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Etho-Archaeology of Manual Laterality: Well Digging by Wild Chimpanzees

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Key Words

Chimpanzee · Handedness · Laterality · Drinking technology · Artefact

Abstract

We present the first indirect test of manually lateralized behaviour in non-human primates, based on wells dug for drinking water by wild chimpanzees (*Pan troglodytes schweinfurthii*). Apes at Toro-Semliki Wildlife Reserve, in Uganda, dig bimanually in sandy riverbeds, leaving behind paired piles of excavated sand. The volumes of left- versus right-side piles do not differ, suggesting a lack of behavioural laterality, but this needs to be verified by further, direct observational data.

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Introduction

Studies of the evolutionary origins of human handedness (laterality of manual function) are vexedly difficult [McManus, 2002]. As with studies of the evolution of neuromuscular (but not skeletal, see Auerbach and Ruff [2006] and Sarringhaus et al. [2005]) asymmetries, palaeo-anthropologists and prehistorians must rely on proxy measures. We will never see our ancestors using their upper limbs differentially nor will we have access to their soft tissues. Thus, attempts at reconstructing the phylogenetic roots of handedness must rely on inference based on indirect measures, usually as taken from artefacts, e.g. as described by Toth [1985], Phillipson [1997] and Rugg and Mullane [2001].

Studies of manual laterality in living apes, especially in nature, may be useful, because, at least in principle, behavioural data may be used to validate morphological data. However, in practice, suitable behavioural data are scarce because the vast majority of wild populations are not observable at close enough range. For the chimpanzee, more than 50 populations have been studied across Africa, yet only a handful are ful-

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Fig. 1. Fresh well in riverbed (with scale object). Note fingermarks at the head of the ‘triangle’ and knuckleprints between tailings.

ly habituated to such scrutiny. Thus, the primatologist is usually placed in a similar situation to that of the palaeo-anthropologist of being forced to rely on inference. We report here the first use of indirect evidence to test for laterality, based on artefacts left behind after the apes have gone; this proxy measure (etho-archaeology, see McGrew et al. [2003]) is based on the products of behaviour, rather than on behaviour itself.

Chimpanzees in the Toro-Semliki Wildlife Reserve in western Uganda dig holes (‘wells’) in sandy riverbeds, in order to get drinking water [Hunt and McGrew, 2002]. More often in the dry season, they dig by hand and sometimes use compressed wedges of leaves or pith as ‘sponges’ to extract the water that seeps into the bottom of the cavity. (We found no signs of digging sticks, which were not needed; we easily mimicked the wells by using our hands alone.) The excavated wet sand is discarded beside the well, where for up to 48 h the darker, damp pile contrasts with the lighter, dry sand of the riverbed substrate. The moist surface also clearly imprints the knuckle- and footprints of the apes, allowing the wells to be distinguished from those of other animals, e.g. baboons (*Papio anubis*, see Hamilton et al. [1978]). (For details of the wells and associated sponges, see Hunt and McGrew [2002], p. 46.)

Previous observations at Semliki showed that the apes sometimes dig with both hands, alternating left and right, producing a distinctive, triangle-shaped hole, with the apex of the triangle being the entry point for the scooping hands, and the two basal corners being the exit points for the left and right scoops of sand (fig. 1). This provided the opportunity for a test of lateralized manual function.

Observational studies of behavioural laterality of hand use by wild chimpanzees show individual lateralization for complex foraging tasks (e.g. extractive tool use) but lack of individual lateralization for other tasks (e.g. picking up objects; see review in McGrew and Marchant [1997]). With one exception (Lonsdorf and Hopkins' [2005] claim of left-handedness for insect extraction), all previous studies of wild chimpanzees have found no population level laterality for any behavioural pattern [Boesch, 1991; Sugiyama et al., 1993; McGrew and Marchant, 2001; Corp and Byrne, 2004]. Experimental studies of behavioural laterality of hand use by captive chimpanzees show a more mixed picture, but at least some [Hopkins and Cantalupo, 2005; Hopkins et al., 2005] show an incomplete but significant right-sided bias in hand use at the population level. These past studies yield competing predictions to be tested on the etho-archaeological data here: if the apes are right-handed, then the right-side piles of sand should be bigger; on the other hand, if the apes are not lateralized, then the left and right piles should not differ.

Methods

On July 5 and 6, 2006, we found 91 wells along a 950-m stretch of the lower reaches of the Mugiri River (0°89' N, 30°39' E). The sandy riverbed was 2–5 m wide and mostly shaded; water was just disappearing below the surface as the dry season progressed, leaving a smooth, moist substrate.

Twenty-five wells had intact paired tailings, while others had been made one-handed ($n = 38$) or had been disturbed by movements of the apes ($n = 28$). For these 25, we measured the maximum length, width and height to the nearest centimetre, in order to calculate a crude volume of the left and right excavated piles of sand. We could not distinguish which individual apes made the wells, and because the study community numbered 40–50, all data were pooled for descriptive analysis at the population level.

Results

At Semliki, we found that the mean volumes (length \times width \times height) of left (10,697 cm³) versus right (11,759 cm³) piles of sand did not differ. The number of wells in which the volume of left-side tailing exceeded right-side volume ($n = 12$) did not differ from those in which right-side volume exceeded left ($n = 13$). When left-side volume exceeded right, the *extent* (right/left) of difference (mean = 1.92) was no different from the reverse (left/right) when right-side volume exceeded left (mean = 2.22). In short, the constructed products (artefacts) of digging were not lateralized, indicating overall ambilaterality in hand use or an equivalent number of left- and right-biased individuals for the pooled data set. The data are mute for individual lateralization, as they are for all human palaeo-archaeological data [Phillipson, 1997] and for all non-human data based on artefacts [Rutledge and Hunt, 2004]. We know of only one other study of lateralized artefacts in a non-human spe-

cies: when Caledonian crows (*Corvus moneduloides*) make probing tools from the leaves of the *Pandanus* palm, they leave lateralized templates from where the tool is excised [Hunt et al., 2001]. These data show left-biased *tool-making* at the species level, but later studies of *tool use* both in nature [Rutledge and Hunt, 2004] and in captivity [Weir et al., 2004] show individual level lateralization only, suggesting a disjunct between manufacture and use. For the apes' wells, the artefacts (well plus paired piles of sand) are made, but then the cavity becomes a receptacle to be acted upon by a different behavioural pattern, sponging, for which we yet have no behavioural laterality data.

As with any indirect evidence, this proxy measure needs to be validated with direct, observational data, but the finding of non-lateralized artefacts is congruent with the general picture for chimpanzees in nature.

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