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The nature of culture

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> 'Townley . . . had said one word only, and that one of the shortest in the language, but Ernest was in a fit state for innoculation, and the minute particle of virus set about working immediately'. (Samuel Butler, 'The Way of All Flesh', 1903).

CULTURE AND BIOEVOLUTION

Niko Tinbergen laid great stress on the essential importance of cultural evolution for the understanding of human behaviour although he never, of course, made it a central subject of his research interests. In a short cautionary note about the future of humanity he wrote for example that 'our unique position in the modern world is due to the consequences of our cultural evolution, which . . . has . . . progressively . . . superimposed (itself) on our still ongoing genetic evolution' and that 'we transfer . . . . , from one generation to the next, not only our genetic heritage but also (our) accumulated non-genetically acquired . . . experience' (Tinbergen, 1977, see also Tinbergen, 1976). Niko's insights into the details of the processes of cultural evolution went much further than his writings reflect, however. A casual but memorable conversation between him and Konrad Lorenz in Stuttgart, Germany in 1959, at which I happened to be present, revealed that clearly. The role of song behaviour as a species-isolating mechanism in some sympatric birds had somehow cropped up. They were considering the selective forces that might have shaped the divergence of song patterns in such situations when Niko raised the important question: Selection of what? Surely not genes since the song of these birds was likely to be learned, not innate. Konrad suggested that song traditions were being selected but Niko considered that it might be better to think of song memory traces being selected. Would memory evolution always cooperate with gene evolution? In the 20 minutes or so that followed, without ever mentioning the word culture, if I remember correctly, they had worked out between them the essentials of a modern theory of cultural evolution. There were however several later dialogues at the Ravenglass field camp where Niko actually pursued similar arguments explicitly in relation to human culture. In recent years, I have tried again and again to recapture some of the threads of those discussions. Needless to say, besides imperfect recollections, this essay also takes into account some of the theoretical ideas and empirical findings (these latter are still scarce) of many scholars that since Tinbergen's times have made cultural evolution a more definite subject of their interest (notably Campbell, 1969; Bajema, 1972; Dawkins, 1976; Cavalli-Sforza and Feldman, 1981; Lumsden and Wilson, 1981; Boyd and Richerson, 1985).

It is time to heed the maestro's ever-recurring admonitions about defining one's terms. Indeed, the word culture is commonly used with several meanings. For the purposes of this essay it is necessary to circumscribe its definition to behavioural culture. Culture will thus mean here the ensemble of traditional behaviours that is characteristic of a population. Traditional behaviours are those that individuals take over from others through some form of social learning. Sometimes media (for example newspapers, books, television) intervene in this process of transmission. Behaviour patterns that organisms acquire via genetic inheritance (for example hatching, crowing, smiling, crying) or by individual learning (key-pecking, soft landing, nose-picking, masturbating) are excluded by this definition. This trichotomous classification of behaviour is avowedly simplistic but here it is conceptually useful. Some illustrative examples of cultural behaviour could be birds nesting in a traditional area, singing a certain dialect and mobbing particular predators, or humans wearing a particular dress, speaking a certain language, reading a certain bestseller, and worshipping a particular god. Material objects by the above definition are not really part of culture, but they are often convenient referents for the cultural behaviour that produced them or is elicited by them (the book or the clothing in the above examples). The definition however appears to be able to accommodate without much strain most other, less tangible 'contents' of culture commonly listed in anthropology textbooks (Harris, 1987): knowledge, beliefs, rituals, institutions, customs, fashions, symbols, etc.

Culture is clearly not a universal attribute of all organisms. In fact, only two or three decades ago it was thought that only humans were endowed with culture. This opinion is no longer held. Cultures, or at least protocultures, have now been documented in many animals (Bonner, 1980), but it is also true that the phenomenon only occurs in a proportion of the more advanced species. The permissive trait, as suggested by the above definition of culture, is that they must be capable of social learning, a competence that comes about through biological evolution. Even when this basic capability is already present, culture is the product of a lengthy historical development. The cultural behaviours proper for knights, Scots, or 'yuppies' are clearly not god-given but have developed gradually over a long time. Their common ancestors 50 000 years ago, the Cromagnons, certainly did not show the cultural traits we now associate with these groups. The cultural evolution process has long been recognized as having at least superficial similarities with that which drives biological evolution. A more thorough anlaysis of the potential analogy has however begun only recently. The intention of this essay is essentially to explore how far the similarities between biological and cultural evolution actually go.

Consideration of how the capacity for culture might have emerged affords the opportunity to briefly recapitulate the salient characteristics of biological evolution. It is a game that genes are simply fated to play as a consequence of their particular molecular properties (Dawkins, 1976). The essential property is that they are capable of self-replication that is not always perfect. Since the gene mutants that arise in this way interact with and compete for an environmental niche in which to survive and replicate, it follows that they will frequently differ in replication potential, that is in fitness. The consequence is gene selection. In different niches different mutations may be the fittest, and this eventually results in speciation. Genes capable of instructing the synthesis of buffering devices, a membrane or even a soma, against environmental variability are likely to have fitness advantages. Gene mutants that could instruct devices that added motility and also sensitivity, behaviour in short, would, given the right circumstances, be even fitter. Which responses followed which stimuli was initially determined exclusively by genetic instruction (innate behaviour). In environments that were more variable over time and space, selection pressure arose for mutations that could instruct neural structures capable of learning. The capacity, for example, to attach existing responses to arbitrary stimuli that happen to be predictive of fitness-influencing events (classical conditioning) or to modify behaviour in such a way as to influence the likelihood of such events (instrumental learning) as a consequence of individual experience obviously magnifies the adaptability of organisms (Staddon, 1983). Mutants extending memory capacities so that a representation of the environment and the self was feasible signified a further bonus. An internal off-line behaviour simulation would become possible, which could even include creative innovation (insight learning). Generally, learning is a device instructed by genes that allows the individual to acquire knowledge about the world and itself over and above that implicitly contained in its genetic code. It is naturally also associated with costs, such as more complex brains and some behavioural instability.

SOCIAL LEARNING AND CULTURE

When an organism acquires behaviour through individual learning, the process is often lengthy, risky and laborious. Genes giving rise to structures that enabled animals to take over the already extant experience of conspecifics would often yield a fitness advantage. The essential characteristic of social learning (imitation, observation, instruction learning) is indeed that individuals in one way or another take over knowledge from others. The precise mechanisms supporting this transmission of information vary considerably (Zentall and Galef, 1988).

Pigeons, as do many other species, tend to breed at sites close to those where they themselves were bred. Successive generations keep to traditional breeding grounds and this is not for want of mobility, as they may migrate far in between breeding. Through an imprinting-like process, juveniles store information about the location where they grow up. This enables them to navigate back to the home area later (Schmidt-Koenig, 1965). It is not only the geographical location to which the young birds imprint but also to the particular habitat in which they were raised, to cliffs or buildings for example. As adults they will then show a preference for the same type of surroundings in which they grew up (Delius, unpublished observations; Klopfer and Hailman, 1965). This does not come about by the youngsters directly imitating the parents but rather by the parents bringing their youngsters up where they can only learn about one thing. There is often a debate about whether this represents true social learning, but it certainly serves to maintain familial traditions.

Seeing several flock members fly to a particular site usually induces other pigeons to follow. Such socially facilitated behaviour need not involve any learning, often being based on innate behaviour (Tinbergen, 1953). But at the same time follower pigeons can hardly fail to learn about the association between, for example, granaries and grain, something that the leading pigeons already knew (Murton *et al.*, 1972). In some altricial species the parents lead their young to sites where the food that they themselves prefer predominates and each of the young learns on its own to find and deal efficiently with these items (Subowski, 1989). Thus again traditions may simply be maintained by parents biasing the learning opportunities of their offspring. Oystercatchers prey on mussels using one of two techniques, stabbing or hammering. Youngsters appear to learn the particular technique that the parents used through observation and participation (Norton Griffiths, 1967; but see Meire and Ervynick, 1986). In a similar context female cats with kittens may even display behaviour analogous to teaching by repeatedly bringing home and releasing live prey just to catch it again. Kittens gradually join the repeated chases and eventually learn to to do the final killing themselves (Chesler, 1969; Ewer, 1969).

Contrived non-natural modes of food gathering have been experimentally arranged to arise through imitative instrumental learning in several species. Having seen another pigeon obtain food from an electromagnetic dispenser after performing the somewhat arbitrary behaviour of pecking an illuminated disc considerably facilitates the subsequent acquisition of that same skill by observer pigeons. A number of experiments show that the information the observer acquires can be multifarious: knowledge of the fact that food is to be found in the particular environment; that it is available at a particular place within that environment; that performance of certain acts make that food more available, and so on. It is rare, however, for an observer to produce the correct food-yielding behaviour on the first attempt. Rather, the observer is only quicker at learning what has to be done. An opportunity to perform the target behaviour while observing is helpful but learning is also facilitated when key-pecking is only possible after a delay (Alderks, 1986; Biederman *et al.*, 1986; Hogan, 1986).

Lefebvre (1986) set up an artificial feeding tradition among a flock of urban pigeons. They captured a few flock members and trained them to feed by piercing a tight paper sheet covering their food troughs. When they were released and were back with their flock, the latter was offered paper-covered troughs. The trained birds immediately began to pierce and feed. Soon no fewer than two dozen other birds had acquired the paper-piercing technique. In a control flock that did not have pretrained demonstrators it took almost three times as long before a bird 'invented' paper piercing by himself, but once that happened, the cultural trait spread just as fast among that flock. Novel feeding cultures occasionally arise naturally among free-ranging animals. A Japanese female macaque named Imo discovered in 1953 that sweet potatoes which she had accidently dropped in a brook tasted better than unwashed, earthy ones and began to actively wash them before consumption. By 1958 all the younger monkeys in her band had imitated her: a potato-washing culture had arisen. Other Japanese monkey groups have never developed this tradition in spite of similar opportunities, but some have developed other local traditions (Nishida, 1987).

Social learning can also be mediated by classic conditioning. Wild-caught blackbirds exhibit mobbing behaviour when they see an owl. Curio *et al.* (1978) arranged it that a predator-naive, hand-raised blackbird saw a novel inoffensive plastic bottle, while an experienced bird actually mobbed an owl. Mobbing acts as an unconditioned stimulus: the naive blackbird began to mob too (unconditioned response, *see* social facilitation above). The bottle functioned as a conditioned stimulus as it always preceded and accompanied the owl-mobbing by the model. After a few pairings, conditioned mobbing could be demonstrated. In the absence of any model the observer blackbird now mobbed whenever the bottle was presented. The acquired bottle-mobbing habit could in turn serve as model for new observers. Thus a novel mobbing tradition or culture had been set up among blackbirds.

The cultural nature of songbird song is so well known that only the most essential characteristics and the most common variants of the underlying process will be mentioned. Song varieties that young birds hear from their father or his neighbours are memorized during a critical period. This imprinting usually takes place before the youngsters can themselves sing. Later the sub-adults learn to match the auditory template with their own song. Barring occasional errors, this leads to a fairly accurate replication of the songs originally heard. Normally this mode of song acquisition leads to the emergence of song dialects characteristic of local populations within a given species (Barker and Cunningham, 1985; Catchpole, 1986). Some species continue to be able to acquire songs all their lives and some may even imitate the sound of other species. There are almost 4000 species of songbirds and it is resonably certain that, except for a few, all sing according to traditions. This suggests that their common ancestor, the original songbird living about 40 million years ago, already had a song culture, long before our primate ancestors had any culture.

Most other taxonomic bird groups have innate songs but parrots are also well known for learning vocalizations by imitation. Since parrots are only distantly related to songbirds, but closely related to birds that have innate vocalizations, their cultures must have arisen, independently (Kroodsma and Miller, 1982).

In the human species, social learning is almost obligatory and often involves yet another, more refined variant. Having previously seen somebody light a camp fire is certainly of assistance if one had to do the same thing for the first time. The demonstrator performs on the basis of

information stored in his or her memory. The behaviour thus produced is seen by the observer, who in turn stores these perceptions in memory, only to convert them again into behaviour at a later date. In such cases, the model has to perform for the observer to be able to memorize the actions. Language, however, enables an energetically more economical form of memory transfer. Simply being told how to light a camp fire is usually sufficient for a reasonable emulation. In most situations where human individuals adopt behavioural traits from others, language plays an important supportive, if not sole mediating role.

It has, indeed, been argued that language might have arisen evolutionarily as an extension of social learning, as a vehicle for instruction, whereby recipes for behaviour could be transmitted in an abstract symbolic way, in a code that might be related to that of memory (Catania, 1985; Delius, 1990). For a *Homo habilis* hunter a million years ago it must have been awkward to demonstrate to novices how to stalk antelopes; it would have been much easier to tell them how it should be done. Linguistic messages function like an almost effortless short circuit between the memories of individuals. Accordingly, it accounts for much of the sophistication of human culture *vis à vis* animal culture. Indeed, linguistic communication, spoken or written, is sometimes the only medium by which many human traditions can be transmitted. Writing greatly amplifies the multiplicative power of language. Most importantly, it disposes of the necessity for the model and the observer to have to coincide in time and space for transmission to be possible. In a way, it makes social learning possible in an asocial setting. Modern communication media extend this even further.

MNEMOBIOLOGY AND MEMES

Generally, learning, whether individual or social, can be conceived as a process whereby experiental information is stored into memory. Cultural traits, defined earlier as behavioural items acquired through social learning, are therefore also represented as particular contents in the memory of the individual bearers of culture.

Information storage is necessarily dependent on physicochemical state changes in memory-supporting structures. According to neurobiological findings, learning (social or otherwise) leads first to volatile changes, lasting only tens of seconds or minutes. Only when learning is sufficiently incisive in one way or another, will the relevant memory traces be consolidated into a more durable format lasting months or years. Culture as a rather persistent phenomenon is obviously heavily dependent on these long-term memories.

Long-term memory, according to current evidence, is laid down as structural brain modifications. Memory deposition chiefly involves changes at the level of the interneuronal transmission sites, the synapses (Morris *et al.*, 1988; Dudai, 1989). Due to the particular patterns of coactivation of pre- and postsynaptic neurons arising during learning, some of these synapses pass from a state of relative inefficiency to a state of relative efficiency, from an inactivated to an activated condition, rather like bits in computer memory that are set from a 0 off-state to a 1 on-state. In some instances, learning even seems to lead to the budding of additional synapses and to the growth of neuronal ramifications supporting them (Horn, 1986). However, much as computer memory also stores information when bits pass from a 1 to a 0 state, there seems to be instances where learning is associated with synapses passing from an activated to an inactivated state or even disappearing, sometimes together with their supportive structures (Wallhäusser and Scheich, 1987). That specifically social learning is also associated with such neural modifications is best documented for songbird vocalizations (Devoogd *et al.*, 1985).

A pigeon brain contains perhaps 10^{10}, the human brain maybe 10^{15}, synapses that are variable in the above sense. Such plastic synapses have to be thought of as the critical components of neural networks functioning as associative arrays. It has been shown mathematically and confirmed empirically that neural networks incorporating large numbers of modifiable junctions are able to store vast quantities of information in a very organized manner. An important property of associative network storage is that the information is content- and not address-retrievable (as in computers), and furthermore that it is stored in a highly distributed but still partially overlapping way (Palm, 1982). Special versions of these networks show interesting additional properties, such as being capable of self organization, stimulus pattern categorization, pattern completion or complex stimulus-response conversions (Kohonen, 1984; Rummelhardt and McClelland, 1986).

Any cultural trait taken over by a given individual from another individual must accordingly be thought of as the transfer of a particular pattern of activated/inactivated synapses from the associative networks of one brain to another. Different traits must be thought of as being coded by topologically different synaptic patterns, that is, a given cultural trait borne by an individual is encoded informationally as a particular configuration of modified synapses in his or her brain (Figure 6.1). Naturally the synaptic constellation that a trait has in one brain will not be geometrically arranged in exactly the same way as the pattern that the same trait has in another brain: the brains of different individuals are likely to be too different for that. Functionally however, the two patterns could still be equivalent when effectively identical traits were represented in memory. In any case, following Dawkins (1976), synaptic patterns that code cultural traits will be called memes, by analogy with the molecular patterns that code biological traits and which are called genes.

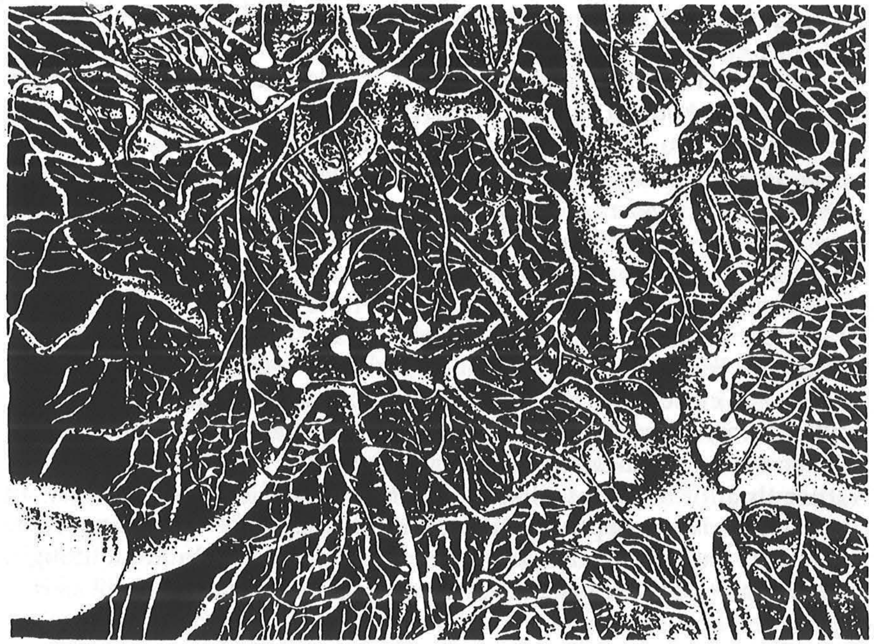

Figure 6.1 A meme as a constellation of activated neuronal synapses lodged somewhere in the brain of an individual

The process of cultural heritage can be seen as passing on these synaptic constellations or memes from one individual to another, or, and that is important, to several other individuals. Obviously it is not a bodily replication of material structures, as is usual with genes, but social learning nonetheless brings about a multiplicative transfer of equivalent structures. Even among genes, however, replication can sometimes be less than direct. Retrovirus RNA genes for example depend heavily on mediation by host cellular machinery for reproduction (Davies *et* *al.*, 1980). Memes are capable of instructing, not protein synthesis as genes do, but behaviour. However, genes can do that too indirectly through protein synthesis. On the other hand meme replication, by involving neurostructural modifications, is invariably associated with the induction of protein synthesis.

Genes can be conceived as specific molecules that code information according to a well understood scheme. Until the 1950s however, genes were largely hypothetical constructs that could not be linked to anything more specific than approximate sites on chromosomes. Memetics is not yet as advanced as genetics. Memes are still largely abstract inferential entities, though we know that they are information coded in neural structures. It is possible and even likely that the memetic code is less universal and more complex than the genetic one. However, the way in which genes code innate behaviour, say the suckling reflex or the crying response of babies, is anything but simple and unitary. Some authors (Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1985) nevertheless prefer to speak of cultural traits or cultural variants rather than of memes (or culturgenes; Lumsden and Wilson, 1981). That seems linguistically cumbersome. Memes stress the transmittance of coded information rather than of behaviour itself, which is a physical impossibility. In genetics it is conceptually important to separate the phenotypic characters and the genes that determine it. It must be admitted, though, that because of the unsatisfactory state of memetics we are still as rule forced to allude to memes by way of trait descriptions.

The important point is that memes have the same essential properties that make genes the key protagonists of an evolutionary process (Dawkins, 1976). They are obviously capable of replication, even if in a roundabout way. Replication is reasonably faithful but not perfect, that is, memes mutate. New song variants arise among songbirds, new words are coined, new rituals are derived and new fads emerge among humans. Not all meme variants are equally effective in reproducing themselves. Some memes spread rapidly in a population, others become extinct. 'I know something, but I won't tell anybody' is a nonstarter as memes go, but 'I will tell you a sure way to save tax' stands for a meme likely to multiply (Ball, 1984). Different memes have different cultural fitnesses, that is, memes vary in their potential to produce memetic offspring.

GENE/MEME SYMBIOSES

There are two characteristics that seem to make the memes of an individual plainly different from his genes. One is that his memes are lodged in the brain that was instructed by his genes, i.e. the former depend on the latter. The other is that the individual's genes come from his parents, but his memes can and often do originate from other conspecifics besides his parents (friends and teachers for example). A host-guest relationship is not at all exceptional among genes themselves, the genes of many symbiotic organisms residing in organisms instructed by the genes of other organisms. Any average human, for example, is normally host to billions of symbiotic organisms belonging to perhaps a thousand different species (Hohorst, 1981). His phenotype is not determined by his human genes but also by the genes of all the symbionts he happens to be infected with. The symbiont species an individual carries usually have a very varied provenance, with only a few being likely to have come from his parents.

Three kinds of organismic symbioses are distinguished: mutualism, where both partner species benefit from the association in terms of Darwinian fitness (gastric flora of ruminants, for example); commensalism, where the fitness of the guest is furthered by the association with little if any fitness cost or gain to the host (intestinal flora of man, for example); and parasitism, where the symbiont profits on fitness at the expense of the fitness of the host (tapeworms in humans, for example; Smith and Douglas, 1987). A striking instance of a symbiosis of the mutualistic kind are the mitochondria, extranuclear cytoplasmatic organelles of eukaryotic organisms. Mitochondria have their own DNA, which replicates independently of the host-cell DNA. The ancestors of mitochondria some 2 billion years ago were almost certainly parasites in prekaryotic organisms, much as viruses are parasites in present day cells (Margulis, 1981). Nowadays, mitochondria are highly integrated into the higher organisms and are not capable of independent existence. On the other hand, essential processes of host cell respiration are controlled by mitochondria and accordingly they are prominent in metabollically very active neurons. In fact, even the slightest behaviour, the most fleeting thought produced by a eukaryotic animal absolutely presupposes the activity of these obligatory symbionts. Infection is always through the egg cytoplasm; sperm do not carry mitochondria. Mitochondrial DNA undergoes an evolution of its own. Mutant mitochondria emerge occasionally, may replicate and can be favoured or disfavoured by natural selection. The selective agency is the intracellular environment, largely but not exclusively controlled by the host cells' nuclear genes (Cann *et al.*, 1987).

Many parasitic species can influence the behaviour of their hosts in very specific ways (Moore, 1984). The rabies virus, for example, massively invades the host's salivary glands and causes them to secrete profuse quantities of infected saliva, but it also invades the nervous system and influences its functioning so as to inhibit swallowing and increase aggressiveness. The sick animal therefore bites with a large reservoir of infested saliva and is thus very likely to infect its victim, which as a rule is no relation and might even belong to another species (Christie, 1981). But it is apparent that the rabies virus furthers its fitness at the cost of the host's fitness, partly by manipulating the latter's behaviour.

Parasites inevitably generate selection pressure for host mutants that are somehow able to prevent or inhibit infection and/or multiplication of the parasites. Immunological reactions that counteract infections, but also innate behaviour that minimizes chances of infection (pelage grooming, clear water drinking, avoidance of sick conspecifics, for example) promote host fitness. Conversely parasites are under natural selection to increase their ability to infect and replicate. Since they often reproduce at high rates within the host organism, evolutionary adaptation to the immune reactions of the host (or to drug treatment) can come about by selection of resistant mutants within a single host individual. This often mimics Lamarckian evolution because the 'offspring' infection passed onto the next host expresses what appears to be a trait acquired by the 'parent' infect (antibiotic resistance, for instance; Futuyma, 1986).

There is obviously also selective pressure upon host organisms to develop mechanisms for resisting infection or turning parasite organisms into mutualists, or at least into commensals, if at all possible. A too-virulent parasite can potentially kill its host before there has been transmission to further hosts, and thus kill itself and its kin. Restrained virulence may be a better fitness strategy. Parasites may therefore also be under some selection pressure to become mutualists or at least commensals (Anderson and May, 1982) but it competes with opposing pressures that tend to make parasites more infectious. An improved immunological response by a host will generate a selective pressure favouring parasite mutants that can overcome it. This coevolutionary arms-race game is biased by the fact that the usually smaller symbionts have, in general, a much faster generational turnover than the larger hosts. Consequently the relative rates of adaptation and counteradaptation are in favour of parasites rather than hosts.

In so far as memes are material structures (arrays of modified synapses) that reside in host organisms and can multiply independently of them, they can be viewed as analogous to the genes of symbionts. In particular, memes are similar to the genes of those symbionts that invade the brain of their host and influence its functioning in ways that affect the host's behaviour. Memes are replicating coded information packages, which infect some higher animals and manipulate their behaviour. Furthermore their replication, analogously to that of symbiont genes, is not tied to the gene reproduction of host organisms.

When dealing with organismic symbioses, one distinguishes between the genetic fitness of hosts and the genetic fitness of guests even though they are both intimately intertwined. Similarly it is essential to differentiate between the genetic (biological) fitness of bearers of cultural traits and the memetic (cultural) fitness of the cultural traits themselves (Ball, 1984). As is the case in symbionts, specific memes or memomes (meme complexes, in analogy to genomes) could in principle survive and reproduce to the advantage, indifference or detriment of the genetic fitness of their hosts, so that cultural traits could be mutualists, commensals or parasites.

Initially, at the phylogenetically protocultural stage, memes must necessarily have been mutualists simply because the capacity for culture, the genetically determined ability for social learning, can only have spread within a population of organisms if individuals having that competence were biologically fitter than those that did not have it. The genetic fitness advantage of an individual was determined by the actual cultural traits made possible by that capacity, in other words the first few memes at least must have furthered the hosts genes. Social learning among some early hominids, for example, can be imagined to have promoted efficient modes of hunting, efficient ways of toolmaking and efficient styles of communication, giving social learners an edge over less educable competitors. Memes at this early stage can be considered as devices by which genes amplified their fitness (Lumsden and Wilson, 1981). They were then close to the slave-like symbionts of genes, much as mitochondria are today. Slaves though, have a well-known bent towards independence. The question is whether genes can manage to keep memes under control past the initial protocultural stage.

Symbionts, as explained earlier, are normally subject to the evolutionary process within their hosts and not just when they are transmitted between hosts. The same can be said of memes. Variability of covert and overt behaviour due to many causes, but not least to neural system noise, continuously generates new potential memes, or meme mutants, within an individual. While still resident in that same individual these mutants are selected by the same innate processes that make learning generally an adaptive process (Staddon, 1983; Gould and Marler, 1987). During overt learning, any otherwise neutral events that circumstantially precede and predict innately appetitive or aversive events, come to be sought or avoided through classic conditioning. Similarly, any arbitrary behavioural response which happens for some reason to generate or produce such reinforcements is correspondingly enhanced or suppressed through instrumental conditioning. During covert learning (insight learning), any event or response identified by behavioural simulation within the memory model of reality as being likely to lead to reward or punishment is retained in, or rejected from, the mind. Eventually, such imagined behaviour is tested when put into practice. Conversely, any responses or strategies that are no longer effective in yielding appetitive or avoiding aversive reinforcement extinguish and are finally forgotten.

In short, any individual learning (including imagining events, ideating, inventing and creating) is a process based on variation and selection, that is analogous to biological evolution (Pringle, 1951; Changeux *et al.*, 1984; Staddon, 1983). Emergent meme mutants in that context can be considered as having replicated well within a host organism, in the sense that the corresponding memory traces have become better consolidated through redundant storage. Unsuccessful meme mutants in the same context are those that cannot establish themselves in the memory of even one host. Incipient meme variants, like symbiotic gene mutants, are thus selected within their hosts, and not only as they spread to new hosts. Effectively every potential meme undergoes a kind of genetically instituted quality control before it has a chance to be passed to other hosts. The commonly held view that cultural evolution is Lamarckian (Medawar, 1976), that it involves the transmission of acquired traits, ignores that fact that the acquisition of those traits is itself the result of a Darwinian intrahost process.

The variation and selection principle however also operates as memes are transmitted from individual to individual by social learning. Imperfect transmission is clearly a frequent source of meme mutation. Potential hosts on the other hand are not completely passive regarding the memes on offer. Host bioevolution can be expected to have ensured that recipient individuals are choosy as to which meme variants they pick up. Young songbirds as a rule only imprint on songs similar to those typical of their species. Obviously an innate mechanism precludes the acceptance of songs that are too aberrant (Catchpole, 1986). A frequen assessment criterion among human seems to be how many carriers of a given meme offer themselves as models. If many conspecifics exhibit a given cultural trait the likelihood that the meme is biologically adaptive is high. If a meme was drastically unadaptive it would literally kill off its hosts, so reducing their number. Another sign of biological meme quality are obvious signs of fitness exhibited by the bearer of a given trait. If an individual is visibly successful, being, for example the strong alpha male of a group of primates, having access to choice food and many females, then the memes he carries are likely to be fitness-promoting and worth acquiring (Boyd and Richerson, 1985).

Even when taken over from other hosts, memes will still have to be consolidated and maintained in the memory of the recipient. Much the same selection mechanisms that operated on the memes generated within an individual, as discussed earlier, will also apply in this situation. There are parallels in symbiont biology. The gene-instructed immune system is an impressively sophisticated mechanism designed to select symbiont variants in the interest of host fitness. It is effective in censoring symbiont varieties, independently of whether they arise through mutations within an individual or whether they enter that individual by infection.

Since genes create the environment on which memes thrive, they should in principle be able to select memes such that only those contributing to their biological fitness can survive and proliferate. Culture at this stage of the game is only one more strategy 'invented' by some genomes to succeed in the harshly competitive game of phylogeny.

PARASITIC MEMES

How discerning can gene-instructed brains be about the memes they are prepared to harbour? The corresponding filter mechanism for symbionts, the immune system of vertebrates, definitely falls short of being perfect. Commensal and even parasitic organisms often get past its scrutiny and manage to infect some, or even many, individuals. Could at least the occasional commensal meme arise and spread in a similar way? Even though penalized by the need for a larger brain, an increased ability for social learning, i.e. an augmented capacity for memes, has obviously conferred a biological advantage in some higher animal species. As long as most of the larger number of memes thus made possible were advantageous to the host, gene selection for indiscriminate reduction of general imitation learning capacities would be weak. Selection for gene mutants that instruct mechanisms capable of controlling more specifically which memes to accept and which to reject would arise, however. The preceding section sketched some mechanisms that could perform this function. But, discrimination between similar meme alleles, some of which promote the genetic fitness of their hosts and others that do not, can demand very clever decision mechanisms. Their instruction is likely to require a slow-to-evolve cooperation of many genes.

If memes were solely cooperative with genes, one would expect the transmission of the former to be closely coupled with the transmission of the latter. According to the genetic selfish altruism principle (Hamilton, 1964), the transmission of mutualist memes should occur mainly between genetically related individuals and less between unrelated individuals. Among primitive cultures most biologically beneficial memes are indeed transmitted from parents to children, and only a few such memes are passed on between non-kin (Hewlett and Cavalli-Sforza, 1986). Unrelated individuals on the other hand are likely to be genetic competitors and should accordingly be suspected of attempting to pass harmful memes to each other. That may be why the search for a solicitor, a stockbroker or a physician among one's relatives is commonplace when one needs critical advice. Still, the fact is that even in protocultures such as those of songbirds, memes are being passed among genetically unrelated individuals.

Mutant memes not contributing to the genetic fitness of their hosts can proliferate if their cultural fitness is high, that is if they are 'catchy', if they can overcome the above-mentioned filters and do not appreciably impair their host's biological fitness. A few biologically useless but inoffensive cultural traits embedded among many cultural traits promoting gene fitness will not generate a strong genetic selective pressure towards mechanisms ensuring their removal. Commensal memes seem an almost inevitable development in any advanced culture. Even in the case of bird culture there are considerable doubts whether all song variants exhibited by a given species are associated with a definite advantage in biological fitness (Barker and Cunningham, 1985).

In human culture biologically innocuous fads or crazes of one kind or another are certainly legion. Pointed rather than round collar tips, two- rather than three-button jackets seem unlikely to make any difference to the survival and the reproduction of wearer, even though generally dressing to keep warm certainly does. Interestingly such commensal memes often occur linked to other memes whose function it is to attach purported biological significance to these. Pointed collars and three-button jackets, for example, were said to be indicative of virility when they were fashionable. On a more global scale, music, literature, and the arts as a whole involve large and complex meme ensembles that are probably neither beneficial nor harmful to the genes of most of their carriers. They can be seen as commensals that have colonized a special mental niche, namely the brain structures that more normally control curiosity and exploration, behaviours that contribute much to genome fitness.

Memes, due to the fact that they can manipulate the behaviour of their hosts, are predestined to increase their memetic fitness at a cost of some host biological fitness. They have it in their hands, as it were, to put their hosts' behaviour to work on their transmission rather than that of their hosts' genes, not unlike the rabies virus. Meme mutations analogous to parasites, that have high cultural fitness at the expense of host vigour, seem nearly inevitable. It is easy to see, for example, how memes inducing drug-taking get past gene-instructed censoring. Addictive drugs happen to activate the reward-signalling mechanism that is so important for learning, even though they are not in fact fitness-promoting, as are the stimuli that normally drive these reward circuits. In much the same way as saccharin fools the alimentary system, so does morphine fool the reinforcement system (Falk and Feingold, 1987).

Innate evaluation mechanisms in humans seem undiscerning about the optimal measure of resource seeking and holding efforts. Attempts to get the best out of the environment are certainly biologically advantageous to an individual, but at some point the returns cease to justify the investment. It is even suspected, for example, that birds occasionally miss mating opportunities on account of exaggerated territorial aggression. Among humans, greed often inhibits fertility. Many a successful parasitic meme profits from the quest for capital riches rather than for genetic fitness. Much of the commercial culture that pervades the civilized world is a certain consequence of this.

Celibacy is an obvious parasite meme that causes a reduction of host reproduction. It is part of a meme complex, a memome that manipulates the brains of hosts so that it reduced their sexual activity but increases instead their proselytizing behaviour, much as the rabies virus inhibits the reproductive behaviour of its host in favour of infective behaviour. Incidentally, certain organismic parasites go one step further and actually castrate their hosts as a means to increase their own fitness (Baudoin, 1975). Among Catholics the celibacy meme carried by one set of hosts is compensated by a linked meme expressing itself in the demand that the remainder of the memome carriers should commit themselves to relentless reproduction. On the other hand, competing memes that instruct the use of contraceptives have spread among Western cultures in recent years, to the extent that relevant populations are numerically decreasing. Contraceptives of course sever the innate link between reproduction and pleasure that normally ensures fertility.

The host's genome should in principle counteradapt against parasitic memes, but the faster evolutionary pace of memes versus genes makes that difficult. Moreover, selection for gene mutants against infection by specific memes can only become effective as these memes spread and are already part of the population's cultural heritage. As an analogy, a partial resistance against myxomatosis only began to emerge as a genetic trait among Australian rabbits after the disease had taken the character of a pandemic and the rabbits were close to extinction (Fenner and Ratcliffe, 1965). Still, gene mutations that somehow ensure brains immune to invasion by parasite memes are at an advantage against those that do not. However, meme mutations bypassing that resistance are culturally selected for, and so there is again a coevolutionary arms-race: hosts evolve improved censoring, memes evolve enhanced propagation.

This all suggests that in an advanced culture parasitic memes should be able to proliferate. Genes are unlikely to be able to devise innate defences against each and every one of the myriads of biologically harmful meme mutants that arise in as variegated a culture as the human one. One has even to consider the possibility that parasitic memes, such as those responsible for environmental pollution, could eradicate their human hosts, even before the genes of AIDS manage to do so.

CULTURAL EVOLUTION

Cultural evolution is the inevitable spin-off from the imperfect replicative properties of memes. Memes reproduce and mutate as they establish themselves in a given brain, and as they transmit themselves to other brains. The survival and the reproductive efficiency of different memes is not identical as they compete for and interact with their environmental niche. Some memes spread explosively, others are only mildly successful, while many become extinct. Different memes have differing cultural fitnesses, much as different genes have differing biological fitnesses. In short, the memetic information lodged in the collective memory of a given cultural ensemble is subject to variation and selection. Memes have to be viewed as independently evolving entities whose core habitat happens to be the brains of some higher animals and whose phenotypoic expression is the cultural behaviour of these same animals. In their essentials they are not too different from, for example, influenza viruses that inhabit the naso-oral cavities of vertebrates and express themselves in the sneezing and coughing behaviour of their hosts (Yamashita *et al.*, 1988).

The multitude of species and subspecies populating the earth is doubtlessly the most striking product of genetic evolution (Minkhoff, 1983; Futuyama, 1986). Speciation consists of the emergence of assemblies of mutually adjusted genes (genomes) adapted to survive and reproduce in different ecological niches. Subcultures and cultures can be similarly understood as distinct coadapted assemblies of memes, as populations of memomes, which thrive in different socioecological niches. An at least temporary isolation between pools of genes facilitates biological speciation. Restriction of meme flow for whatever reason, but often due to geographical separation between host populations, is an important factor in cultural speciation. Media and mobility are the antithesis of cultural speciation, as they facilitate the transport of memes between previously isolated cultures. The almost universal spreading of the Coca-Cola subculture in the late 1940s, and the MacDonald's subculture in the early 1980s, are witness to this. On the other hand, the tendency for like to mate with like, that is assortive mating according to characteristics such as height, eye colour, personality, etc., helps to maintain biological distinctiveness. The tendency for individuals of like culture to stick together, illustrated by both the isolation of immigrant communities and the insulation of social classes, in turn aids the preservation of cultural specificities.

When only a few individuals are the founders of a large population then the latter's genetic composition reflects its restricted ancestry. The analogue of this founder effect that favours the emergence of new species on islands also effects cultural evolution. It is known, for example, that only a few chaffinches colonized the Chatham Islands in the South Pacific in about 1900. The present population of this bird, some 35 generations hence, still has an aberrant and reduced song repertoire, a dialect that differs from that of the parent population living in New Zealand. No doubt this reflects the few and individaul song styles that the founders brought with them and passed on to their descendants (Baker and Jenkins, 1987).

Competition is a very salient characteristic of biological evolution. The replicative and instructive activities of genes are dependent on environmental resources. Finite resources limit reproduction and their partitioning leads to various forms of competition between genomes. In organisms capable of behaving, competitiveness frequently surfaces in the guise of agonistic behaviour. Aggression for food and space, strife about social rank and contests for sexual partners are examples. Memes also compete for limited resources, primarily for synaptic space in hosts, but also for the means that they need to reproduce themselves (principally a share of the hosts' behaviour). It is not surprising therefore that memes should also instruct their hosts to behave competitively, even agonistically on their behalf. Among humans at any rate, culturally driven aggressive behaviour is sadly often in evidence, even in its most extreme forms. Brawls among soccer fans, murder among political partisans, wars between religious sects, are events that challenge again and again our naive belief in human morality and rationality.

Biological evolution, however, also yields cooperative behaviour. Each member in a bird flock, for instance, benefits in fitness from the fact that the antipredator vigilance is enhanced by socializing: many eyes see more than two (Tinbergen, 1953). Culturally determined behaviour of this kind is extremely widespread, at least among humans. Religious sects, learned societies, political parties, etc., clearly arise because the memes concerned are more effective jointly than singly in spreading themselves.

The simple fact that blood relatives share varying proportions of genes generates selective pressure for the emergence of an accordingly graded altruistic disposition among them (Hamilton, 1964). Analogously, individuals can share many, few or no memes, yielding a gradation of memetic kinships. In advanced cultures with institutions such as schools and universities, large numbers of memes are transmitted among unrelated persons. Altruistic behaviour of a markedly parental quality by professors towards their 'best' pupils (i.e. those that have adopted many of their memes) is not uncommon. Culturally based helping behaviour among genetically unrelated people that have some beliefs or traditions in common is widespread: Muslims help Muslims, freemasons aid freemasons, fraternity members assist fraternity members, etc. In fact, cultural altruism may often simply reinforce or formalize the other biologically viable form of altruism, namely reciprocal altruism that, among animals at least relies on only a rather indefinite fellowship (Trivers, 1985).

Competition between biological kin groups can, however, also enhance strife. Capuchin monkey bands composed mainly of relations, for example, engage in quite warlike aggression against other bands about trees in fruit or stray females (Delius, unpublished observations). To an even greater extent, the same applies to cultural kin groups. Indeed, all too frequently Protestants and Catholics, Sikhs and Hindus and many other such groups choose to kill each other. Meme selfishness may on occasions even override gene altruism. Differing political allegiances for instance can make mortal foes of even close blood relatives, as documented by several tragic Spanish Civil War episodes.

Every culture seems to contain items that are in some way extravagant, involving effort, expense or inconvenience that appears disproportionate relative to the pay-off, return or advantage the items provide. Megalithic stone circles, pyramids, gothic cathedrals, tulipomania, operatic performances, fanciful fashions are some examples. Can these be compared to biological extravaganzas such as elk antlers, bird of paradise plumage, manakin dances or orchid flowers? In the biological context it is coevolution that most often brings about extraordinary traits. Whenever the evolution of two or more kinds of organisms is closely interdependent, in the sense that each kind is a selection agency affecting the evolution of the other, then there is scope for unpredictable, sometimes spectacular developments (Futayama and Slatkin, 1983).

Males and females of one species are often involved in such runaway games through sexual selection. Within each sex there is competition for the best sexual partners. Females, who invest heavily during reproduction, can gain much by choosing males with characteristics that promise offspring of quality. This generates selection for males that have such characteristics, but also leads to breeding females having ever stronger preferences. The ensuing feedback spiral can give rise to unusual features such as the peacock's tail or the bowerbird's bower (Borgia, 1986). Mutualistic memes that are like extensions of genes are bound to get caught up in this sort of game. The whole birdsong culture is strongly suspected to be a memetic offshoot of gene-based sexual selection (Catchpole, 1987). Among humans, sex-differentiated dress fashions have probably originated in the same way.

Meme reproduction itself at first sight seems to be of an asexual kind, much as the simple budding or cloning typical of such organisms as virus and bacteria (Jackson *et al.*, 1986). According to detailed questionnaire investigations by Cavalli-Sforza *et al.* (1982) on the cultural traits of American college students, the meme occasioning art museum visits for instance, appears to derive solely from the meme borne by just one other model person (father). However, the propagation of the meme motivating churchgoing among this population appears to require the fusion of appropriate memes carried by two persons (the parents). Other memes, for instance that eliciting jogging, usually descends from several memes born by friends, celebrities, etc., but not the parents. It was argued earlier that host genomes may in fact tend to bias memetic reproduction towards a multifusional mode involving several source memes ('do what everybody does'). It is uncertain, however, whether this primitive isogamic 'sexuality' of memes can support anything like cultural sexual selection.

Cultural trait luxuriation is more likely to be produced by the same kind of coevolutionary tangles effective in complex biological communities which occupy elaborate niches such as the humid tropics. There the survival and reproduction chances of any organism are mainly determined by the ecological context created by the other organisms, rather than by the physical conditions of the habitat. The intricate and dynamic web of organismal interactions characterizing such communities has led to the evolution of innumerable freaks, such as flowers that look like bees, caterpillars that look like snakes, moths that look like hummingbirds, butterflies that look like other butterflies, and so forth. Analogously, how well a meme succeeds depends largely on the cultural context in which it finds itself. For example, once a set of Muslim or Catholic memes has established itself in a brain, it generates a strong bias for the acceptance of further memes of Muslim or Catholic type, but also for the rejection of any Buddhist or Hindu memes. A runaway process leading to exaggeration and fanaticism becomes a strong possibility in such a context. From there to pyramid and cathedral building may be just a step further. More generally, the selection of memes by memes must doubtlessly be a major factor in cultural evolution. The arbitrary developments that such an inherently unstable arrangement can produce are intuitively boundless.

If memes select memes, can memes also select genes? In certain circumstances they undoubtedly do. Different socially learned songs, for example, definitely promote and sustain the genetical differences between several sympatric bird species (Thielcke, 1973). That is of course precisely what Tinbergen and Lorenz had assumed during that remarkable 1959 conversation mentioned at the beginning of this essay. Given that culturally transmitted song dialects also influence intraspecific mating preferences of songbirds, they are also bound to have subtle effects on their population genetics, even if the effects are difficult to pinpiont (Barker and Cunningham, 1985). During the Ravenglass discussions Niko Tinbergen often considered whether cultural processes such as language, birth control or modern medicine, were not importantly affecting the course of human biological evolution. A few years later he seemed to be certain about it. His worry was then that cultural evolution in several respects was outstripping biological evolution at a dangerously accelerating pace (Tinbergen, 1977). He wrote: 'It is an illusion to believe . . . that cultural evolution (entails) unmitigated progress'. The overall course of cultural evolution, he concluded, needed a rational and urgent correction. 'Time is running out', Niko warned us, and that is no less true today than it was then.

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REFERENCES

Alderks, C.E. (1986) Observational learning in the pigeon: effects of model's rate of response and percentage of reinforcement. *Animal Learning Behaviour*, **14**, 331–35.

Anderson, R.M. and May, R.M. (eds) (1982) *Population biology of infectious diseases*, Springer, Berlin.

Baker, A.J. and Jenkins, P.F. (1987) Founder effect and cultural evolution of songs in an isolated population of chaffinches, *Fringilla coelebs*, in the Chatham Islands. *Animal Behaviour*, **35**, 1793–1803.

Bajema, C.J. (1972) Transmission of information about the environment in the human species: a cybernetic view of genetic and cultural evolution. *Social Biology*, **19**, 224–26.

Ball, I.A. (1984) Memes as replicators. *Ethology and Sociobiology*, **5**, 145–61.

Barker, M.C. and Cunningham, M.A. (1985) The biology of bird song dialects. *Behavioural and Brain Sciences*, **8**, 85–133.

Baudoin, M. (1975) Host castration as a parasitic strategy. *Evolution*, **29**, 335–52.

Biederman, G.B., Robertson, H.A. and Vaughan, M. (1986) Observational learning of two visual discriminations by pigeons: a within-subject design. *Journal for the Experimental Analysis of Behaviour*, **46**, 45–9.

Bonner, J.T. (1980) *The evolution of culture in animals*, Princeton University Press, Princeton.

Borgia, G. (1986) Sexual selection in bowerbirds. *Scientific American*, **256**, 70–79.

Boyd, R. and Richerson, P.J.V. (1985) *Culture and the evolutionary process*, Chicago University Press, Chicago.

Campbell, D.T. (1969) Variation and selective retention in sociocultural evolution. *General Systematics Yearbook*, **14**, 69–85.

Cann, R.L., Stoneking, M. and Wilson, A.C. (1987) Mitochondrial DNA and human evolution. *Nature*, **325**, 31–36.

Catania, C. (1985) Rule governed behaviour and the origins of language, in *Behaviour analysis and contemporary psychology*, (eds C.F. Lowe, M. Richelle, D.E. Blackman and C.M. Bradshaw), Erlbaum, London, pp. 135–156.

Catchpole, C.K. (1986). The biology and evolution of bird songs. *Perspectives in Biology and Medicine*, **30**, 47–62.

Catchpole, C.K. (1987) Bird song, sexual selection and female choice. *Trends in Ecology and Evolution*, **2**, 94–97.

Cavalli-Sforza, L.L. and Feldman, M.W. (1981) *Cultural transmission and evolution, a quantitative approach*, Princeton University Press, Princeton.

Cavalli-Sforza, L.L., Feldman, M.W., Chen, K.H. and Dornbusch, S.M. (1982) Theory and observation in cultural transmission. *Science* **218**, 19–27.

Chesler, P. (1969) Maternal influence in learning by observation in kittens. *Science* **166**, 901–903.

Changeaux, J.-P., Heideman, T. and Patte, P. 1984. Learning by selection, in *The biology of learning* (eds P. Marler and H.S. Terrace), Springer, Berlin, pp. 115–133.

Christie, A.B. (1981) Rabies. *Journal of Infection*, **3**, 201–218.

Curio, E., Ernst, E. and Vieth, W. (1978) Cultural transmission of enemy recognition: one function of mobbing. *Science*, **202**, 899–901.

Davies, B.D., Dulbecco, R., Eisen, H.N. and Ginsberg, H.S. (eds) (1980) *Microbiology*, Harper and Row, Philadelphia.

Dawkins, R. (1976) *The selfish gene*. Oxford University Press, Oxford

Delius, J.D. (1989) Of mind memes and brain bugs, a natural history of culture, in *The nature of culture*, (ed W.A. Koch), Brockmeyer, Bochum, pp. 26–79

Delius, J.D. (1990) Sapient sauropsids and hollering hominids, in *Geneses of language*, (ed W. Koch). Brockmeyer, Bochum, pp. 1–29.

Devoogd, T.J., Nixdorf,B. and Nottebohm, F. (1985) Synaptogenesis and changes in synaptic morphology related to acquisition of a new behaviour. *Brain Research*, **329**, 304–308.

Dudai, Y. (1989) *The neurobiology of memory: concepts, findings, trends*. Oxford University Press, Oxford.

Falk, J.L. and Feingold, D.A. (1987) Environmental and cultural factors in the behavioral action of drugs, in *Psychopharmacology: the third generation of progress*, (ed H.Y. Meltzer), Raven Press, New York, pp. 1503–1509.

Fenner, F. and Ratcliffe, F.N. (1965) *Myxomatosis*, Cambridge University Press, Cambridge.

Futuyma, D.J. (1986) *Evolutionary biology*, 2nd edn, Sinauer, Sunderland, Mass.

Futuyma, D.J. and Slatkin, M. (1983) *Coevolution*, Sinauer, Sunderland, Mass.

Ewer, R.F. (1969) The 'instinct to teach'. *Nature*, **222**, 698.

Gould, J.L. and Marler, P.(1987) Learning by instinct. *Scientific American*, **256**, 62–73.

Hamilton, W.D. (1964) The evolution of social behavior. *Journal of Theoretical Biology*, **7**, 1–52.

Harris, M. (1987) *Cultural anthropology*, Harper and Row, New York.

Hewlett, B.S. and Cavalli-Sforza, L.L. (1986) Cultural transmission among Aka pygmies. *American Anthropologist*, **88**, 922–34.

Hogan, D.E. (1986) Observational learning of a conditional hue discrimination in pigeons. *Learning and Motivation*, **17**, 40–58.

Hohorst, W. (1981) Parasitologie, in *Biologie*, (eds D. Starck, K. Fiedler, P. Harth and J. Richter), Verlag Chemie, Weinheim, S. 765–808.

Horn, G. (1986) Imprinting, learning, and memory. *Behavioral neuroscience*, **100**, 825–32.

Jackson, J.B.C., Buss, L.W. and Cook, R.E. (eds) (1986) *Population biology and evolution of clonal organisms*, Yale University Press, New Haven.

Klopfer, P.H. and Hailman, J.P. (1965) Habitat selection in birds. *Advances in the Study of Behavior*, **1**, 279–303.

Kohonen, T. (1984) *Self organization and associative memory*, Springer, Berlin.

Kroodsma, D.E. and Miller, E.H. (eds) (1982) *Acoustic communication in birds*, Academic Press, New York.

Lefebvre, L. (1986) Cultural diffusion of a novel food-finding behaviour in urban pigeons: an experimental field test. *Ethology*, **71**, 295–304.

Lumsden, C.J. and Wilson, E.O. (1981) *Genes, mind and culture, the coevolutionary process*, Havard University Press, Cambridge, Mass.

Margulis, L. (1981) *Symbiosis in cell evolution*, Freeman, San Fransisco.

Medawar, P.B. (1976) Does ethology throw any light on human behaviour? in *Growing points in ethology*, (eds P.P.G. Bateson and R.A. Hinde), Cambridge University Press, Cambridge, pp. 497–506.

Meire, P.M. and Ervynick, A. (1986) Are oystercatchers (*Haemotopus ostralegus*) selecting the most profitable mussels (*Mytilus edulis*)? *Animal Behavior*, **34**, 1427–35.

Minkhoff, E.C. (1983) *Evolutionary biology*, Addison Wesley, Reading, Mass.

Moore, J. (1984) Parasites that change the behaviour of their host. *Scientific American*, **250**, 82–89.

Morris, R.G.M., Kandel, E.R. and Squire, L.R. (1988) Learning and memory. *Trends in Neuroscience*, **11**, 125–79.

Murton, R.K., Coombs, C.F.B. and Thearle, R.J.P. (1972) Ecological studies of the feral pigeon. Flock behaviour and social organization. *Journal of Applied Ecology*, **9**, 875–89.

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

Norton-Griffiths, M. (1967) Some ecological aspects of feeding behaviour of the oystercatcher *Haematopus ostralegus* on the edible mussel *Mytilus edulis*. *Ibis*, **109**, 412–24.

Palm, G. (1982) *Associative memory*. Springer, Berlin.

Pringle, J.W.S. (1951) On the parallel between learning and evolution. *Behaviour*, **3**, 174–215.

Rummelhardt D.E. and McClelland, J.L. (1986) *Parallel distributed processing. Exploration in the microstructure of cognition*. MIT Press, Cambridge, Mass.

Schmidt-Koenig, K. (1965) Current problems in bird orientation. *Advances in the Study of Behavior*, **1**, 217–78.

Smith, D.C. and Douglas, A.E. (1987) *The biology of symbiosis*, Arnold, London.

Staddon, J.E.R. (1983) *Adaptive behaviour and learning*, Cambridge University Press, Cambridge.

Subowski, M.D. (1989) Recognition in ethology. *Perspectives in Ethology*, **8**, 137–71.

Thielke, G. (1973) *Die Wirkung erlernter Signale auf die Artbildung*, Universitätsverlag, Konstanz.

Tinbergen, N. (1953) *Social behaviour in animals*, Methuen, London.

Tinbergen, N. (1976) Ethology in a changing world, in *Growing Points in Ethology*, (eds P.P.G. Bateson and R.A. Hinde), Cambridge University Press, Cambridge, pp. 507–27.

Tinbergen, N. (1977) Time is running out, unpublished manuscript.

Trivers, R. (1985) *Social evolution*, Cummings, Menlo Park, CA.

Wallhäusser, E. and Scheich, H. (1987) Auditory imprinting leads to differential 2-deoxyglucose uptake and dendritic spine loss in the chick rostral forebrain. *Developmental Brain Research*, **31**, 29–44.

Yamashita, M., Krystal, M., Fitch, W.M. and Palese P. (1988) Influenza B virus evolution: co-circulating lineages and comparison of evolutionary patter with those of influenza A and C viruses. *Virology*, **163**, 112–22.

Zentall, T.R. and Galef, B.G. Jr (eds) (1988) *Social learning: psychological and biological perspectives*. Erlbaum, Hillsdale.