Chimpanzees are well known for their tool using abilities. Numerous studies have documented variability in tool use among chimpanzees and the role that social learning and other factors play in their development. There are also findings on hand use in both captive and wild chimpanzees; however, less understood are the potential roles of genetic and non-genetic mechanisms in determining individual differences in tool use skill and laterality. Here, we examined heritability in tool use skill and handedness for a probing task in a sample of 243 captive chimpanzees. Quantitative genetic analysis, based on the extant pedigrees, showed that overall both tool use skill and handedness were significantly heritable. Significant heritability in motor skill was evident in two genetically distinct populations of apes, and between two cohorts that received different early social rearing experiences. We further found that motor skill decreased with age and that males were more commonly left-handed than females. Collectively, these data suggest that though non-genetic factors do influence tool use performance and handedness in chimpanzees, genetic factors also play a significant role, as has been reported in humans.

1. Introduction

Tool use has been described in many species, but apart from humans, the complexity and variability found in chimpanzees is unmatched in the animal kingdom [1–6]. A variety of forms of tool use have been described in different great apes throughout Africa and Asia, and it has been suggested that social learning and local traditions have perpetuated within- and between-community variation in the acquisition of tool use in chimpanzees [6–8] and other great apes [9]. Many have suggested that the evolution of tool manufacture and use in humans had profound effects on a variety of complex cognitive functions such as language and speech, as well as increased brain size and complexity, including lateralization in structure and function in hand use [10–16]. Specifically, it has been hypothesized that the left hemisphere’s specialization for praxic and speech functions evolved from adaptation in early hominids for tool manufacture and use [14,17,18]. In these evolutionary models, speech co-opted neural and biological systems involved in manual motor actions, such as prehensile grasping and tool use, with increasing selection for fine motor skill necessary for the articulation of speech in early humans, after the split from the common ancestor with chimpanzees.

Although there are now very good descriptions of various forms of tool use in many communities of chimpanzees, far less is known about the mechanisms that underlie individual and phylogenetic variability. Studies in wild and captive apes have demonstrated that learning to use tools can take many years [19–21].
Moreover, there is some evidence that females show a greater propensity and interest in tools and learn to use them at an earlier age than males [22,23]. Indeed, the claim that females have a greater propensity to use tools has also been reported in captive bonobos (Pan paniscus), a species for which evidence of tool use in the wild is relatively sparse [24,25]. One interpretation of the sex difference in tool use in chimpanzees is that female offspring spend more time in closer proximity to their mother when she is using tools compared with male offspring. The greater proximity of the female offspring affords them greater opportunity to learn the necessary actions and substrates needed for successful tool use.

Less studied but arguably equally important is tool use performance in both wild and captive chimpanzees and indeed, all primates [26–35]. As noted above, most studies of tool use in wild and captive chimpanzees have focused on the role that subject characteristics such as sex, age or rearing experience have on the usage frequency of different tools rather than their actual performance [36,37].

This is unfortunate, because presumably better performance or skill on a given tool-use task, particularly those that yield access to food resources, would likely be beneficial to the individual. In humans, there is a rich body of research on the effects of subject, experimental and genetic influences on motor skill. For instance, there is evidence of sex differences in tool use, with female humans reported to show better performance on fine motor tasks, whereas males perform better on tasks requiring more ballistic movements [38]. There is also a large body of data showing age-related changes in motor skill in humans [39], and there is evidence that tool-use learning and skill are both heritable [40,41].

In this report, we examined the role of both genetic and non-genetic factors on individual differences in motor performance and hand use for a probing tool-use task in chimpanzees using quantitative genetic analyses. At one level of analysis, we quantified motor skill on a precision tool-use task and assessed the relative contributions of genetic and non-genetic factors to individual variation in performance. Because no study like this has been previously conducted in chimpanzees (nor any non-human primates, as far as we know), we were essentially testing two heuristic explanations for how individual differences in motor skill might vary in the chimpanzees. From a purely operant conditioning perspective, individual performance would be primarily mediated by their reinforcement history on the task. Subjects that were better or worse would receive differential rates of reinforcement and therefore performance would improve at different rates across individuals, but the relatedness of the individuals would explain little variability in performance. This would lead to the prediction that heritability would essentially be zero and that other non-genetic factors would largely explain individual differences in performance. The alternative hypothesis would, in contrast, propose that inherent differences in motor skill for tool use would reflect potential genetic mechanisms. These initial genetic predispositions could interact with operant mechanisms, leading to differential rates of acquisition and performance, but unlike the operant explanation, inherent initial differences in skill would be attributable to genetic factors. This hypothesis would predict that at least some degree of heritability in motor skill would be found in the chimpanzees.

In addition to tool-use skill, we also assessed heritability in hand preference. Although historically many have argued that non-genetic mechanisms govern the expression of behavioural asymmetries in non-human vertebrates, including handedness [42], there is increasing evidence that this view is no longer tenable. For instance, fish can be selectively bred for lateralized eye preferences when viewing a predator [43]. In primates, there is evidence that handedness can run in families, as well as evidence in chimpanzees of small-to-moderate heritability in hand use for reaching, manual gestures and coordinated bimanual actions [44]. Because handedness in chimpanzees has been previously found to be heritable, we hypothesized that significant heritability in hand use would be found for the tool-use task employed in this study. Finally, we tested for genetic correlations between motor skill performance and hand preference measures. These analyses were performed to assess whether similar genes explain individual variation in motor skill and hand preference.

2. Methods

(a) Subjects

A total of 243 captive chimpanzees were observed, including 148 females and 95 males. The chimpanzees were housed at two facilities: the Yerkes National Primate Research Center (YNPRC) of Emory University (n = 90) and the Michale E. Keeling Center for Comparative Medicine and Research of the University of Texas MD Anderson Cancer Center (UTMDACC; n = 153). Between the two facilities, the chimpanzees ranged in age from 5 to 51 years (mean = 27.21 years, s.d. = 9.64). There were 133 mother-reared (MR), 57 human-reared (HR) and 53 wild-caught (WC) chimpanzees in the combined sample. All of the research was approved by the local Institutional Animal Care and Use Committees and followed the guidelines for the ethical use of chimpanzees in research outlined by the Institute of Medicine.

We defined a HR chimpanzee as an animal that was separated from his or her mother within the first 30 days of life, owing to unresponsive care, injury or illness [45,46]. These chimpanzees were placed in incubators, fed standard human infant formula and cared for by humans until they could sufficiently care for themselves, at which time they were placed with other infants of the same age until they were three years of age [45,46]. At three years of age, the HR chimpanzees were integrated into larger social groups of adult and subadult chimpanzees. MR chimpanzees were not separated from their mother for at least the first 30 days of life and were raised in ‘nuclear’ family groups of chimpanzees, with group sizes ranging from four to twenty individuals.

It should be noted that the subset of HR chimpanzees in this study were raised in this manner because their biological mothers did not exhibit adequate maternal care at birth, and this required intervention in order to protect the infants’ well-being. Thus, the chimpanzees in this study were not HR with the goal of subsequently determining the effects of early-life experiences on development. The study we present here is opportunistic and retrospective; that is to say, we took advantage of the fact that some of the chimpanzees received different rearing experiences to determine whether this might have long-term consequences for tool-use behaviour. Finally, the WC individuals were generally older and were brought to captivity from the wild prior to 1974, when the Convention on International Trade in Endangered Species (CITES) banned all importation of chimpanzees.

Each chimpanzee colony was genetically isolated, in the sense that they both populated from different founder chimpanzees that were imported into the USA prior to the CITES ban in 1974. Indeed, many of the chimpanzees within the pedigrees had estimated birth dates in the 1940s, when some of these research colonies were originally formed [47]. Within each colony,
The stick into the hole during each attempted probe. Time per motor planning and hand-to-eye coordination. In addition to it is the insertion that requires the greatest fine motor skill, stance, the hand used to insert the stick was recorded because them. If the tool became unusable, a new tool was offered to by either handing it directly to them or by dropping it near device on the enclosure, each subject was supplied with a tool material and procedures were used at the two facilities. 

Table 1. Pedigree structure of the chimpanzee sample.

<table>
<thead>
<tr>
<th>relationship</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>parent–offspring</td>
<td>380</td>
</tr>
<tr>
<td>full-siblings</td>
<td>24</td>
</tr>
<tr>
<td>half-siblings</td>
<td>375</td>
</tr>
<tr>
<td>grandparent–grandchildren</td>
<td>116</td>
</tr>
<tr>
<td>avuncular</td>
<td>12</td>
</tr>
<tr>
<td>second degree</td>
<td>6</td>
</tr>
<tr>
<td>third degree</td>
<td>191</td>
</tr>
<tr>
<td>fourth degree</td>
<td>24</td>
</tr>
</tbody>
</table>

pedigrees were well documented from the founder animals to the current populations. For all offspring, the mothers were known, but paternity was not always known or reported in the records. 

(b) Materials
The device and general methods have been described in detail elsewhere [36]. Briefly, the task employed was designed to simulate the motor demands of termite fishing in wild chimpanzees [2]. The motor and cognitive requirements of termite fishing were simulated using threaded polyvinylchloride (PVC) pipes (approx. 4 cm in diameter and approx. 20 cm in length) attached to threaded PVC bases that were affixed to the subjects’ home enclosures at multiple locations approximately 60–80 cm above the ground or floor. The pipes were fitted with a disc in one end with a 7 mm hole cut out to greatly reduce the size of the opening available for tool insertion, thus increasing the motor demands of the task. The other end was closed with a removable screw-on cap. The pipes were filled with a preferred food substance that would adhere to the tool, such as BBQ sauce, mustard, yogurt, syrup or apple sauce, before being screwed into the bases. The chimpanzees were provided with flexible, thin ‘lollipop’ sticks (approx. 11 cm in length and 4 mm in diameter, like those used to make large lollipops) made out of tightly rolled, thin paper. The animals used the lollipop sticks to dip into the small hole of the pipe and retrieve the food (figure 1). Identical materials and procedures were used at the two facilities.

(c) Procedure
Prior to testing, all of the chimpanzees had been exposed to a simulated termite fishing tool-use task similar to that described in this study. This form of tool use is used as an enrichment simulation. To test for shared maternal effects (c²) on the phenotypes, we created a matrix identifying individuals that were born to the same mother and this variable was included as a covariate. We used the bivariate heritability estimate function within SOLAR. We used the software package SOLAR [57]. SOLAR uses a variance components approach to estimate the polygenic component of heritability when considering the entire pedigree (table 1). Consistent with approaches used by others [48–56], to estimate heritability, we included sex, rearing history and age as covariates in the estimates of heritability to account for their influence on phenotypic variation. To test for shared maternal effects (c²) on the phenotypes, we used the bivariate heritability estimate function within SOLAR to quantify genetic correlations between the different traits.

(d) Data analysis
Hand preferences were characterized in several ways. First, for each subject, a handedness index was derived following the formula HI = (R – L)/(R + L). Positive HI values reflected right-hand biases and negative values reflected left-hand biases. The absolute value of the handedness score reflected the magnitude of hand preference. For all analyses, α was set at p ≤ 0.05, and all post hoc tests were conducted using Tukey’s honestly significant difference test. The average time per successful dip for each hand was calculated using the following formula: average left time = total left time/total left frequency, and average right time = total right time/right frequency. To eliminate differences between chimpanzee colonies in their exposure to this tool-use device, the mean latency scores were converted to standardized z-scores within the YNPRC and UTMDACC cohorts.

(e) Heritability analysis
Heritability (h²) is the proportion of total phenotypic variance that is attributable to additive genetic sources. Total phenotypic variance is constrained to a value of 1; therefore, all non-genetic contributions to the phenotype are equal to 1 – h². Many of the chimpanzees in each colony are related and this allowed for an analysis of heritability in tool use and asymmetry using quantitative genetics based on the entire pedigree (table 1). Consistent with approaches used by others [48–56], to estimate heritability, we used the software package SOLAR [57]. SOLAR uses a variance components approach to estimate the polygenic component of variance when considering the entire pedigree (see [48,51,54]). We included sex, rearing history and age as covariates in the estimates of heritability to account for their influence on phenotypic variation. To test for shared maternal effects (c²) on the phenotypes, we used the bivariate heritability estimate function within SOLAR to quantify genetic correlations between the different traits.

3. Results
(a) Quantitative genetic analysis
Prior to any analyses, we used box-plots to determine any outlier data points. For the latency scores, three subjects were removed (two males, one female) owing to extremely high scores (all had z-scores > 3.00). None of the subjects
was removed from the handedness analyses. The results from the overall heritability analyses are shown in table 2. Both tool-use performance and hand use were found to be significantly heritable after adjustment for the covariates sex, age and rearing history. Additionally, for tool-use performance, age was a significant covariate, and subsequent analysis showed that latency increased with age (figure 2). For handedness, both age and sex were significant covariates. Males were found to be more left-handed than females (see table 3 for descriptive information on handedness). Using the bivariate function within SOLAR, we also found a significant genetic correlation between the HI and \( Z_{\text{latency}} \) scores (\( r_g = 0.865, \text{s.e.} = 0.345, p = 0.001 \)) but no environmental correlation (\( r_e = 0.235, \text{s.e.} = 0.141, p = 0.100 \)). Thus, common genes appear to underlie individual variation in both hand use and tool use performance.

To explore both the consistency and magnitude of the observed heritability patterns, we performed several follow-up analyses. First, recall that the YNPRC and UTMACC chimpanzees are genetically isolated groups of apes. That is to say, founder animals were unique to each colony, and no sires or dams were shared between the two facilities. Thus, to assess the consistency in the pattern of heritability, we performed separate analyses on each colony (table 2). For these and subsequent follow-up analyses, we included only those covariates that were significant in the full model analysis (age and sex). Similarly, we also eliminated the tests for maternal effects because this variable was not found to be significant for the full model analysis. Tool-use performance was significantly heritable in both colonies. In terms of hand preference, significant heritability was found in the UTMACC colony, whereas the YNPRC heritability estimates approached conventional levels of statistical significance. Statistical comparisons demonstrated that the UTMACC and YNPRC heritability estimates were not significantly different for either tool use performance or hand preference.

We next considered the potential mediating influence of early rearing experiences on heritability in tool use. For this analysis, we performed separate analyses on the MR and HR chimpanzees and these results are also shown in table 2. Significant heritability in tool-use performance and handedness was found within the MR and HR cohorts. Furthermore, age was a significant covariate for tool-use performance for both the MR and HR chimpanzees. Lastly, for hand preference, age and sex were significant covariates in the MR but not HR chimpanzees.

4. Discussion

Measuring tool-use performance and hand use in a relatively large sample of captive chimpanzees revealed three main findings. First, tool-use performance and hand preference were both significantly heritable. Importantly, heritability in tool performance and hand use was significant in two separate
Table 3. Distribution of hand preference and mean HI values for male and female chimpanzees. Based on the total left- and right-hand frequencies, z-scores were used to evaluate whether the hand preferences of individual subjects deviated significantly from chance. This is the procedure most frequently used in the non-human primate literature (see [58,59]). Subjects with z-scores greater than 1.95 or less than −1.96 were classified as right- and left-handed, respectively. All other subjects were classified as ambiguously handed. Asterisk indicates p = 0.011 for a one-sample t-test on the HI scores, with zero being the estimated HI score for a normally distributed set of data.

<table>
<thead>
<tr>
<th>Tool Use</th>
<th>NL</th>
<th>NA</th>
<th>NR</th>
<th>Mean HI</th>
<th>S.e.</th>
<th>t</th>
</tr>
</thead>
<tbody>
<tr>
<td>Males</td>
<td>43</td>
<td>23</td>
<td>29</td>
<td>−0.144</td>
<td>0.055</td>
<td>−2.59*</td>
</tr>
<tr>
<td>Females</td>
<td>55</td>
<td>35</td>
<td>58</td>
<td>+0.014</td>
<td>0.045</td>
<td>0.31</td>
</tr>
<tr>
<td>Overall</td>
<td>98</td>
<td>58</td>
<td>87</td>
<td>−0.047</td>
<td>0.035</td>
<td>−1.34</td>
</tr>
</tbody>
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In summary, the findings presented here demonstrate that chimpanzee motor skill and handedness when assessed for tool use are significantly heritable. These results are fairly robust as manifested by the evidence that significant heritability was found in (i) two distinct, genetically isolated populations of chimpanzees and (ii) in both MR and HR chimpanzees. To what extent heritability in motor skill is evident in other species or for other motor tasks remains unknown but warrants further study. Notwithstanding, the findings presented here are consistent with the view that the genetic basis for tool use was present in the common ancestor of humans and chimpanzees, and in humans these genes may have been altered and elaborated upon in their functional control over more complex motor actions, such as speech, after their divergence from the genus *Pan*.

**Data accessibility.** The pedigree and behavioural data for this study are available at DRYAD (datadryad.org).

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### References


