<REVIEWS>
Acquisition of Skilled Gathering Techniques in Mahale Chimpanzees

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Chimpanzees show a remarkable ability to organize actions into complex programs, shown most famously in their ability to employ tools in many different ways for subsistence. Chimpanzee tool use has been much studied, with an emphasis on the tool rather than the process of use. We planned instead to examine chimpanzee skills in the broader context of plant-processing techniques, with an emphasis on the process. In particular, we focused on the development of infants in parallel with describing the skills of their mothers. Data were collected from M group chimpanzees in the Mahale Mountains National Park during February–December 1998 and then again June 1999–January 2000. Focal sampling procedures were used to collect data on 14 mother-infant pairs, with 10x40 binoculars to help see the fine details and action sequences recorded on Dictaphone for later transcription.

Central to our work is the measurement of 'complexity' and the degree to which the hands of non-human great apes constrain their cognitive capacities. Several possible measures of complexity, even ones which might have been expected to 'trade off' against each other (e.g. size of action repertoire, and the mean number of such actions used for any given task), do in fact provide converging evidence of complexity (1). Many food plants used by Mahale chimpanzees were relatively simple for them to consume without elaborate techniques. However, complex plant gathering was shown in two circumstances: (1) embedded foods, e.g. pulp from tough-shelled, large fruits; and (2) physically defended leaves, where defences had to be circumvented in order to feed painlessly. In both cases, the techniques employed showed considerable manual dexterity (2), and hierarchical organization (1, 3).

Since leaf-processing varies from simple mouthing to a quite complex task, we were able to make a direct test of the hypothesis—often-assumed—that complex cognition is primarily valuable for *difficult* manual tasks. We compared processing of 8 leaf foods which differed in this way, and strongly confirmed this hypothesis: complex food processing may therefore have selected for cognitive advance in the shared chimpanzee/human line of ancestry (4).

Of cardinal interest was to examine acquisition of skill. The clearest developmental sequence we obtained was for the processing of an embedded food, *Saba florida*. Many of the developmental changes were explicable in terms of chimpanzee maturation: increasing power, reach and manual dexterity with age of infant (5). However, some aspects hinted that social learning mechanisms might also be involved: for instance, we observed some cases where the infant intently watched the mother or another older individual as they fed, frequent synchronized feeding with the mother, and numerous cases of both food solicitation and food sharing. All these circumstances might aid acquisition of complex skills—but did they? We suggest a more conservative evaluation.

Young infants typically depended on their mothers for access to the edible parts of *Saba*. This means that synchronized feeding, intense observation, and food solicitation may reflect no more than an infant's strong motivation to gain food. Social learning cannot therefore be concluded to be necessary from observation of these behaviours, although it often has been in the past. Food sharing, similarly, does not mean that the mother is deliberately sharing *knowledge* with the infant. We found that solicitation peaks very early in the infant's life, at a time when lactation is still essential, and mothers share little food at that time. Later in development, when the infant would be able to gain significant nutrition from solid food, mothers share food virtually on demand. This is most parsimoniously explained as a consequence of a mother optimizing her energy budget. When sharing solid food can aid in reducing lactational demands on the mother, she shares; but not before then, when the infant is most in need of knowledge. Thus, we do not consider that chimpanzee food sharing evolved with a primary function of passive tutoring. But, as a consequence of these factors—the infant's desire for food, and the mother's optimization of energy transfer to the infant—the learning process for the infant may nevertheless be "scaffolded" (6, 7). If relevant information is indeed gained through the infant's (hunger-motivated) observations, and the mother's (energy optimization) food-sharing, this is most likely to involve mechanisms which do not imply any intent on behalf of the mother or infant, such as affordance learning (8) or imitation without intentionality (9, 10). We found no evidence to support the idea that teaching (11) or imitation in the sense of gestural copying (12, 13) were involved in the acquisition of this rather complex natural task.

An unexpected finding was that, when processing *Saba* and *Citrus* fruits, chimpanzees show strong manual laterality which varies in direction between the sexes (14). It is generally accepted that laterality is elicited by a need for skilled manipulation (15-17), so our finding of strong individual hand preferences provides orthogonal evidence that chimpanzees see these tasks as cognitively challenging. However, the sex-linked pattern of manual laterality among the chimpanzee population is unique, as far as we know. Moreover, it may shed light on the origins of the sex difference found in modern day humans, where males are on average slightly more left-handed or ambidextrous than women.

When they handle *Saba* or *Citrus* fruits bimanually, Mahale chimpanzees first grip the whole fruit by laying one hand over another in an extra-strong grip; the choice of hand to apply first is highly lateralized and correlates positively with their later choice of hand for delicate manipulations: it is the "dominant hand", in human terms. We found a significant sex difference in dominant hand (Figure 1), with males tending to left- and females to right-hand dominance. Humans, of course, show population right-handedness in both sexes, normally explained by a species-specific "right-shift" gene (18, 19). Comparing between the sexes, the human pattern—women more strongly lateralized than men—is exactly what would be expected if the right-shift had been superimposed on a pre-human pattern of female right- and male left-handedness. We suggest that the ancestral pattern has been retained in modern chimpanzees, but is only brought out by challenging bimanual manipulations such as *Saba* eating, because as arboreal animals chimpanzees are more generally rewarded for ambidextrality (14).

Plant food processing by great apes therefore proves to be a useful site for meaningful comparison of cognitive skill in the great apes. Past comparisons have been blighted by the species-specific nature of the most compelling evidence: chimpanzee social behaviour and tool-use, gorilla plant-processing, orangutan locomotion and (in one population) tools. Comparing on the 'level playing field' of plant processing, we find that when chimpanzees deal with complex manual problems they employ elaborate, hierarchically-organized programs, as is already known in gorillas. Like gorillas, they show co-ordination both between the two hands and among individual digits in different executive roles, an obvious parallel with humans (20, 21). The parallel is even tighter when their sex-differentiated handedness in a bimanual task is considered, with Mahale chimpanzees presenting a possible model of the original pattern of laterality of the last common ancestor and explaining the sex differences in degree of handedness seen in humans today. However, it is intriguing that in development of these considerable manual skills, we find that most ontogenetic changes can be explained by maturation and energy-optimization strategies of the mother, rather than advanced social learning mechanisms. Within this more mundane picture there is certainly scope for extensive incidental social learning; but it is most likely that simple processes, such as affordance learning and "unintentional" imitation by behaviour-parsing, may underwrite much of the organized complexity and impressive skills of great apes.

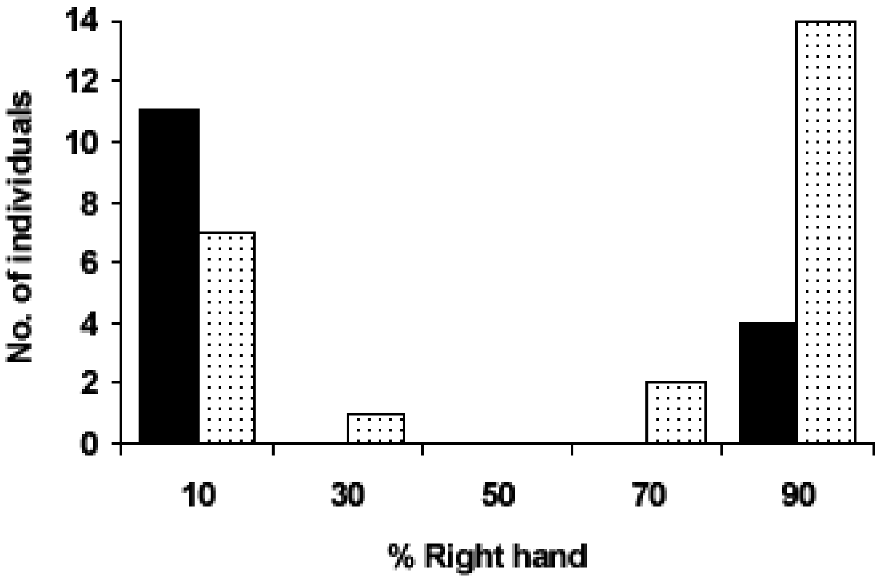

Figure 1. Sex differences in hand preference. Distribution of Mahale chimpanzees, according to the preferred hand for manipulative actions when processing Saba and Citrus fruits. The X-axis shows an individual's degree of right-hand prefernce; thus, 0 = completely left-handed, 50 = ambidextrous, 100 = completely right handed. Males (15 individuals) are shown in black, females (24) in stipple.

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