COGNITIVE SCIENCE Vol 24 (3) 2000, pp.477–508 ISSN 0364-0213

Primate Culture and Social Learning

ANDREW WHITEN
University of St. Andrews

The human primate is a deeply cultural species, our cognition being shaped by culture, and cultural transmission amounting to an "epidemic of mental representations" (Sperber, 1996). The architecture of this aspect of human cognition has been shaped by our evolutionary past in ways that we can now begin to discern through comparative studies of other primates. Processes of social learning (learning from others) are important for cognitive science to understand because they are cognitively complex and take many interrelated forms; they shape traditions, cultures and nonsocial aspects of cognition; and in turn they may be shaped by their cultural context. The study of primate social learning and culture has in recent years enjoyed a renaissance, providing a wealth of new findings, key aspects of which are reviewed. The focus is on cognitive issues, including learning about the consequences, sequential structure and hierarchical organization of actions; relating stored knowledge to the assimilation of new social knowledge; feedback guiding the construction of imitations; conceptual grasp of imitation; and the reciprocal relationship between social learning and culture.

I. INTRODUCTION: COGNITIVE SCIENCE AND SOCIAL LEARNING

Humans are social animals. But one can go further than that: there are ways in which we are more *deeply* social than any other species on earth in our cognitive makeup. This distinctive social 'depth' in human cognition includes extensive penetration of each other's minds ('mindreading' or 'theory of mind'), learning major swathes of what we know and do from the culture we inherit (cultural learning), exploiting cooperation to achieve much greater things than we could individually, and communicating through language (Whiten, 1999a). In these zoologically extraordinary social achievements may lie key explanations for the heights human intellect reaches and the particular ways in which our cognitive system functions.

But distinctive as they are, these human abilities have evolved from prehuman primate foundations. Complex social life must have had a long history among the primates, for it characterizes all the main groups of anthropoids—the monkeys and apes—that have

Direct all correspondence to: A. Whiten, University of St. Andrews, School of Psychology, St. Andrews KY16 9JU, United Kingdom; E-Mail: a.whiten@st.andrews.ac.uk.

proliferated in the last 30 to 40 million years of primate evolution. These societies have been characterized as ‘Machiavellian’ because of the socially-exploitative strategies that so often make for success in them: indeed the ‘Machiavellian Intelligence Hypothesis’ proposes that it is exactly these complexities of social life—rather than physical problem-solving, foraging, tool-making and so forth—that explain important elements of advanced primate cognition, both nonhuman and human. (Whiten, 1999b; Whiten & Byrne, 1988, 1997).

One of the important ways in which primates exploit these complex social worlds is to selectively tap the expertise already acquired by others, either directly, by scrounging resources from them, or more indirectly, by learning from them (Russon, 1997). Anthropoid societies therefore provide us with a potentially very rich source of information about the origins of social learning and the kinds of cultural processes such learning may generate.

This means there is a two-part rationale for why primate social learning is important to a cognitive science aiming primarily to understand human cognition. First, the architecture of the *human* mind is massively adapted to work only in intimate conjunction with an elaborate surrounding culture (Bruner, 1990; Donald, 1991; Tomasello, Kruger & Ratner, 1993; Sperber, 1996): any fundamental understanding of human cognition will have to adequately describe its adaptations for being socially shaped. The second part of the rationale is that we will better understand this inherently social mental architecture if we can establish what it has been constructed from. This requires intelligent analysis of the relevant processes among primates, leading to inferences about ancestral cognitive capacities.

In addition to this overarching rationale, there are a number of more specific reasons why the topic of this paper holds interest for cognitive science. In outlining these next I must also emphasize that they are topics of current controversy among those who actually investigate them. Primate social learning and culture have been studied since the establishment of both psychology and Darwinian theory over a century ago, but critical exchanges in the literature about underlying theories, methods and findings have become most intense in recent years. This appears to be mainly because accumulating critiques showed that very much less had truly been established than received wisdom had portrayed (e.g., Galef, 1988, 1990; Heyes, 1993; Tomasello, 1990, 1994; Visalberghi & Fragaszy, 1990; Whiten & Ham, 1992). In recent years these challenges have stimulated a lively renaissance in studies of primate social learning (and animal social learning more generally), along with much debate about exactly what the new findings mean. Readers wishing to extend their grasp of the field as a whole can be directed to a rich crop of reviews, collections and theoretical analyses that mark the vigour this field has developed in the last decade: Boesch (1996a, b,); Boesch and Tomasello (1998); Box and Gibson (2000); Byrne (1995); Byrne and Russon (1998); Galef (1988, 1990, 1992, 1998); Heyes (1993, 1994); Heyes and Galef, (1996); King (1991, 1994); McGrew (1992, 1998); Mitchell (1994); Moore (1992); Parker and Russon (1996); Russon (1997); Russon, Mitchell, Lefebvre, and Abravanel (1998); Thierry (1994); Tomasello (1990, 1994, 1996); Tomasello and Call (1997); Tomasello, Kruger, and Ratner (1993); Visalberghi and

Fragaszy, (1990); Whiten (1996, 1998b, 2000); Whiten and Ham (1992); and Zentall (1996). Here are five aspects of the interest all this should have for cognitive science more generally.

1. Cognitive Complexity

The most thorough way in which an animal may learn from the actions of another is to *imitate* or copy it. Such a copying process operating across a whole community could lead to population-level similarities of behavior—a 'culture' or 'tradition' in biologists' terminology.

As a form of learning, imitation is generally regarded as quite distinctive and cognitively complex. Heyes (1993) illustrates what is special about imitation by noting that 'when I look down I see something very different when I curtsy than when I see someone else curtsying'. The imitator sees an action performed by another individual (the 'model') from the imitator's perspective, and from this has to generate the actions appropriate to their own action-perspective. This entails more than just a change in visual perspective: the imitator has to reconstruct not merely what the act looks like from their perspective, but what it is to *do it* from their own perspective - they have to recreate the *program of action* that the model used (Whiten & Ham, 1992), without any necessity for external shaping by either positive or negative reinforcement.

What happens in the imitative translation process is a challenging cognitive question. One of the signs of its burgeoning interest in cognitive science is the desire within artificial intelligence to achieve the difficult task of creating robots that can imitate (Demiris & Hayes, 1996). Because animal studies to date have mostly been stuck on the question 'can or does species X imitate?', I think one can as yet point only to the glimmerings of answers to the overarching cognitive question I want to pursue: 'what form does the imitator's representation of the act imitated (the 'model') take?' Even so, we can begin to address here several specific subissues within this general quest: what do primates represent of the sequential, causal or hierarchical structure of others' acts they may learn from?—and what of its intentional structure (for example, what another is *trying* to do)?—what is involved in copying novel acts and what role do action-representations already in place play in this?—what kinds of feedback are used to guide the construction of an act to match a model?—do primates operate with any conception of what it is to imitate?—and finally, can experience in imitation modify the way in which the imitator represents what it imitates? Of course, the answers to such questions may be different for different primates.

2. Varieties of Social Learning

The questions just listed suggest some of the many different forms that imitation might take. But imitation is only one among varied kinds of social learning, differentiation among which is of interest from a cognitive standpoint. One way to conceptualize these is illustrated in Figure 1, which classifies the different processes through which the

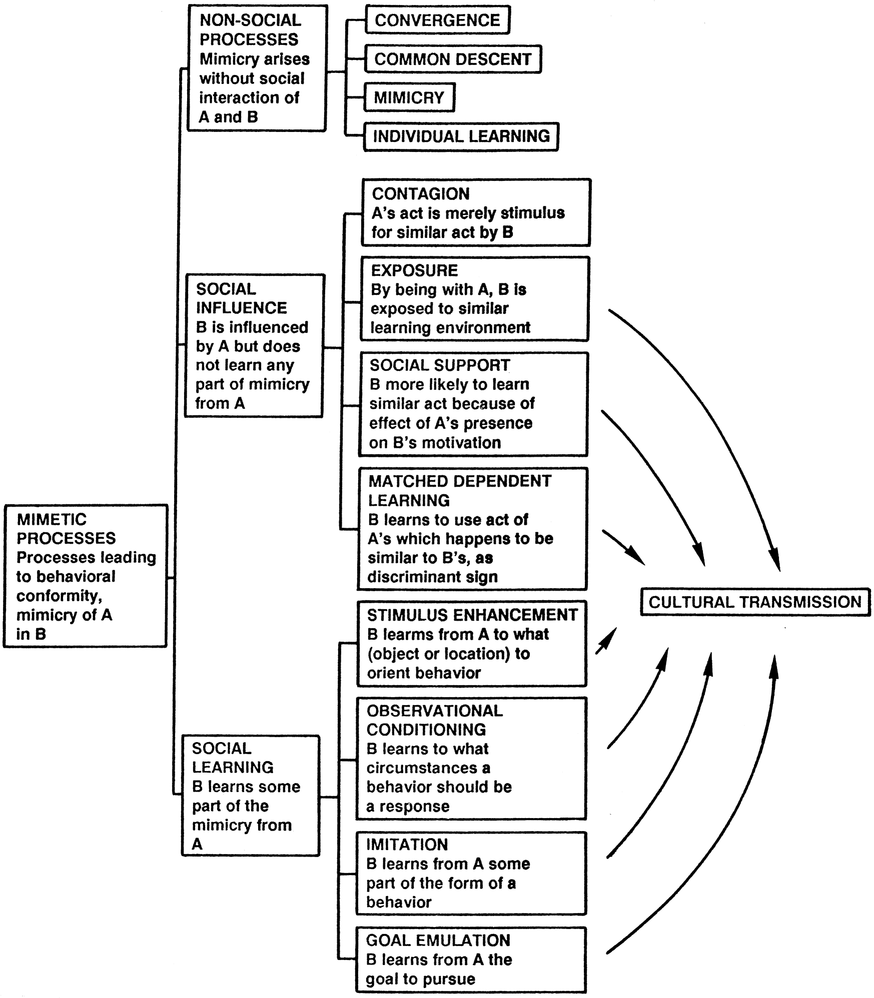


Figure 1. A taxonomy of 'mimetic' processes: those whereby the acts of one individual, B, may be caused to resemble those of individual A (from Whiten and Ham, 1992). For further explanation of terms, see text.

behavior of an individual B may come to be like A's in some way ('mimetic' processes). At the second level (second column), three main categories are discriminated. First is a category (*nonsocial processes*) that includes all those cases that do not even require social interaction between A and B: for example, two apes who never meet but who are faced with similar fruits in their environments, may learn by their own individual efforts (*individual learning*) how to peel the fruit in the same, perhaps optimal, fashion. By contrast, in the category of *social influence* B does affect A in some way: however, unlike in the third category, *social learning,* B does not learn any part of the similarity in acts *from* A: in the case of *exposure,* for example, by simply tending to be with A, B gets exposed to a similar environment which it learns to respond to in a matching fashion.

Note that, as within the specific case of imitation discussed above, the various distinctions in social influence and social learning made in Figure 1 are essentially cognitive ones, discriminating what the imitator selectively represents and utilizes from within the plethora of information made available through the actions of another individual.

Social *learning* is the main category we are concerned with in this paper. In the case where monkey B represents only the special association of monkey A with some location or object—perhaps a branch laden with fruit—we have a case of *stimulus enhancement* (Figure 1). This category is sometimes described as involving A merely drawing B's attention to some locus by its proximity to it, or even by the results of behavior that remain after A has left. However, B's representation of what it is watching may need to be more complex than that. In birds it has been shown that stimulus enhancement of a feeding site may occur only if bird B sees bird A actually succeeding in gaining food there (Palameta & Lefebvre, 1985). Such an effect is not improbable in primates although it has not been formally tested. It would imply that the individual B is able to interpret what it sees as a conjunction of an environmental locus with an act of A that has particular significance. A's act is in fact matched by what B will later attempt itself (i.e., feeding), but A's acts as seen by B will neither look nor feel as it does when A itself feeds, so connecting up the percept with the appropriate response will not follow automatically from the similarity of behavior: some process must be dedicated to connecting up the complex percept with the appropriate action on B's part.

Observational conditioning (Figure 1) is nicely illustrated in studies by Mineka and colleagues (Mineka & Cook, 1988, for a review) in which young monkeys developed fear responses to stimuli they had witnessed others being frightened by. Stimulus enhancement and observational conditioning are treated in the literature as quite distinct processes, but Whiten and Ham (1992) pointed out that they can be interpreted as positive and negative versions of an essentially similar process. In stimulus enhancement an individual B may learn the positive, or appetitive significance of an object or location: in observational conditioning, it learns about negative, or aversive significance. Bearing in mind the nature of stimulus enhancement revealed in birds, as discussed above, the two categories seem symmetric in that they both draw attention to a locus and inherently attach some significance (positive or negative) to it (see Heyes, 1994, for a more elaborate analysis of the similarities and differences between these categories).

The next category is *imitation* (Figure 1), in which B learns some part of the *form* of A's behavior. Strangely, despite specifying 'some part of', this definition has sometimes been misinterpreted as requiring an exact match, or as emphasizing 'motor matching', so a little clarification may be wise. What is required to meet this definition is that there is *some measurable matching* in B's copy of A. As Whiten and Custance (1996) noted, there are many different aspects of the original act that an imitator may or may not match, such as the act's bodily shape, extent, tempo, laterality, orientation and sequential pattern. Each of these might be copied with a greater or lesser degree of fidelity, so we must entertain a very rich conception of the variety of ways in which a pattern of behavior may match its model. Copying of each of these different aspects carries implications, of course, for the way in which the imitator is able to represent and translate into its own output what the model was doing. We shall discuss these in more detail below.

Finally, we have the case where B may *emulate* the outcome of A's action, without copying anything of the form of A's behavior itself. From the perspective of how B represents A's actions, at least two very different senses of 'emulation', a concept first promoted in primatology by Tomasello (1990), should be distinguished. In one, B learns something about the way some part of the physical world works through the consequences of A's actions on it: an example would be learning that a tool can be used as a rake to get food, the case that initially suggested the importance of this distinction in an experiment by Tomasello, Davis-Sasilva, Camak, and Bard (1987). In that experiment, chimpanzees learned from a model to use the rake to gain out-of-reach food, but did not copy certain functionally significant details of the raking actions the model displayed. In such a case what B must presumably represent is the basic causal role the tool plays—in Tomasello's terms, what the tool *affords* in the context in question (Tomasello, 1996). This can be considered more of a technical than social type of understanding, for which a fair test would be whether B could learn the key information just as well if it witnessed the tool doing its job, or other relevant objects 'going through the motions', without seeing A's actions. Heyes, Jaldow, Nokes, and Dawson (1994) approach to such a test was to have the manipulandum operate automatically, without a model touching it. Such a test could be misleading, however, because it remains possible that it will be necessary for a primate B to *perceive A* as having *caused* the tool movement (or in some way be associated with it), even when B is learning more about the nature of the tool movement than about the form of A's action.

Tomasello et al. (1987) had suggested that the chimpanzees they studied were not copying others' behavior but instead were learning about the *results* of that behavior. Assuming that observers learned about results relevant to task solution (e.g., raking the food closer), as opposed to irrelevant results (like disturbing leaves on the ground with the rake), Whiten and Ham decided to add the term 'goal' (rather than 'result') to emulation as a way of marking what might differentiate it from imitation (Figure 1); that is, the emulator copies not all results but just those that are goals of the model (imitation and emulation tend to be treated as synonyms in regular dictionary entries). Tomasello (1998) notes that this terminology suggests a meaning different to that he intended, in which emulation is essentially about the 'affordance' of manipulated objects as outlined in the paragraph above, which need make no reference to the model's 'goals'. However, copying of goals remains a theoretical possibility for which we need a term. Huber (1998) refers both to emulation (*sensu* Tomasello) and goal emulation (*sensu* Whiten and Ham). This is awkward terminology but it does acknowledge both possibilities. That an imitator will recognize a model's goals is more than a theoretical possibility, for Meltzoff (1995) has shown that human infants may attempt to act out what they perceive another as *trying to do*, even when the model is unsuccessful in achieving the result that is its goal. Clearly this ability must depend on kinds of social cognition different to learning only about object affordances per se. Thus despite some interim confusion, the upside of having introduced the term 'goal-emulation' is that it has highlighted the need to recognize these distinctions in the form that observational learning may take. Byrne (1998), Call (1999), Custance, Whiten and Fredman (1999) and Whiten and Ham (1992) each suggested that several further distinctions really need to be recognized within the emulation/imitation concepts, but the multiplicities of these, while demanding the attention of future experimenters, are beyond the scope of the present article. Just one central aspect of the emulation/imitation distinction is discussed further below, where I argue that we should be thinking of an imitation/emulation continuum, rather than a neat dichotomy.

3. Species Differences in Social Learning

To those most concerned with *human* cognitive science, differences among primates in capacities for social learning are relevant because they may shed light upon the sequence of evolutionary changes that shaped the patterns we now see in our own species (see Byrne, this volume). For instance, we shared a common ancestor with chimpanzees only about 5 million years ago, with old world monkeys perhaps 25 million years ago: do we, then, share forms of social learning with the chimpanzee that are in some way intermediate between those we share with the monkeys and those unique to ourselves? Some primate researchers have argued—with varying degrees of conviction—that we do, the intermediate ability in question being certain advanced forms of imitation (e.g., Byrne, 1995; Russon, 1997; Whiten & Byrne, 1991; Whiten & Ham, 1992). However, this is very far from being a consensus. Indeed, the comparative study of social learning can be fairly described as in (fascinating) turmoil, with some workers claiming that the only good evidence for animal imitation is in nonprimates (e.g., Galef, 1992; Heyes, 1993, 1998), others that the reverse is true (i.e., the only good evidence is in primates; Byrne & Tomasello, 1995). This seems partly due to differences in the way various authorities define the principal concepts at stake (notably imitation and emulation) and partly due to differences in methodological approach. Although such debates may at times create more heat than light and appear rather confusing to outsiders, there are signs that they are leading to much needed progress on both fronts: conceptual distinctions that attempt to address the real complexity of primate social learning (e.g., Boesch, 1996; Byrne and Russon, 1998 and commentaries; Tomasello, 1996; Whiten, 1998b; Whiten & Custance, 1996) and methodologies that avoid past weaknesses, whether the refinements be observational (e.g., Boesch, 1996a, b; Russon & Galdikas, 1993, 1995; Tanaka, 1998) or experimental (e.g., Bugnyar & Huber, 1997; Whiten et al., 1996). We shall meet some of these new approaches below. As they are applied systematically in future comparative studies, we can expect that an illuminating phylogeny of social learning will eventually be charted.

4. Culture

“To explain culture, then, is to explain why and how some ideas happen to be contagious. This calls for the development of a true *epidemiology of representations* ” Thus, Sperber (1996, p. 1) pithily expresses a bridge between cognitive science, which studies representations, and the study of culture, seen as “the cumulative effect of countless processes of interindividual transmission through imitation” (1996, p. 3).

But do any primates or other animals really have such a culture? If culture is defined in the most general way as behavioral conformity spread or maintained by nongenetic means, then these means must involve either social learning or social influence of the types indicated in Figure 1. Social influence and stimulus enhancement appear to be widespread among birds and mammals (see Heyes & Galef, 1996), and thus so do cultures, defined in this way. The opening of milk-bottle tops by blue-tits, the spread of which in the UK was carefully documented, was one of the first of many examples (Hinde & Fisher, 1951). Studies with captive birds showed that social enhancement, in which the results of the expert bird’s actions (opened containers) drew the attention of novices to the new food source, would be sufficient to cause the spread of such a behavior in the population (Sherry & Galef, 1984). Stimulus enhancement may be the main way in which young primates learn about what foods to eat and how to find them (Fragaszy & Visalberghi, 1996; Whiten, 1989; Visalberghi, 1994).

However, there is clearly more to human culture than this kind of process. Galef (1992) suggested that since human culture rests upon sophisticated social learning processes that include imitation and teaching, it is misleading to talk of animal ‘culture’ unless transmission occurs through mechanisms this complex. If the mechanisms operative in primates are no more than, say, stimulus enhancement, it might be more proper to say that we have an *analogy* of human culture, rather than any homologous processes that would give a real insight into evolutionary origins. Galef suggested that if we have only an analog we might be best to refrain from talk of ‘culture’ and simply refer to ‘traditions’. Of course, which actual terms we use to highlight this distinction is arbitrary (one could make a similar argument about the ‘corruption’ of the anthropomorphic term, ‘tradition’!), but Galef is making a significant point about the distinction itself. Accordingly we are back to issues of cognition: the nature of the cognitive process of transmission *matters* in understanding what kinds of traditions, or cultures, really operate among nonhuman primates.

Tomasello, Kruger, and Ratner (1993) also emphasized the special nature of what they called ‘cultural learning’ in humans, suggesting that even in young children, true imitation rests upon abilities to recognize the intentional structure of actions in others in a way that other apes do not naturally do. Again, then, what apes have to tell us about the origins of culture is argued to hinge crucially on the cognitive underpinnings of how social learning actually takes place.

5. Experience and the Ontogeny of Social Learning

Tomasello et al. (1993) also raised another interesting linkage between culture and social learning in highlighting the fact that the strongest evidence of human-like imitation in apes is for those that have experienced some degree of interaction with humans, in many cases actually being human-reared (see Call & Tomasello, 1996, for a full account). The apes have experienced some of the inputs from human culture that may be necessary for advanced social learning mechanisms to come into operation. This raises the intriguing possibility that the very ability to imitate or learn in other socially complex ways depends on the experiences gained in early ontogeny.

This suggests a further reason why the subject of primate social learning may have important contributions to make to cognitive science generally. Acknowledging that the human cognitive system is a deeply cultural phenomenon, it was suggested in the section above that primate social learning mechanisms are of interest in understanding the roots of culture. Now we are looking at processes of primate social learning with respect to the converse process, the possibility that the learning processes may themselves be nurtured and shaped *by* the culture in which they are embedded. Are social learning mechanisms, such as the ability to imitate in particular ways, shaped by experiences during development? We do not understand much about this yet, but enough is known to predict that nonhuman primate cognition has much to tell us here that will illuminate the nature of social cognition as it has evolved in the human primate.

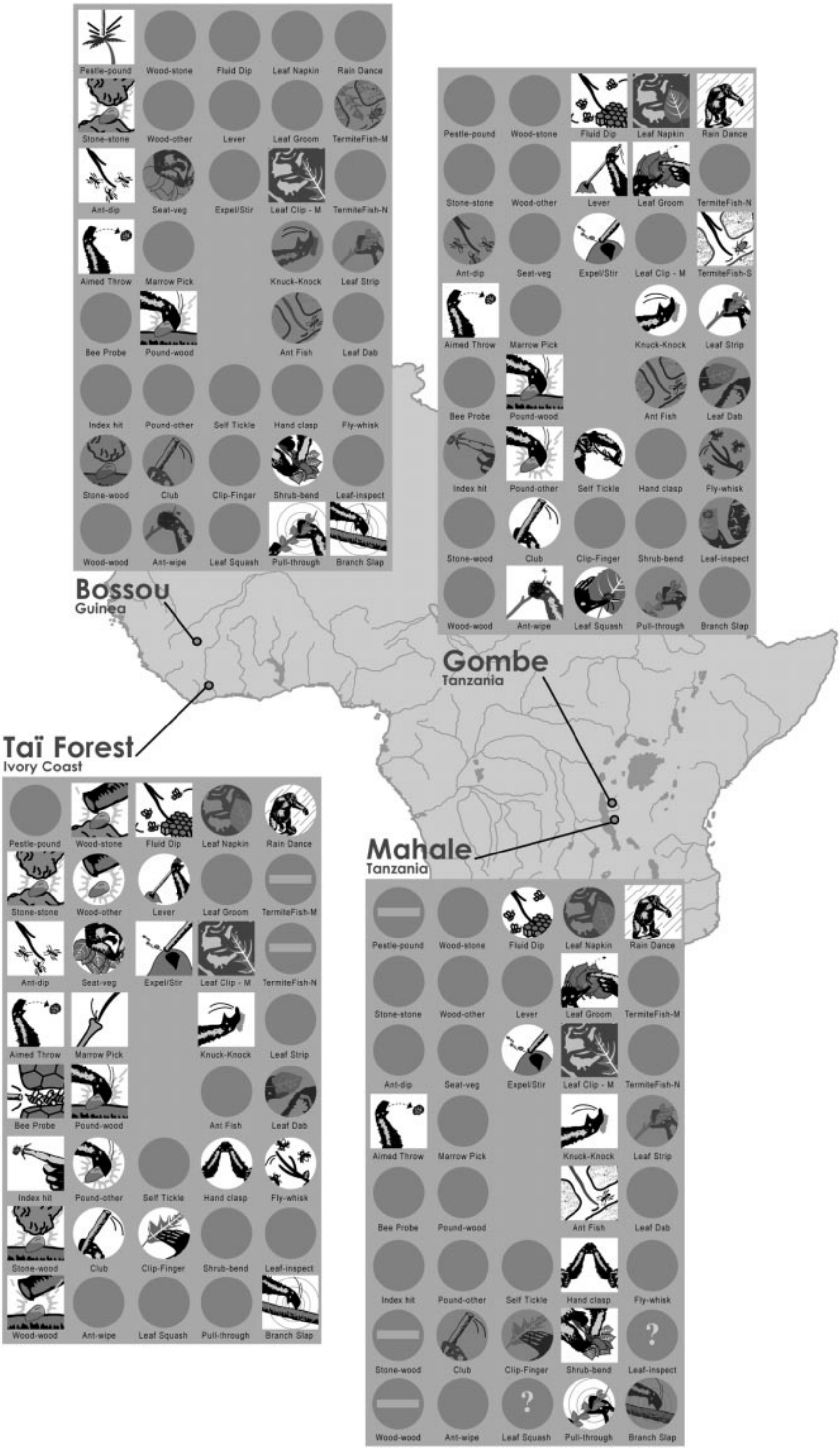
These, then, are some of the main reasons why I think primate social learning processes should be of interest for cognitive science: beginning with the overarching rationale that through comparative primate studies we can better understand the origins of our deeply cultural human cognitive system, I argued that primate social learning is of interest because of cognitive complexities within it, because of the variety of related social learning processes uncovered, because different forms characterize different points in primate phylogeny, and finally because of the ways in which social learning and culture may each shape the other. With these perspectives in mind, we can move on to review key findings from recent years. In doing this, I omit two areas I cannot do justice to within the space available. One is social learning in the vocal/auditory mode (see Whiten and Ham on the contrast with learning in the visual mode; for reviews, see Janik & Slater, 1997; Seyfarth & Cheney, 1997). The other omission concerns teaching, which I have recently discussed elsewhere (Whiten, 1999d; see also Caro & Hauser, 1992: Maestripieri, 1995, for reviews).

In the next section I will look at what we know about primate culture in the natural state, before turning to experimental studies more concerned with the specifics of learning. The field research faces severe limits in concluding anything definite about the underlying learning processes, yet it is the only valid starting point for designing or even making sense of the controlled experiments necessary to uncover these processes. Studies of primates in the wild are important for several reasons that include outlining the possible scope of traditions, as well as identifying the niches in primates' lives where various kinds of social learning may be adaptive.

II. PRIMATE CULTURES?

Chimpanzees: Interpopulation Differences in Technology and Communication

The most elaborate evidence of primate culture is provided by variations in the behavior of chimpanzees (Boesch, 1996a, 1996b; Goodall, 1986; McGrew, 1992, 1998; Nishida,


Bossou
Guinea
Pestle-pound
Wood-stone
Fluid Dip
Leaf Napkin
Rain Dance
Stone-stone
Wood-other
Lever
Leaf Groom
TermiteFish-M
Ant-dip
Seat-veg
Expel/Stir
Leaf Clip - M
TermiteFish-N
Aimed Throw
Marrow Pick
Knuck-Knock
Leaf Strip
Bee Probe
Pound-wood
Ant Fish
Leaf Dab
Index hit
Pound-other
Self Tickle
Hand clasp
Fly-whisk
Stone-wood
Club
Clip-Finger
Shrub-bend
Leaf-inspect
Wood-wood
Ant-wipe
Leaf Squash
Pull-through
Branch Slap
Gombe
Tanzania
Pestle-pound
Wood-stone
Fluid Dip
Leaf Napkin
Rain Dance
Stone-stone
Wood-other
Lever
Leaf Groom
TermiteFish-N
Ant-dip
Seat-veg
Expel/Stir
Leaf Clip - M
TermiteFish-S
Aimed Throw
Marrow Pick
Knuck-Knock
Leaf Strip
Bee Probe
Pound-wood
Ant Fish
Leaf Dab
Index hit
Pound-other
Self Tickle
Hand clasp
Fly-whisk
Stone-wood
Club
Clip-Finger
Shrub-bend
Leaf-inspect
Wood-wood
Ant-wipe
Leaf Squash
Pull-through
Branch Slap
Taï Forest
Ivory Coast
Pestle-pound
Wood-stone
Fluid Dip
Leaf Napkin
Rain Dance
Stone-stone
Wood-other
Lever
Leaf Groom
TermiteFish-M
Ant-dip
Seat-veg
Expel/Stir
Leaf Clip - M
TermiteFish-N
Aimed Throw
Marrow Pick
Knuck-Knock
Leaf Strip
Bee Probe
Pound-wood
Ant Fish
Leaf Dab
Index hit
Pound-other
Self Tickle
Hand clasp
Fly-whisk
Stone-wood
Club
Clip-Finger
Shrub-bend
Leaf-inspect
Wood-wood
Ant-wipe
Leaf Squash
Pull-through
Branch Slap
Mahale
Tanzania
Pestle-pound
Wood-stone
Fluid Dip
Leaf Napkin
Rain Dance
Stone-stone
Wood-other
Lever
Leaf Groom
TermiteFish-M
Ant-dip
Seat-veg
Expel/Stir
Leaf Clip - M
TermiteFish-N
Aimed Throw
Marrow Pick
Knuck-Knock
Leaf Strip
Bee Probe
Pound-wood
Ant Fish
Leaf Dab
Index hit
Pound-other
Self Tickle
Hand clasp
Fly-whisk
Stone-wood
Club
Clip-Finger
Shrub-bend
?
Leaf-inspect
Wood-wood
Ant-wipe
?
Leaf Squash
Pull-through
Branch Slap

1987; Sugiyama, 1997). As long-term studies have become established at different field sites, it has emerged that some behavior patterns are noticeably absent at some sites, yet habitual at others, a fact checked in some cases by visits of the same scientists to different sites (Boesch, 1996a, b; McGrew, 1992). Figure 2 illustrates the richness of these variations.

Two main kinds of chimpanzee behaviors need to be discriminated when we start to interpret the significance of this variation. First, the greatest number of differences concern tool use - candidates for “chimpanzee material culture” (McGrew, 1992). The problem in interpreting these as evidence of traditions that are socially transmitted, as with all foraging techniques, is that there may be physical reasons for the nonuniform distribution: the hard nuts that are cracked at the West African sites, for example, are not present at some more easterly sites. However, specific comparisons have been made that avoid this difficulty. Boesch et al. (1994) found that chimpanzees to the east of the Sassandra-N′Zo river do not crack nuts, despite the fact that those on the west side do, and those on the east have plentiful supplies of nuts and potential tools. The river appears to be a barrier over which the tradition has not passed. McGrew et al. (1997) showed noncracking chimpanzees in Gabon likewise have all the appropriate materials to hand.

It may always be objected that, logically, it is impossible to rule out whether there is some local physical feature, such as the subtle quality of the potential foodstuffs and potential tools, which will explain away the apparent traditions (Tomasello, 1990, 1994). However, in the face of such critiques, field researchers have gone as far as one can reasonably can in testing alternative explanations. An example is Boesch’s comparisons (1996a, b) of ant-dipping at Gombe (McGrew, 1974) and Tai (Boesch & Boesch, 1990). At Gombe chimpanzees use a long wand (average 66 cm) to gather many ants which are then swept off with the free hand and eaten as a large mass. At Tai a shorter stick is used to gather only about 15 ants at a time, which are then swept off with the lips. The Gombe method is overall about four times more efficient, and Boesch has himself checked that the materials are appropriate for using it at Tai: but the chimpanzees, it would appear, have never discovered it. Instead, different traditions persist at the two sites.

Can we say anything about the nature of the transmission process? In the case of nut-cracking to the west of the river barrier, it does not seem possible to discriminate firmly between relatively simple social learning mechanisms (coupled with individual intelligence), like stimulus enhancement, and more complex ones like imitation. In the case of the ant-dipping contrasts, however, it seems difficult to account for the data without concluding that at Gombe the chimpanzees ‘learn some part of the form of a

Figure 2. Distribution of some putative chimpanzee cultures. The four main blocks of icons represent long term field sites where there is reasonable confidence about absence of behavior patterns. This is not a complete picture of such putative cultures, but indicates the richness of the possible cultural variation. Square icons, customary patterns (present in most or all able-bodied individuals); circular clear icons, habitual patterns (performed repeatedly by several individuals); circular faded icons, present; blank discs, absent; barred discs, ecological reason for absence; question mark, uncertain. Data from an ongoing project in collaboration with C. Boesch, J. Goodall, W. C. McGrew, T. Nishida, V. Reynolds, Y. Sugiyama, C. E. G. Tutin, and R. W. Wrangham (see Whiten et al. 1999).

behavior' - that is, imitate - where the 'part' involves at least the use of the swiping action along the dipping wand, held in the other hand.

When we turn to the other category of acts in Figure 2 we also seem to be on stronger inferential grounds with regard to the processes at work. These are differences in communication or other social acts that are inherently less easy to explain away as perhaps individually-learned solutions to idiosyncratic local problems than is the case for foraging techniques (see also de Waal & Seres, 1997). But does that imply they must result from imitation? Tomasello (1996) suggests it does not. An alternative is a process he calls 'ontogenetic ritualization' (earlier termed 'conventionalization') in which one individual's acts are shaped by interaction with another. In the case of the grooming hand-clasp (McGrew & Tutin, 1978), in which two chimpanzees mutually clasp one hand overhead while grooming with the other, that might work by each new individual coming into the tradition having to raise its arm to meet that of its grooming partner, who already has the habit. The plausibility of this is limited insofar as it is not apparent the new groomer needs to clasp hands: but Tomasello's argument underlines the fact that it is typically difficult to isolate the cognitive processes that occur in nature by purely observational, noninterventive means. It is difficult to be really sure of how many of the chimpanzee population differences represent traditions, and how many of such traditions are (if we use Galef's 'imitation' criterion) 'cultures'.

Evidence for Traditions in other Primates

Compared to the richness of chimpanzee interpopulation differences on record, there is little in the literature documenting similar variation for other primates that is not easily explicable by local ecology, such as the particular foodstuffs available. This may be partly because other primates' foraging techniques are not so technological; whereas ant-dipping (for example) affords interpopulation differences in technique, even chimpanzees have not been recorded processing foods nontechnologically in different ways at different sites. Instead they appear to converge on the same optimal method, as presumably do other primates when compared at different sites. Accordingly, although it remains very plausible that social learning of some kind is involved in how wild primates locate, select and process their foods, there are no interpopulation differences that establish social learning processes (let alone specific processes like imitation) in the way that now seems possible for some of the chimpanzee behaviors.

Byrne (1995) has tried to turn this issue somewhat on its head by arguing that *similarities* among a population can evidence social learning. He suggests that similarity of the overall pattern of foraging techniques in mountain gorillas, despite variation in the details of execution (Byrne & Byrne, 1993) evidences acquisition by imitation, because it is difficult to envisage the observed complexity being acquired by individual learning processes. This last step in the argument is difficult to objectively evaluate, however. Just such a pattern of overall similarity, coupled with variation in detail, is also expected in all individually acquired, optimal food processing methods. Tomasello and Call (1997) accordingly class the example as a case of individual learning in their tables of primate social learning studies; more appropriate, I think, would be to say that the data that will test the imitation hypothesis are not yet available.

Other kinds of data than interpopulation differences are relevant to the issue, however. One is where the spread of a behavior through a population can be documented, potentially illustrating various features that have been discriminated in cultural evolution, such as transmission, standardization, persistence, and diffusion across groups or generations (Kroeber, 1928; McGrew, 1998 for a well-informed review). The most famous case of this was the spread of sweet-potato washing and wheat-washing among Japanese macaques (Imanishi, 1957; Nishida, 1987), that became the text-book example, alongside chimpanzee tool use, to illustrate ‘culture’ and ‘imitation’ in primates (Whiten & Ham, 1992). However, scrutiny of the data by Galef (1990) highlighted the fact that the rate of diffusion of the behavior was very slow and steady, not accelerating as one might expect in the case of imitation. It has now become not uncommon to say that it has thus been shown that Japanese macaques did not learn the techniques by imitation, but as with the gorilla case mentioned above, it is more proper simply to acknowledge that the data on the spread of the behavior per se do not decide the case.

Some variations in nonfeeding behaviors, however, seem particularly difficult to interpret as being acquired by individual learning processes. One is stone-handling, a curious act in which stones are manipulated in various ways, including being rubbed together to make a ‘click-clacking’ sound, then dropped without further use. Despite its apparent uselessness, the origins and spread of this as a habit, from a single individual to all youngsters in one group of Japanese macaques, has been amply documented (Huffman, 1996). It seems difficult to see how mere stimulus enhancement should make this happen, suggesting some kind of emulative or imitative effect (this is a nice case in which to wonder just what the difference between emulation and imitation would really be; see below for further discussion). Another Japanese macaque example comes from Tanaka’s (1995) finding that techniques for grooming ecto-parasite eggs from others’ fur differ among matrilineal groups. A longitudinal study documented in fine detail how a change in one female’s technique was subsequently adopted by her kin, (Tanaka, 1998). This involved modifying an action used to search for louse eggs, so as to remove them as well, a change that seems only explicable by appeal to an imitative process, as Tanaka concludes.

Mindful of Galef’s concerns about the rate of spread of putative traditions, Lefebvre (1995) has since analyzed the time course of a number of documented cases of diffusions of novel behaviors in various monkey and chimpanzee studies. Of 17 independent cases, 13 did show the kind of rising (accelerating) curve predicted if some process of social transmission is involved. Lefebvre suggested that “the fact that Japanese macaques provided all of the nonaccelerating cases, whereas all six chimpanzee sets showed acceleration . . . may perhaps be linked to the differences between monkey and ape social learning pointed out by Visalberghi and Fragaszy (1990) and Whiten and Ham (1992)” (p. 234). However, the rising curves could be caused by several of the processes distinguished in Figure 1. The curves suggest that social traditions did develop in most cases, but the underlying cognitive processes remain to be specified. The most powerful way to discriminate these is through appropriate experimentation.

III. EXPERIMENTAL STUDIES OF SOCIAL LEARNING PROCESSES

Further below I shall focus on a series of cognitive issues in social learning, many of which rest upon the results obtained in experimental studies. To set these in proper context, I shall in this section offer an overview of the experimental literature as a whole, but it will perforce need to be brief and selective. More details on many of the studies are available in other recent reviews that the present one complements, notably those of Tomasello (1996) and Tomasello and Call (1997).

Whiten and Ham (1992) tabulated the many experimental studies of primate social learning that have taken place over the last century, and Tomasello and Call's (1997: tables 9.2, 9.3) extension and update rises to over 50 studies. The bulk of these early studies are not very illuminating with respect to cognitive issues that interest us now, principally because they did not incorporate the procedures needed to discriminate simpler processes like stimulus enhancement from more complex ones like imitation. Many claims to have demonstrated 'imitation' are nowadays doubted for this reason.

More recent experimental studies, interpreted critically within the framework of possible explanations indicated in Figure 1, had by the early 1990s generated a skeptical attitude in several authors with respect to the long-standing assumption that primates are ready imitators. Tomasello, Davis-Dasilva, Camak and Bard (1987), in the first experimental study of social learning in chimpanzees to use conspecific models, found that subjects who watched another chimpanzee use a rake to gain out-of-reach food were quicker to successfully use the rake themselves, when compared to subjects who had not watched the model. However, the observer subjects did not copy the particular two-step technique the model had developed for when food was at the edge of the presentation platform and more difficult to retrieve; instead they tended to use their own methods, frequently without success. This was the kind of learning that led Tomasello to emphasize the category of emulation. Emulation goes beyond stimulus enhancement insofar as the subject is not merely attracted to a locus, but learns something about changes of state that are possible in the world - in this case, something about the causal relationship between tool and food: but it then uses its own behavioral strategies to try to exploit that knowledge, rather than imitating those the model used.

Other recent experiments with apes have painted a similar picture (Call & Tomasello, 1994, 1995; Paquette, 1992; Nagell, Olguin & Tomasello, 1993; Sumita, Kitahari-Frisch & Norikoshi, 1985). Experiments with monkeys in the same period likewise failed to find evidence of imitation (Adams-Curtis, 1987; Antinucci & Visalberghi, 1986; Fragaszy & Visalberghi, 1989; Visalberghi, 1987; Visalberghi & Trinca, 1989; Westergaard & Fragaszy, 1987; Westergaard & Lindquist, 1987). Visalberghi and Fragaszy (1990), reviewing their own and similar experiments, concluded that there was evidence of social learning only at the level of stimulus enhancement.

More recently, experimental evidence of advanced social learning in both apes and monkeys has been confirmed. In some studies, the apes have been actively encouraged to imitate, in an attempt to discover, in the current climate of doubt, whether they have the basic competence to do so. In one of these studies, by Tomasello, Savage-Rumbaugh and Kruger (1993), three chimpanzees that had been reared by humans were rated as imitating a battery of actions to the same extent as did a comparison group of young children (three mother-reared chimpanzees, however, scored significantly lower than the other groups). In a study by Custance, Whiten and Bard (1995), two chimpanzees trained to 'do as I do' on request were exposed to a battery of 48 new actions. Coders blind to what each subject had watched were able to successfully identify matches in a highly significant, although not large number of cases - 13 for one subject, 20 for the other. Miles, Mitchell and Harper (1996) report similarly positive results for this 'Simon says' procedure in an orangutan, although the coding procedure did not appear to be blind to what the subject had in fact witnessed in each case.

In a different kind of study by Whiten et al. (1996), chimpanzee subjects were not encouraged to imitate but were simply presented with (human) models opening an 'artificial fruit' (Figure 3) in one of two alternative ways. To open the fruit, several defenses had to be removed, as happens in many natural primates foods. In one experiment the defenses were a pair of bolts that were either poked out through the back, or pulled out at the front with a twisting motion, after which a lid was opened to gain the edible treat inside. In another experiment, a pin was spun round and removed using one of two different methods, after which a handle could be disabled by either pulling it out or turning it to one side, allowing the lid to be opened. Chimpanzees were found to copy the method they witnessed being used to remove the bolts, as did young children. However, while the children also imitated the method of handle removal, the chimpanzees did not - all tended to use the same method of pulling out. Thus, in a situation where young children learned a technique with quite high fidelity, chimpanzees did not copy all they witnessed so faithfully.

Applying this method to capuchin monkeys has also produced evidence of more sophisticated social learning than the earlier work referred to above (Custance, Whiten & Fredman, 1999). These monkeys did not copy some of the features that chimpanzees did, like twisting, but they did show signs of the overall approach they saw the model perform, more than is consistent with only stimulus enhancement. Custance et al. suggested these monkeys' performance could be described as emulation or a simple form of imitation (the gray area between imitation and emulation will be discussed more below). Bugnyar and Huber (1997) found that two of five marmosets showed strong signs of imitating the way in which a conspecific model opened a doorway to retrieve food. The conclusion that these two monkeys were imitating was supported by a microanalysis demonstrating that the probability of the relevant combination of actions was extremely unlikely to have occurred by chance.

These studies of imitation have therefore passed through a period in which the long-held assumption that monkeys and apes are ready imitators was seriously in question. Now, evidence with qualified support for the original assumption is emerging from more

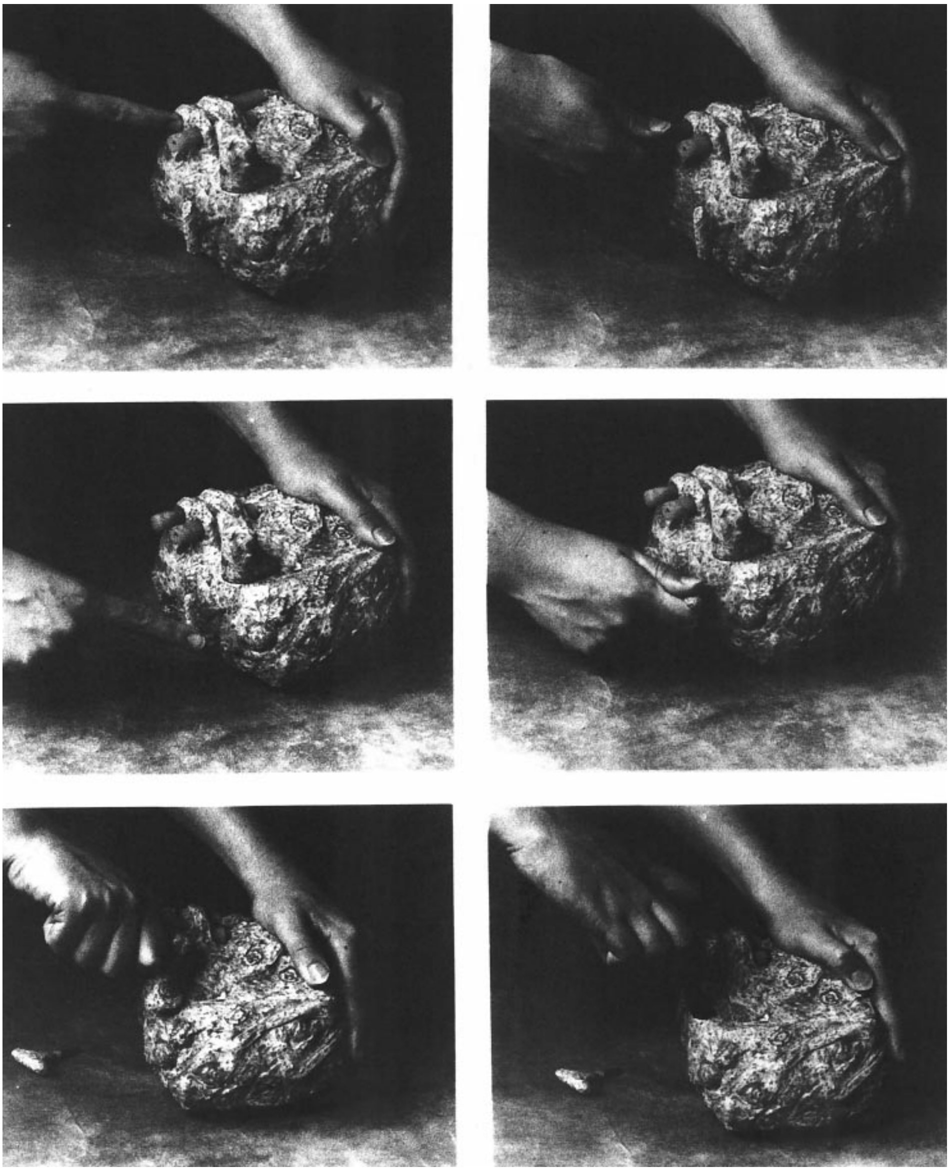


Figure 3. An artificial 'fruit', showing examples of alternative acts used to remove defenses: poke versus twist bolt; spin versus turn pin; turn versus pull handle.

rigorous and imaginative approaches (Russon, 1997). This forms a basis for discussion of a number of particular cognitive issues in the study of social learning, to which we now turn. It has to be emphasized, however, that most of the empirical effort so far has gone into answering basic questions of the kind: 'do they imitate?'; 'have they got culture?': research actually tackling the issue of what is going on, cognitively, is in its infancy.

IV. EIGHT COGNITIVE ISSUES IN SOCIAL LEARNING

1. Copying the Sequential Structure of Actions

The success of chimpanzees in opening our artificial fruits suggested that it would be feasible to present the ‘whole fruit’ with all defenses in place, an experiment in which the cognitive implications of various possible kinds of social learning become more interesting. This was what the artificial fruit was designed to do originally, but we began cautiously because our subjects were juveniles and the experiment was done at a period of general skepticism about the imitative powers of primates.

In demonstrating opening of the ‘whole’ artificial fruit to four adult chimpanzees, two alternative sequences of actions were used (Whiten, 1998b), as well as variants on each component technique, generating four different patterns:

1. Twist far bolt - Twist near bolt - Spin pin - Turn handle - Lift Lid
2. Poke far bolt - Poke near bolt - Turn pin - Pull handle - Lift Lid
3. Spin pin - Turn handle - Twist far bolt - Twist near bolt - Lift Lid
4. Turn pin - Pull handle - Poke far bolt - Poke near bolt - Lift Lid

Each subject saw the fruit opened three times using one of these sequences before they were allowed their own attempt. They saw the sequence again before each of a second and third attempt they were allowed. On their third attempt, but not before, a statistically significant tendency emerged for subjects to follow the sequential order they had witnessed. In fact the sequence was perfectly matched for three subjects, with just one reversal for the fourth subject, who took the bolts out in the opposite order to that he had witnessed.

This is the first demonstration of an animal imitating the sequential structure of the acts it witnesses. Considering the implications of this for how the imitator is able to represent what it has watched the model do, Whiten (1998b) suggested that these chimpanzees were able to extract and remember the basic *plan* of the action sequence. This raises the possibility that we are seeing here a manifestation of a simple kind of ‘mindreading’—a capacity studied in other experiments with respect to attributions of states like ignorance, knowledge and attention (Whiten, 1996, 1998a; see Povinelli, this volume). Of course like all mindreading, a mental structure would here be being recognized in a behavioral pattern. However, these results do not allow us to discriminate between whether the chimpanzee subjects were representing what they saw as sequential structure in what the model is doing (or attempting), or instead as the sequence in which the fruit comes apart, which we might think of as a kind of ‘sequential emulation’.

2. Emulation versus Imitation

Recall that Tomasello distinguished emulation as a process different from imitation. Emulation and imitation tend to be treated in the literature as an either/or dichotomy, with emulation treated as the cognitively inferior processs; Byrne and Tomasello (1995), for example, suggest that the results interpreted by Heyes, Dawson and Nokes (1992) as demonstrating imitation in rats may reflect ‘only’ emulation.

However, it may be misleading to think of an absolute dichotomy here in how the subject represents what it has witnessed in the model performance. Whiten and Ham (1992) suggested that chimpanzee subjects in the experiment of Tomasello et al. (1987), described above, might represent the model in a number of possible ways consistent with the finding that they did not copy details; expressed roughly, in English, alternatives include ‘rake food’ and ‘food can be got with rake’, among others. The second of these seems to emphasize the ‘affordance’ of the tool that Tomasello refers to, but the first can reasonably be described as *imitation* of what the model is doing, but just at a relatively schematic level. When the imitator comes to make its own attempt, it might fill in this schematic representation with appropriate techniques it holds in memory. Whiten and Ham (1992) suggested experimental manipulations that could discriminate such alternative representations.

But another way in which a dichotomy may be unhelpful is that movements of objects caused by a model might be represented in essentially the same way as bodily movements. Copying hammering that is constituted by a fist movement, or by a hammer-tool movement, might be done through essentially similar representations of the structure of the act, so that it would be misleading to distinguish emulation from imitation simply by whether what is copied lies in the ‘object’ versus the ‘bodily’ domains (Whiten & Custance, 1996).

It may thus be appropriate to think of imitation versus emulation as a useful but qualified distinction, that makes sense only in relative terms in a particular context, rather than in absolute terms. For example, in artificial fruit experiments, of those subjects that copied pushing the bolts out, some copied poking, while others used their own technique like using the ball of the hand. So it makes sense to say that relative to each other, the first group are imitators, the second emulators. But of those who poked, some copied use of the digit they saw used, others used other digits to poke: so at this level of analysis the latter subgroup of these is emulating *relative to* the imitators performing the more faithful copy.

Which is more intelligent? Imitation or emulation? In general the literature appears to assume that imitation is the more sophisticated cognitive process; species from apes to rats have been demoted from claims of imitation to ‘mere’ emulation. Yet there is an important sense in which a relatively emulative approach to social learning may be an intelligent one for an individual to take (Whiten & Ham, 1992; Byrne & Russon, 1998): emulation implies that the learner can select from the model’s performance just the new information it needs, and then efficiently combine it with its own practical knowledge to deal with the task in its own way. In some cases, this seems to be supported; for example, chimpanzees who emulated in pulling out the handle from the artificial fruit opened it quicker than children who were relative imitators in more faithfully copying the turning actions some of them witnessed (although, aren’t humans supposed to be the more intelligent species?). However, not all primate emulators are superior in this way: an example comes from the Tomasello et al. (1987) study, in which the authors noted that if subjects *had copied* the model’s two-step act they would not have failed as often as they did through their less effective emulations.

Myowa-Yamakoshi and Matsuzawa (1999) found that when tested with a battery of actions in a 'do-as-I-do' paradigm, chimpanzees were more ready copiers of actions that involved applying an object to another or to oneself, than manipulations of an object by itself, suggesting that chimpanzees may naturally operate closer to the 'emulation' end of the continuum outlined above. This might appear consistent with the observations of Inoue-Nakamura and Matsuzawa (1997), who could not discern any instances of imitation during the gradual mastery of stone tools by wild chimpanzees. However, Yut, Greenfield and Boehm (1995; Greenfield & Maynard, 1999) came to an opposing conclusion because they found that young chimpanzees observing termite-fishing devoted close visual attention not merely to the ends of the act, but to all stages of the means involved. Any imitative consequences of such information gathering are, as noted earlier, difficult if not impossible to discern in the long periods of playful practice such youngsters typically show in the wild.

That in our experimental studies we find some copying at both detailed and more schematic levels suggests the hypothesis that our chimpanzee subjects are selective in what they take from their observations of both means and ends; where they have the means already within their repertoire to achieve an end attained by a model, they may apply their own means even when it is different; where they are ignorant of relevant means they may pay close attention and pick up potentially useful details of technique.

3. Copying the Hierarchical Structure of Actions

Byrne and Byrne (1993) showed that several of the foraging behaviors of mountain gorillas show a hierarchical organization, an example of which is shown in Figure 4. The complexity of this led the authors to suspect the technique must be learned by observation. That individuals have idiosyncratic ways of achieving the various steps (using different manual grips, for example) led Byrne to develop the concept of what he has called 'program-level' imitation (Byrne, 1995).

Byrne and Russon (1998) define program-level imitation (PLI) formally as "copying the structural organization of a complex process (including the sequence of stages, subroutine structure, and bimanual co-ordination), by observation of the behavior of another individual, while furnishing the extract details of actions by individual learning." This is clearly of interest with respect to how the imitator represents what it imitates. However, I think there are good reasons why a category of PLI is counterproductive, and more progress will be made if the four elements included in the definition above (lack of copied detail, but copying of sequential, bimanual and subroutine structure) are separated and the more important ones assessed independently (Whiten, 1998c). The reasons for this, briefly, are as follows

First, the final phrase of the definition neglects the fact that no imitation is exact, as emphasized by Whiten and Ham's definition. All imitation has a schematic character, varying in fidelity according to the features it assimilates—features of various kinds including sequence, tempo, orientation and shape of various elements within the act as a whole, as discussed earlier (Whiten & Custance, 1996). In any one case, just how much

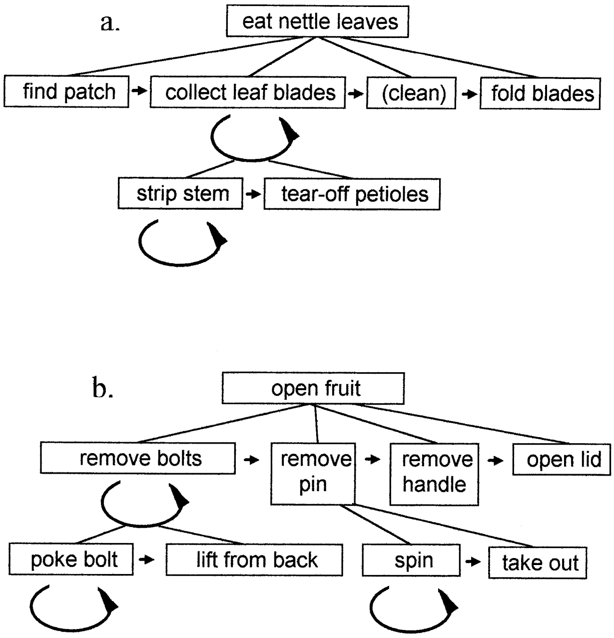


Figure 4. (a) Hierarchical program for nettle eating by gorillas (based on Byrne and Russon, 1998, Figure 2). (b) Hierarchical structure of artificial fruit-opening, using same conventions as (a), after Whiten (1998b). Circular arrows indicated actions repeated to a criterion before proceeding to the next action to the right.

detail gets copied is an interesting cognitive and empirical question, but because fidelity is inherently a continuum, to try to use this to shape a categorical definition, like PLI, will only cause confusion.

The other three elements are also logically separable. Whether sequential organization is copied can be answered independently of the other issues, as discussed above as the first ‘cognitive issue’. How much detail is assimilated in addition to any sequence-copying is a separate question. In fact, some detail was copied by chimpanzees and children in imitation of the artificial fruit sequence, but not all; as noted above, this doesn’t help to decide if this case exemplified PLI or not - yes, because not all detail was copied? - or no, because *some* detail was copied?.

The imitating of ‘subroutine structure’, or hierarchical organization, can similarly be logically distinguished from any necessity for sequential and/or bimanual co-ordination, as well as from the question of fidelity of copying. This seems the important core of Byrne and Russon’s contribution—the hypothesis that hierarchical structure might be imitated—leaving aside the other three elements for independent assessment in any one case.

This then leaves the question of how to objectively check for the imitation of hierarchical structure. This, of course, is different from demonstrating that a candidate act for imitation is itself hierarchically organized, as Byrne and Russon do. Possibly all skilled acts are hierarchically organized and this seems clear in the gorilla foraging examples that

Byrne considers. However, *imitation of the hierarchy* has not been demonstrated for these skills - indeed social learning *per se* remains an untested hypothesis, for the reasons discussed earlier (see also Tomasello & Call, 1997 and peer commentary on Byrne and Russon). The other cases offered in evidence by Byrne and Russon concern the actions of rehabilitant orangutans (Russon & Galidikas, 1993, 1995). This is puzzling because these seem to show the reverse of what is implied by the definition of PLI: the best evidence of imitation is at the level of what Byrne and Russon call 'action level' imitation, with little sign that the orangutans copy the hierarchical program that characterizes the original human forms of the acts concerned, like making fires (Matheson & Fragaszy, 1998; Whiten, 1998b,c).

Accordingly, imitation of hierarchical structure is an interesting cognitive possibility but one that is yet to be tested in nonhuman primates. The route to this may be clearer if set out first in a clear experimental context. Figure 4 shows the hierarchical structure of the artificial fruit experiment opening sequence, alongside an equivalent one for gorilla foraging on nettles. Do the results reported above for the artificial fruit indicate that this hierarchical structure was copied? Surely not: it could just be that imitators represent what they saw in terms of a simple sequential plan or program: far bolt - near bolt - pin - handle - lid (if that is the sequence they saw). Or, insofar as we may guess that if offered a fruit with the bolts already out they would continue to remove the remaining defenses, a set of rules may have been acquired of the type: - if far bolt out, remove near bolt - if bolts out, remove pin - if pin out, remove handle - if all defenses out, open lid.

So what *would* show imitation of hierarchical structure as such? One criterion might be that an imitator, once acting on a particular node in Figure 4, persists until the outcome of that node is achieved. Thus, once embarked on removal of a bolt, that would be completed before removal of another item. At one higher level, both bolts would be removed before another defense were tackled. This is in fact what happened in Trial 3 of the experiment. So can we conclude they had copied a 'bolts' subgoal/subroutine? The problem here is that because the bolts were removed consecutively, it may have been just that *sequence* that was being copied. One could of course perform a different model sequence, like far-bolt, pin, handle, near-bolt, but then if the subject itself performed both bolt removals consecutively (perhaps because chimps have a natural tendency to 'hierarchize' in this way) they would not be imitating what they saw! It seems, then, that demonstrating imitation of hierarchy as such requires a purpose-built design in which the same elements are constructed into different hierarchical configurations. The results of the sequence imitation experiment, in which subjects showed no evidence of imitation in the first trials, suggests that such a design should not hinge on what subjects do in their first attempt: the design must be resistant to the effects of individual learning at this stage, including the possibility of individual processes that may tend to 'hierarchize' whatever elements the subject has learned by observing the model. The difficulty of framing this experimentally emphasizes the extra difficulty of ever being able to recognizing the phenomenon in purely naturalistic contexts. We have developed such an experimental approach and found that young children do copy hierarchical structure (see Figure 5). It is planned to apply this test to chimpanzees.

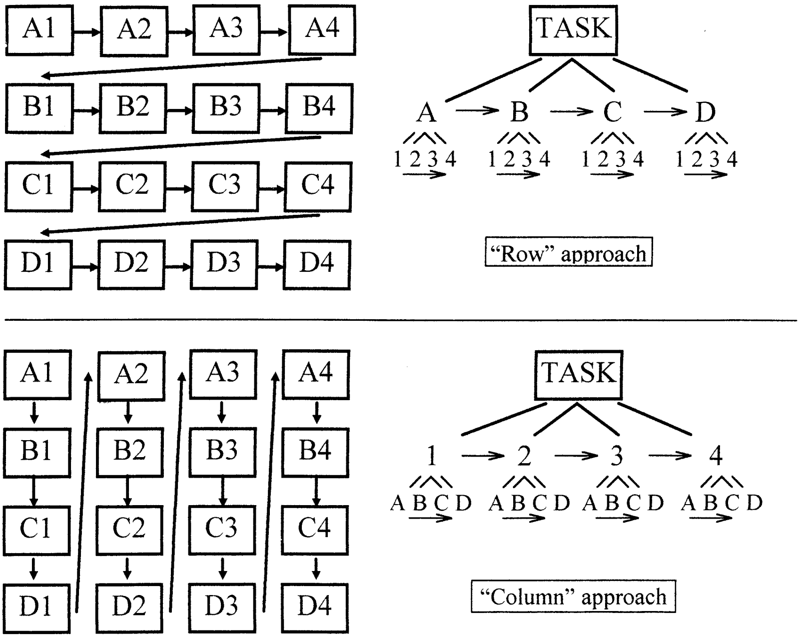


Figure 5. Schematic design of experiment to test for imitation of hierarchical structure. Sixteen actions are modeled, giving access to a reward. One model shows these actions performed 'row-wise' (top), the other 'column-wise' (bottom). Whether subjects copy the hierarchical and/or sequential structure instantiated in these alternatives (represented on right) can then be measured. Imitation of the hierarchical but not the sequential structures shown has been shown for a sample of three-year-old children, using an artificial fruit designed for testing of both children and chimpanzees (Whiten, 1999c); the latter remain to be tested.

4. Imitation of Novel Acts

Within the social learning literature, some authors argue that 'true' imitation should only be recognized when the act imitated is novel (e.g., Byrne & Tomasello, 1995), whereas others argue this constraint would neglect copying that is nevertheless cognitively interesting (Gardner & Heyes, 1998, Huber, 1998, Zentall, 1998). Whiten and Custance (1996) took a position somewhat in between, arguing that novelty cannot be an all or none matter. Even at the end of a continuum where an imitated act might be judged relatively novel, it is likely that the act draws in some ways on acts the subject has performed before: indeed it may be that imitation is only possible where the animal can make links between the 'new' act it sees in the model, and some aspects of its existing behavioral repertoire. Custance, Whiten and Bard (1994) trained chimpanzee subjects to 'Do what I do' using a set of training actions and then tested them with new ones: analysis of videotapes showed several cases in which the subject responded by first performing an act already trained, and then modifying this to create the new one. For example, having been trained to copy touching one's armpit, one subject responded to the new act of touching elbow by raising her arm, touching her armpit, then groping her hand along her arm to reach her elbow.

Byrne and Russon (1998) are among the authors who argue for novelty as a cardinal feature of imitation, suggesting such novelty could arise in program-level imitation as subjects combine acts already in their repertoire. Imitation of sequential patterning, discussed above, shows this aspect of novelty and to that extent is a powerful demonstration of imitation (Whiten, 1998b). However, it is still dangerous to see novelty as an absolute in such combinations: if the component acts (poking, pulling, and so on) are in some sense already 'in the repertoire', these acts may have been performed in the past in various sequential orders, and indeed in various hierarchical relationships. The role of existing knowledge in learning relatively new behavior through imitation is clearly important (if difficult) to investigate in trying to understand how imitators represent what they imitate.

5. Achievement of an Imitative Match: Feedback

Heyes (1993) described imitation as 'an especially demanding variety of visual-tactile cross-modal performance'. Mitchell (1994) refers to imitation as 'kinesthetic-visual matching'. The assumption in both these analyses is that imitation based on visual input utilizes kinaesthetic and/or proprioceptive stimulation to guide its implementation in the imitator. This seems to neglect the possible role of visual feedback. Although such visual-visual matching would not strictly be a 'cross-modal' process, it would still be inherently complex because of the transformation that is required, from the behavior seen in the other to what it needs to look like when similarly performed by the imitator.

The role of these different forms of feedback have yet to be systematically investigated: we do not know, for example, what happens to imitative capacities in blindfolded subjects. Indeed we do not even know how critical feedback *per se* is: might 'ballistic' imitation be possible in a human or nonhuman primate, involving the construction of an action plan or motor program that can create an act recognisably like the model's, without benefit or either visual or kinaesthetic feedback?

Some studies do allow us to infer that the kinaesthetic form of feedback can do the job in some cases at least. In the 'do-as-I-do' experiment of Custance et al. (1994, 1995), subjects were able to imitate acts that involved parts of their body they simply could not see (facial expressions, head movements, touching parts of the body out-of-sight) just as well as those in sight.

6. Can Primates Hold a Concept of Imitation?

The fact that the do-as-I-do experiment is possible at all suggests that the subjects have some kind of concept of imitation—that is really what the method depends upon. Only humans, chimpanzees, an orangutan and dolphins have so far shown evidence of this achievement (Hayes & Hayes, 1952; Xitco, 1988; Herman, Pack & Morrel-Samuels, 1993; Custance et al., 1995; Miles et al., 1996; Harley, Xitco, Roitblat & Herman, 1998). Mitchell and Anderson (1993) made a concerted attempt to train a macaque monkey to imitate on request, without success. Perhaps, then, the apes (and dolphins) know when they are imitating, in a way that species who cannot learn to imitate 'to order' cannot. This may have implications for the nature and reality of culture in those species that hold such a concept, for it could be argued that one thing differentiating humans from most of the many animal species with traditions is that humans have some concept of cultural conventions, being aware of when they are flouting or conforming to such conventions. Knowing you are imitating is a step towards this, and is a kind of ‘metarepresentation’ (mentally representing some mental process or representation) that may link it with other abilities to represent ‘states of mind’ (Boyd & Richerson, 1996; Whiten, 1996, in press a; Suddendorf, 1998, 1999; and see Povinelli, this volume). Such ideas have potential links with the two final points of discussion.

7. The Relation Between Imitation and Culture

Heyes (1993) acknowledged that imitation can mediate social transmission, which is of course essential for any possibility of culture: nevertheless, she argued that imitation is ‘insignificant in relation to culture’. The reason is simply that imitation ‘does not insulate information from modification through individual learning in the retention period between acquisition and retransmission’. In other words, there is ample scope for whatever is socially transmitted to be corrupted or otherwise modified by individual learning before the next transmission, which might be a whole generation later. This is an important concern, particularly in the case of long-lived primates that are highly exploratory and quick to learn.

The study of sequence learning (Whiten, 1998b) produced a surprising result in this respect. Imitation was not apparent in the first trials, but appeared in Trial 3. Given that subjects had mostly succeeded in opening the fruit in the early trials, this was unexpected. It is generally assumed that in any experiment the important point at which to check for imitation is in Trial 1, because after that the subjects’ performance may be influenced by the habits they form. Instead, subjects appeared to begin by trying various patterns of approach (incorporating from the start some specific techniques they had seen, like poking and twisting, that are not in fact necessary but only performed by the model to check for imitation) and then converged on the sequential pattern of the model. This is a tendency that would tend to negate the kind of corruption that Heyes (1993) considered. Of course, it would only be an adaptive way to behave in a species where there are considerable benefits to imitation, compared to individual learning.

Perhaps chimpanzees are one such species. Boesch (1996a) uses the term ‘canalization’ to express his proposition that some chimpanzee traditions of the kind described earlier can only be explained if social learning is part of a process that actively restricts experimentation with alternative methods. Evidence for this is that of 14 methods used by Zoo chimpanzees when provided with nut-cracking facilities, only 6 were seen in wild Tai chimpanzees cracking nuts (although some were seen in other contexts, like stabbing with a stick). In studying the imitation of artificial-fruit opening by young children, we found they were often particularly faithful copiers, ignoring nonsocial information they could have exploited to be more efficient. We concluded that this is perhaps because in general culture is so important to humans (Whiten et al., 1996). ‘Canalized’ copying may often be an adaptive strategy, even in an intelligent species.

8. Imitation and Enculturation

The strongest and most elaborate evidence of imitation in primates comes from apes that have had much experience with humans, being reared by them or otherwise exposed to many of the experiences that human children receive in interacting with their elders - loosely termed ‘enculturation’ (Tomasello et al., 1993; Call & Tomasello, 1996). Call and Tomasello note that various aspects of these experiences could be the ones that make the difference and at present we do not know which these are. They suggest, however, that close interaction with humans leads to an understanding of intention - ‘an understanding of behavior as intentional in the sense of differentiating means from ends’ (p. 392) - that wild-living apes may lack.

Whiten (1993) suggested that alternatively, those apes who have performed relatively unimpressively in imitation experiments are the odd ones out: human enculturation may provide experiences that laboratory chimpanzees lack, but which are present in some form in the wild. These could be experiences derived from early attempts at imitating, that begin a developmental upward spiral of imitative efforts and competence, perhaps in conjunction with the kind of canalization process outlined by Boesch (1996a). I feel that some of the detailed interpopulation differences now dissected by Boesch (1996a, b) represent evidence of imitation as compelling as that from the experimental literature, consistent with these subjects having benefited from ‘chimpanzee enculturation’ (Whiten, 1993). Just what happens during the developmental process is one more cognitive issue demanding imaginative study.

V. SUMMARY, CONCLUSIONS, AND QUESTIONS FOR THE FUTURE

For cognitive scientists, the principal matter to be understood in ‘culture’ is the array of cognitive processes whereby information transmission between individuals takes place. In this paper I have focused upon the processes generally regarded as the most complex of these, generally referred to as imitation and emulation. The relationship between these processes in nonhuman primates and the complex forms of social learning found in our own species is the reason for my selectivity. However, it should be emphasized that if we were to shift the focus to understanding how nonhuman primate traditions typically operate, attention to a wider range of observational learning processes (as indicated in Figure 1) becomes more appropriate (McGrew, 1998; Whiten & Ham, 1992). We don’t really know the role these simpler mechanisms play in the human case, possibly in concert with the more complex ones of imitation and teaching.

Psychologists studying primate social learning have begun to shift their attention beyond the question of whether any particular species imitates or has culture, to the cognitive processes underlying the transmission process. The multitude of recent critiques of earlier approaches to studying observational learning has led to new methods that have turned out to have much potential for this purpose. Some of these, developed because of the particular demands of working with nonverbal subjects, have yet to be applied fully to study human subjects but they have much potential for this purpose. There now seems enormous scope for cross-fertilization between cognitive scientists studying nonhuman and human primates, both in these methodological approaches and the theoretical issues that have driven their development (Whiten, 2000; Whiten & Brown, 1999).

This is apparent for each of the eight cognitive issues discussed in this paper. Thus, experiments designed to test for the copying of sequential and hierarchical structure in actions have been developed, but only relatively recently, so we have *some* results comparing the performance of chimpanzees and human children on these (showing both similarities and differences between them), but a comprehensive comparison remains a fascinating future step. Developmental psychologists have sometimes approached these topics from intriguingly different theoretical and methodological standpoints (Want & Harris, 1998). For example, whereas our tests have been designed to test for the copying *of* sequential or hierarchical action structures, Bauer and Mandler (1989) were concerned to test whether particular kinds of causally structured sequential patterns made copying easier for young children than patterns lacking this structure, implying a role for perception of these structures in the children's representations. There seems much potential for cross-pollination between these approaches and the cognitive concerns they have been designed to address.

The recent debates among animal researchers have highlighted how little we know of certain social transmission processes, in both nonhuman and human primates. Thus, the argument that it is only when the acts concerned are novel that imitation becomes of real cognitive interest leads us to the more interesting question of exactly what role existing knowledge plays in such copying - and we find we don't really know. As I illustrated earlier, there are contexts in which both chimpanzee and child appear to emulate to good effect, where a plausible explanatory hypothesis is that having watched a model perform an act, the subject uses their stored knowledge to 'short-cut' to task-solution achieved by their own methods, rather than the one they witnessed. However, there are also situations where the subject instead steadfastly copies what they saw, even when this involves a less competent outcome than they are independently capable of. What rules govern the adopted copying 'strategy' (e.g., relatively imitative or relatively emulative; relying much on world knowledge or devaluing this in favor of social information) remain poorly understood. These are issues raised by the primate research reviewed here and addressable—for both child and chimp—by extensions of the methods being developed.

While tackling these questions about transmission from individual A to individual B, sight should not be lost of the wider cultural context that makes sense of them. As Sperber (1996) has emphasized, cognitive science omits an important aspect of understanding mental representations if it neglects the processes whereby representations spread from brain to brain. Strangely, the experimental methods described above have not yet been applied to the successive transmission of behavior across a population of individuals, yet they seem eminently suitable to do this. This should tell us how action structures and the representations they imply change during population diffusion. However, to finally pick up the eighth cognitive issue discussed in the paper, the pattern of cultural spread and change will clearly be influenced by the capacities of the individuals that constitute it. That individuals reared in a particular culture may to some extent *learn* useful approaches to social learning - learning to imitate, for example - is one hypothesis suggested by recent findings. Again, this is an empirical question eminently answerable using the experimental tools now to hand.

Acknowledgments: For comments on earlier drafts of this paper I am grateful to Debbie Custance, Vincent Janik, Bill McGrew, Adam Miklosa, Chris Moore, Jim Moore, Peter Slater, Chuck Snowdon, Joanne Tanner, and Mike Tomasello.

REFERENCES

Adams-Curtis, L. E. (1987). Social context of manipulative behaviour in *Cebus apella. American Journal of Primatology, 12,* 325.

Antinucci, F., & Visalberghi, E. (1986). Tool-use in *Cebus apella*: A case study. *International Journal of Primatology, 7,* 349–361.

Bauer, P. J., & Mandler, J. M. (1989). One thing follows another: Effects of temporal structure on 1- to 2-year-olds' recall of events. *Developmental Psychology, 28,* 197–206.

Boesch, C. (1996a). The emergence of cultures among wild chimpanzees. In W. G. Runciman, J. Maynard-Smith & R. I. M. Dunbar (Eds.), *Evolution of social behaviour patterns in primates and man* (pp. 251–268). Oxford: Oxford University Press.

Boesch, C. (1996b). Three approaches for assessing chimpanzee culture. In A. E. Russon, K. A. Bard & S. T. Parker (Eds.), *Reaching into thought: The minds of the great apes* (pp. 404–429). Cambridge: Cambridge University Press.

Boesch, C., & Boesch, H. (1990). Tool use and tool making in wild chimpanzees. *Folia Primatologica, 54,* 1–15.

Boesch, C., Marchesi, P., Marchesi, N., Fruth, B., & Joulian, F. (1994). Is nut cracking in wild chimpanzees cultural behaviour? *Journal of Human Evolution,* 4, 325–338.

Box, H. O., & Gibson, K. R. (2000). *Mammalian social learning: Comparative and ecological perspectives* (Symposia of the Zoological Society of London, 72). Cambridge: Cambridge University Press.

Boyd, R., & Richerson, P.J. (1996). Why culture is common, but cultural evolution is rare. In W. G. Runciman, J. Maynard Smith, & R. I. M. Dunbar (Eds.), *Evolution of social behaviour patterns in primates and man* (pp. 77–93). Oxford: Oxford University Press.

Bugnyar, T., & Huber, L. (1997). Push or pull: An experimental study on imitation in marmosets. *Animal Behaviour, 54,* 817–831.

Byrne, R. W. Commentary on Boesch, C. and Tomasello, M. Chimpanzee and human culture. *Current Anthropology, 39,* 604–605.

Byrne, R. W., & Tomasello, M. (1995). Do rats ape? *Animal Behaviour, 50,* 1417–1420.

Byrne, R. W. (1995). *The thinking ape*. Oxford: Oxford University Press.

Byrne, R. W. & Byrne, J. M. E. (1993). Complex leaf-gathering skills of mountain gorillas (*Gorilla g. beringei*): Variability and standardization. *American Journal of Primatology, 31,* 241–261.

Byrne, R. W. and Russon, A. E. (1998). Learning by imitation: a hierarchical approach. *Behavioral and Brain Sciences, 21,* 667–721.

Call, J. (1999). Levels of imitation and cognitive mechanisms in orangutans. In S. T. Parker, R. W. Mitchell, & H. L. Miles (Eds.), *The mentalities of orangutans and gorillas* (pp. 316–341). Cambridge: Cambridge University Press.

Call, J., & Tomasello, M. (1994). The social learning of tool use by orangutans (*Pongo pymaeus). Human Evolution,* 9, 297–313.

Call, J. & Tomasello, M. (1995). The use of social information in the problem-solving of orangutans (*Pongo pygmaeus*) and human children (*Homo sapiens*). *Journal of Comparative Psychology, 109,* 308–320.

Call, J., & Tomasello, M. (1996). The effect of humans on the cognitive development of apes. In A. E. Russon, K.A Bard, & S. T. Parker (Eds.), *Reaching into thought: The minds of the great apes* (pp. 371–403). Cambridge: Cambridge University Press.

Caro, T. M., & Hauser, M. D. (1992). Is there teaching in nonhuman animals? *Quarterly Review of Biology, 67,* 151–174.

Custance, D. M., Whiten, A. & Bard, K. A. (1994). The development of gestural imitation and self-recognition in chimpanzees (*Pan troglodytes*) and children. In J. J. Roeder, B. Thierry, J. R. Anderson & N.

Herrenschmidt (Eds.), *Current primatology: Selected proceeding of the XIVth Congress of the International Primatological Society, Strasbourg, Vol 2. Social Development, Learning, and Development*. pp. 381–387. Strasbourg: Universite Louis Pasteur.

Custance, D. M., Whiten, A., & Bard, K. A. (1995). Can young chimpanzees imitate arbitrary actions? Hayes and Hayes (1952) revisited. *Behaviour,* 132, 839–858.

Custance, D. M., Whiten, A., Fredman, T. (1999). Social learning of an artificial fruit task in capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology, 113*, 1–11.

Demiris, J., & Hayes, G. (1996). Imitative learning mechanisms in robots and humans. Paper presented at the 5th European Workshop on Learning Robots, Bari, Italy.

de Waal, F. B. M., & Seres, M. (1997). Propagation of handclasp grooming among captive chimpanzees. *American Journal of Primatology, 43,* 339–346.

Donald, M. (1991). *Origins of the human mind: Three stages in the evolution of culture and cognition*. Cambridge, MA: Harvard University Press.

Fragaszy, D. M., & Visalberghi, E. (1989). Social influences on the aquisition and use of tools in tufted capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology, 103,* 159–170.

Fragaszy, D. M., & Visalberghi, E. (1996). Social learning in monkeys: Primate 'primacy' reconsidered. In C. M Heyes, & B. G Galef, Jr. (Eds.), *Social learning in animals: The roots of culture* (pp. 65–84). London: Academic Press.

Galef, B. G., Jr. (1992). The question of animal culture. *Human Nature, 3,* 157–178.

Galef, B. G., Jr. (1988). Imitation in animals: History, definitions, and interpretation of data from the psychological laboratory. In T. Zentall & B. Galef (Eds.), *Social learning: Psychological and biological perspectives* (pp. 3–28). Hillsdale, NJ: Erlbaum.

Galef, B. G., Jr. (1990). Tradition in animals: Field observations and laboratory analyses. In M. Bekoff & D. Jamieson (Eds.), *Interpretations and explanations in the study of behaviour: Comparative perspectives* (pp. 74–95). Boulder, CO: Westview Press.

Galef, B. G., Jr. (1998). Recent progress in studies of imitation and social learning in animals. In Sabourin, M., Craik, F. and Robert, M. (Eds.) *Advances in psychological science, Vol. 2: Biological and cognitive aspects* (pp. 275–299). Congress Proceedings, XXVI International Congress of Psychology. Montreal. Psychology Press.

Gardner, M., & Heyes, C. (1998). Splitting, lumping and priming. *Behavioral and Brain Sciences, 21*, 690–691.

Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behaviour*. Cambridge, MA: Harvard University Press.

Greenfield, P. M., & Maynard, A. E. (1999). Cultural apprenticeship and cultural change: The ontogeny of tool use in cross-species perspective. In S. T. Parker, J. Langer & M. L. McKinney (Eds.) *The evolution of behavioral ontogeny*. Santa Fe: SAR Press.

Harley, H. E., Xitco, M. J., Roitblat, H. L. and Herman, L. M. (1998). Imitation of human models by bottlenose dolphins. Napoli Social Learning Conference, Naples, July 1998.

Hayes, K. J., & Hayes, C. (1952). Imitation in a home-reared chimpanzee. *Journal of Comparative Psychology, 45*, 450–459.

Herman, L. M., Pack, A. A. and Morrel-Samuels, P. (1993). Representational and conceptual skills of dolphins. In H. L. Roitblat, L. M. Herman, P. E. Nachtigall (Eds.) *Language and communication: Comparative perspectives* (pp. 403–442). Hillsdale, NJ: Lawrence Erlbaum.

Heyes, C. M. (1993). Imitation, culture and cognition. *Animal Behaviour, 46,* 999–1010.

Heyes, C. M. (1994). Social learning in animals: Categories and mechanisms. *Biological Reviews, 69*, 207–231.

Heyes, C. M. (1995). Imitation and flattery: A reply to Byrne and Tomasello. *Animal Behaviour, 50,* 1421–1424.

Heyes, C. M. (1998). Theory of mind in nonhuman primates. *Behavioral and Brain Sciences, 21,* 101–148.

Heyes, C. M. and Galef, B. G. Jr. (Eds.). (1996). *Social learning in animals: The roots of culture*. London: Academic Press.

Heyes, C. M., Dawson, G. R., & Nokes, T. (1992). Imitation in rats: Initial responding and transfer evidence. *Quarterly Journal of Experimental Psychology, 45b,* 59–71.

Heyes, C. M., Jaldow, E., Nokes, T., & Dawson, G. R. (1994). Imitation in rats: The role of demonstrator action. *Behavioral processes, 32*, 173–182.

Hinde, R. A., & Fisher, J. (1951). Further observations on the opening of milk bottles by birds. *British Birds, 34,* 393–396.

Hogan, D. E. (1988). Learning and imitation by pigeons. In T. R. Zentall & B. G. Galef (Eds.), *Social learning: Psychological and biological perspectives* (pp. 225–238). Hillsdale, NJ: Erlbaum.

Huber, L. (1998). Movement imitation as faithful copying in the absence of insight. *Behavioral and Brain Sciences, 21,* 694.

Huffman, M. A. (1996). Acquisition of innovative cultural behaviours in nonhuman primates: A case study of stone handling, a socially transmitted behaviour in Japanese macaques. In C. M Heyes, & B. G Galef, Jr. (Eds.), *Social learning in animals: The roots of culture* (pp. 267–289). London: Academic Press.

Imanishi, K. (1957). Identification: A process of enculturation in the subhuman society of *Macaca fuscata. Primates,* 1, 1–29.

Inoue-Nakamura, N., & Matsuzawa, T. (1997). Development of stone tool use by wild chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology, 111,* 159–173.

Janik, V., & Slater, P. J. B. (1997). Vocal learning in mammals. *Advances in the Study of Behaviour, 26,* 59–99.

King, B. J. (1991). Social information transfer in monkeys, apes, and hominids. *Yearbook of Physical Anthropology, 34,* 97–115.

King, B. J. (1994). *The information continuum*. Santa Fe, NM: SAR Press.

Kroeber, A. L. (1928). Sub-human culture beginnings. *Quaterly Review of Biology, 3,* 325–342.

Lefebvre, L. (1995). Culturally transmitted feeding behaviour in primates: evidence for accelerating learning rates. *Primates, 36*, 227–239.

Maestirpieri, D. (1995). Maternal encouragement in nonhuman primates and the question of animal teaching. *Human Nature, 6,* 361–378.

McGrew, W. C. (1974). Tool use by wild chimpanzees in feeding upon driver ants. *Journal of Human Evolution, 3,* 501–508.

McGrew, W. C. (1992). *Chimpanzee material culture: Implications for human evolution*. Cambridge, MA: Cambridge University Press.

McGrew, W. C. (1998). Culture in non-human primates? *Annual Review of Anthropology, 27,* 301–328.

McGrew, W. C., & Tutin, C. E. G. (1978). Evidence for a social custom in wild chimpanzees? *Man, 13,* 234–251.

McGrew, W. C., Ham, R. M., White, L. J. T., Tutin, C. E. G., & Fernandez, M. (1997). Why don't chimpanzees in Gabon crack nuts? *International Journal of Primatology, 18*(3), 353–374.

Matheson, M. D. & Fragaszy, D. M. (1998). Imitation is not the "holy grail" of comparative cognition. *Behavioral and Brain Sciences, 21,* 697–698.

Meltzoff, A. (1995). Understanding the intentions of others: Re-enactment of intended acts by 18-month-old children. *Developmental Psychology, 31,* 838–850.

Miles, H. L., Mitchell, R. W. & Harper, S. (1996). Simon says: the development of imitation in an enculturated orangutan. In A. E. Russon, S. T. Parker, & K.A. Bard (Eds.), *Reaching into thought: The minds of the great apes*. Cambridge, MA: Cambridge University Press

Mineka, S., & Cook, M. (1988). Social learning and the acquisition of snake fear in monkeys. In T. Zentall & B. Galef (Eds.), *Social learning: Psychological and biological perspectives* (pp. 51–73). Hillsdale, NJ: Erlbaum.

Mitchell, R. W. (1994). The evolution of primate cognition: Simulation, self-knowledge, and knowledge of other minds. In D. Quiatt & J. Itani (Eds.), *Hominid culture in primate perspective* (pp. 177–232). Boulder, CO: University Press of Colorado.

Mitchell, R. W., & Anderson, J. R. (1993). Discrimination learning of scratching, but failure to obtain imitation and self-recognition in a long-tailed macaque. *Primates, 34,* 301–309.

Moore, B. R. (1992). Avian movement imitation and a new form of mimicry: Tracing the evolution of a complex form of learning. *Behaviour, 122,* 231–263.

Myowa-Yamakoshi, M. & Matsuzawa, T. (1999). Factors influencing imitation of manipulatory actions in chimpanzees (Pan troglodytes). *Journal of Comparative Psychology 113*, 128–136.

Nagell, K., Olguin, R. S., & Tomasello, M. (1993). Processes of social learning in the tool use of chimpanzees (*Pan troglodytes*) and human children (*Homo sapiens*). *Journal of Comparative Psychology, 107,* 174–186.

Nishida, T. (1987). Local traditions and cultural transmission. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), *Primate societies* (pp. 462–474). Chicago: University of Chicago Press.

Palameta, B., & Lefebvre, L. (1985). The social transmission of a food-finding technique in pigeons: What is learned? *Animal Behaviour, 33,* 892–896.

Paquette, D. (1992a). Discovering and learning tool-use for fishing honey by captive chimpanzees. *Human Evolution, 7,* 17–30.

Parker, S. T. & Russon, A. E. (1996). On the wild side of culture and cognition in the great apes. In A. E. Russon, S. T. Parker & K.A. Bard (Eds.) *Reaching into thought: The minds of the great apes* (pp. 430–450). Cambridge: Cambridge University Press.

Quiatt, D., & Reynolds, V. (1993). *Primate behavior: Information, social knowledge and the evolution of culture*. Cambridge: Cambridge University Press.

Russon, A. E., & Galdikas, B. M. F. (1993). Imitation in ex-captive orangutans (*Pongo pygmaeus*). *Journal of Comparative Psychology, 107,* 147–161.

Russon, A. E., & Galdikas, B. M. F. (1995). Constraints on great ape imitation: model and action selectivity in rehabilitant orangutan imitation (*Pongo pygmaeus*). *Journal of Comparative Psychology, 109,* 5–17.

Russon, A. E. (1997). Exploiting the expertise of others. In Whiten, A. & R. W. Byrne (Eds.), *Machiavellian intelligence II: Evaluations and extensions* (pp. 174–206). Cambridge: Cambridge University Press.

Russon, A. E. (1999). Orangutan's imitation of tool use: A cognitive interpretation. In S. T. Parker, H. L. Miles, & R. M. Mitchell (Eds.), *The mentalities of gorillas and orangutans* (pp. 117–146). Cambridge: Cambridge University Press.

Russon, A. E., Mitchell, R. W., Lefebvre, L., & Abravanel, E. (1998). The comparative evolution of imitation. In J. Langer & M. Killen (Eds.), *Piaget, evolution and development* (pp. 103–143). Hillsdale, NJ: Erlbaum.

Seyfarth, R. D., & Cheney, D. L. (1997). Some general features of vocal development in non-human primates. In C. Snowdon and Hausberger (Eds.) *Social influences on vocal development* (pp. 249–273). Cambridge: Cambridge University Press.

Sherry, D. F., & Galef, B. G. (1984). Cultural transmission without imitation: Milk bottle opening by birds. *Animal Behaviour, 32,* 937–938.

Sperber, D. (1996). *Explaining culture: A naturalistic approach*. Cambridge, MA Blackwell.

Suddendorf, T. (1998). Simpler for evolution: Secondary representation in apes, children and ancestors. *Behavioral and Brain Science, 21,* 131.

Suddendorf, T. (1999). The rise of the metamind. In M. C. Corballis & S. E. G. Lea (Eds.), *The descent of mind*. Oxford: Oxford University Press.

Sugiyama, Y. (1997). Social tradition and the use of tool-composites by wild chimpanzees. *Evolutionary Anthropology, 6,* 23–27.

Sumita, K., Kitahar-Frisch, J., & Norikoshi, K. (1985). The acquisition of stone-tool use in captive chimpanzees. *Primates, 26*, 168–181.

Suzuki, S., Kuroda, S., & Nishihara, T. (1995). Tool-set for termite fishing by chimpanzees in the Nodoki Forest, Congo. *Behavior*, *132*, 129–235.

Tanaka, I. (1995). Matrilineal distribution of louse egg-handling techniques during grooming in free-ranging Japanese macaques. *American Journal of Physical Anthropology, 98,* 197–201.

Tanaka, I. (1998). Social diffusion of modified louse egg-handling techniques during grooming in free-ranging Japanese macaques. *Animal Behaviour, 56,* 1229–1236.

Thierry, B. (1994). Social transmission, tradition and culture in primates: from the epiphenomenon to the phenomenon. *Tech. Cult, 23–24,* 91–119.

Tomasello, M. & Call, J. (1997). *Primate cognition*. Oxford: Oxford University Press.

Tomasello, M. (1990). Cultural transmission in the tool use and communicatory signalling of chimpanzees? In S. Parker & K. Gibson (Eds.), *Language and intelligence in monkeys and apes: Comparative developmental perspectives* (pp. 274–311). Cambridge: Cambridge University Press.

Tomasello, M. (1994). The question of chimpanzee culture. In R. W. Wrangham, W. C. McGrew, F. B. M. de Waal, & P. Heltne (Eds.) *Chimpanzee cultures* (pp. 301–317). Cambridge, MA: Harvard University Press.

Tomasello, M. (1996). Do apes ape? In C. M. Heyes & B.G. Galef (Eds.), *Social learning in animals: The roots of culture*. London: Academic Press.

Tomasello, M., Davis-Dasilva, M., Camak, L., & Bard, K. (1987). Observational learning of tool-use by young chimpanzees. *Human Evolution, 2,* 175–183.

Tomasello, M., Kruger, A. C., & Ratner, H. H. (1993). Cultural learning. *Behavioral and Brain Sciences, 16,* 495–552.

Tomasello, M., Savage-Rumbaugh, E. S., & Kruger, A. C. (1993). Imitative learning of actions on objects by children, chimpanzees and enculturated chimpanzees. *Child Development, 64,* 1688–1705.

Visalberghi, E. (1987). Acquisition of nut-cracking behaviour by 2 capuchin monkeys (*Cebus apella*). *Folia Primatologica, 49,* 168–181.

Visalberghi, E. (1994). Learning processes and feeding behaivour in monkeys. In B. G. Galef, M. Mainardi, & P. Valsecchi (Eds.), *Behavioral aspects of feeding* (pp. 257–270). Chur, Switzerland: Harwood Academic.

Visalberghi, E., & Fragaszy, D. (1990). Do monkeys ape? In S. Parker & K. Gibson (Eds.), *Language and intelligence in monkeys and apes: Comparative developmental perspectives* (pp. 247–273). Cambridge, U.K: Cambridge University Press.

Visalberghi, E., & Trinca, L. (1989). Tool use in capuchin monkeys: distinguishing between performing and understanding. *Primates, 30,* 511–521.

Westergaard, C. G., & Fragaszy, D. (1987). The manufacture and use of tools by capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology 101,* 159–168.

Westergaard, G. C., & Lindquist, T. (1987). Manipulation of objects in a captive group of lion-tailed macaques (Macaca silenus). *American Journal of Primatology, 12,* 231–234.

Whiten, A. (1989). Transmission processes in primate cultural evolution. *Trends in Ecology and Evolution, 4,* 61–62.

Whiten, A. (1993). Human enculturation, chimpanzee enculturation and the nature of imitation. *Behavioral and Brain Sciences, 16,* 538–539.

Whiten, A. (1996). Imitation, pretence and mindreading: Secondary representation in comparative psychology and developmental psychology? In A. E. Russon, S. T. Parker, & K.A. Bard (Eds.), *Reaching into thought: The minds of the great apes*. Cambridge, U.K.: Cambridge University Press.

Whiten, A. (1998a). Evolutionary and developmental origins of the mindreading system. In J. Langer and M. Killen (Eds.), *Piaget, evolution and development.* Hillsdale, NJ: Lawrence Erlbaum.

Whiten, A. (1998b). Imitation of the sequential structure of actions by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology, 112,* 270–281.

Whiten, A. (1998c). How imitators represent the imitated: The vital experiments. Commentary on Byrne & Russon: Learning by imitation: A hierarchical approach. *Behavioral and Brain Sciences 21*, 707–708.

Whiten, A. (1999a). The evolution of deep social mind in humans. In M. Corballis & S. Lea (Eds.), *The descent of mind* (pp. 155–175). Oxford: Oxford University Press.

Whiten, A. (1999b) The Machiavellian hypothesis. In R. Wilson & F. Keil (Eds.), *MIT. Encyclopedia of the cognitive sciences*. Cambridge, MA: MIT Press.

Whiten, A. (1999c). Imitation of sequential and hierarchical structure in action: experimental studies with children and chimpanzees. *Proceedings of the Artificial Intelligence and Simulation of Behaviour Convention, Edinburgh*. (pp. 38–45) April.

Whiten, A. (1999d) Parental encouragement in *Gorilla* in comparative perspective. Implications for social cognition. In: S. T. Parker, H. L. Miles, and R.W. Mitchell (Eds.), *The mentality of gorillas and orangutans.* (pp. 342–366). Cambridge: Cambridge University Press.

Whiten, A. (2000). Chimpanzee cognition and the question of mental re-representation. In D. Sperber (Ed.), *Metarepresentations*. Oxford: Oxford University Press.

Whiten, A., & Brown, J. (1999). Imitation and the reading of other minds: perspectives from the study of autism, normal children and non-human primates. In S. Braten (Ed.), *Intersubjective communication and emotion in ontogeny: A sourcebook.* Cambridge: Cambridge University Press.

Whiten, A., & Byrne, R. W. (1991). The emergence of metarepresentation in human ontogeny and primate phylogeny. In A. Whiten (Ed.), *Natural theories of mind: Evolution, development and simulation of everyday mindreading* (pp. 267–281). Oxford: Basil Blackwell.

Whiten, A. & Byrne, R.W., Eds. (1997). *Machiavellian intelligence II: Evaluations and extensions*. Cambridge: Cambridge University Press.

Whiten, A., & Custance, D. M. (1996). Studies of imitation in chimpanzees and children. In C. M Heyes, & B. G Galef, Jr. (Eds.), *Social learning in animals: The roots of culture* (pp. 291–318). London: Academic Press.

Whiten, A., Custance, D. M., Gomez, J.-C., Teixidor, P., & Bard, K. A. (1996). Imitative learning of artificial fruit processing in children (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology, 110,* 3–14.

Whiten, A., & Ham, R. (1992). On the nature and evolution of imitation in the animal kingdom: reappraisal of a century of research. In P. J. B. Slater, J. S. Rosenblatt, C. Beer, & M. Milinski (Eds.), *Advances in the study of behavior* (pp. 239–283). San Diego: Academic Press.

Xitco, M. J. (1988). Mimicry of modeled behaviours by bottlenose dolphins. Master's thesis, University of Hawaii.

Yamakoshi, G., & Sugiyama, Y. (1995). Pestlepounding behavior of wild chimpanzees at Bossou, Guinea: A newly observed tool-using behavior. *Primates, 36,* 489–500.

Yut, E., Greenfield, P. M., & Boehm, C. (1995). Gone fishin': Developmental changes in attention and their relation to the development of insect fishing technology in young chimpanzees in the wild. Poster presented at Jean Piaget Society Meeting, Berkeley, California.

Zentall, T. R. (1996). An analysis of imitative learning in animals. In C. M. Heyes & B. G. Galef (Eds.), *Social learning in animals: The roots of culture* (pp. 221–243). New York: Academic Press.

Zentall, T. R. (1998). Insufficient support for either response "priming" or "program-level" imitation. *Behavioral and Brain Sciences, 21,* 708–709.