Social transmission, tradition and culture in primates: from the epiphenomenon to the phenomenon

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Résumé
On examine les conséquences et la signification de la propagation de comportements socialement acquis chez les primates non humains. Les comportements acquis ne sont parfois que des modes transitoires, ils peuvent aussi se transmettre d'une génération à l'autre et donner lieu à des traditions. Ils concernent généralement les activités de subsistance, les soins du corps ou les signaux de communication mais ils n'ont parfois aucune utilité directe. Leur aspect stéréotypé peut résulter aussi bien de contraintes sociales qu'écologiques. Dans certains cas, cependant, leur forme apparaît arbitraire du point de vue des facteurs de l'environnement. Ce n'est que chez le chimpanzé que l'on rapporte l'accumulation de plusieurs dizaines de traditions. Le fait que les primates non humains n'intéralisent pas leurs propres traditions et qu'ils ne puissent que difficilement produire des copies fidèles limite vraisemblablement la stabilisation et l'accumulation des modifications acquises. On conclut que ces traditions ne sont pas des adaptations par elles-mêmes mais qu'elles représentent, à l'échelle des populations, un effet secondaire des facultés d'apprentissage individuelles. Il reste que de tels épiphénomènes ont pu jouer un rôle actif dans l'émergence du phénomène culturel chez les premiers hominidés.

Mots-clés: acquisition sociale, modelage, propagation, accumulation, adaptation.

Abstract
The consequences and meaning of the propagation of socially acquired patterns in populations of non-human primates are reviewed. Acquired patterns may represent temporary fashions, they may also be transmitted from one generation to the next and give rise to traditions. They mainly concern subsistence activities, body care or social communication but they sometimes have no direct utility. A fair degree of stereotypy may occur in propagated patterns both from social and ecological shaping. However, in some cases, forms appear arbitrary with regard to environmental constraints. The accumulation of dozens of traditions is known in chimpanzees only. Lack of faithful copying and failure to internalize traditions likely limit the stabilization and accumulation of refinements in non-human primates. It is concluded that these traditions are not adaptations per se but represent side-effects of individual learning abilities at the population level. However, such epiphenomena might have been instrumental in the emergence of the cultural phenomenon in early hominids.

Key-words: social acquisition, patterning, propagation, accumulation, adaptation.
When attempting to tackle the question of culture-like behaviours in animals, the discussion inescapably leads to the meaning of 'culture', then follows an essentialist debate about the definition of culture, aimed at settling the animal problem... Looking at the beginning of culture is like considering the origin of life. An information-storing organisation has emerged but it vanishes as we get to its roots. In the early stages, some elements of the phenomenon are already present and look like the phenomenon, but others are lacking and yet the whole phenomenon is not there. Reminiscent of 'protolife', the concept of 'protoculture' was proposed to account for these stages, both in non-human primates ('pre-culture': Kawai, 1965; Kawamura, 1972; Menzel et al., 1972) and early hominids (Hallowell, 1961), but that only avoids the problem, the question of boundaries remains. Living non-human primates are not our ancestors, and there is a discontinuity between animal and human achievements. While the gap between non-human primates and mankind has been crossed at least once by early hominids, they have left only a few traces of their material culture. By studying non-human primate traditions, our goal is to provide insights about how culture might have gradually emerged. The main question addressed in this paper is not whether or not animals have culture, but where culture may come from. Before considering the evolutionary significance of socially acquired patterns in non-human primates, their features and conditions of occurrence will be first reviewed.

**Features and Conditions of Occurrence of Socially Acquired Patterns**

**Innovation**

For social transmission to occur, individual acquisition must have taken place beforehand. Innovation may concern the eating of a new food item, the discovery of a technique, the development of a social tactic. It can be the invention of a new pattern in a stable environment, or occur as a response to environmental change; either a new pattern is discovered or an old one is altered in form or purpose (Kummer & Goodall, 1985). The likelihood of innovation depends on environmental opportunities and time available for exploration by individuals. Free time provided by captivity, or novel patterns produced through play, for instance, may promote innovation (Beck, 1980; Fagen, 1981). Social constraints also affect the appearance of novelty. In captive Guinea baboons (*Papio papio*), the proximity of dominant individuals limited subordinates' foraging success (Pallaud & Lepoivre, 1985); in hamadryas baboons (*Papio hamadryas*), subordinate females were more effective in exploiting resources at the periphery of the group than the highest-ranking female, occupied more socially (Sigg, 1980).

One outcome of innovation is the appearance of idiosyncratic patterns. The primatological literature is rich in reports of particular behaviours that have never spread to conspecifics (e.g., Beck, 1980; Kummer & Goodall, 1985; Visalberghi & Fragaszy, 1990a). In most cases, we have no information on how these patterns appeared, and any learning process may account for them. In fact, innovation is inseparable from learning. Trial-and-error and associative learning probably account for most instances of discovery. While chimpanzees (*Pan troglodytes*) can mentally solve problems involving the use of tool (see Premack & Woodruff, 1978), monkeys seem to have a poor understanding of the combinations of actions and means necessary to succeed in complex tasks; brown capuchin monkeys (*Cebus apella*), for example, failed to master problems that required prediction of the effects
produced by the subject's use of tool (Visalberghi & Limongelli, 1994), and Tonkean macaques (*Macaca tonkeana*) seemed unable to coordinate their forces to lift heavy stones (Petit et al., 1992). Chance probably plays a major role in discovery, as suggested by many anecdotes. For instance, Kummer and Goodall (1985) report that olive baboons (*Papio anubis*) near lake Tanganyika used to dig in the gravel, searching for scraps, "One day when the lake was rough and the successive breaking of large waves made drinking difficult, an adolescent male, Asparagus, was observed to dig a hole near the high water mark, wait for a wave to fill it, then quickly drink as the wave retreated"; presumably, drinking water that filled holes dug while searching for food subsequently resulted in the digging of holes for the purpose of drinking (Kummer & Goodall, 1985). Serendipity also leads to human inventions, but insights from intentional synthesis obviously contribute to human achievements to an extent unknown among non-human primates (Kroeber, 1928; Lévi-Strauss, 1952).

**Mechanisms of social transmission**

With regard to the social transmission of acquired behaviour in non-human primates, it has been inferred for long that they are able to learn by 'observation' or 'imitation'; the results of experimental studies have recently questioned this stance (Galef, 1988; Visalberghi & Fragaszy, 1990a; Whiten & Ham, 1992; but see Heyes, 1993). A number of reports indicate that great apes can imitate, in the sense of replication of a model's action (e.g., Russon & Galdikas, 1993). However, in an experimental study, juvenile chimpanzees were found to be unable to reproduce the acts of a conspecific demonstrator in a relatively complex task -- raking in food using a T-bar (Tomasello et al., 1987; Nagell et al., 1993); onlookers behaved more successfully than control subjects, however, and the authors argue that they learned something about results; they also appear to have recognized that the tool has a function in solving the problem. It could also be that the solution involved some understanding of the goal (Whiten & Ham, 1992). However, the possibility that animals can imitate simple acts remains a controversial topic (e.g., Heyes, 1993; Russon & Galdikas, 1993; Tomasello et al., 1993a).

With regard to monkeys, they appear unable to attribute mental states to others, which would preclude them imputing purposes to others (Cheney & Seyfarth, 1990; Povinelli et al., 1991). We have little information on the processes of information transfer. The drawing of attention of an individual towards the location of another or its object of interest ('stimulus enhancement') is an important mechanism of information transfer, increasing the probability of individual learning. In some cases, monkeys may recognize a relationship between the outcome of a conspecific's acts and some features of these acts (for example, holding an object in the case of tool use). A stimulus might be associated with the positive or negative reactions of conspecifics, the outcome of which is social conditioning (Jouventin et al., 1976; Mineka & Cook, 1988). Also, the probability of occurrence of a pattern already present in the individual's repertoire might be increased throughout 'social facilitation' (i.e., contagion). The transmission of food preferences, for instance (see Hikami et al., 1990), might involve any of these processes, and several processes may occur simultaneously in monkeys and apes as well.

The spread of food-washing in a group of Japanese macaques (*Macaca fuscata*) (Kawai, 1965; Nishida, 1987) has been recently questioned as an example of imitation in non-human primates. Galef (1990) has pointed out...
the slow propagation of the behaviour, much lower than would be expected if imitation took place. Brushing food is common in monkeys, and group-members might have acquired the behaviour through simple processes: learning a relationship between food-brushing and water, or associating food and water, or even following the demonstrator then discovering food-washing individually. The loading of our language with human representation has probably hampered initial descriptions of the phenomenon. In a study of the acquisition of food-washing in brown capuchin monkeys and longtailed macaques (Macaca fascicularis), subjects were given access to water and sand-covered food (Visalberghi & Fragaszy, 1990b). At first, subjects dunked fruits, retrieved them, and then dunked them back into water; only later did subjects start to unambiguously clean food before eating it. As emphasized by the authors, labelling food-dunking as washing would have obscured the fact that initial manipulation was exploratory and playful, "behaviour patterns relating food and water may become established in a functional pattern as a consequence of their association with cleaned food, but they do not appear to serve a cleaning function" (Visalberghi & Fragaszy, 1990b). Such considerations are relevant to processes of social transmission. Stating that "an individual observes another one washing its food" implicitly means that the observing individual is aware of the cleaning function of the behaviour. While this may be correct from a human perspective, it may be misleading in terms of the monkey Umwelt. That the subject watches an action does not imply that it comprehends it.

Adults sometimes punish inappropriate responses of immatures or reinforce good ones (Nishida, 1987); although adults' motivations are unclear, this might be an effective form of social conditioning. Such behaviour represents teaching, as defined by Caro and Hauser (1992) -- in modifying its behaviour, an individual facilitates learning by an observer. However, teaching about behaviour patterns not already present in the repertoire has never been described in monkeys. In chimpanzees, two cases of intentional teaching have been claimed: in the wild, a mother stimulated her offspring and oriented its tools in the context of cracking nuts (Boesch, 1991); in captivity, a female trained in sign-langage molded the hands of a juvenile into the sign appropriate to context (Fouts et al., 1989). Suggestive though they are, the latter cases should not lead us to forget that information transfer in non-human primates primarily relies on indirect modes; intentional instruction remains the exception rather the rule, and imitating seems limited to simple acts. There is not "a passion for imitation" (Bates et al., 1991) as stated for humans.

Propagation
The complexity and frequency of occurrence of the new pattern, the innovator's social status, as well as onlookers' abilities to recognize the utility of the pattern may all affect the probability and speed of propagation; it may be a matter of days or months... As information transfer occurs between interacting partners, propagation is channelled by social networks. Priority of access to incentives favours the spread of new food-processing patterns among dominant individuals (Hauser, 1988; Kawai et al., 1992). In the kin-structured organization of Japanese macaques, innovations first spread among peers, and preferentially among partners belonging to the same lineage (Kawai, 1965; Huffman, 1984; Scheurer & Thierry, 1985). In Guinea baboons, relatedness appears less influential (Petit & Thierry, 1993). Some individuals -- the oldest ones, in particular -- may never acquire
the new pattern and the spread within the group remains incomplete.

Distinctions have been made between 'dissemination' and 'diffusion'. While dissemination is a within-group propagation, diffusion is the spread of a pattern from one group to another (McGrew & Tutin, 1978). Diffusion might occur through the transfer of migrating individuals (McGrew & Collins, 1985; Hauser, 1988), it might also stem from the fission of one group into two ('founder effect', Burton & Bick, 1972). Besides such synchronic propagation, the transmission of patterns may be diachronic, in which case it is called a 'tradition'. In principle, to qualify as tradition, a pattern should persist in learners after the death of the demonstrator; in practice, there is usually more than one possible demonstrator in the field, so we can only check whether the pattern is retained from one generation to the next. In chimpanzees, the main channel of information transfer seems to be from mother to offspring (Goodall, 1986; McGrew, 1992). In provisioned Japanese macaques, after the initial phase of dissemination in the population, new patterns were learned from elders at an early age (Kawai, 1965; Huffman, 1984). The term 'tradition' emphasizes the historical consequences of the phenomenon; it makes sense since a new pattern may become socially inherited on a long-term basis. However, it must be stressed that the existence of traditions is an outcome of the fact that information transfer may occur among overlapping generations. Tradition and dissemination involve the same processes of information transfer, they do not differ in kind.

Disseminated patterns may appear then vanish from the repertoire of the group (Boesch, 1993). Goodall (1986) reports the occurrence of such 'fashions' in a community of wild chimpanzees living in the Gombe National Park, Tanzania. For instance, a juvenile female started to display 'wrist-shaking', a rapid to-and-fro shaking of the hand when threatening another individual. The following week, another young female, a playmate of the former, began to wrist-shake in various contexts. The gesture was displayed by both individuals during the following year but less and less often and the pattern was gradually extinguished. Some data suggest that acquired patterns are highly susceptible to extinction. In a study of vervet monkeys (Cercopithecus aethiops) in Amboseli, Kenya, a 14-old female was seen dipping dry pods into the well of an acacia containing an exudate: after a few minutes, the female removed the pods and consumed them; in the following month, most group-members were successively observed feeding on pods dipped in exudate (Hauser, 1988). The technique improved access to a source of water and allowed the hard seeds of the dry pods to soften; it occurred during a period of drought, it had never been observed in 7 years of observation of the population. It is not known whether the adult female discovered the technique or remembered it. If the pattern arose in response to the drought, it may as well be lost when ecological pressures are relaxed; as noted by the author, experienced individuals may be a privileged source of knowledge, and the survival of a pattern is highly dependent on such variables as individual life expectancy and group-size (Hauser, 1988). On the other hand, providing that ecological conditions do not change (see Huffman, 1984), traditions may endure long periods. In the case of Japanese macaques at Koshima, food-washing appeared as a response to provisioning by human beings, and has been maintained in the group for more than thirty years (Kawai et al., 1992). In Gombe chimpanzees, Goodall (1986) describes the technique of leaf-spong-ing - chewing some leaves, dipping this 'sponge' into a tree-hole to get out water and drink it. This technique was already
established when the study began and is still present three decades later.

According to Tomasello et al. (1993a), many human traditions show uniformity, i.e. patterns are learned by all individuals belonging to a given community. Although this does not hold true for every pattern even in human beings, it must be underlined that incomplete propagation seems the rule in monkeys. In contrast, some patterns may be eventually practiced by virtually all group members in chimpanzees (Boesch, 1993).

Utility

Many socially acquired patterns in non-human primates are related to the selection, acquisition and processing of food (Nishida, 1987). While groups of Japanese macaques near Osaka dug and ate the roots of yams and lilies, this was not seen at Takasakiyama where these plants were also present (Kawamura, 1965). In one population of lowland gorillas (Gorilla g. gorilla) in Gabon, individuals consumed weaver ants but ignored a particular species of termite; another population, 250 km apart, showed the opposite picture: the termite was included in the diet but not weaver ants, although both insect species were available (Tutin & Fernandez, 1992). Many but not all populations of chimpanzees use tools to fish for ants, termites or honey (Goodall, 1986; McGrew, 1992; Sugiyama, 1993).

Acquired habits may also concern communication signals. Several peculiar patterns used in aggressive displays or solicitations have been reported in chimpanzees (Goodall, 1986; Tomasello, 1990). Among them, the best documented is the leaf-clipping display, described in communities inhabiting the Mahale mountains in Tanzania (Nishida, 1980). An individual picked several stiff leaves and pulled them apart with teeth. In removing the leaf blade, a noisy sound was produced. This behaviour was mainly performed as a courtship display: the female often responded by approaching for copulation; the behaviour also sometimes occurred when individuals were frustrated by lack of access to an incentive. This display has been reported in two other places. At Bossou, Guinea, it mainly occurred as a frustration response and was rarely performed in a sexual context (Sugiyama, 1981). In the Tai forest, Ivory Coast, it was part of the drumming display of males. However, at all sites, the display seemed to act primarily as a ritualized displacement (McGrew, 1992).

Patterns related to subsistence activities, body care and social communication are reinforced by direct benefits to the performers. However, the utility is sometimes less obvious. In a captive group of Guinea baboons, young males learned to break a concrete structure using stones (Petit & Thierry, 1993); while the task might be self-rewarding, it did not bring gain. As this instance of dissemination occurred in a captive setting, its significance may be questioned. But we also know of the propagation of apparently non-purposeful behaviours in free-ranging groups. In the eighties, a tradition arose in the Japanese macaques of Arashiyama (Huffman, 1984). Young individuals frequently handled stones: manipulations included carrying, rolling and clacking stones, gathering them into piles, and scattering. This practice was reported in two other groups of the same species, it had no consequences and looked like play. In chimpanzees inhabiting the Mahale mountains, McGrew and Tutin (1978) have described a particular posture of social grooming that they named the ‘grooming-hand-clasp’: both participants in the session sit facing one another, each one simultaneously extending an arm overhead and grasping the other’s hand, meanwhile the opposite hand is used to groom the partner’s underarm area. Here again, the habit did not meet
particular needs. It occurred frequently and has been reported in only one other locality (Ghiglieri, 1984).

**Patterning**

As pointed out by McGrew (1992), recognizing propagation requires some degree of stereotypy: the transmitted pattern needs to be a norm, i.e. shown by a significant proportion of the population in an identifiable form. Measurement and comparison of patterns have been applied to the products of behaviour (Boesch & Boesch, 1993; McGrew, 1992; Sugiyama, 1993). In making tools, chimpanzees both select their material and modify it through a sequence of actions. Their artefacts have different usages and they may display a fair degree of stereotypy. In fishing for termites, chimpanzees may use hard sticks to dig into termite mounds; then, they pick flexible twigs, grass blades or pieces of bark which they may shorten or peel before probing termite tunnels. For dipping into underground nests of ants, they choose long branches which they strip to obtain smooth wands (Goodall, 1986; McGrew, 1992). Sticks employed in fishing for honey are larger than those aimed to ant-dipping (Boesch & Boesch, 1993). A chimpanzee may produce various tools from the same raw material. It may pick a leaf and strip the blade in preparing a probe, it may chew the leaf to make a sponge, or destroy it when displaying sexual solicitation, it may also use the leaf without modification to wipe away dirt (Nishida, 1980).

Acquired communication patterns must be quite stereotyped to be understood by conspecifics. Communication involves both the production of a pattern and its comprehension. Tomasello (1990) argues that signals may be acquired either by imitation or 'conventionalization'. In the latter process, an individual learns that a given action sequence produces a predictable reaction in the recipient; through repetition of the sequence, the recipient anticipates the action and responds only to part of the initial sequence, thereby reinforcing an increasingly formalized form. This is a social shaping process. Comparing the 'pant-hoots' of male chimpanzees at Gombe and Mahale, Mitani et al. (1992) have found subtle intergroup differences in the spectral and temporal features of this long-distance call. The two populations are separated by less than 200 km and such dialectal variation is unlikely to be explained by genetic factors; as hypothesized by the authors, it may reflect a shaping process: some variants would have been reinforced over time to match a locale-specific vocal type ('action-based learning', Marler & Nelson, 1993).

In spite of patterning, some variation may occur in the performances of different individuals and thus in the reproduction of patterns. It was argued that a distinctive feature of human cultures lies in the faithful reproduction of patterns (Tomasello et al., 1993a). Though there may be some truth in such a statement, it is difficult to test empirically. According to the level of analysis, it may be concluded that two chimpanzees display the same overall technique to crack nuts using stone hammers and anvils, or that each of them employ idiosyncratic techniques because they differ in the position of the fingers holding the hammer (Boesch, 1993). In species able to imitate, a pattern may be altered by innovative improvements and copying errors. Even in human beings, cultural elements do not exist in identical forms, they are abstractions of ideal types. Culture is a perpetually recreated phenomenon which depends on a balance between the respective importance of individual variations and social conformism (Boyd & Richerson, 1985). When indirect modes of transmission operate, the lack of information about patterns obliges individuals to rediscover at least part of
them, which favours variation and limits transmission fidelity. On the other hand, actions are constrained by the context, and patterns may eventually reappear as an outcome of environmental shaping. On operational grounds, it is difficult to distinguish between factors responsible for the emergence of patterns.

In monkeys, which seem to rely mainly on indirect processes of social transmission, we should expect noticeable transformation of initial patterns throughout the propagation process. When examining the food-processing behaviours of Koshima macaques, it indeed appears that the diversity of patterns increased with time. In the sixties, there were few variants of potato-processing: rolling the potato in water, brushing off the sand by hand, or dipping the potato into the sea after gnawing it once or twice (‘seasoning’) (Kawai, 1965). Twenty years later, additional variants were observed: rinsing, brushing against the bottom, collecting immersed potatoes, usurping cleaned potatoes from others; similar diversification was documented for wheat washing (Kawai et al., 1992). In the absence of data about mechanisms of transmission, a conservative stance would assume that some relation between water and food was socially learned but that the different types arose through individual learning. In the case of stone-handling at Arashiyama (Huffman & Quiatt, 1986), several variants might be performed by individuals, but it is still unknown to which extent social influences have played a role in their occurrence.

**Arbitrariness**

For methodological reasons, when variations between populations are found to be correlated either to genetic or ecological differences, they cannot be regarded as originating from social transmission. For example, the fact that the chimpanzees of one Mahale community did not fish for termites like those of Gombe was explained by the virtual absence of a particular genus of termites in the first site (Nishida & Uehara, 1980; McGrew & Collins, 1985). But the distinction between factors is not always so simple. An ecological change or some peculiarity in the habitat may give rise to an elaboration which disseminates or becomes traditional. The food-processing habits of groups of Japanese and vervet monkeys stand as such cases. Physical and social factors often interact, and trying to separate them would be vain (Nishida, 1987; McGrew, 1992).

Arbitrariness is not a straightforward concept, it is a matter of extent (McGrew & Tutin, 1978), i.e. there may be gradation in arbitrariness. Many socially transmitted patterns are arbitrary with regard to the environment to some extent, otherwise they could have not appeared. When stone-playing occurred in a few groups of Japanese macaques, such an event was only one among many possible others, it cannot be said to be an obligatory product of ecological conditions. But this historical contingency was also related to the presence of a stony ground in the habitat, and perhaps free-time availability (Huffman, 1984); moreover, the various forms of handling recorded at Arashiyama seemed to exhaust most of the combinations open to a macaque in manipulating small stones, therefore they also depended on physical constraints. In captive rhesus macaques (*Macaca mulatta*), an abnormal stereotypy consisting in covering the eyes with the hands was performed by most individuals in the colony; while various abnormal behaviour patterns usually occur in deprived conditions, their convergence into one main pattern was peculiar, but might have been induced by artificial light-dark conditions (Thierry, 1984). Patterns detached from environmental constraints bring clearer instances of arbitrariness. In fishing for termites, chimpanzees may use segment
of vines that they insert into the mound; McGrew (1992) noted that at one site (Mt Assirik, Senegal), only one end of the vine tool was employed, while at Gombe individuals employed both ends of the tool, which seemed a useless response to a low return of termites. The difference seems gratuitous. The same remark may be made with regard to the appearance and disappearance of 'fashions'. At Tai, the leaf-clipping display was performed for years by males in the drumming context; then, within one month, it started to be used during rest, not only by males but by other age-and-sex classes too (Boesch, 1993). Leaf-clipping may be regarded as iconic when expressing frustration or excitation (making noise and destroying objects), but it is less so when performed during resting or in a sexual context. When the form of acquired signals is no longer related to their use, it becomes a convention. (Transition from iconic to non-iconic meaning is a well recognized process in the evolution of human language; Eco, 1988.) Finally, it may be noted that apes reared in a human environment may acquire lexical signs by mere exposure, without direct training (Savage-Rumbaugh, 1991).

**Internalization**

The lack of a referential system elaborate enough to express thoughts obviously impairs any communication about shared beliefs and conceptualized norms in animals. However, this is not the whole story. Some have denied great apes the capacity to construct arbitrary forms (failure to plan, Holloway, 1969), or to imitate (failure to ascribe intentionality to conspecifics, Tomasello et al., 1993a); although these authors have probably gone too far (see above), few people would disagree that non-human primates lack certain human cognitive abilities. When a form is reproduced by a human being, whatever it originates from environmental shaping and/or intentional design, it is liable to be recognized as reflecting a particular 'style' by another human being, which supposes the reading -- and interpretation -- of socially embedded rules (see King, 1991). More generally, the identity of groups is based on the recognition of traditions. Ethnographs testify that people are aware that they have norms and may report about them (Kroeber & Kluckhohn, 1952). In contrast, there is no indice that non-human primates can attribute a meaning to their own traditions: they seem unable to internalize collective frames of reference.

Inevitably, the question of meaning has been raised with respect to the stone artefacts left by early hominids (Leroi-Gourhan, 1964; Berthelet & Chavaillon, 1993). While some anthropologists believe that types are designs related to cultural boundaries (e.g., Holloway, 1969; Wynn, 1989), others stress that types result from an interaction between raw material, technique and design, which makes it difficult to sort out stylistic and functional variables (e.g., Stiles, 1979). However, when artefacts come to be recognizably 'standardized' -- i.e., designed to be of similar size and shape, an event unseen in apes -- this should reflect the existence of shared ideas about appropriate shapes, i.e. shared cultural representations (see Wynn, 1989; Donald, 1991; Berthelet & Chavaillon, 1993).

**Accumulation**

In monkeys, habits in space utilization and diet selection have rarely been documented (Kawamura, 1965; Marais, 1969; Nishida, 1987), and there is no strong evidence about the existence of acquired variation in communication signals (but see Stephenson, 1973; Green, 1975; Maeda & Masataka, 1987). The instances of dissemination and tradition previously discussed represent isolated events. While it is probable that socially acquired variations between populations of monkeys are
underestimated, known instances of propagated patterns are rare. With regard to apes, data are too incomplete to draw firm conclusions, although an impressive diversity of habits has been described for the chimpanzee, both across and within regions (reviewed in Goodall, 1986; Tomasello, 1990; McGrew, 1992; Boesch & Boesch, 1993; Sugiyama, 1993). At Bossou, chimpanzees use stone hammers and anvils of stone to crack open oil palm nuts and eat the kernel; at Taï, chimpanzees also possess sophisticated lithic techniques to exploit hard nuts, but they do not apply it to the oil-palm nut; at Gombe, chimpanzees feed on the fruit of the oil palm tree, they chew the fibrous outer husk, but reject the nut; at Mahale, chimpanzees seem to ignore the palm nuts present in their range. When comparing Gombe and Mahale populations, which both inhabit the eastern shore of the lake Tanganyika, it appears that they differ by at least fifty consumed food items available at both sites, seven patterns of tool-use, and several communication signals; even then, such an account does not scant justice to innumerable variations in techniques of food-processing, most of the differences probably being traditional. Thus, it is understandable that students of wild chimpanzees use the term ‘culture’ to describe the chimp world. Implicit in this usage is the belief that ‘culture is an accumulation of traditions’. Far from being trivial, number of traditions is a significant parameter which reflects the acknowledged fact that culture is a cumulative process. Hence, McGrew (1992) has repeatedly called for the rise of an ethnology of chimpanzees.

Rather than to a mere addition of traditions dealing with different behaviour patterns, accumulation may also refer to a succession of modifications brought to a single pattern. The lack of explicit communication and instruction severely constrains the ability of chimpanzees to gradually improve a technique through generations (Tomasello et al., 1993a). In human beings, cultural artefacts can act as external representations that keep record of previous experience (Donald, 1991); the reading of artefacts stabilizes traditions, individuals can build upon, which favours the accumulation of improvements. In this respect, the failure of non-human primates in internalizing their traditions limits the extent of the cumulative process.

From this review, it appears that a number of aspects of human culture may be found in non-human primates. Ascribing culture to them or not depends on the criteria used to define the phenomenon. Culture may be what is non-genetically inherited (see Kroeber and Kluckhohn, 1952), what is transmitted by imitation (Boyd & Richerson, 1985; Tomasello, 1990; Galef, 1992), what depends on a succession of refinements (Tomasello et al., 1993a), what involves the generation of arbitrary forms (Holloway, 1969), what is mediated by symbols (Bain, 1942; White, 1959; Weiss, 1973; Sahlins, 1976) or what rests on internalized norms (see Kroeber & Kluckhohn, 1952; Lévi-Strauss, 1967; Keesing, 1974). McGrew and Tutin (1978) have also proposed an operational definition of culture which requires that several conditions be met, including the occurrence of innovation, dissemination, diffusion, tradition and patterning. However, when anthropologists refer to culture, they assume the existence of language as the medium of most behaviours, habits and norms, which means that there is no homology between animal and human traditions (Weiss, 1973; Washburn & Benedict, 1979). This leaves the emergence of culture and language in early hominids in the shadow. Rather than considering performances of monkeys and apes from an anthropocentric perspective, it is more productive to recognize that animal
constructs are of another order than human ones, and assess their evolutionary significance on their own (Leroi-Gourhan, 1964; Galef, 1992).

FUNCTION AND EVOLUTION
Common fallacies

It is generally assumed that cultural transmission in humans is adaptive because it avoids the costs and errors of individual learning; risks entailed by trial and error are lowered and the probability of discovering an advantageous behaviour is increased (Boyd & Richerson, 1985); by creating culture, humans beings provide themselves with own ecological niche (Hardesty, 1972). Closely similar statements have been expressed with regard to socially acquired patterns in non-human primates. Kummer (1971) enumerates three reasons why traditions should be superior to individual learning: experimenting directly with the environment may be dangerous (e.g., poisonous food plants or predators), some environmental situations are too rare to permit direct experience for every individual (e.g., in case of drought, an elder may hold information about available water sources), not every group member may discover a new pattern (tradition pools individual achievements). In short, dangerous, rare and difficult individual discoveries are favourably perpetuated by tradition, which multiplies the benefits of an experience without the high costs of individual discovery (Kummer, 1971). Nishida (1987) adds that traditions may open an ecological niche not exploited by other animals; for example, cracking hard nuts provides important nutrients not available to others.

Stating that socially acquired patterns may bring specific advantages is sound. But assuming uncritically that animal traditions are a direct outcome of natural selection (e.g., Wilson, 1975) arises from several misunderstandings (see Williams, 1966; Gould & Lewontin, 1979; Lewontin, 1979; Gould, 1989). First of all, in considering non-human primates' achievements as the beginnings of human culture, we are at risk of the retrospect fallacy. Any overemphasis of the subsequent history of a character may lead to consider fitness as granted. The evolutionary process is a blind, tinkering process (Jacob, 1977), and the existence of every character must be accounted for on its own. Also, in speculating about selection, we should keep in mind that the characters at stake are individual learning abilities, not categories such as 'traditions': rather than real objects, the latter are human mental constructs, and we must avoid reifying them. Lastly, in distinguishing between proximate and ultimate levels of causation, it is possible to assert that the evolution of sophisticated learning abilities in non-human primates are the proximate means by which traditions may ultimately appear. This stance neglects the fact that an organism is not a mosaic of characters but an integrated phenotype where characters are liable to produce multiple effects. Before ensuring the propagation of acquired patterns, learning and cognitive abilities primarily evolved as means to attribute meanings to the world, cope with environmental variations, manage in finding food, face adversaries or cooperate with partners (Humphrey, 1976; Milton, 1981; Cheney & Seyfarth, 1990).

Meaningless patterns?

Through their learning abilities, individuals may acquire efficient patterns, but they may also make errors and sometimes perform counterproductive behaviours, this is normal. But at the population level, it is commonly held that patterns are propagated because they are adaptive. Some believe that only adaptive patterns can became fixed through tradition while non-adaptive ones are eliminated (Burton & Bick, 1972; Lumsden & Wilson, 1981). In evolutionary
biology, 'adaptation' supposes that a character has been shaped by natural selection for its current function, but some characters may have an effect without having been selected for; these cannot be said to have a function (Williams, 1966; Gould & Vrba, 1982). When there are no more termites to catch, there is no adaptive sense in a tool-reversing habit. Even adaptationists would acknowledge the non-necessary nature of the grooming-hand-clasp or stone-handling habits. Nevertheless, they would say that such patterns are residuals of the evolutionary process, and that what matters is that most socially acquired patterns are beneficial. Efficiency may be difficult to assess. After all, the grooming-hand-clasp is a practical way for chimpanzees to mutually uncover the underarm area for grooming it; and stone-handling might have filled the activity vacuum induced by provisioning the Japanese macaques (Huffman, 1984). Before ascribing meaning to patterns, we have to scrutinize their proximate causes. In this respect, the existence of dialects provides a case.

A few instances of intergroup variation in vocalizations have been reported in non-human primates (Green, 1975; Maeda & Masataka, 1987; Mitani et al., 1992). Mitani et al. (1992) suggest that it would be advantageous for chimpanzees to be able to discriminate the long-distance calls of their fellow community members from those of others. The question may be approached by considering bird-song dialects. In many oscine birds, sets of individuals share features that differ discretely from vocal characteristics of other sets. Two main functions have been proposed for the occurrence of dialects (Baker & Cunningham, 1985). First, song learned following dispersal permits neighborhood song convergence and allows admittance to the local group; a male copying the song of another male would gain an advantage in obtaining a territory and attracting a mate in the context of a few adjacent holders. According to a second hypothesis, song learned prior to dispersal allows population recognition; females would prefer natal dialect males, which would limit gene flow between adjacent populations and preserve genetic adaptation to local conditions. However, these two hypotheses do not fit the data, one only applies to a highly localized geographic scale, the other only accounts for dialect populations of hundreds of birds, and many species do not conform to the predictions derived from one or the other hypotheses (see Mundinger, 1982; Baker & Cunningham, 1985). A third hypothesis may fully explain the phenomenon, namely the null hypothesis. Song learning would have evolved as a mechanism for transmitting from one generation to the next complex signals representing the species-specific vocal repertoire, thereby permitting mate-selection or species-recognition; patterns of geographic variation would be an epiphenomenon, a secondary effect of the ability to copy song (Andrew, 1962; Slater & Ince, 1979; Mundinger, 1982; Wiens, 1982). Similar reasoning may be applied to non-human primate dialects. There is no need for further evolutionary explanation. In addition, the fact that dialectal drifts are little pronounced in monkeys and apes may be accounted for by lesser vocal learning abilities in comparison to song-birds (see Snowdon, 1990).

There is no reason to assume that social learning involves abilities different from those required to learn in the physical environment (Dennett, 1987; Hauser, 1988; Visalberghi & Fragaszy, 1990a). When individuals gifted with elaborated learning abilities live in proximity, it is unescapable that they may learn something from each other, all the more so if they possess high cognitive capacities and frequently interact2. Traditions may then emerge at the
population level and carry along advantageous as well as non-advantageous patterns. If traditions bring benefits, it is an outcome of chance instead of design (see Williams, 1966).

**Tradition drifts**

Once a self-supporting historical process is launched, random variation resulting from small sampling and copying errors (in acquisition or performance) may induce tradition drifts. This has been assumed independently for song-bird dialects, non-human primate traditions and human cultures (see Burton & Bick, 1972; Cavalli-Sforza & Feldman, 1981; Boyd & Richerson, 1985; Baker & Cunningham, 1985; Lynch et al., 1989; Burton, 1992). Individual improvement of patterns is also liable to alter a tradition; however, non-human primates data do not permit to distinguish between chance and such 'guided variation', as labeled by Boyd and Richerson (1985). All the same, for a drift to occur, there must be a fair degree of fidelity in the transmission of patterns. In Japanese macaques, a number of variants have been described for food-washing and stone-handling; the important role of indirect social transmission in the species probably precluded the canalization of the tradition in one direction.

It must be added that the extent of tradition drifts appears quite limited in the social organizations of monkeys. In vervets, it has been shown that immatures have to learn the contextual meaning of signals (Cheney & Seyfarth, 1990). No shift in meaning of the vocalizations has yet been reported. For instance, the correspondence between three different alarm calls and the categories of predators that they signal was consistent from one group to another in the field; it seemed not to be affected by tradition, even though it was shown to vary in captive settings, free from natural predators (Brown et al., 1992). In spite of variations, the form of social organization is mainly species-specific. As individual traits are in part genetically determined, the variance in the social environment which results from the contributions of every group member is partly heritable (Altman & Altman, 1979). In given ecological conditions, the converging action of similarly built individuals tend to pull social organizations towards equifinal states (Thierry, 1994). Even in chimpanzees, where habits have been described with regard to many subsistence activities and several communication signals, the same fundamental patterns of organization have been reported in all parts of Africa where the species has been observed. Though fluctuations may be expected in some patterns, the lack of communication about internalized social norms impairs the starting of directional drifts, thus preventing any significant shift to occur in the rules regulating social relations.

**Conclusion**

While many socially acquired patterns may contribute to the survival of individuals, there is no sign that their consequences at the population level were designed by natural selection. Consequently, the traditions observed in most non-human primates may be considered as epiphenomena. That contrasts with the human cultural phenomenon, the creation of which is viewed as the human mode of adaptation (Hardesty, 1972). Given the involvement of language in their development, human beings cannot normally exist without culture. In contrast, it seems that non-human primates may be deprived from their traditions without ceasing to behave normally.

With regard to great apes such as chimpanzees, our conclusions remain less sure. On the one hand, the lack of instruction by elders means that each generation of chimpanzees struggles to reach the level of skill of the previous one.
(Tomasello, 1990). While the use of "hammers" to crack open hard nuts has been reported in several regions of West Africa, chimpanzees in East Africa have never been observed to do this although nuts may be looked upon as a key ecological resource, there are even some chimpanzee communities where the use of tools is rare (Tomasello, 1990; McGrew, 1992). On the other hand, once sufficiently stable epigenetical alterations have occurred as a consequence of behaviour, changes in the conditions of adaptation are liable to give rise to novel selective processes, those involved in niche construction in particular (Odling-Smee, 1988). We have no means of deciding whether chimpanzees' accumulations of traditions are long-lasting enough to sustain such evolutionary processes.

Some authors conclude that the emergence of human culture cannot represent an elaboration upon non-human primate-like traditions. The basic argument is that the evolution of sophisticated cognitive abilities for other purposes would have subsequently allowed cultural transmission in early hominids (Sahlins, 1976; Galef, 1992). Current thinking about processes of transmission and retention supports this argument. Social information transfer allows the communication of phenotypic traits from one individual to another. As imitation and teaching ensure better replication than more indirect modes of transmission, natural selection would have favoured reliance on such processes (Boyd & Richerson, 1985; Tomasello et al., 1993a). But random variations and even rational choices may threaten faithful transmission, and psychological processes that promote social conformism should have also occurred; this is as easier if the transmitted patterns are arbitrary and their utility difficult to assess (Boyd & Richerson, 1985; Heyes, 1993). Norms and symbols, favoured by anthropologists as markers of culture, are such patterns.

Such a line of reasoning assumes that some psychological advances should have occurred prior to the onset of the cultural machinery. We may indeed speculate that some intellectual accomplishments were critical to the process (e.g., the semiotic stage [Piaget, 1967] or the mimetic stage [Donald, 1991]). However, we cannot ignore the fact that any progress made by early hominids occurred in a cultural context probably equal or superior to those observed in present-day chimpanzees. Non-adaptations represent a primary source of raw material for future evolutionary change (Gould & Vrba, 1982); the incidental existence of traditions at the population level might have been instrumental in favouring any psychological change. The ability to compare techniques, recognize dialects or use non-iconic communication signals may be subjected to selective pressures; growing awareness of individuals about their own traditions may induce feedback effects on the cultural phenomenon itself, like mirrors reflecting each other to infinity. That elements of culture may be read by its own actors can multiply the potential outputs permitted by the accumulation of a number of traditions, and turns what at first emerged as an epiphenomenon into a genuine phenomenon.

Of course, in the absence of fossil evidence, there is little hope of going further in such speculation. However, apes having learned to use lexical symbols seem to achieve more than their laboratory counterparts (Tomasello et al., 1993b). Whether such subjects may learn patterns directly from each other is presently under investigation (Fouts et al., 1989; Toth et al., 1993), this might provide insights about apes' ability or inability to communicate about common norms. Admittedly, the rearing environment of these subjects is
monitored by human beings. Such artificial conditions may be viewed as the cultural equivalent of in vitro fecundation in embryology. Although we cannot expect apes to go beyond the stage of a few cell divisions, any of their achievements or failures would be valuable.

FOOTNOTES

1 From an evolutionary point of view, requiring that traditions be transmitted through verbal language to qualify as culture is a creationist stance, no more no less (Hallowell, 1961; Holloway, 1969). Provisionally seeing culture as an outcome of the accumulation of traditions - without specification of the number of traditions required to qualify or any assumption about qualitative leaps - could help understanding its emergence.

2 That some of the highest human intellectual achievements (e.g., art and mathematics) may be secondary outputs of mental abilities selected for other purposes is a concern as old as the theory of natural selection; a controversy arose between Wallace and Darwin about the subject (Gould & Vrba, 1982). The emergence of elaborate performances (e.g., use of tools) in non-human primates has been similarly suggested as stemming from a general ability for problem-solving, only expressed when favourable environmental conditions are provided (Beck, 1980; Kummer, 1992; McGrew, 1992).

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