Cultural primatology comes of age

Frans B. M. de Waal

The chimpanzee keeps inching closer to humanity. After decades of patiently gathering information, the heads of seven field-sites pool their knowledge to reveal the astonishing variation in tool technology and social customs in chimpanzees across Africa.

The question of whether animals have culture is a bit like asking whether chickens can fly. Compared with an albatross or a falcon, perhaps not, but chickens do have wings, they do flap them, and they can get up in the trees. Similarly, viewed from the cultural heights achieved by humans in art, cuisine, science and politics, other animals seem to be nowhere in sight. But what if we change perspective, and don't measure them by our standards? This is what Kinji Imanishi, a Japanese anthropologist, proposed in the early 1950s[1]. In an imaginary debate between an evolutionist, a layman, a monkey and a wasp, Imanishi suggested that culture — defined as the non-genetic transmission of habits — was entirely possible, and even likely, for animals other than humans.

This insight prepared the minds of primatologists for the spread of potato washing among macaques on the tiny Japanese island of Koshima (Fig. 1). One juvenile female pioneered the habit of carrying sweet potatoes to the water to clean off the dirt. Her mother and closest peers soon followed, and the habit spread to others. Within a decade, the whole of the population under middle age was washing potatoes[2]. But Western anthropologists and psychologists were distinctly uncomfortable with application of the 'culture' label to mere monkeys. This led to definitions of culture that required linguistic mediation, a high speed of behavioural change, or full-blown imitation[3–5]. Soon the debate shifted to the question of whether monkeys and apes actually 'ape'. In drawing such lines, the critics echoed earlier views that designated our species as the only one to possess culture[6].

If animal groups vary in a single behaviour such as potato washing, there is, perhaps, not much reason to use a loaded term such as 'culture' — 'group-specific trait' or 'tradition' should do instead. But the first intimation that things might not be so simple with regard to our closest relatives came in 1992, with William McGrew's review of chimpanzee tool-use in the wild[7]. Since then, new observations have appeared, one by one, in the primatological journals. And now, on page 682 of this issue, comes the grand synthesis by Andrew Whiten and his colleagues[8], describing the various habits of chimpanzees at no less than seven well-established field sites. The record is so impressive that it will be hard to keep these apes out of the cultural domain without once again moving the goalposts.

The evidence comes from a survey of all suspected cultural variants in wild chimpanzees, including behaviour patterns never published before. Some populations, for example, fish for ants with short sticks, eating the prey off the stick one by one. But at least one population has developed the more efficient technique of accumulating many ants on a long wand, after which all insects are swept into the mouth with a single hand motion.

After compiling a first list, Whiten *et al.*[8] rated behaviour patterns on a scale from customary to absent at each field site, and the ecology of each site was taken into account. For instance, chimpanzees will not sleep in ground nests (as opposed to tree nests) at sites with high leopard or lion predation. Such ecologically explainable differences were excluded from the list, leaving no fewer than 39 behaviour patterns — far more than reported for any other animal — that vary across chimpanzee communities in Africa.

Genes determine general abilities, such as tool use, but it is hard to imagine that they instruct apes how exactly to fish for ants or whether or not to make cushy seats out of vegetation. Moreover, Whiten and colleagues found no evidence that habits vary more between, than within, the three existing subspecies of chimpanzee. So genetics cannot account for the observed variability. Take the two best-known communities: those studied by Jane Goodall in Gombe National Park, and by Toshisada Nishida in the Mahale Mountains, both in Tanzania. The two sites are only 170 km apart, and both are inhabited by the Eastern subspecies

F. B. M. DE WAAL

C. BOESCH

Figure 1 **Japanese monkey washing potatoes. About half a century ago, a juvenile Japanese macaque developed sweet-potato washing on the island of Koshima. The habit spread to the rest of the population. None of these monkeys is still alive today, but their descendants are still washing potatoes.**

Figure 2 **Transmitting culture — this chimpanzee shares the nut that she has just cracked open. Nut-cracking, one of the best-studied cultural variants, is acquired by young chimpanzees only after many years of practice.**

(*Pan troglodytes schweinfurthii*). In Mahale, grooming apes customarily clasp two hands together high above their heads — something never seen in 40 years at Gombe[9].

Studies of chimpanzees in captivity support the emerging picture of cultural apes. Because captive groups are relatively young, new habits often develop and their spread can be carefully charted[10]. Also, new techniques can be demonstrated to the apes by human experimenters, to see how faithfully they are copied[11]. All in all, the evidence is overwhelming that chimpanzees have a remarkable ability to invent new customs and technologies, and that they pass these on socially rather than genetically (Fig. 2).

The definition of culture will no doubt keep changing, but Whiten *et al.*[8] rightly take the position, common in the life sciences, that mechanisms are of secondary importance. In the same way that the definition of respiration doesn't specify whether the process takes place through skin, lungs or gills, the concept of cultural propagation does not specify whether it rests on imitation, teaching or language. The 'culture' label befits any species, such as the chimpanzee, in which one community can readily be distinguished from another by its unique suite of behavioural characteristics. Biologically speaking, humans have never been alone — now the same can be said of culture. □

Frans B. M. de Waal is at Living Links, The Yerkes Regional Primate Research Center and Department of Psychology, Emory University, Atlanta, Georgia 30329, USA.
e-mail: dewaal@emory.edu

1. Itani, J. & Nishimura, A. in *Precultural Primate Behavior* (ed. Menzel, E. W. Jr) 26–50 (Karger, Basel, 1973).
2. Watanabe, K. in *The Ethological Roots of Culture* (eds Gardner, R. A., Chiarelli, A. B., Gardner, B. T. & Plooij, F. X.) 81–94 (Kluwer, Dordrecht, 1994).
3. Galef, B. G. *Hum. Nature* **3,** 157–178 (1990).
4. Premack, D. & Premack, A. J. in *Companion Encyclopedia of Anthropology* (ed. Ingold, T.) 350–365 (Routledge, London, 1994).
5. Tomasello, M., Kruger, A. C. & Ratner, H. H. *Behav. Brain Sci.* **16,** 495–552 (1993).
6. Kroeber, A. L. & Kluckhohn, C. *Pap. Peabody Mus. Am. Archeol. Ethnol.* **47,** 41–72 (1952).
7. McGrew, W. C. *Chimpanzee Material Culture: Implications for Human Evolution* (Cambridge Univ. Press, 1992).
8. Whiten, A. *et al. Nature* **399,** 682–685 (1999).
9. McGrew, W. C. & Tutin, C. E. G. *Man* **13,** 243–251 (1978).
10. de Waal, F. B. M. & Seres, M. *Am. J. Primatol.* **43,** 339–346 (1997).
11. Whiten, A. *J. Comp. Psychol.* **112,** 270–281 (1998).

Enzymes

Picking a winner

Roger Sheldon

Enzymes are remarkable catalysts that perform their tasks with alacrity in water at room temperature, and with a high degree of regioselectivity (for example, substitution at a particular position in an aromatic ring) and enantioselectivity (for a particular optical isomer). Because of the trend towards more environmentally friendly processes, and drugs that are more effective and cause fewer side effects (such as optically pure isomers), biocatalysis is rapidly becoming an attractive option for the manufacture of fine chemicals. The industrial application of certain enzymes, for example most hydrolytic enzymes, is relatively straightforward, whereas for others, such as the reduction–oxidation, or redox, enzymes, the need for enzyme cofactors makes their use more problematic. Nonetheless, it is precisely these enzymes that mediate the most interesting synthetic conversions.

A major challenge in biocatalysis is to harness the enormous potential of the ubiquitous cytochrome P450 monooxygenases[1]. These enzymes play key roles in the biosynthesis of prostaglandins and steroids, among others, and in the detoxification of foreign substances in the body, including drugs, pesticides and petroleum hydrocarbons. They are promiscuous catalysts, using molecular oxygen to insert an oxygen atom into a number of substrates. Many of these conversions are of potential industrial interest, for example in the production of pure enantiomers of epoxides. Unfortunately, they suffer from several drawbacks — low stability and turnover rates and the need for a complex cofactor regeneration system — that prohibit their industrial application. The paper by Arnold and co-workers on page 670 of this issue[2] constitutes an important step towards the ultimate goal of commercial viability. They successfully apply the technique of 'directed evolution', using random mutagenesis and DNA shuffling, to develop mutants of a bacterial cytochrome P450 enzyme that efficiently use hydrogen peroxide (H_20_2) as the source of oxygen, thereby bypassing the need for cofactor regeneration.

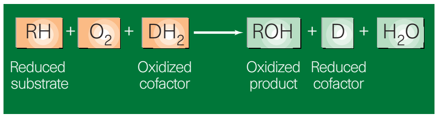

Figure 1 **Oxidation–reduction reaction catalysed by cytochrome P450 monooxygenases.**

Cytochrome P450 monooxygenases catalyse redox reactions, which involve taking one oxygen atom from O_2 and inserting it into a substrate (hence the name monooxygenase). The second oxygen atom is reduced to water (Fig. 1). Cytochromes have an iron-containing porphyrin group (a haem complex) that catalyses electron-transfer processes by cycling between oxidized and reduced forms of iron. Cytochrome P450 (the name is derived from the fact that its spectrum exhibits a characteristic peak around 450 nm) differs from other cytochromes in that it uses O_2 and a reducing source to oxidize substrates. The necessary reducing source is provided by the cofactor system, which cycles between D and DH_2 (Fig. 1).

The cofactor, a nicotinamide adenine dinucleotide (NAD or NADPH), is regenerated *in vivo* by a complex system involving multiple redox proteins, the reducing agents being ultimately derived from an energy source such as glucose. The need for a complex cofactor regeneration system, along with the poor stability of these enzymes outside the cell, dictates that fermentation is the best way to perform such reactions in practice. But the complexity of fermentation processes limits the application of these enzymes to expensive products such as steroids. Their scope could be expanded if it were possible to use the isolated enzymes. Indeed, the need for cofactor regeneration can be circumvented altogether by using H_2O_2 as the oxygen source in the so-called 'peroxide shunt' pathway[1] (Fig. 2). Unfortunately, this is not very efficient, and in order to be synthetically viable would have to be improved considerably. This was the starting point for the study by Arnold and co-workers[2].

After aeons of evolution, through mutation and Darwinian selection, enzymes are ideally suited to the tasks they perform *in vivo*. They have not evolved for the purpose of producing chemicals on an industrial scale, and so often lack the necessary features, such as stability outside the cell and high turnover rates. But, using the tools of modern biotechnology, it is now possible to mimic the evolution of enzymes *in vitro* — so-called directed evolution — in weeks rather than millions of years. The advent of error-prone polymerase chain reaction (PCR) has made it possible to selectively target the gene encoding a particular enzyme and generate a library of genes containing point mutations. Recombination produces further mutations that can be screened to find variants leading to superior enzymes[3]. It is a relatively easy task to make thousands of mutants, but the real key to success is developing an assay that can pick out the useful ones.

For their directed evolution study Arnold and co-workers[2] chose the widely studied cytochrome $P450_{cam}$ from the bacterium *Pseudomonas putida*, the structure of which has been determined by X-ray diffraction. This enzyme catalyses the hydroxylation of camphor *in vivo*, showing only weak activity towards naphthalene — a component of coal tar used to manufacture dyes and resins. The hydroxylation of naphthalene with H_2O_2 was chosen as the model reaction to be studied, presumably because a bicyclic aromatic leads to more highly conjugated, and therefore more highly coloured, products.