
<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 ambidexterity (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

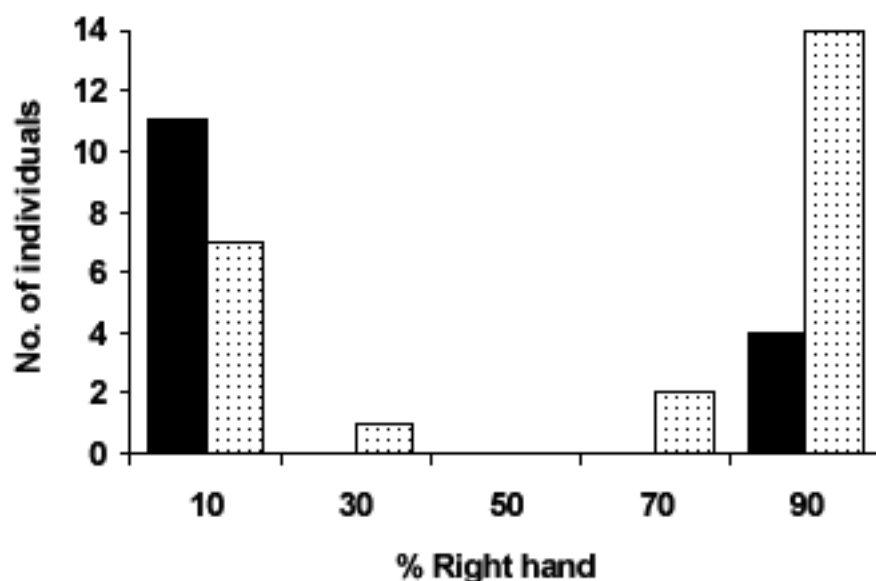


Figure 1. Sex differences in hand preference. Distribution of Mahale chimpanzees, according to the preferred hand for manipulative actions when processing *Saba* and *Citrus* fruits. The X-axis shows an individual's degree of right-hand preference; thus, 0 = completely left-handed, 50 = ambidextrous,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

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.

References

- (1) Byrne RW, Corp N, Byrne JME 2001. Estimating

- the complexity of animal behaviour: How mountain gorillas eat thistles. *Behaviour* 138: 525-557.
- (2) Byrne RW, Corp N, Byrne JM 2001. Manual dexterity in the gorilla: bimanual and digit role differentiation in a natural task. *Animal Cognition* 4: 347-361.
 - (3) Byrne RW, Russon AE 1998. Learning by imitation: a hierarchical approach. *Behav Brain Sci* 21: 667-721.
 - (4) Corp N, Byrne RW 2002. Leaf processing of wild chimpanzees: Physically defended leaves reveal complex manual skills. *Ethology* 108: 1-24.
 - (5) Corp N, Byrne RW 2002. The ontogeny of manual skill in wild chimpanzees: Evidence from feeding on the fruit of *Saba florida*. *Behaviour* 139: 137-168.
 - (6) Bruner J 1970. The growth and structure of skill. In Connolly KJ, (ed) *Mechanisms of Motor Skill Development*, pp 63-94. Academic Press: New York.
 - (7) Wood D 1989. Social interaction as tutoring. In Bornstein MH, Bruner JS, (eds) *Interaction in Human Development*, pp 59-80. Lawrence Erlbaum Associates: Hillsdale, New Jersey.
 - (8) Tomasello M, Kruger AC, Ratner HH 1993. Cultural learning. *Behav Brain Sci* 16: 495-552.
 - (9) Byrne RW 1999. Imitation without intentionality. Using string parsing to copy the organization of behaviour. *Animal Cognition* 2: 63-72.
 - (10) Byrne RW 2002. Imitation of complex novel actions: what does the evidence from animals mean? *Advances in the Study of Behavior* 31: 77-105.
 - (11) Boesch C 1991. Teaching among wild chimpanzees. *Anim Behav* 41: 530-532.
 - (12) Cusance DM, Whiten A, Bard KA 1994. The development of gestural imitation and self-recognition in chimpanzees (*Pan troglodytes*) and children. In Roeder JJ, Thierry B, Anderson JR, Herrenschmidt N, (eds) *Current Primatology. Vol. 2: Social Development, Learning and Behaviour*, pp 381-387. Université Louis Pasteur: Strasbourg.
 - (13) Whiten A, Cusance DM, Gomez J-C, Teixidor P, Bard KA 1996. Imitative learning of artificial fruit processing in children (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). *J Comp Psychol* 110: 3-14.
 - (14) Corp N, Byrne RW 2003. Sex differences in chimpanzee handedness. *Am J Phys Anthropol* 121: in press.
 - (15) McGrew WC, Marchant LF 1996. On which side of the apes? Ethological study of laterality of hand use. In McGrew WC, Marchant LF, Nishida T, (eds) *Great Ape Societies*, pp 255-272. Cambridge University Press: Cambridge.
 - (16) McGrew WC, Marchant LF 1999. Laterality of hand use pays off in foraging success for wild chimpanzees. *Primates* 40: 509-513.
 - (17) Corballis MC 1991. *The Lopsided Ape*. Oxford: Oxford University Press.
 - (18) Annett M 1985. *Left, Right, Hand and Brain: The Right Shift Theory*. London: Lawrence Erlbaum.
 - (19) McManus IC 1985. Handedness, language dominance and aphasia: a genetic model. *Psychological Medicine Monograph Supplement* 8: 1-40.
 - (20) Frigaszy DM 1998. How non-human primates use their hands. In Connolly KJ, (ed) *The Psychobiology of the Hand*, pp 77-96. Mac Keith Press: Cambridge.
 - (21) Boesch C, Boesch H 1990. Tool use and tool making in wild chimpanzees. *Folia Primatol* 54: 86-99.