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<NOTE>

Wild Chimpanzees at Mahale are not Manually Lateralised for Throwing

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INTRODUCTION

The importance of throwing has figured consistently and prominently in scenarios about the evolutionary origins of human behaviour^{1,2}. The utility of imparting force to airborne projectile weapons, launched ballistically, is obvious, whether to deter, punish or subdue predators, prey, or competitors. Other functions of throwing are less obvious but could be equally useful, such as bringing down hanging fruit, gaining others' attention, shattering large objects into fragments, etc. Scenarios have stressed a number of important variables, such as posture (especially bipedality), sensorimotor skill (especially hand-eye coordination), cerebral asymmetry, etc. Calvin¹ linked all of these to the evolutionary origins of language. However, few of these ideas have been tested empirically.

One way to tackle evolutionary aspects of human throwing is to look at throwing performance in our nearest living relations. Although throwing has been known in both wild³ and captive⁴ chimpanzees for almost a century, quantitative studies are few; often they are sub-

sumed in broader studies of manual behaviour, e.g. ref. 5. Furthermore, studies often do not distinguish between aimed (targeted) throwing *versus* unaimed (perhaps better termed hurling) throwing, underarm *versus* overarm delivery, or one-handed *versus* two-handed throwing.

Several studies of manual laterality in throwing by captive chimpanzees have been published, and all have reported population-level, right-sided bias^{6–8}. Others have incorporated these reported findings into comprehensive accounts of the origin of handedness, e.g. ref. 9.

We can find no published quantitative data on manual laterality in throwing from *any* non-human primate species in nature, much less from chimpanzees. One obvious reason for this absence is that, unlike in the artificial conditions of captivity, wild primates throw only rarely. Here we report such a dataset, collected ethologically from a population of chimpanzees in nature, over an extended period, in an effort to balance the picture.

METHODS

The subjects were the eastern chimpanzees (*Pan troglodytes schweinfurthii*) of M group in the Mahale Mountains of western Tanzania^{10,11}. This population has been studied since 1965, making it the second-oldest field study of chimpanzees; the apes are fully habituated to close-range behavioural observation. The Mahale ethogram is well-known and described; Nishida *et al.*¹² listed 10 kinds of throwing.

We recorded all observed occurrences of throwing, using *ad lib.* sampling, that is, regardless of whether behaviour was being scan-sampled or focal-subject-sampled¹³. We interrupted normal protocols, in order to note the identity of the thrower, target, etc. Nishida recorded his data from 1999–2004, when he mostly followed males, hence the shortage of data on females. McGrew and Marchant recorded their data in 1996. Here we report data only on unimanual *versus* bimanual data, and on the hand(s) involved. Each throw is considered an independent data-point, as the chimpanzees always repositioned themselves between throws, usually to pick up another object.

RESULTS

We recorded 556 throws by 16 individuals (Table 1); the median number of throws per subject was 33 (range: 9–72). Of these, 63 (11%) were done two-handed, usually in agonistic charging displays; almost half of these were done by two high-ranking adult males (DE, $n = 17$; FN, $n = 13$). These appeared to be unaimed and perforce were done bipedally; they are considered no further here.

One-handed throwing was unlateralized. Only 4 (BB, CT, IV, OR) of the 16 individuals showed statistically significant (Binomial test, two-tailed, $p < 0.05$) laterality; three were biased to the right versus one to the left. The remaining 12 subjects showed ambilateral performance. Overall, nine individuals showed (non-significantly) more right-sided throws, six showed left-sided throws (a non-significant difference, $n = 15$, $x = 6$, $p = 0.60$), and one was tied. Descriptively overall, of one-handed throws, 226 (46%) were done with the left hand versus 267 (54%) with the right hand.

Table 1. Laterality of throwing by wild chimpanzees (n=16) of Mahale's M group.

Name	Year of Birth	Total Throws	Both Hands	Left Hand	Right Hand	R vs. L p<0.05
AL	1982	46	1	21	24	
BB	1981	37	2	26	9	L
CD	1991	34	1	18	15	
CE	1998	11	0	3	8	
CT	1985	32	1	6	25	R
DE	1963	27	17	3	7	
DG	1981	21	3	10	8	
DW	1988	36	2	17	17	
FN	1978	70	13	27	30	
IV	1993	20	1	4	15	R
MC	1996	64	9	28	27	
OR	1991	47	7	10	30	R
OS	1998	14	0	5	9	
PM	1988	16	1	10	5	
PR	1991	72	4	35	33	
XM	1995	9	1	3	5	
TOTAL		556	63	226 (46%)	267 (54%)	

L = stat. sig. left bias; R = stat. sig. right bias; blank = not stat. sig. diff.

All chimpanzees are males, except for IV (bolded).

DISCUSSION

These results clearly contrast with those from the most thorough study done in captivity: Hopkins *et al.*⁷ found that of 89 subjects with six or more data-points, 50 were right-biased, 23 were left-biased, and 16 were unbiased. We have no explanation of this remarkable difference, although it joins a long list of behavioural contrasts between nature and captivity, in which captive chimpanzees are lateralised, while wild chimpanzees are not (see summary in ref. 14). We can find no reports of two-handed throwing by captive chimpanzees; whether this is because such behaviour was not reported, or because it is absent, remains to be seen.

Earlier, McGrew and Marchant¹⁵ hypothesised that captive chimpanzees might be biased toward right-sidedness by their lengthy (sometimes lifetime) association with human caretakers, most of whom will have been right-handed. However, a recent extensive study of four great ape species (see below) found species-level right-sided laterality in captive chimpanzees, at least based on a single bimanual measure¹⁶.

The implications for the evolutionary origins of human handedness are no clearer than the present state of play of contradictory studies of behavioural laterality. Handedness in living *Homo sapiens* could be a derived trait (of uncertain time-depth) or a primitive trait that could date back as far as the last common ancestor of the present African apes and humans (perhaps as long ago as 6–7 million years). Results on manual laterality for the only living Asian great ape, the orang-utan, *Pongo pygmaeus*, are confusing, as according to Hopkins *et al.*¹⁶, they are a left-handed species.

What is clear is that chimpanzees both in captivity and in nature habitually throw, despite being non-linguistic quadrupeds. Thus it is not necessary to invoke bipedal

stance or co-evolved language to explain the evolutionary origins of throwing in the hominin lineage, and if the results from nature are to be believed, neither is it necessary to link throwing to manual lateralisation.

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<NOTE>

Playful Drumming by Immature Wild Chimpanzees at Mahale: Do They Enjoy Making Sounds?

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INTRODUCTION

Before the Mahale Mountains National Park was established in 1985, several villages of Tongwe people lived in the forest. Although many years have passed since the people left, we can still sometimes find the remains of human artifacts on the forest floor while observing chimpanzees. Here, I report the rare cases where immature chimpanzees found and drummed on clay pots discarded by the former villagers and discuss their playful nature in relation to the origin of music.

OBSERVATIONS

(1) Case of an 11-Year-Old Adolescent Male, Cadmus (CD) (25 Nov. 2002)

While CD was playing with a 4-year-old male infant (OS) in a thicket, CD found at 10:13:59 a clay cooking pot (about 40-cm diameter, 30-cm high, with a 14-cm diameter hole at the bottom). He lifted it with his left hand and approached OS with a play-face. OS approached and touched CD, but soon returned to his mother to suckle.

At 10:15:29, an estrous adolescent female (QA) showed leaf-clipping courtship near CD, who did not respond. At 10:15:39, CD lifted the pot with both hands, put it on his head like a helmet, and tapped 31 times on its

side with his right palm. Then he stamped on the ground four times and pounded the pot three times with his left fist. After stamping on the ground twice, he again tapped on the pot's side with his right palm 14 times (Figure 1).



Figure 1. CD puts a pot on his head and taps it with his palm.

At 10:16:42, CD lowered his head, placed the pot on the ground, and kicked its rim twice with his right heel. Then he lowered one side of the rim with his right hand and kicked the rim with his right heel ten times. At 10:17:19, CD stood up, kicked backward, and pushed the pot with his right sole. The pot rolled off, and he left.

In total, CD drummed 60 times: 45 times with his right palm, three times with his left fist, and 12 times with his right heel. He calmly drummed with no pilo-erection. His face was not visible when he put the pot on his head, but he drummed on it on the ground with no facial expression. He generally tapped lightly and did not make loud sounds. Although he might have heard the pot's large resonance from inside it, the sounds did not seem to attract others. No one approached CD during his drumming, even though six chimpanzees rested within 10 m: OS and his mother, a 1-year-old male infant (TD) and his mother, an adult male (DG), and an adolescent female (QA).

(2) Case of a 6-Year-Old Juvenile Male, Michio (MC) (14 Feb. 2003)

At 10:46:56, while MC was walking in a thicket, he found a large clay water pot that was about 50-cm high, with a 45-cm diameter, a narrow neck, and an 18-cm diameter mouth. He slapped the bottom of it three times with his left palm, rolled it, and slapped it once with his right palm. Then he stepped onto it with both feet, soon got off it, lowered the pot's mouth to the ground, and slapped its bottom with his left palm. He then pushed and rolled it, slapped it simultaneously with both palms, and slapped it nine times with both hands in turns. At 10:47:19, he stopped but soon started playing again in various ways (Figure 2, Video 1: available online at [mahale.main.jp/PAN/19_2/19\(2\)_05.html](http://mahale.main.jp/PAN/19_2/19(2)_05.html)): slapping the pot with his palms, pushing and rolling it, stamping on it with his soles, kicking it with his heels, stepping up onto