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OH-65: The earliest evidence for right-handedness in the fossil record

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A B S T R A C T

Labial striations on the anterior teeth have been documented in numerous European pre-Neandertal and Neandertal fossils and serve as evidence for handedness. OH-65, dated at 1.8 mya, shows a concentration of oblique striations on, especially, the left I^1 and right I^1, I^2 and C^1, which signal that it was right-handed. From these patterns we contend that OH-65 was habitually using the right hand, over the left, in manipulating objects during some kind of oral processing. In living humans right-handedness is generally correlated with brain lateralization, although the strength of the association is questioned by some. We propose that as more specimens are found, right-handedness, as seen in living *Homo*, will most probably be typical of these early hominins.

1. Introduction

OH-65, found in Olduvai Bed I, is a mostly intact maxilla dated to ~1.8 mya. The specimen was found in a stream channel, close to the lake margin in a tuffaceous, silty sandstone. It is associated with Oldowan tools and large mammals, some of which bear cut marked surfaces (Blumenschine et al., 2003). The maxilla preserves all 16 teeth (Fig. 1a) and is attributed by those authors to be an adult *Homo habilis*. It preserves evidence of using the labial faces of its anterior teeth as a cutting platform. In his description, Clarke (2012: 422) noted that there is "a network of fine, randomly-oriented striations" on the labial faces of the central incisors, with many fewer striations on the lateral incisors and canines (Fig. 1b, c). We have examined the original and an epoxy cast of the maxilla. We note that the striations are not found on any faces of the premolars and molars, but are concentrated on the labial faces of the two central incisors with some expression in the lateral incisors and canines, especially on the right side. The lingual surfaces are mostly free of striations and those present are superficial, more typical of dietary striations as defined by Krueger and Ungar (2009). These are much fainter than the labial striations we describe here (they observed them at 100×; our analysis is at 20×) and are attributed mainly to dietary, manipulative or abrasive factors, not produced by tools (Krueger and Ungar, 2009). The OH-65 lingual striations are few and show no pattern of directionality.

Distinctive labial striations, like those on OH-65, are not randomly arranged, having been described in European Neandertals and the Sima de los Huesos fossils (Bermúdez de Castro et al., 1988; Pérez-Pérez et al., 2003; Lozano et al., 2009; Frayer et al., 2010, 2012; Volpato et al., 2012; Estalrrich and Rosas, 2013; Fiore et al., 2015). Experimental work has shown that these scratches were most likely produced when a stone tool was used to process material gripped between the anterior teeth and the tool occasionally struck the labial face leaving a permanent striation (Fig. 2). Bermúdez de Castro et al. (1988) and Lozano et al. (2009) performed experiments, having volunteers with mouth guards pull with the left (or right) hand and cut with the opposite hand. They documented a right (or left) obliquity of striations when one hand was favored for processing. Right oblique striations were produced by right-handers; left oblique by left-handers.

To evaluate the morphology of the scratches, Frayer et al. (2010) scored several prehistoric ovicaprid teeth with hand-held chert

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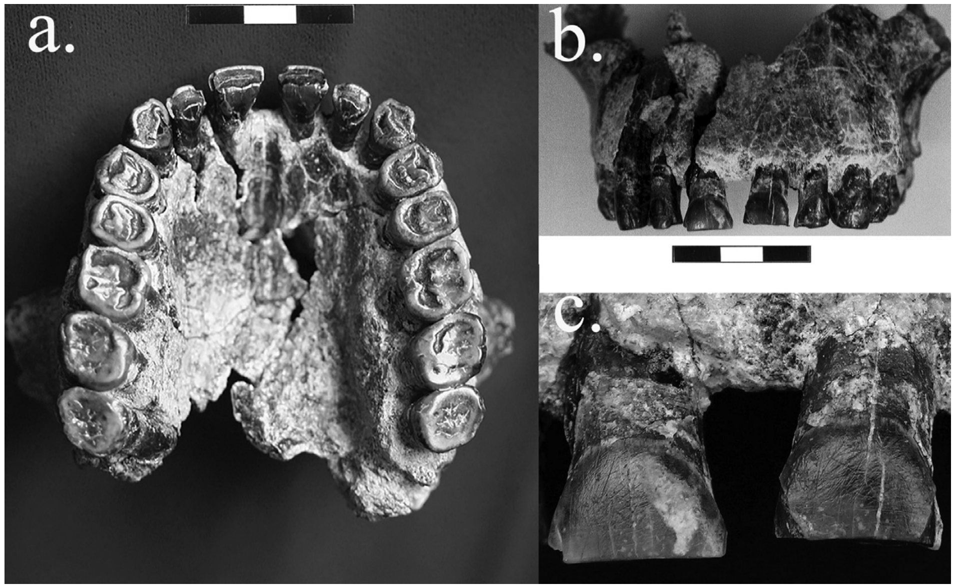

Figure 1. Three perspectives of the OH-65 maxilla. a. Palatal view; b. labial view; c. close-up of the two central incisors showing concentration of labial striations.

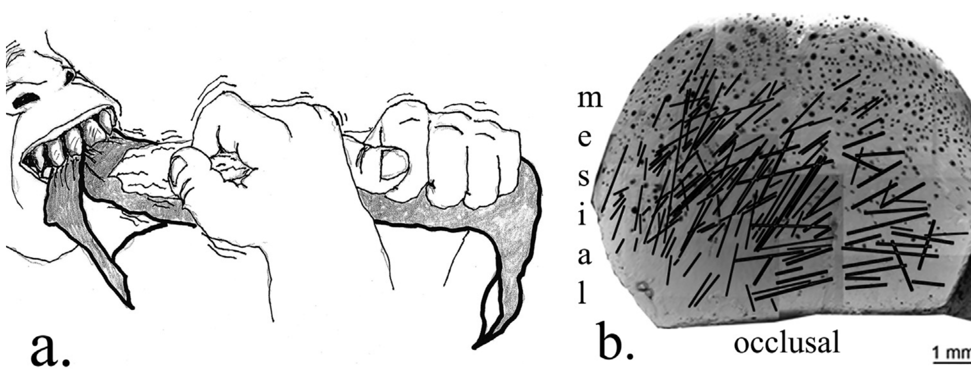

Figure 2. a. Experimental evidence suggests these labial scratches were produced when material was processed with one hand pulling the object and the other cutting it with a stone tool. Depicted here is a right-hander pulling with the left and cutting with the right. Many scratches are found on the labial face, but right oblique scratches are produced by this action (i.e., striations beginning in the superior right portion of the image). b. A stereomicroscopic composite of the sputter-coated cast of left I^1 used in the analysis. The dense concentrations of striations show that the tooth surface was repeatedly modified by a stone tool and the majority of striations are right oblique. The black dot "bubbles" are artifacts of the casting and sputter-coating.

tools. We found that under SEM, the striae on the ovicaprid teeth have a V-shape form with secondary striae and microridges inside the scratch. These are produced by the edge of the stone tool, but compared to cut marks in bone are less distinct (e.g., Olsen and Shipman, 1988), likely related to the hardness of the enamel and the less direct force applied to the tooth surface (Frayer et al., 2010). Antemortem and postmortem rounding and smoothing of the striation edges also affect the appearance of the striations under the microscope. In OH-65 the overall morphology of the marks with the V-shaped signature and secondary striae within the striations closely resembles the experimental marks on the ovicaprids.

1.1. Handedness and brain asymmetry in nonhominins

Various studies have reported handedness in mammals from kangaroos to chimpanzees (Giljov et al., 2015; Marchant, 2015) and limb preference in other animals (e. g., Forrester et al., 2013; Versace and Vallortigara, 2015). Ströckens et al. (2013: 569) conclude after a survey of 119 species from fish to donkeys to primates that the "findings … support the position that population-level asymmetries in limb preferences per se are a common feature among vertebrates, while the strong and consistent rightward population-level asymmetry observed for human handedness is not." Controversy involves higher primates, especially chimpanzees, where some show no consistent handedness in the wild (McGrew and Marchant, 1997; Marchant and McGrew, 2013; Marchant, 2015) and others show a sex difference in bimanual tasks, with males more likely left-handed and females right-handed (Corp and Bryne, 2004; Llorente et al., 2011). On the contrary, in a large survey of great apes Hopkins et al. (2011) tallied 536 chimpanzee adults and juveniles and arrived at 63: 37 right to left ratio, when considering only these two categories in the bimanual tube test. Bonobos ($n = 118$) show no similar ratios with a 50: 50 preference for the right or left hand (Hopkins et al., 2011, Table 2; Supplementary Online Material [SOM] Table 1). However, in these same tube tests chimpanzees have a very high frequency of "ambiguous" hand preference. Thus, when "ambiguous" is included, the ratios in adult and juveniles are 50 right: 22 ambiguous: 29 left (SOM Table 1). No equivalent frequencies are given for humans (Hopkins et al., 2011), but based on other bimanual tasks of tool use, humans show a consistent right-handed bias in bimanual tasks, with a low frequency of ambidexterity or ambiguous hand