

The maker not the tool:
The cognitive significance of great ape manual skills.

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Tool-use by chimpanzees has attracted disproportionate attention among primatologists, because of an understandable wish to understand the evolutionary origins of hominin tool use. In archaeology and paleoanthropology, a focus on made-objects is inevitable: there is nothing else to study. However, it is evidently object-directed manual skills, enabling the objects to be made, that are critical in understanding the evolutionary origins of stone-tool manufacture. In this chapter I review object-directed manual skills in living great apes, making comparison where possible with hominin abilities that can be inferred from the archaeological record. To this end, 'translations' of terminology between the research traditions are offered. Much of the evidence comes from observation of apes gathering plants that present physical problems for handling and consumption, in addition to the more patchy data from tool use in captivity and the field. The living great apes, like ourselves, build up novel hierarchical structures involving regular sequences of elementary actions, showing co-ordinated manual role differentiation, in modular organizations with the option of iterating subroutines. Further, great apes appear able to use imitation of skilled practitioners as one source of information for this process, implying some ability to 'see' below the surface level of action and understand the motor planning of other individual; however, that process does not necessarily involve understanding cause-and-effect or the intentions of other individuals. Finally I consider whether a living non-human ape could effectively knap stone, and if not, what competence is lacking.

Only two years after Louis Leakey (1961) defined Man's origin as the point at which an ape-like creature first made tools to "a regular and set pattern", Jane Goodall (1963) published her evidence that the chimpanzees of Gombe did just that. The 40 years that followed have seen many attempts to sharpen definitions—of human, of tool, and of what counts as a regular and set pattern—to avoid the unfortunate syllogism that these facts point toward, and to gain a better understanding of the origins and development of tool-making in humans. We now know that the chimpanzee *Pan troglodytes* is not alone among living great apes in making tools (e.g. see Fox, Sitompul and van Schaik, 1999), that chimpanzees make many different types of tool for different purposes (Boesch & Boesch, 1990; Goodall, 1986; Nishida, 1986), and that the styles of tool-making differ between chimpanzee communities (McGrew, 1992; McGrew, Tutin, & Baldwin, 1979). Meanwhile, archaeological evidence has pushed the origins of flaked stone tools

way back (Roche, Deleignes, Brugal, Feibel, Kibunjia, Mourre, et al., 1999), beyond the comfortable period when tall, large-brained ancestral humans lived over much of the Old World, to African strata in which the few hominin bones are of small animals with chimpanzee-sized brains, species not even classified in the genus *Homo*. These facts may seem to encourage “continuity” theorizing, until the tools themselves are examined. The fact is, there is a big difference between the most elaborate chimpanzee tool, a green twig stripped of its leaves, and the 2.3 Mya stone tools showing organized sequential detachment of flakes. Put bluntly, any of us can make any chimpanzee tool, without training and in a few seconds, but stone knapping is an esoteric and difficult skill which excites admiration and awe even today. No living ape has learnt to remove a flake in the way even 2.3 Mya hominins could (Toth, Schick, Savage-Rumbaugh, Sevcik, & Rumbaugh, 1993; Wright, 1972). Are all efforts to understand pre-hominin origins of human tool making doomed to disappointment?

Part of the difficulty with answering this question is the difference in evidence from living great apes and extinct hominins. Behavioural observation of apes allows us to identify tools made from grass, vine and woody material, tools that entirely comprise chimpanzee tool manufacture; but we see only a snapshot in time, lacking any historical record (or even definite fossils of chimpanzee ancestors). The only *stone* tool-use by chimpanzees, for cracking nuts (Boesch & Boesch, 1990; Sugiyama & Koman, 1979), involves selection of found objects, thus leaving no archaeological record except small piles of rocks. Conversely, the archaeological record of early hominins entirely omits tools made of plant material, which presumably these creatures were at least as well able to fashion as are modern chimpanzees; but this is compensated by a rich time-series of tools, some associated with bones of particular hominin species. If we insist on parity by ignoring tools made of non-fossilizing plant material, tool-making becomes once more “uniquely human”: but ignoring evidence is no way to make progress. (Unfortunately, just this approach remains frequent in more popular treatments of human origins.) Even when direct comparison between tools of apes and hominins *has* been made, it has inevitably been at a highly abstract level; and claims have been controversial (McGrew, 1987; Wynn & McGrew, 1989). This paper will argue for another way: let us back off from this close-focus upon tools, stone or otherwise, and concentrate instead on their psychological significance.

Surely the reason that for hundreds of years scholars have been content to define our species as “Man the Tool-maker” is not because of any special symbolic meaning of tools, but the fact that making tools is smart. Finding a delicately flaked stone arrowhead in the ground is exciting to most people because of what it tells them about the mind of the tool-maker. The real

significance of the earliest stone tools in the fossil record is the deductions they allow us to make about the cognitive psychology of long-extinct hominins. The slight change of emphasis immediately enables progress: we *can* compare two million year old hominins and modern chimpanzees on the metric of psychological capacity, no matter where our evidence for those capacities comes from. The lesson has perhaps been better grasped by paleo-archaeologists—who have long attempted to reconstruct behaviour from the use of debitage, flaking sequences, cut marks on bones, disposition of tools on floors and so on—than by primatologists, held in thrall by the tyranny of the tool as detached object. Chimpanzees are the only ape species commonly to make tools in the wild, and this has led to an inordinate concentration on the chimpanzee, much puzzlement about the relative lack of tools in other great apes (e.g. McGrew, 1989), and theories that awkwardly postulate the secondary loss of tool-making abilities in apes other than chimpanzees (e.g. Parker and Gibson, 1979). Let us instead concentrate our analyses upon the *process*: of tool making, tool using, or any comparably skilled manual activities. This brings immediate advantages from the point of view of the evolutionary psychologist. Study is no longer restricted to species that make tools (which effectively meant to one species of ape, the chimpanzee), but can be widened to any species that uses its hands or equivalent effector organs in interesting ways: even raccoons, squirrels and parrots. That will allow more genuinely comparative study. For reconstructing the evolution of human psychology, by examining the manual dexterity and flexibility of non-human primates, starting with the great apes, we have some prospect of gaining important clues to the evolutionary origin of technological skill. One aim of the current paper, then, is to present a brief overview of the **object-directed manual skills of the living great apes**, as presently known, in order that paleo-archaeologists may make informed comparisons with the corresponding manual skills they deduce from the fossil record.

An additional problem in making productive comparisons between skills of living apes and extinct hominins is that the two traditions of study have proceeded independently, and each has needed to use technical terms. Often, wishing to avoid cumbersome jargon, researchers have recruited everyday words and given them new, operational definitions. Unfortunately, the same words may have been given very different definitions, a problem sometimes further compounded by slightly different everyday meanings in English and French. For instance, “technique” has been defined as “the practical manner of accomplishing a particular task” (Inizan, Reduron-Ballinger, Roche, & Tixier, 1999), and “an ordered sequence of elements of manual skill, coordinated so that the whole performance serves to {accomplish a purpose}” (Byrne & Byrne, 1993b). These definitions may not sound incompatible, but in reality it is clear that Inizan et al use the term for how a local purpose is achieved, such as whether a stone

hammer or a soft hammer is used for percussion flaking, whereas Byrne and Byrne use it to describe the overall organization of a task—almost the exact reverse. These terms are understood perfectly by cognate researchers, but as soon as the two traditions attempt to talk to each other, problems are likely to arise. To make any sort of worthwhile comparison, it is first necessary to make terms mutually comprehensible. A secondary aim of this paper, then, is to provide an approximate **translation of terminology** to allow better communication between cognitive archaeology and cognitive primatology. Thus, whenever I introduce and define a term used by primatologists to describe great ape manual capacities, I will attempt to provide the equivalent term that has been used to describe equivalent behaviour within knapping (Bril, Roux, & Dietrich, 2000; Inizan, et al., 1999; Roux, 2000).

Although I will not ignore the tool-making and tool-use unique of the chimpanzee (and to one tool-using population of Sumatran orangutan *Pongo abelii*, a population which is now probably extinct), I will concentrate on the preparation of “hard-to-process” plants for consumption, a task that confronts all apes to a greater or lesser extent. My terminology was developed originally while working with mountain gorillas *Gorilla beringei* engaged in terrestrial herb feeding. Research employed both real-time observations in the field (Byrne & Byrne, 1991, 1993b), and more detailed analysis of video records of gorilla behaviour in the laboratory (Byrne, Corp, & Byrne, 2001a, 2001b). The definitions were subsequently refined through extension to chimpanzees, where difficult fruit processing was also examined (Corp & Byrne, 2002a, 2002b); and to describe the compensations employed by snare-injured chimpanzees and gorillas who cope with these challenging feeding tasks (Byrne & Stokes, 2002; Stokes & Byrne, 2001). Comparable work has begun on the Bornean orangutan *Pongo pygmaeus* (Russon, 1998).

Manual challenges of plants

In this paper, the emphasis will be on plants which present special difficulties, and the impression might be gained that most foods of great apes are hard to process, or that apes are specialists on the more intractable plants found within their ranges. Compared with their closest feeding competitors, the Old World monkeys, there may be some truth in this view (Byrne, 1997); however, great apes do of course avoid difficulties when they can. Most strikingly, chimpanzees and western gorillas relish figs *Ficus* spp. (Wrangham et al., 1993). Because of the fig’s unusual pollination method, its fruits normally contain living fig wasps and thus provide protein as well as sugars. In regions of high density and year-round availability of figs, availability of this balanced diet means that chimpanzees are able to avoid many of the problematic foods they must eat elsewhere. For instance, at Budongo and Kibale, Uganda, chimpanzees do not feed

on social insects and so no individuals in these populations engage in regular tool-use. The abundance of figs in the ranges of some chimpanzee populations is therefore rather an annoyance for cognitive psychologists! Because it is precisely when they are engaged with manually challenging foods that we see the cognitive capacities of apes most clearly displayed, fleshy fruits provide little useful information about manual skills. Even within leaf-eating tasks, we have found that it is only the physically “defended” leaves which reveal many of the manual capacities of most interest for comparison with hominid abilities, including an overall hierarchical task organization (Corp & Byrne, 2002a).

Some of the plant-processing tasks that elicit complex manual strategies from great apes are tasks readily comprehensible to Europeans and Americans who—like myself—are already familiar with the some of challenges they would present for handling. This is the case because the plants eaten by some great apes, such as mountain gorillas, are plants of the temperate zone and as such are matched by closely related forms in the Holarctic. For instance, the nettle *Laportea alatis*, like the nettles familiar to northern Europeans, is more or less covered by stinging hairs. The sting mechanism only activates as the leaf matures, so the topmost immature leaves on a stem are relatively safe to touch. Stings are found all over mature leaves, the leaf underside is less protected than the edges or upper surface. Worst to touch are the stems, both that of the leaf (the petiole) or the main upright stem, which are densely covered by stings. As children sometimes discover by trial and error, but are often told, a firm grip is less painful, because the sting mechanism is delicate and can often be crushed before it triggers; conversely, a light touch can be very unpleasant. (Hence the English phrase, “grasping the nettle”.) For the mountain gorillas of Karisoke, Rwanda, *Laportea* leaves are one of the four most frequent plants items in the diet (Watts, 1984). This is not surprising since they are rich in protein and low in indigestible lignin (Waterman, Choo, Vedder, & Watts, 1983). However, the reactions of young gorillas show that they find contact with nettle plants painful and aversive, just as humans do (*pers obs.*). Other plants of similar importance in gorilla diet, like the thistle *Carduus nyassanus* and the bedstraw *Galium ruwenzoriense* share the same genus and the same difficulties for handling as common wayside plants of late summer in Europe and America. *Galium* is a clambering plant, adapted to this way of growing by numerous minute hooks on the edges of leaf and stem; these hooks hinder swallowing, and could easily trigger choking. Like all the terrestrial herbs staple to gorilla diet, *Carduus* is highly nutritious, but it is defended from animals by long, tough spines on the leaves and the winged extensions of the stem.

Chimpanzees are restricted to tropical zones, and the challenges they face in plant-handling are less familiar. Two plants in particular have been found to test the manual abilities of

chimpanzees. These are the leaves of *Broussonettia papyrifera*, a South-East Asian tree introduced to Budongo, Uganda, in a failed attempt to establish paper-making. Its leaves are covered on one side with woolly hairs that, like the hooks of *Galium*, make swallowing difficult (Stokes, 1999; Stokes & Byrne, 2001), and *Saba florida*, a vine whose baseball-sized fruits are delicious and high in sugars, but which are difficult to open neatly enough to gain the flesh (Corp & Byrne, 2002b). Orangutans have attracted far less study than chimpanzees or mountain gorillas (though even less has yet been possible with western gorillas *Gorilla gorilla* or bonobos *Pan paniscus*, whose manual skills in the wild remain sadly unexplored). However, orangutans; approach to the problem of obtaining the nutritious meristem of new leaves of the palm *Borassodendron borneensis*, defended by razor-sharp edges of the surrounding leaf petioles, shows many parallels with the manual skills of Africa great apes (Russon, 1998).

The smallest functional units of action

Suppose a leaf needs to be folded, as is the case when a gorilla eats nettle (because folding wraps a whole bundle of stinging nettle leaves and exposes only the relatively sting-free leaf underside). There are many ways for an ape to do it. Holding with precision grips of thumb and first finger of a different hand at either end, one hand may be rotated until the leaf is folded, then the thumb of the other hand moved to hold both leaf ends; or, holding only one end of the leaf with a scissor grip of digits 2 and 3 (Christel, 1993; Marzke & Wullstein, 1995; Napier, 1961), the index finger of the other hand can push the leaf tip over until it can be held by opposition of thumb against the two fingers; and so on. There are literally dozens of ways of achieving this single function (Byrne & Byrne, 1993b). They presumably vary in efficiency, for instance in how quickly the job can be done, whether the method is reliable in every case, and whether the hand can simultaneously be used for another purpose—perhaps retaining already-folded leaves to add to the bundle. However, in a sense, the variation is unimportant compared to the fact that any of the alternatives allow the job to be done. (Although practically-inclined readers may be interested to know that for a gorilla, much the most popular and apparently efficient method is to fold a bundle of nettle leaves over the thumb of the hand grasping the bundle with a power grip, using a tip-to-tip precision grip of the complementary hand, then re-grasp the folded bundle with the thumb over which it was folded.)

Distinguishing every variant that differed in the digits involved and the overall form of movements made, we found that gorillas employ a very large number these elementary units of action, which we called *elements*. For instance, in gorillas eating the pith and leaves of *Carduus* thistle, we found 222 elements in detailed analysis of data from 14 individuals processing up to

40 handfuls of thistle (Byrne et al., 2001b). Moreover, we showed that this count had by no means reached asymptote, and the same was true for other plant-processing tasks. Such variation may have rather little significance in terms of the overall range of tasks which can be tackled, and in any case we had no way in the field of measuring the mechanical efficiency of each variant, or charting the changes in motor proficiency during development. Instead, we ‘lumped’ elements that resulted in the same change made to the plant material. For thistle, there were 46 *functionally distinct elements*, and this estimate was found to be much closer to asymptote. When the functionally distinct elements for two other leaf-processing tasks were combined (see Byrne and Byrne, 1993), we found a total set of 53. This approach offers a simple way of comparing tasks in their manual complexity at a relatively elemental level (Byrne et al., 2001b); when comparable analysis has been performed for other great apes, it will be possible to compare species and populations that use their skills for very different tasks.

Our FUNCTIONALLY DISTINCT ELEMENT is probably closest to the term ELEMENTARY GESTURE used in the analysis of knapped stone (Bril et al., 2000), although it is perhaps more conservative in potentially lumping together very different ways for achieving the general effect with the plant material. (In practice, because we think that this lowest level of variation in ape data is mainly a matter of trivial differences in grips and the specific fingers involved, we would suspect that counts of elements from human and ape might reasonably be compared.)

Presumably, in both living ape and hominin, the mode of effect and practical use of each functionally distinct element of action are mostly discovered by trial and error, but sometimes imitation may also be valuable. Anecdotal evidence suggests this is sometimes the case in gorillas (Byrne, 1999 p.343-5). Mountain gorillas forage out of visual contact with other adults; only as an infant does a gorilla have the chance to watch closely while another individual is feeding; its own mother. At adolescence, all female gorillas leave their natal group and move away to join another group, sometimes moving more than once. However, a female joining a group whose range is in a different habitat to her that in which she grew up has no opportunity to learn locally-appropriate skills by imitation. Intriguingly one such female, Picasso, whose natal range did not include nettle, never learnt the “folding” described at the start of this section. Moreover, her juvenile offspring also failed to learn the trick. Perhaps folding is difficult to discover without a model to copy, and until one of Picasso’s descendants gets a lucky break and either discovers folding for itself or sees another gorilla doing it, they may be in for a painful time eating nettle leaves.

Coordination of the hand

Most manual actions of monkeys are carried out with a single hand, and often the other hand is in use simultaneously to support the body. The more upright body-carriage of great apes allows bimanual use of the hands, particularly if the animal is in the sitting posture favoured by gorillas. In addition, the mobile lips of great apes, especially the chimpanzee, mean that the mouth can sometimes be used almost as a “third hand”. Most obviously, two hands can be used jointly to apply double the force to an object. Such symmetrical bimanual use of the hand is presumably relatively straightforward for the brain to program. In contrast, *asymmetric bimanual action*, in which the two hands are used in different and complementary ways (and for this reason it is sometimes called “complementary bimanual action”), likely demands considerable neural flexibility.

Asymmetric bimanual processing displays what has been called manual role differentiation (Elliott & Connolly, 1984), in which the two hands must separately achieve different functions in different ways, yet be coordinated together both in space and time. As an example, consider how asymmetric bimanual action is central to a gorilla’s processing of nettle to eat. In processing a single plant, four different uses of asymmetric bimanual hand action may be employed: if the ground is soft, in order for the leaves to be efficiently stripped off the stem the other hand will be needed to support the stem base securely; then, it is essential that the two hands can be opposed to twist-off or tear-apart the leaf blades from the petioles, which are discarded; next, any debris that contaminates the bundle will be picked out, with delicate use of tip-to-tip precision grip of one hand while the other loosely retains the bundle; finally, the folding of the leaves to encase the parcel in a single leaf underside crucially depends on asymmetric bimanual action. The assignment of hand to role is highly lateralized: a gorilla that uses the right hand to hold the leaf-bundle and the left to fold it over, will hardly ever reverse these roles. For a given task, and a given animal, the asymmetry in manual action is highly stable.

Asymmetric bimanual hand use with manual role differentiation is apparently rare or absent in monkey species (but see Boinski, Quatrone and Swartz, 2001), yet it has been widely reported in great apes (e.g. Boesch & Boesch, 1990; Byrne & Byrne, 1991; Byrne et al., 2001a; Fox et al., 1999; Russon, 1998; see also (Fragaszy, 1998). The importance of this ability for chimpanzees, when they crack nuts with hammer and anvil, can clearly be seen in Boesch and Boesch’s (1993) analysis of hand posture in this task.

Coordination can also occur within a single hand, if the digits can be controlled independently. This *digit role differentiation* is probably impossible for most mammals, including monkeys, and certainly has not been described until recently (Byrne et al., 2001a). Once again, however, it may well be rather routine for great apes. For instance, nettle processing would be

inefficient if each plant had to be dealt with separately: often the plants are rather small and yield few leaf blades to eat, especially from the perspective of a huge silverback male gorilla. However, in fact it is routine to see a part-processed bundle of leaves retained in part of the hand (either digits 2 and 3, or 4 and 5, are commonly used), while a new plant is processed to the same stage (Byrne & Byrne, 1991). The accumulation may take place (1) once the leaves of a stem have been stripped off in a compact whorl; or (2) it may be delayed until leaf petioles have also been detached, thus allowing the iteration of a longer sequence of processing actions. Either way, the facility enables the edible part of several plants to be accumulated, and critically relies on digit role differentiation (Byrne et al., 2001a). All the main food plants of mountain gorillas are processed in ways that rely on this within-the-hand accumulation (Byrne & Byrne, 1991), illustrating the importance of digit role differentiation for this species. The ability has not been studied in other great apes, but a review by Frigaszy (1998) points out it may be important to them also: for instance, nut-cracking chimpanzees hold intact nuts in the same hand that they use to position and support a nut on an anvil for striking.

Within writing on stone knapping, little has been made of the importance of bimanual asymmetric coordination between the hands and digit role differentiation within the hand: perhaps, because these abilities are so familiar in our own species that their absences is unimaginable in other hominins. Bimanual asymmetric coordination would appear to be absolutely essential for any skilled stone working to take place, and digit role differentiation—while perhaps not essential—is certainly used routinely when a stone's position is adjusted within the hand by a modern stone knapper.

So far, we have considered skill at what has been called the “action level” (Byrne & Russon, 1998). Effectiveness at this level is a matter of (1) how well an action is carried out, the gradual increase in *efficiency of motor movement* that comes with long practice (something that cannot be effectively studied in observational studies of wild animals, although it is a prominent part of discussions of skill in humans e.g. Welford, 1968); (2) the *size of repertoire* of functionally distinct elements of action, providing both different ways of achieving effects (in stone knapping parlance, different TECHNIQUES to achieve a similar end: Inizan et al, 1999) and alternative ways of achieving a single effect. Having several alternative ways to achieve the same purpose sounds like unnecessary redundancy, but for an animal that may need to forage in tall trees while safely supporting its bulk, the option to carry out a normally bimanual action with one hand may be critical. This sort of flexibility also confers an unexpected benefit on great apes: the chance to survive after maiming of the hands, which sadly occurs in many areas of Africa as a consequence of snares set by humans. Young apes are highly curious, and liable to explore novel objects with

their hands, with grim consequences (Stokes, Quiatt, & Reynolds, 1999). Not all die of their injuries, however, and those that survive have been found to show quite remarkable accommodations to their severe disablement (Byrne & Stokes, 2003; Byrne & Stokes, 2002; Stokes & Byrne, 2001), using a very different range of action elements to achieve the same functions as their able-bodied counterparts, but nevertheless achieving comparable feeding efficiency.

To deal with complex manual problems however, another type of skill is also required: the ability to build up programmes of goal-directed action out of constituent elements of action, and it is to this ability we turn next.

Building up elements into hierarchical organization

In principle, the organization of a programme of goal-directed actions might be *linear*: a string of elements, joined together into a chain of actions whose sequential application achieves the desired effect. This possibility has great attraction to psychologists within the learning theory tradition, because of the computational simplicity or “parsimony” of the associative process needed to construct linear strings. (Indeed, the assumption that associative chaining could account for all human behaviour was central to the doctrine of behaviourism.) Imitative learning of string-like structures of action—called “action level imitation by Byrne & Russon, 1998—can be accommodated by an associative process, with some modification of the basic theory (Heyes & Ray, 2000).

No doubt, some animals can only acquire novel complex behaviour by action-level imitation, producing an undifferentiated linear sequence of actions; many animals probably do so frequently; and even humans certainly do so sometimes. Consider, for instance, the ability to mimic the style and mannerisms of another person that some comics use to devastating satirical effect. More significantly, we may copy in a linear fashion when we cannot “see below the surface” of a smooth performance to understand its organization, and in the process of imitation we may gain more insight into that organization.

However, it is now thoroughly accepted within psychology that human skills are normally *hierarchically* organized (Chomsky, 1959; Miller, Galanter, & Pribram, 1960; Newell & Simon, 1972), and that this applies at every point from tying shoelaces to constructing a novel sentence. Increasingly, there is evidence that the manual skills of great apes also show hierarchical organization: they are structured more like a branching tree than a linear chain, and large branches or small twigs can be dealt with as units, allowing great flexibility. Gorillas, for instance, are able both to *omit* parts of an otherwise rather standardized sequence of actions, if there is no

need on occasion to perform one particular action, or alternatively to *repeat* a section of the normal program iteratively to a criterion (Byrne & Byrne, 1993b). The section of program repeated, and thus treated as a single module, may be short or quite long. (A *program* in this context is an organized sequence of motor actions used to process potential food into a form suitable for ingestion; a *module* is a section of a program that can be treated as an independent unit, for instance by repetition, omission or use in a different program altogether.) In nettle eating, the whole sequence of *pull a stem into range, hold the base while the other hand strips up the stem, grasp the petioles to twist or lever them off the leaf blades* may be repeated, while already-processed leaf blades are retained in the lower fingers of one hand, showing that this sequence can form a module. This allows a gorilla to accumulate a larger handful of nettle leaves to eat. Modules which achieve a common function may be *shared* between two otherwise very different programs. And unlike the “fixed action patterns” of classical ethology, a gorilla’s program for dealing with plant food can be *interrupted*—provided the interruption occurs at a module boundary—and resumed smoothly later, allowing individuals often to stop mid-process, scan the environment, interact vocally with others, etc. before continuing to process the same handful. Orangutans also organize their motor planning in a hierarchical way (Byrne & Russon, 1998; Russon, 1998), as do chimpanzees (Stokes & Byrne, 2001).

Hierarchical organization of learned behaviour is likely common to all great apes (the manual behaviour of the bonobo has not yet been studied under natural conditions, but in captivity the species appears to have similar manual abilities to the chimpanzee). The ability to schedule novel hierarchical structures, themselves composed of smaller, familiar components, means that great apes have *generative* manual skill (Case, 1985; Corballis, 1991): a limited range of basic motor components can be combined in many different ways to produce a potentially unlimited range of skills. Most animals, even other non-human primates, show no such generative ability in their actions: essentially, their motor repertoires are fixed, and all that can be learnt is in under what circumstances to use an action, and how firmly or gently it should be applied. The fact that the living apes, our closest relatives, show generativity in manual skills is significant for two reasons. Most relevant to this chapter, generative manual ability is an important precursor of hominin tool construction; but in addition, it means that the closest to syntax in the natural behaviour of great apes is in the hand action, not their voices (which are restricted to a fixed and presumably innate repertoire of signals: Marler & Tenaza, 1977). Hierarchically organized structures of manual action, in which the constituent modules are themselves built up out of more elementary action components, have been called **TECHNIQUES** in primate work, a very different usage from that of archaeology. The closest

equivalent in archaeology is probably the PLAN OF ACTION (Bril et al., 2000), or METHOD (Inizan et al., 1999). The term SEQUENTIAL ORGANIZATION has also been used, but it is important to realize that in knapping as in ape plant preparation the organization is hierarchical, not simply a linear sequence.

The pattern of variance in the gorilla data (i.e. *idiosyncratic* at low levels of description, such as the precise form of elements or the manual laterality, but highly *standardized* at the level of the overall structure) has been used to argue for the importance of program-level imitation in acquisition (Byrne, 1998; Byrne & Byrne, 1993a; Byrne & Russon, 1998). In *program-level imitation* the imitator ‘sees’ and copies the underlying planning structure, but may well use its own way of achieving many of the actions copied (Note that slavish copying of low-level manual elements may well be inefficient, whereas trial-and-error exploration often efficiently homes in on the optimum.) The idea that apes can learn by program-level imitation has been subsequently supported by analysis of the behaviour of disabled chimpanzees in the wild (Byrne & Stokes, 2002; Stokes & Byrne, 2001). Young apes are highly curious, and vulnerable to disabling and often fatal injuries when they explore snares set to catch other animals. Nevertheless, some survive, and go on to manage to eat foods which require complex processing. If their normal skills developed solely by individual exploration, one would expect highly idiosyncratic techniques to be acquired by disabled animals. However, if imitation is necessary to acquire a skilled technique, and the only available model (the mother) is able-bodied, then hers is the technique that must perforce be acquired. The latter pattern was found: disabled apes use the same overall method as able-bodied ones, working round the local problems caused by their disablement.

In program-level imitation, what is essential is the opportunity to watch a skilled performer at work *for a long time*: only then can statistical regularities in the behaviour betray the underlying planning structure (Byrne, 2002, 2003). Young apes have abundant opportunities of this kind, and perhaps the same was true of the children of hominin knappers. Teaching, in contrast, may be less important when great apes learn elaborate motor skills. Active demonstration was seen only twice in an 11 year project on the acquisition of chimpanzee nut-cracking (Boesch, 1991b) and has not been noted again since. None at all was seen in a study of acquisition of *Saba florida* processing, the most complex plant feeding task for the Mahale, Tanzania, chimpanzee population (Corp & Byrne, 2002b). Instead, both studies noted that the behaviour of mother chimpanzees makes many opportunities available to their infants that may have beneficial consequences for their learning. In particular, mothers allow infants and juveniles to watch them closely, scrounge food, and interact with aspects of their own food preparation

(e.g. stone tools). However, Corp and Byrne questioned whether the mothers intend (or are adapted to produce) an effect upon learning. They noted that despite repeated begging by infants below 1 year, mothers do not share *Saba florida* pith, while when the infant is over one year they share readily, even sometimes offering the pith. This pattern is more consistent with a nutritional effect: below a year, lactation cannot be replaced or reduced by supplemental pith feeding, whereas the infant is presumably at least as well able to learn about the task.

Could a living great ape learn to knap stone?

Living great apes evidently possess many manual skills that are directly comparable to those of hominin stone knappers. Their hands are surprisingly dextrous, allowing a range of precision as well as power grips (especially in the gorilla, whose relatively long thumb and short fingers are most similar in proportion to those of modern humans). A large range of differentiated manual actions are performed, specific to functions required for particular tasks. This gives ample testament to apes' ability to learn novel motor actions, including deftly coordinated bimanual actions, in which the two hands take complementary roles simultaneously. In addition, fingers can be independently manipulated, allowing a single hand to carry out two different functions at once: for instance, picking up a small object while retaining a tight bundle of stems in other fingers. Dependent upon the flexibility of motor learning in all great apes, the extensive repertoire of manual actions for achieving different functions seems to be learnt mainly by individual exploration and trial and error, because the fine details vary idiosyncratically across the population. However, chains of different actions can be built up into complex programs, at least 5 steps in length, and these more elaborate constructions are learnt partly by imitation. The process of constructing action sequences from smaller components is hierarchical, allowing flexibility in response to environmental need, efficient modular organization, and enlargement of the repertoire in a generative and 'productive' way. These abilities would appear to allow the rudiments of stone knapping to

be done, although certainly would not be sufficient to account for the stone tools of early modern humans, which show clear evidence of being made to a preconceived plan ¹.

So, why do living apes *not* make stone tools? Before jumping to conclusions about cognitive limitations, it may be worth noting that most living apes do not make tools at all, although there is little doubt they are capable of doing so, and readily do in captivity when given tasks experimentally (McGrew, 1989). It is evident that bonobos, gorillas, almost all orangutans, and some populations of chimpanzees, have no reason in the wild to embark on tool-making: they manage just fine in their environment without needing tools. (Some part of the reason for this is no doubt the absence of tasks for which a tool is a suitable solution, but much more often it will be due to the availability of alternative, simpler sources of the same nutrients.) Might modern apes be capable of knapping? Experimental studies in captivity suggest that the answer is probably no. Both an orangutan and a bonobo have learned to flake a stone in order to obtain a sharp flake (Toth et al., 1993; Wright, 1972). However, the orangutan was extensively trained by the experimenter, and had the advantage that the core was held in place artificially for it. The bonobo, a ‘language’ trained ape, was simply shown simple knapping by the experimenter, and presented with a task that depended on cutting a rope. Rather than knap a hand-held rock, it preferred to throw the rock at the hard ground: this was effective in shattering the rock, and the bonobo then carefully selected a sharp flake to use. Since this was in fact effective, and the ape clearly understood the cause-and-effect of sharp flakes and cutting, it is hard to know what to make of its ‘failure’ to knap in classic

¹ It is controversial whether some or all of the stone tools of earlier hominins would also require the ability to envisage the finished product in advance and so guide the entire process of flaking. For most pre-*sapiens* tools, variation in types is extensive and no advance plan is evident. In contrast, the Acheulean hand-axe and the Levallois flake are relatively standardized, suggesting a real plan [Mithen, 1996 #1726]. However, Davidson (2002; Davidson and Noble, 1993)[#3384; #201] interprets these distinctive forms more prosaically. He argues that much of the ‘standardization’ of the hand-axe reflects selection by modern archaeologists, and that in fact the distribution of ancient bifaces includes a wide range of forms. Moreover, he suggests that the desired product was usually the *flakes* not the final core, which thus represents the leftover stone from which no more flakes can be detached. Dibble (1987, 1989)[#3383; #205] earlier suggested that much of the patterning in artefacts of the French Mousterian can be explained in terms of the processes of reduction, given differential availability of raw materials. Davidson goes further, interpreting the large, ‘final’ flake of the Levallois technique as a (failed) attempt to open up the core to allow more detachments (i.e. produce an acute angle at its edge), making the point that in the cases where this was successful the core would have been flaked further, so the evidence necessarily no longer exists. Needless to say, these views are not accepted by many researchers, but resolution of this controversy will require new evidence.

hominin fashion: if you can invent a safe and effective method, why bother to imitate a riskier and trickier one?

Alternatively, it may very well be that no living great ape is capable of learning the motor skill involved in aiming a *powerful and accurate* blow at an object held in the other hand: it is the combination that may be beyond them, because there is no doubt that living apes have both great limb power and delicate precision ability, in separate contexts (Goodall, 1986). Some evidence for this conjecture comes from manual laterality, which appears to develop mainly in the context of “difficult” tasks². All the skilled plant preparation of the mountain gorilla is highly lateralized at the individual level (Byrne & Byrne, 1991). Most of the natural manual behaviour of chimpanzees, like that of monkeys, lacks clear lateralization: in captivity, individual lateral preferences are found with repetitive tasks, but their significance—both statistical and functional—is controversial (Marchant & McGrew, 1996; McGrew & Marchant, 2001; Warren, 1980). The exceptions to this generalization, cases where chimpanzees do develop strong individual lateralization in the wild, are mostly tasks that require skilled use of tools or aimed percussion of objects (Boesch, 1991a; McGrew & Marchant, 1996; McGrew, Marchant, Wrangham, & Klein, 1999; Sugiyama, Fushimi, Sakura, & Matsuzawa, 1993). For this reason, lateral specialization has often been associated with skilled tool use (e.g. McGrew and Marchant, 1996). Alternatively, Byrne & Byrne (1991; see & Byrne, Corp and Byrne, 2001) noted the cognitive complexity of asymmetric bimanual coordination, also a feature of those chimpanzee tasks eliciting individual laterality, and—crucially—found in all the highly lateralized but non tool-using gorilla activities. Byrne and Byrne suggested that it was instead asymmetric bimanual coordination that benefited from strong lateralization: when the two hands need to take distinctively different roles in a single task, it pays not to switch roles between left and right hands. The correlation with tool-use and percussion is a coincidence of the particular chimpanzee tasks that needed bimanual coordination.

Humans, of course, also show population-level manual laterality, “handedness”, and this has generally been assumed to be critical to the highest echelons of manual skill, as for

² It is not really clear in what aspect of the tasks this difficulties resides. McGrew and Marchant (1999)[#2543] argue that laterality makes for increased neural efficiency, and support this with evidence that more highly lateralized chimpanzees are quicker at processing. However, Byrne and Byrne (1991), who showed the same correlation in gorillas, noted that hand *preference* inevitably meant an asymmetry in practice, and more practice will anyway lead to greater efficiency.

instance in writing. It is therefore intriguing that gorilla leaf-eating tasks—which are more complex in various ways than pith-extraction tasks—show weak but statistically significant population right-handedness (Byrne & Byrne, 1991; Byrne et al., 2001a). Gorillas are more likely to be lateralized so that precise actions are performed right-handed, with the left hand as a support. Could it be that manual role differentiation not only predisposes apes towards strong laterality, but also benefits from an inherited population bias towards particular hand assignment—right handed precision? This speculation is supported by Hopkins’ (1995) study of an asymmetric bimanual task in captivity, where strong individual laterality and significant population right-handedness were found, whereas no population effects had been detected in wild chimpanzee tasks. Now, however, population-level manual laterality has at last been found in wild chimpanzees, when eating *Saba florida* (Corp & Byrne, 2003), with females showing right- and males left-handedness. Importantly for the present discussion, this task requires both great *power* (to tear open the hard fruits), and delicate *precision* (to remove flesh without loss), in close alternation. If the expressed laterality is a sign of difficulty for the apes, it may well be beyond the capability of a modern chimpanzee, gorilla or orangutan, to exert the combination of power and precise aim in a single task that is required to knap stone.

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