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Of mind memes and brain bugs; a natural history of culture[1]

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Colleague at Bochum University: "You have set a flea in my ear". Discjockey on German radio: "The song is a proper earwig". Report in an English newspaper: "The idea was obviously infectious". Passenger on an international flight: "What a contagious, nonsensical habit!". American performance artist: "Language is a virus".

1. Introduction

Consultation of dictionaries reveals that in common parlance the word "culture" is hopelessly overloaded with meaning. For the purposes of this essay it is necessary to strip its definition down to a bare, manageable minimum. Culture will be taken to mean behavioural culture. It is

the ensemble of behavioural traits that characterize specific human groups in the sense that members of such a group at a given period of time tend to hunt with this or that technique, sow seeds in this or that way, adore this or that god, speak this or that dialect, wear this or that dress, greet in this or that manner, build this or that kind of housing, cultivate this or that kind of music, respect this or that institution and so forth. Furthermore, it will be understood that the behavioural traits that constitute a culture are passed on among the members of the population by individuals taking them over from other individuals. The transmission of cultural items occurs through learning by observation of others, by imitation, through instruction, through tradition. The transmission may be direct or may involve intermediaries such as letters, newspapers, advertisements, books, records, videotapes, radio, television.

Behavioural traits that are transmitted from parents to children by biological inheritance, such as the coordination patterns of suckling, crying, smiling, sleeping and the organic bounds of perceptual, cognitive and motor capacities of individuals, are thus not part of culture. However, in what precise instances or situations such innate behaviour or behavioural capacities are realized or exhibited may well be culturally determined in the above sense. Conversely, genetically transmitted behavioural traits may predispose or limit the transmission of cultural traits, an issue that will be of much interest later. Also excluded from the definition of culture are behavioural traits that individuals do not learn from others but develop, learn or invent by themselves, thumb-sucking, nose-picking, walking, running, being examples[2]. However, as soon as other individuals begin to imitate, to copy such behaviour it becomes a cultural item. Thus culture does not include traits that are innate or that are learned individually but only those that are learned from others, directly or through media[3].

The restriction to behavioural traits excludes material items such as land, buildings, clothing, money, slaves, weapons, waste, pollution etc. as elements of culture. However, the particular mode of fabrication, creation, use, appreciation, administration, transmission, destruction, etc. of such goods through particular forms of manufacture, bequest, barter, sale, distribution, robbery, conquest, arson, carelessness, etc. very often are determined by cultural traits. Material goods may also support, enable, constrain, motivate, influence, etc. the emergence, transmission and realization of cultural traits (see for example the effect of hoola-hoop rings, Rubik's cubes, miniskirts, jeans, bowler hats, steam engines, aeroplanes, computers on cultural behaviour). Books, records, films, pictures and suchlike are particular cases. If read, listened, viewed or appreciated, their contents become culture but if not they are only goods, or tokens in cultural rituals (buying, giving, lending, collecting, storing, burning). Material products of cultural behaviour often loom large in more popular conceptions of culture because they are perceptible, because they endure. Flint axes, cave paintings, pyramids, gothic cathedrals, etc. stand for the cultures that generated them, for the many behavioural traits that these encompassed.

The cultural behaviour of present day human populations such as !kungs, Bavarians, untouchables, francophones, concert-goers, cowboys, rockers, yuppies, bank managers, boilermakers or whatever, is the product of historical processes. Cromagnons, Neanderthals and their contemporaries 50 thousand years ago certainly did not exhibit anything like as sophisticated a cultural behaviour as present day human groups do. The protohominid ancestors of modern man living about 4 million years ago had only wisps of culture, if that. Modern relations of ancestral species living 70 million years ago, insectivores and prosimians, are devoid of any cultural behaviour to speak of. A capacity for culture had to evolve first. Therapsid dinosaurs living 200 million years ago and forerunners of

all mammals very probably did not possess any cultural traits. Mechanisms that enable a cultural transmission of behaviour had to emerge through the process of biological evolution. Thereafter cultures arose, developed and diverged over time, over many generations.

The nature of processes that underlie the phenomenon of cultural evolution is the theme of this essay. More precisely it is the analogy between the cultural evolutionary process and the biological evolutionary process. The superficial similarities between these two processes have repeatedly been noted in the last hundred years or so. An analysis of the correspondences however has only begun in recent years. As an introduction to the subject it is convenient to present first an encapsulated characterization of biological evolution, the better understood of the two processes. This affords the opportunity to consider how the capacity for culture might have emerged as a biological characteristic of certain organisms.

2. Biological evolution

The game of biological evolution began 3.5 billion or so years ago with the chance emergence of stable molecules or molecule-systems capable of almost perfect self-replication. Any molecule varieties generated by non-perfect replication that were not themselves capable of replication were out of the game. The varieties capable of replication inevitably competed for environmental resources, as the assembly of duplicate molecules is only possible through requisition of matter and energy from the surrounding medium. Those molecules that were the most efficient in drawing on the environment replicated most often, would leave more offspring and would eventually, over generations, oust the less efficient. The medium in which these replicating molecules existed was with certainty not homogeneous; different varieties of replicator molecules came to dominate in different environmental patches. Replicator mutants that were capable of synthesizing molecular envelopes that buffered them from the external environment would be at an advantage in terms of stability over those that could not. They had provided themselves with a milieu intérieur and had become proper organisms.

If, over and above that, mutants arose that could synthesize means for motility, a contractile molecular appendage, a flagellum for example, these replicator species would be able to move into the sections of the habitat richest in resources and best suited for replication. Molecular receptors tuned to key environmental chemicals that could start and stop locomotion would make such movement goal-seeking. Proper behaviour had then arisen. Which responses followed which stimuli for very, very many generations were determined by mechanisms exclusively instructed by genes (innate behaviour). As long as the organisms lived in a very constant environment this signified no disadvantage but as soon as they spread into environments that were more variable over time and space, behaviour determined by individual experiences would become an advantage. That is, selection pressure arose for gene mutations that were able to instruct neural structures capable of learning. Learning to attach existing approach or avoidance responses to novel stimuli that were predictive of good or bad events (classical conditioning) or learning to produce novel responses that lead to advantageous conditions or to suppress responses that yielded disadvantageous conditions (instrumental learning) on the basis of past experience are forms of learning that are still widespread among animals. The actual act of learning does not need to involve behavioural activity. An organism may register contingencies between stimuli it observes passively (latent learning). Furthermore it may use the representation of the world and its own behaviour that it has previously stored by such means into memory to internally simulate real situations and thereby identify

off-line potential behaviours that are likely to yield positive pay-offs when used de facto (insight learning). In general, learning is a device instructed by genes that allows the individual to acquire knowledge about the world and itself over and above that which is implicitly contained in its genetic code. Each individual at this stage has to learn by itself though, often an effortful and lengthy process in a none-too-consistent environment.

Summarizing, biological evolution is the plain consequence of the not totally perfect self-replication that characterizes certain organic molecules. Within populations of a given species molecularly (genetically) coded information is replicated and transmitted from one generation to the next. The replication is not completely faithful and every now and then new information is generated. Over generations novel information arises in this way at a steady rate. The chances of being transmitted from generation to generation is not equal for all varieties of information. Individual organisms that are synthesized under the instruction of the particular genetic information that they happen to embody vary in their capacity for survival and reproduction. The genetic information present in a population of organisms is subject to selection, as it progresses through successive generations, on the criterion of whether it is adapted to environmental conditions in terms of the fitness to reproduce itself. The capacities for behaviour and learning are consequences of this adaptation process.

3. Imitation Learning

Mutants that can instruct neural substrates with the capability for imitation learning, whereby an individual can directly take over the experience of others, are a further evolutionary step forward in adaptability. Social facilitation may have been a preadaptive step that preceded the evolutionary emergence of this kind of learning. It refers to the phenomenon that perceiving others performing certain behaviours can motivate some animals to execute the same behaviour. Such a contagiousness of behaviour is often adaptive. Buzzing bees swarming out are a signal for hive mates to follow suit in what is then likely to be a successful communal attack on a large enemy. Many gulls flying towards a particular spot at sea are likely to indicate that there is food there; following them is likely to result in successful foraging. Several pigeons hurriedly flying away from a clearing are likely to indicate that a predator is about; flock mates will be well advised to leave as well even though they themselves might not have seen or heard the predator. Socially facilitated behaviour of this kind need not involve any learning; it often is based on innate behaviour, but it can provide opportunities for learning. Learning in such a context can hardly be anything but imitative in nature. Seeing other pigeons approach stubble fields will trigger socially facilitated following but at the same time the individual pigeons can hardly fail to learn about the association between stubble fields and grain and begin to approach stubble fields by themselves after a few such experiences. In this example the observers that learn perform the relevant behaviour virtually at the same time as the models perform it. It is a further stage of sophistication when the imitator stores into its memory the behaviour it saw its model perform without necessarily performing that behaviour at the time, a kind of latent imitation learning. Having idly watched a mechanic at the service station change the wheel of a car is of assistance to a driver if he later has to deal with a flat tyre himself.

Learning is generally a process by which knowledge, an assembly of information that represents reality, is stored in the brain as the contents of memory. The car mechanic in the above example performed on the basis of information stored in his memory and so did the driver afterwards. The contents of memory were transformed into behaviour by the demonstrator, and, in the observer, lead to perceptions about the behaviour which he stored in his

memory, to convert them again later into behaviour. Still the model had to perform for the observer to be able to store. A more efficient and more advanced form of imitation would be possible if a more direct transfer of memory contents were possible. In most situations where human individuals take over behavioural traits from others, linguistic communication plays an important supportive, if not sole, mediating role. Elsewhere I have argued that language might have arisen evolutionarily as an extension of imitation learning, as a vehicle for instruction, whereby recipes for behaviour are transmitted in an abstract symbolic way. Linguistic messages function like an almost effortless short-circuiting between the information-storing structures of individuals. For a <u>Homo habilis</u> a million years ago it must have been awkward to demonstrate to a dozen novices how to stalk an antelope; it would have been much easier to tell them how it should be done. Language plays a major role in the transmission of human cultural contents and that makes for much of the sophistication of human culture <u>vis-à-vis</u> animal culture. It also potentiates information transmission. Being told verbally how to change a car tyre is sufficient for reasonable performance. Such instruction costs little in terms of energy and time. Linguistic communication, spoken or written, is sometimes the only medium by which certain human behavioural traits can be transmitted from individual to individual. Written language much amplifies the culture transmitting power of language. Most importantly, it breaks with the necessity that the model and the observer have to coincide in time and space for memory content transmission to be possible.

The detailed processes mediating imitation or observational learning at even sublinguistic levels vary considerably. Some concrete examples may serve to illustrate this variety. Individuals of many bird species will breed at locations close to those where they themselves were bred. Successive generations keep to traditional breeding grounds. This is not due to a lack of mobility, as many of the same species will migrate every autumn over thousands of kilometers before returning in spring to breed only a few hundred meters from their site of birth. It has been demonstrated that this is due to an imprinting-like process. Juvenile birds store information about the geographical location of the site where they grow up. They can use this knowledge to navigate back to the home area at a later time. It is not only the geographical location on which young birds are imprinted but also the particular habitat in which they were raised, say broad-leaved deciduous woods or coniferous evergreen forests. As adults they will then show a preference for whatever surroundings they grew up in. Familial traditions are set up in this way. Note though that strictly they do not come about by the youngsters imitating the parents but rather by the parents bringing their youngsters up where they can only learn about one thing. It is borderline whether one wishes to call this learning imitative or not.

Many bird species eat a variety of foods. Given individuals, however, often have marked preferences for particular items among these potential foods. The food they tend to choose is that which their parents fed them when they were young. This is ensured by an imprinting to the sight, smell and taste of the food they had as youngsters. In some species the parents lead their young to sites where the food that they like predominates. Each of the young then learns on its own to find and deal efficiently with these items. Thus again traditions may simply be maintained by parents biasing the learning opportunities of their offspring. Whether this is designated imitation learning or not is again an academic matter. In yet other species, the special technique by which individuals obtain food varies, even though all feed on the same items. Youngsters appear to learn the particular alternative techniques from the parents by observation and participation. In some species behaviour analogous to teaching may occur. It is characteristic of female cats with kittens that they bring home live mice and birds, release them in the presence of

the young just to catch them again. Kittens will begin to participate in these repeated chases.

Contrived non-natural modes of food gathering can be experimentally arranged to arise through proper imitation learning in some species. Having seen another pigeon obtain food from an electromagnetic dispenser, after performing the somewhat arbitrary behaviour of pecking an illuminated disc that acts as a switch, considerably facilitates the subsequent acquisition of the same skill by observer pigeons. A number of experiments show that the information that the observer acquires can be multifarious: knowledge as to the fact that food is to be had in the particular environment, that it is available at a particular site; that performance of certain acts make that food available, that other acts are not conducive to getting food and so on. It is rare though that the observer will produce the correct food-yielding behaviour on the first attempt. Instead, having observed a model, he is quicker at learning by himself what has to be done.

Observational learning of this kind may be further facilitated if pigeons have the opportunity to perform the target behaviour while they observe rather than only at some later time. This may have to do with the fact that in that way no long term retention in memory is needed but perhaps also because social facilitation potentiates the learning process. Seeing other pigeons peck facilitates or even induces, or motivates pecking. The behaviour is contagious. A strong tendency to peck definitely facilitates the acquisition of instrumental pecking for food on a response key. Accordingly it also helps if in the above context the pigeons meant to imitate are hungry when they observe. Incidentally, observing a partly skilled model is better than seeing a perfectly skilled one perform.

An artificial feeding tradition was inserted among a flock of feral urban pigeons by capturing a few of their members and training them to get at grain by piercing a tight paper sheeting covering special troughs. When they were released back into their flock in the wild they, along with their mates, were 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 feeding 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 itself but once that happened the new cultural trait spread just as rapidly in that flock.

Avian imitation learning can be mediated by classical conditioning. Wild-caught blackbirds show a special mobbing behaviour when they see an owl (and also other predators). They stay close to it, show signs of high excitation and give off warning calls. A stuffed owl is often sufficient to elicit this response. In an experiment it is possible to arrange for a blackbird (the model) to see a stuffed owl which is concealed to another as yet naive blackbird (the observer). Instead it sees a novel but innocuous object such as a white plastic bottle. The model mobs the owl. This behaviour is contagious; it is an unconditioned stimulus for the observer to begin to mob as well (the unconditioned response). The white bottle seen by the observer functions as a conditioned stimulus. It always precedes and accompanies the mobbing by the model. After a few pairings (exposures of the model to the owl, of the observer to the mobbing model and the bottle) a conditioned response can be demonstrated in the observer. In the absence of any model the ex-observer mobs whenever it is shown the bottle. Its acquired bottle-mobbing habit can serve as a model for new observers. A bottle-mobbing tradition among blackbirds has been initiated: a new miniculture has been set up.

4. Song Culture

Three or four decades ago culture was seen as a purely human phenomenon. Meantime many animals have been found to have behavioural cultures in the sense defined earlier in this essay. Granted, none of the animal cultures entail as many or as complex behavioural traits as those found in present day human populations. Animal cultures are far simpler but the principles by which they come about are qualitatively equivalent to those by which human culture functions. Animal cultures are often labelled as protocultures to characterize their relative simplicity. But then our hominid ancestors 3 million years ago also possessed only protocultures.

Although some species of mammals and in particular primates exhibit protocultural behaviour, here we focus on such behaviour in birds. There are good reasons to do so. A very large number of bird species, perhaps as many as 5000, exhibit a special kind of protocultural behaviour, namely song cultures. For one taxonomic group of birds, the oscines (the songbirds proper) comprising about 4000 different species world-wide there are reasonable grounds to believe that all but a few species have song cultures. Some hundred or so songbird species have been adequately examined so far and virtually all have turned out to have songs determined by tradition. The exceptions are brood-parasitic species like cuckoos, cowbirds and widowbirds that lay their eggs in other birds' nests and have these raise their young. It is reasonably certain that all songbirds proper descend from a common ancestor that split off from the remaining bird stock about 40 million years ago. It is very probable that this ancestral species already had the capacity for song culture which it then passed on to all descendent species. This would make birdsong cultures the oldest cultures extant, since human culture originated only some 3 million years ago, perhaps building upon protocultural roots of primate ancestors, dating back to at most some 15 million years ago.

Much is known about the song of some selected songbird species, arguably more than is in fact known about any single human cultural trait. The chief fact underlying avian song culture is that each individual songbird learns its song from another individual or individuals by imitation. The typical course of events is that the young nestling or fledgling, a chaffinch for example, still incapable of singing because of the incomplete development of its vocal apparatus, the syrinx, hears its father or male neighbours sing (females rarely if ever sing). It stores a representation of what it hears into its auditory memory. If it is a male it becomes capable of vocalizing under the influence of male hormones when a few months old. It begins to vocalize by producing a wide variety of sound patterns. Those sounds that match its auditory memory template are retained in its repertoire, those that do not are lost. By and by the variety is reduced and only a sound sequence that coincides closely with song that it heard as a youngster is retained and produced henceforth. If the fledgling is prevented from hearing a model then the song that develops in the trial-and-error self-learning period bears no similarity with that produced by its normal conspecifics. It has no auditory template that can be matched by trial and error vocalization learning. If the youngster is surgically deafened soon after it heard the model it does not develop a model-like song either, since it has no means to check the match between its own vocalizations and the auditory template. If it is deafened after its own song has crystallised the latter is initially maintained and only degrades slowly.

If hatchlings are given to adoptive parents of another species they end up producing a song similar to that of the adoptive parents. Hand-raised young will also store templates of song heard from a tape recorder although that is usually less effective than hearing it from a life model. This happens, provided that the adoptive or tutoring song is not too different from those of its own species. Experiments have shown that there are innate limits as to

the sounds that fledglings will store as templates. If the model songs are too wildly different from the species' characteristic song style, they will be only very roughly taken over, or even not at all. Moreover it would seem that young songbirds have sufficient innate information about their species-specific song that, if it is offered along with other alternatives, they will store it preferentially.

Female songbirds do not normally sing but if artificially injected with male sexual hormone as adults they do. Since they then also produce the parental song they must also have memorized a template, one that they normally do not convert into vocalizations. There is evidence though that they use the auditory template to recognize males of their own species, perhaps even discriminating those singing their fathers' dialect. Much is known, incidentally, about the neural substrates of bird song. Song is principally controlled by the left half of the brain. A number of well identified, interconnected neural structures are involved. In species that learn new songs each spring new nerve cells that form new synapses are incorporated into some of these structures under the joint influence of testosterone (male hormone) and auditory stimulation. In fact the avian song system has become a model preparation for the study of the neuronal basis of learning.

While members of several songbird species normally only take over songs from their father, several also store templates of songs produced by neighbours. Although in some species the repertoire of a given male is restricted to one song, in many species the repertoire includes several dozen songs and individuals of exceptional species may even command several hundred different songs or song elements. Even further, some species will continue to pick up templates from neighbours throughout their life. A few species (starlings, mockingbirds, hill-mynahs, and among non-songbirds, parrots) will occasionally even incorporate songs and sounds from non-conspecific species into their repertoire.

In an experiment hand-raised young bullfinches were exposed to an artificial song, a simple flute melody. As adults they produced a good rendition of this melody and furthermore sang it to their own young who in turn learned from them. They again transmitted it to the next generation. An artificial song tradition had been set up. In the wild the transmission of song by delayed imitation learning results in the formation of regional dialects. The song copying fidelity is high but occasionally slight deviations or errors occur. In some species new song elements may also arise through a process more akin to invention than to copying errors, by combination and development of preexisting elements for example. The overall result of this slightly imperfect transmission is that, within a species, the populations of a given geographical area will sing a particular song variant or song repertoire, those of another area a different variant or repertoire. The reader needs to know that by and large youngsters remain in the area where they were born. Transitions from one dialect area to another may be gradual, that is with intermediate kinds of song, or quite abrupt. In any dialect area there will be a few birds that sing aberrant songs; in some cases these go back to errors of transmission, in others to immigrants from other dialect areas. Newcomers in some instances will eventually acquire the correct local dialect. Since many songbird species can hold a large repertoire of songs or song elements, the structure and composition of dialects can be quite complicated. The song culture of a bird population may thus be a composite of many separate cultural items of which any given individual may only bear some. The function, if any, of bird dialects is a much disputed issue. It seems likely that the capacity for learned song, instead of innate song, arose by the process of sexual selection possibly in the special context of speciation (the emergence of a new species). Present day songbird females appear to prefer those males of their own species that exhibit the most elaborate song.

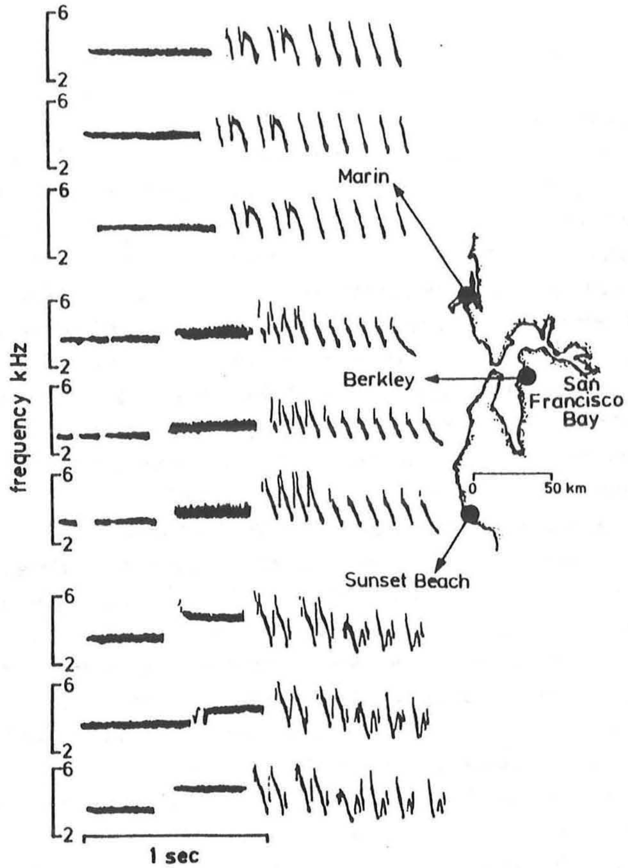

Fig. 1 Song dialects of song sparrows in the San Francisco area. Each sonogram represents the song of an individual bird. Individuals that live in the same area have similar songs. From Marler and and Hamilton (1966), modified.

Originally perhaps they did so because elaborate song was a sign of male vigour or because it conveyed the surest sign that the male belonged to the right species, namely its own. The initial preferences lead to a runaway effect, known technically as sexual selection. Males with an ever own. The initial preferences lead to a runaway effect, known technically as sexual selection. Males with an ever more complex song are most likely to mate and produce offspring. Females that chose such males were more likely to have reproductively successful offspring and so forth. Since a genetically encoded transmission of elaborate song is certain to be inefficient as compared to a transmission by imitation learning, selection pressure for this latter mode ensued. But the evolution of complex learned song by itself does not explain the existence of regional song dialects. A simple but not unlikely explanation for the emergence of song dialects is that they are inevitable side products of the evolution of song learning, not having any particular function. As an analogy, there is no doubt that language as such is an advantageous asset, but whether speaking Chinese or German, for instance, is associated with a Darwinian fitness advantage is doubtful except in the sense that among Chinese it is not particularly adaptive to speak German and vice versa. There is nothing in sexual selection that will prevent the complex songs of different populations drifting apart. That would mean that dialects, unlike song learning itself, confer no fitness gain to the individual songbird.

An alternative explanation for dialects is that they increase the genetic fitness of their singers quite directly. They are learned markers for the gene pool of local songbird populations that are specially adapted to local environmental conditions. Local song dialects would be indicators for individuals stemming from a given pool. Local dialects would give females the possibility of selecting males of the same pool thus drawing fitness gains from fusing its genes with coadapted ones. Support for this hypothesis, however, has not been particularly forthcoming.

5. Memes

Song varieties that are transmitted through imitation learning are stored as auditory templates in the songbird's memory. Through motor learning these contents of memory come to control behaviour. In fact a separate motor template of song is then assembled in memory and controls vocal output directly. More generally, learning, whether classical, instrumental or whatever, can be conceived as a process by which particular information is stored into memory. Learning by imitation is no exception in this respect. Verbal or written instructions, if effective in yielding learning also lead to the deposition of new memory contents. Cultural traits, defined earlier as behavioural items that are acquired through imitation, instruction and related processes, 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. Long-term memory contents are laid down in patterns of structural brain modifications. Memory deposition involves changes in submicroscopic nervous structures, the synapses. Synapses are structural arrangements that establish information-transmitting contacts between neurons. Due to the particular patterns of simultaneous activation of pre- and postsynaptic neurons that arise during learning, certain synapses pass from a state of relative inefficiency to a state of relative efficiency, from what in neurophysiological slang is called a "cold" state to a "hot" state, somewhat like bits in a computer memory that are set from a 0 off-state to a 1 on-state. In some instances learning may even lead to formation of new synapses or the deletion of old synapses. Much as computer memory bits also store information when they pass from a 1 to a 0 state there seem to be instances where learning is associated with synapses passing from a hot to a cold state or even disappearing altogether.

The human brain contains perhaps 10^{15} variable synapses. Such plastic synapses have to be thought of as the critical components of neural networks that function as associative arrays. Synapses in these networks that are doubly activated in temporal coincidence modify their transmitting properties. It has been shown mathematically and checked empirically that associative 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- (as in computers) retrievable and furthermore that it is stored in a highly distributed way. Special versions of these networks show interesting properties such as being capable of self organisation, or being capable of categorizing input patterns.

Any cultural trait that is taken over by a given individual from another individual must accordingly be thought of as the transfer of a particular pattern of synaptic hotspots within the associative networks of one brain to the associative networks of another brain. Different traits must be thought of as being coded by topologically different hotspot patterns. That is, a given cultural trait borne by an individual is encoded informationally as a particular pattern of modified synapses in his brain. Naturally the hotspot pattern 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. For that, the brains of different individuals are likely to be too different. But functionally the two hotspot patterns would still be equivalent, at least to the extent that the effective memory contents representing the trait were identical. As an analogy the reader may think of the same text passage stored on two different kinds of floppy-discs by two different computers: spatially not identical but informationally equivalent.

Culture as represented in an individual's brain is accordingly nothing but a large collection of configurations of hot synapses that are able to instruct cultural behaviour. Each cultural trait is coded by such neuronal constellations. The cultural heritage process can be conceived of as a passing on of these constellations from one individual to another, or to several others. Obviously it is not a bodily replication of the structures but there is nonetheless a multiple transfer of equivalent structures. Biological traits are said to be coded in genes (sequences of the bases adenine, thymine, cytosine and guanine along the backbone of the DNA molecules). Analogously, cultural traits can be said to be coded in memes (constellations of activated and non-activated synapses within neural memory networks). It is true that genes replicate in a quite direct manner whereas memes do so more indirectly through mediating communicative behaviour among individuals. But even among genes, replication can sometimes be less than straight. Parasitic RNA retroviruses, the aids virus being a notorious example, have genes that replicate quite indirectly. They have, as it were, to borrow the DNA and the DNA-instructed cellular machinery of host organisms to achieve reproduction. Memes are capable of instructing, not protein synthesis as genes do, but behaviour. Indirectly, through protein synthesis genes can do that too. Much as genes, memes can remain dormant for periods of time. They may need to be activated by specific events before they are translated into behaviour.

The material configurations in neural memory that code behavioural cultural traits can be said to be memes in analogy to genes. Memes formally share the essential properties that make genes the key protagonists of an evolutionary process. They are obviously capable of replication, even if in a somewhat roundabout way through one or another kind of imitation or instruction learning. Replication is reasonably faithful but not perfect, that is, memes mutate. New song variants arise among songbirds, new words are coined, new rituals are created, new fads emerge among humans. Meme mutations may not seem to be always truly random, but that needs to be looked into more carefully later. In any case random variability is not a precondition for an evolutionary game though it is a salient characteristic of Darwinian evolution.

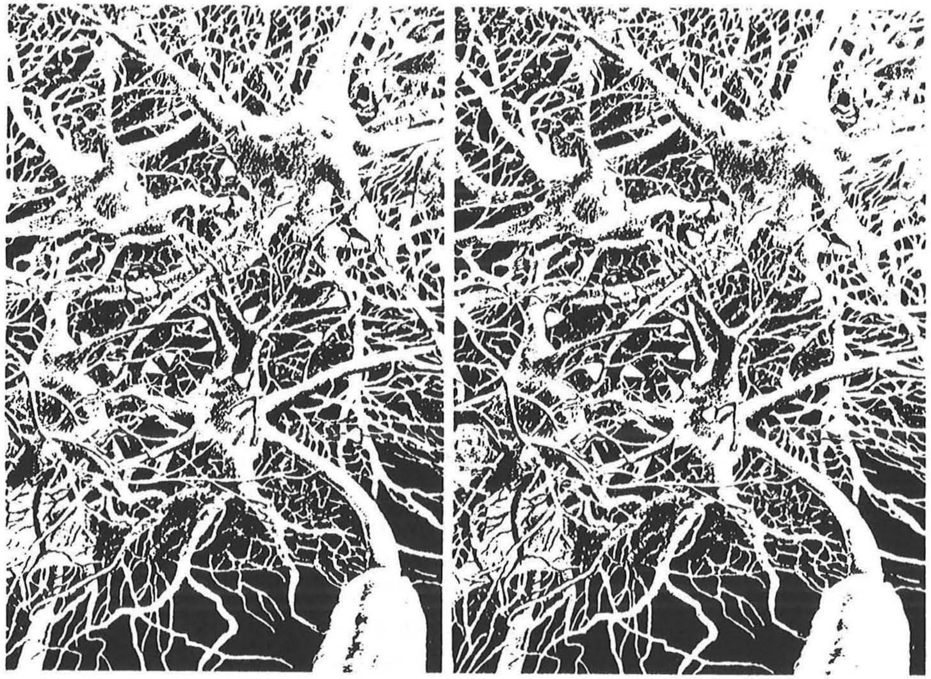

Fig. 2. A cultural trait encoded as a pattern of activated synapses somewhere in the brains of two different individuals (schematic).

That memes are subject to selection, to differential replication, is obvious. Not all cultural trait 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. Different memes can be seen to have different cultural fitnesses, that is memes vary in their potential to produce memetic offspring.

Thanks to molecular genetics, genes can be conceived of as material structures, as specific molecules that code information according to a well understood scheme (sequence of base triplets determine which amino acids are strung together during protein synthesis). Until the fifties, though, 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 still are largely abstract inferential entities, though we know that they are information coded in neural structures. It is possible and even very 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 nevertheless prefer to speak of cultural traits or cultural variants rather than of memes (or culturegenes). That seems linguistically cumbersome. The word meme is a convenient stand-in. Moreover it stresses the transmittance of coded information, rather than of behaviour itself which is a physical impossibility. In genetics it is conceptually essential to separate between a phenotypic character and the genes that determine it. The term gene as used in the context of evolutionary argument can often also be a shorthand for quite complex molecular arrangements that are not made explicit or that are not even precisely known. When discussing the distribution of sickle-cell anaemia among Africans in relation to malaria infection it is for example usual and convenient to talk of "a" haemoglobin gene and its mutations. That ignores the fact that, by a more precise account, at the very least a dozen different, not yet fully understood DNA complexes are implicated in the synthesis of blood pigment. No doubt meme complexes exist in the same kind of way.

6. Symbiosis

Whatever their structure, memes are usually lodged in organisms that are instructed by genes. It may seem that this is a very special circumstance that invalidates or strongly limits any analogy between memes and genes. But this host-guest relationship is common among genes themselves. Many genes lodge in organisms instructed by other genes. Symbiotic organisms, and therefore their genes, are regularly guests of host organisms expressed by other genes. Any human individual for example is normally host to billions of symbiotic organisms belonging to perhaps a thousand different species. A person's precise phenotype is thus not only determined by human genes but also by the genes of all the symbionts that he carries. Three categories of symbionts are distinguished: mutualists, where the host species benefit from the association in terms of Darwinian fitness (gastric flora of ruminants, for example), commensals, which cause neither appreciable fitness cost nor gain to the host (intestinal flora in man, for example) and parasites, which occasion fitness losses to the host (tapeworms in humans, for example). This characterization of symbionts is not always immutable. A given symbiont species can, for example, turn from commensalist to parasite in particular situations. Entamoeba coli, frequently an inoffensive intestinal commensal in humans can become a deadly parasite if the host's health is weakened by other agents.

Striking mutualist symbionts are the mitochondria, extranuclear cytoplasmatic organelles of eukaryotic organisms. Mitochondria have their own DNA that replicates independently of the host cell's nuclear 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. Nowadays, mitochondria are highly integrated into the higher organisms and not capable of independent outside existence.

On their side the host organisms are totally dependent on their mitochondria. Essential processes of cell respiration are controlled by mitochondria. Mitochondria are quite prominent in nerve cells, particularly in presynaptic terminals, as these are metabolically very active. In fact, even the slightest behaviour produced by a human individual absolutely presupposes the activity of these obligatory symbionts in his neurons.

Despite this close dependence on host genes, mitochondrial DNA is subject to an evolution of its own. Mutant mitochondria can emerge, replicate and be favoured or disfavoured by natural selection. The selective agency is mostly the intracellular environment, largely controlled by the host cell's nuclear genes. Sometimes, though, the external environment in which the host organism operates can affect this milieu intérieur in ways that impinge on the fitness of mitochondrial mutants and lead to an evolution of the mitochondria within the individual host. To the extent that the selected mitochondria come to be part of the oocytes' cytoplasm the host's offspring will (maternally) inherit these mitochondria (spermatozoids do not normally contribute mitochondria).

The introns that constitute an appreciable proportion of the genomic DNA of higher animals may be a peculiar instance of commensalism. Unlike from the exon sections they do not instruct protein synthesis as the RNA sections into which the introns translate are edited out by special enzymes. The introns, however, replicate normally during reproduction and growth. It seems that they are functionless gene mutants that are hitching a ride. Introns do not contribute to the fitness of the organism, but do not cause sufficient fitness loss as to be seriously selected against. In certain plants, however, some introns seem to have turned into pathogenic viroids.

Symbionts are frequently responsible for what seems to be a Lamarckian evolutionary process based on the transmission of individually acquired, phenotypical characteristics. An example pertaining to parasites has much practical consequence. When human hosts are infected by pathogenic bacteria they are often treated with antibiotics. If the treatment is not radical enough, randomly generated bacterial mutants that happen to be resistant to the antibiotic survive and the infection will rekindle. The bacterial infection has adapted to changed environmental conditions. The infection that is now passed to other individuals superficially would seem to have an acquired antibiotic resistance, but strictly speaking the resistance is the product of a definitely Darwinian process.

Many different species of parasites invade the nervous tissue of vertebrate hosts and cause behavioural modifications. Encephalitis symptoms of various kinds caused by several different viruses, but also by some bacteria, some fungi, some protozoa and even some helminths, are dramatic examples. Sometimes parasites manipulate the behaviour of their hosts in quite specific ways. The rabies virus infects many different animals but is mainly canids (dogs and their relatives). The hosts' salivary glands are massively invaded by the virus, causing them to secrete infected saliva profusely (foam about the mouth). The virus also invades the nervous system and somehow influences its functioning so as to increase the aggressivness of the host (a previously tame pet will become viciously rabid). At the same time the rabies virus induces an aversion to water so that the animals are said to be hydrophobic. The swallowing of saliva is inhibited. The sick animal is thus highly likely to bite with a large reservoir of infested, undiluted saliva and thus very likely to infect its victim through the wound. In other words, the host's behaviour is influenced by the virus so as to maximise the latter's transmission and replication. The rabies virus furthers its Darwinian fitness at the cost of the host's fitness, partly by manipulating its behaviour. In a sense a rabid dog ceases to be a servant to its own genes, but rather becomes a slave to its viral genes.

The trematode Dicrocoelium is a liver-fluke in sheep. The eggs of this parasite are passed out with the excrement of these animals. Snails that feed on the excrement are intermediary hosts to the first stage larvae (cercariae) that develop from the eggs. The larvae invade dermal glands

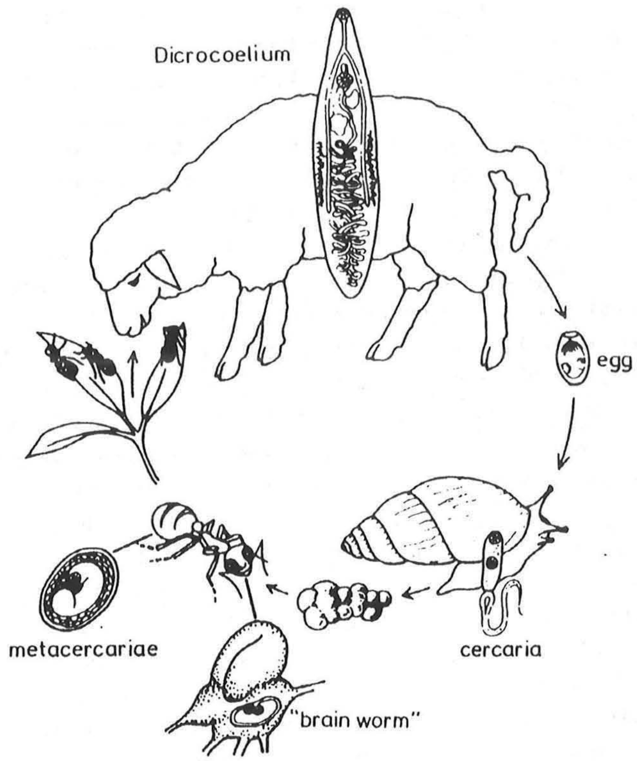

Fig. 3. The reproductive cycle of the liver fluke Dicrocoelium (see text for explanations). From Hohorst (1981), modified.

of the snails and are excreted with the mucus that these produce. Ants who regulary feed on this material are then intermediary hosts to the trematodes' second stage larvae (metacercariae). The majority of the metacercariae infect the abdomen of the ant but one or two regularly find their way into the ant's brain, more precisely to their suboesophageal ganglion and somehow modify its functioning so that the ant comes to exhibit an unusual, pathological behaviour. It climbs upwards on the stems of the vegetation and clamps itself fast onto the upper leaves. The parasites manipulate the host's behaviour to their advantage and to its disadvantage. When the leaves and ants are eaten by sheep these infect themselves with the metacercariae. The latter find their way to the liver and develop into liver-flukes. The cycle can begin again.

Parasites generate selection pressures favouring host mutants capable of preventing or inhibiting infection and multiplication. Immunological reactions that counteract infections but also behaviour that minimizes chances of infection (pelage grooming, clear water drinking, avoidance of sick conspecifics, and so forth) promotes host fitness. Conversely parasites are under natural selection to increase their ability to invade and replicate. Since many reproduce at high rates within the host organism, evolutionary adaptation to immune reactions of the host or even to drug treatments can emerge through selection of resistant mutants even within a single host individual.
The evolution of host and parasites tend to become highly interdependent, often taking the form of an "arms race". Better known examples of such antagonistic coevolution are prey species under selection for better antipredator behaviour and predators that are selected for better predatory behaviour. Predators incidentally, can be said, in some wider sense, to be parasites of their prey. By and large neither ever wins the game, it just escalates: gazelles flee ever faster, cheetahs chase ever faster, figuratively speaking.

A too infectious parasite that kills its host before it has infected a new host kills itself. A parasitic way of life harbours the risk of extinction. Restrained infectiousness may lead to better longer term guest fitness. A mutualistic relationship is inherently more stable. Parasites may thus be under some selection pressure to become mutualists or at least commensals. The asexual clonal mode of reproduction that characterizes many symbionts facilitates the evolution of this restraint that otherwise might require unlikely group selection processes. There is very obviously also selection pressure upon the host organisms to turn parasites, if at all possible, first into commensals and then into mutualists. Similar cooperative coevolution has very visibly shaped the relationship between certain flowering plants and pollinating insects and birds. These latter are in some wider sense also mutualist symbionts. Coevolution of this kind may well be the path by which, presumably, the parasitic ancestors of mitochondria were turned into cooperating mutualists. But there is no certainty that such a process will occur in every instance as it competes with selective pressures that tend to make parasites more virulent. The very large number of existing parasitic species are witness to this. The symbiont-host coevolutionary game is biased in favour of the frequently small symbionts that have a much faster generational turnover than the larger hosts. The potentially higher rate of evolutionary counter- or coadaptation favours the symbionts. That within that framework a parasitic way of life continues to be viable is evident.

7. Memes as Mutualists

In as far as memes are material structures (arrays of modified synapses) that reside in host organisms and that can multiply independently of them, they can be viewed as analogous to the genes of symbionts. In particular, memes can be seen as being similar to genes of symbionts that invade the brain of their hosts and influence its functioning in ways that affect the host's behaviour. Memes are replicating coded information packages that infect some higher animals and manipulate their behaviour. As symbionts can, many memes sometimes survive as passive "spores" (as temporarily forgotten ideas, unread books, unpublished manuscripts, mislaid floppy-discs for example).

In the context of symbiont biology it is essential to distinguish between the genetic fitness of hosts and the genetic fitness of symbionts even though they are often 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[4]. As is the case in symbionts, specific memes or memomes (meme complexes) may survive and reproduce to the advantage, indifference or detriment of the genetic fitness of their hosts, so that cultural traits could be the equivalents to mutualists, commensals or parasites.

Initially, at the phylogenetically protocultural stage memes must forcibly have been mutualists simply because the capacity for culture, the genetically coded ability for imitation learning, can only have spread within a population of organisms if individuals that had 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 that were made possible by that capacity, in other words the first few memes at least must have furthered the host's genes. Imitation learning among some early hominids for example can be imagined to have promoted efficient modes of hunting, efficient ways of tool-making, efficient styles of communication that would have given them an edge over less educable competitors. New gene mutants of hosts furthered guest memes by synthesizing brains that could be easily infected by them. But such mutations were only selected for, if the memes they enabled resulted in an adaptive

advantage for them. Memes at this early stage can be visualized as devices by which the genes of hosts amplified their fitness through a learning capacity extension. They were then close to slave-like symbionts of genes, much as mitochondria are today. Slaves though, have a well-known bent towards independence. How would genes manage to keep memes subdued past the protocultural stages?

Many symbionts, as described before, are subject to evolution within their hosts and not only as they are transmitted from host to host. The same can be said of memes. Individual learning, inventiveness, creativity and thinking continuously generate new potential memes, or meme mutants, within an individual. Within the individual these mutants are selected by various mechanisms. The main selection occurs through the basic principles that make learning generally an adaptive process. In the course of the phylogenetic history of a given species certain events have consistently signalled to its members either a gain in biological fitness (food, sex, or dominance for example) or a loss in fitness (pain, cold, or defeat for instance). Such events tend to acquire a special innate status, they become so-called primary unconditioned reinforcers, appetitive or aversive. They are classes of events that the organisms innately seek or avoid. During learning any otherwise neutral events, that circumstantially precede and predict such reinforcement, come to be sought or avoided through classical conditioning. Similarly, any arbitrary behavioural response, that happens for some reason to generate or produce such reinforcement, is correspondingly enhanced or suppressed through instrumental conditioning. Furthermore, any behavioural plan or strategy that is identified through insight or ideation, as being likely to lead to one or the other kind of reinforcement is retained in or rejected from the mind. At the very latest, thought-up behaviour is put to the test when put into practice. Conversely, any responses or strategies that are no longer effective in yielding appetitive or avoiding aversive end states extinguish and are finally forgotten. Every potential meme undergoes a kind of quality control before it has a chance to be passed to other hosts.

More generally, any learning, ideating, inventing or creating by an individual is, as pointed out by many authors, a process based on variation and selection that has similarities to biological evolution. Emergent meme mutants in that context can be seen as having replicated well within a host organism in the sense that the corresponding memory traces have become better consolidated through redundant, replicate storage. Unsuccessful meme mutants in the same context are those that can not establish themselves in the memory of even one host. Incipient meme variants, just like many symbiotic genes, are selected within their hosts, and not only as they spread to new hosts. The common affirmation that cultural evolution is Lamarckian, that it involves the transmission of acquired traits, ignores the fact that the acquisition of those traits is itself the result of an intrahost Darwinian process. Memes are equivalent in this respect to genes of symbionts which, as described earlier, are often involved in evolution that superficially seems to obey Lamarckian rules, but in fact is truly Darwinian.

The variation and selection principle however also operates as memes are transmitted from indvidual to individual by whatever form of imitation or instruction learning. Imperfect or erroneous transmission is an obvious further source of meme variation, of meme mutations. Potential hosts on the other hand are not completely passive vis-à-vis memes. Host bioevolution can be expected to have ensured that recipient individuals are choosy as to which meme variants they pick up among the many that are on offer. Innate mechanisms that evaluate meme quality in the sense of furthering genetic fitness, will be inevitably selected for[5]. A frequent assessment criterion 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 reducing their number. Another sign of meme quality are obvious signs of biological fitness exhibited by the bearer of a given trait. If an individual is visibly successful, for example by being the strapping alpha male of a group of primates that has access to choice food and many females, then the memes he carries are likely to be fitness promoting and worth taking over by younger group members.

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 operate on the memes that are generated within an individual and that we 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 a remarkable coincidence that it also operates on a variation/selection principle analogous to biological evolution and it is no coincidence that in the past it has been considered a helpful model for understanding learning and memory. However that may be, 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.

To be able to pick up memes one needs opportunities to do so. One way is to socialize, to cultivate acquaintance with others. As a corollary the capacity for imitation learning, for culture, enhances social behaviour. There are parallels in symbiont-host co-evolution. Herbivores for example must seek out conspecifics for infection with their mutualist gastric fauna on which they depend for the digestion of cellulose. This may be one reason for the frequency of herding behaviour among grazing species. There is furthermore evidence that herbivores seek the company of apparently healthy individuals and avoid contact with obviously sick individuals. Culture induced sociality should thus include the avoidance of contact with the culturally aberrant individuals as a trait.

Compressed, the argument of this chapter is that, since genes create the environment on which memes thrive, they have it in their means to filter, to censor, to select memes such that only those that contribute to their biological fitness can survive and proliferate. Culture, in other words, at this point of the argument is yet another strategy "invented" by some genomes to make it in the harshly competitive game of phylogeny. It consists in genes cultivating tame memes in their garden and getting them to work for the masters.

8. Memes as Parasites

How efficient are innate meme-censoring mechanisms? How discerning can gene-instructed brains be about the memes they harbour? The analogous filter mechanism for symbionts, the immune system of vertebrate hosts that we referred to above, for example, definitely falls short of being perfect. Commensal and even parasitic organisms often get past its scrutiny and manage to infect at least some 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 learning by imitation and instruction, that is an augmented capacity for memes, has obviously meant a biological advantage among some higher animal species. As long as the greater proportion 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 chapter sketched one or two mechanisms that could do some of that. However, discrimination between similar meme alleles (variants, mutants), 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 the close cooperation of several genes, in other words the assembly of so-called supergenes. These are known to be slow to evolve.

Mutant memes that do not contribute 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 are hardly going to generate a strong genetic selective pressure towards mechanisms ensuring their removal. Commensal memes (knowledge, beliefs, habits, customs, fashions, rituals, etc. that make no difference to the genetic fitness of their bearers) seem an almost inevitable historical development in any lineage capable of culture. With respect to bird culture it is indeed hard to show that this or that song variety is connected with a biological fitness advantage, even though general more complex song repertoires have been shown to be more adaptive than simpler ones.

In human culture biologically innocuous fads or crazes of one kind or another seem to be legion. Round or pointed collar tips, three or two-button jackets seem unlikely to make any difference to the survival and the reproduction of wearers, even though generally dressing that keeps warm certainly does. It is interesting that often such commensal memes occur linked to other memes whose function it is to attach purported biological significance to these. Round collars and two-button jackets have for example, in a certain fashion period, been said to be "sissy", to be indicative of lacking virility. More globally, music, literature, the arts as a whole involve large and complex meme ensembles that probably are neither beneficial nor harmful to the genes of most of their carriers. They can be conceived as commensals that have colonized a special mental niche, namely the brain structures that more normally control curiosity and exploration, behaviours that normally also contribute much to genome fitness.

Memes, by the fact that they can manipulate the behaviour of their hosts, are in some ways preadapted towards increasing 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 the 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. Drug taking and dangerous sports are likely to be expressions of such memes. In both cases it is easy to see how these memes 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 activate these reward circuits. Much in the same way as saccharin fools the nutrition apparatus, so does morphine fool the reinforcement apparatus. A meme that expresses itself in addictive drug-taking has no trouble in bypassing genetic censure. Playful activity within limits no doubt furthers host viability in several ways. But where is the border to excessive and violent activity that curtails survival and reproduction? An individual has only limited innate information as to when play behaviour begins to reduce Darwinian fitness. It is on the basis of this uncertainty that injurious boxing and excessive jogging persist as cultural traits.

Innate dispositions fomenting biologically adaptive status-seeking create niches for mutualist memes that aid and abet social advance. Frequently though, this is an avenue for parasitic memes. Skin tatoos for instance, are an almost obligatory trait in some cultures. They are the expression of a meme that is definitely associated with

loss of genetic fitness. Tatooing often leads to illness and death through infections. Nonetheless the meme is obviously "catchy", fashionable. That is so because tatoos are perceived as conferring social standing, an attribute that within bounds certainly promotes biological fitness. Genes clearly do not provide humans with sufficient discernment to evaluate fitness gains and losses associated with tatooing. The meme thrives on this uncertainty. Genes, or rather the relevant dispositions that they instruct seem to be similarly undiscerning about resource seeking and holding efforts. Attempting to get the best of the environment is certainly biologically advantageous to an indvidual but at some point the returns cease to justify the costs. It is suspected for example, that occasionally birds 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 consequence of this[6].

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 reduces 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, there are organismic parasites that go one step further and actually castrate their hosts as a means to increase their own fitness. At least within one well known subculture 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. Memes that instruct the use of contraceptives have in recent years spread among Western cultures to the extent that the relevant populations are decreasing in numbers. Clearly the birth control memes reduce the Darwinian fitness of these groups as compared with that of other nations that are still increasing their population. Notice that contraceptives sever the natural link between pleasure and reproduction that normally ensures fertility.

One expects the host's genome, exposed to the selective pressure created by parasitic memes, to counteradapt but, as in the case of the parasite-host arms-race, the faster reproduction rate of memes versus that of genes make counter-adaptation a difficult undertaking. 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, a viral infection, only began to emerge as a genetic trait among rabbits in Australia after the disease had taken the character of a pandemic and the rabbits were close to extinction. The same, although worldwide, development may threaten the human species in connection with the aids virus. No doubt, gene mutations that somehow ensure brains that are resistant, or immune to invasion by parasite memes are at an advantage against those that do not. However, counteradapting meme mutations that bypass the resistance are culturally selected for and so we have a process akin to the coevolutionary arms-race that we know from parasites: hosts evolve improved censoring, memes evolve enhanced propagation.

Meme replication is critically dependent on the availability of host brains. If they reduce host fitness too drastically memes might eventually find themselves without hosts. A meme that promotes suicide is not likely to spread much. At least one ritual mass suicide has in the recent past lead to the extinction of the members of a religious sect, and as a consequence of its memes. As among symbionts there is some selective pressure for less virulent memes. Nevertheless harakiri and kamikaze suicides are persistent cultural traits. A similarity with the bubonic plague comes to mind. There the microbes have to kill the human hosts to ensure the spread of the infection. The fleas as intermediary hosts, only leave and seek new

hosts (rats) when the cadavers cool. These spread the fleas about and with them the pathogens. Preaching suicide may only be successful if done by example, that is meme propagation only becomes effective as the host is killed.

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 selfishness principle, the transmission of mutualist memes should occur mainly between genetically related individuals and less between unrelated individuals. The former are a kin group within which the so-called inclusive fitness mechanism promotes altruism. Such gene-induced altruism has to do with the fact that any given gene borne by an individual is likely to also be present as an identical copy in close relatives, with a probability that is defined by the degree of relatedness. Evolution is indifferent as to which particular identical copy replicates as long as some replicate. Furthering the fitness of a relative, even if at some cost, is thus a reasonable evolutionary strategy for an organism. Among primitive cultures most beneficial memes are indeed transmitted from parents to children, and some more between other relatives. Only few biologically "good" memes are passed on among non-kin. Non-kin on the other hand are mostly genetic competitors, a constellation that promotes selfishness. Non-relations should accordingly be bent on passing harmful memes to each other. Instances in which persons for example passed profitable inside stock-market information to family members, but spread misleading and damaging rumours to the general public are regularly publicised. It is also true though that potential recipients are often wary about taking over memes of any consequence from non-relations. The search for a solicitor, a stockbroker, or a physician among one's relatives when in need of critical advice is commonplace. Friends may however take the role of relatives in such situations. Reciprocity involving a kind of contract between individuals, often in the form of simple friendship, is in fact another altruistic arrangement that can be supported by genes. We shall see later that memes can potentiate this parasite checking strategy.

Whatever the details may be, the sheer fact that parasitic genes are abundant suggests that parasitic memes should also be able to proliferate[7]. Genes are unlikely to be able to come up with 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 nuclear power politics or environmental pollution, could eradicate their human hosts once and for all, even before the parasitic aids virus genes manage to do so.

9. Cultural evolution

Cultural evolution is the inevitable spin-off of an information-creating, information-transmitting,information-translating and information-selecting process. Within a culture the information survives coded as memes in the minds of its participants. Memes express themselves in behavioural traits. Memes reproduce as they consolidate themselves in a given brain and as they are transmitted to other brains. Replication is reasonably faithful, but cultural innovations, meme mutations arise at an appreciable rate. Over time there is a steady renewal of memes. The survival and the reproductive efficiency of all cultural traits is not identical. Some memes spread explosively, other memes are only mildly successful, while many memes eventually go extinct. Cultural traits come and go. Different memes have differing cultural fitness much as different genes have differing biological fitness. 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 phenotypic

expression is the cultural behaviour of these. In their essentials they are not too different from, for example, flu viruses that inhabit the naso-oral cavities of vertebrates and express themselves in host sneezing and coughing behaviour.

Are there cultural equivalents for the more prominent phenomena of biological evolution? The multitude of species and subspecies that populate the earth is perhaps the most striking product of genetic evolution. Speciation consists in the emergence of assemblies of mutually adjusted genes (genomes) that are 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 reasons, but often enough 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 forties and fifties and the MacDonald's subculture in the eighties are witness to this. On the other hand, the tendency for like to mate with like, that is assortative mating according to characteristics such as height, eye colour, personality, etc., helps to maintain biological distinctivness. The tendency for indviduals of like culture to stick together, illustrated by 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 affects 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 individual song styles that the founders brought with them and passed on to their descendants.

Competition is the most 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 that are capable of behaving, the 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 (a share of hosts' behaviour together with the associated time and energy expenditure, often also a share of extraorganismal means such as writing utensils, publicity space, television time and so on). 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 antipredator vigilance is enhanced by socializing: many eyes see more than two. Culturally determined behaviour of the same kind is extremly widespread at least among humans. Religious sects, learned societies, political parties, etc. clearly arise because members are more effective jointly

than singly in spreading the beliefs, the gospel, the memes they bear.

Biological evolution can furthermore promote altruism. It often does so, as was already explained, through the kin selection process. Animal parents behave altruistically towards their offspring because they are furthering their own (replicate) genes that these carry. Aunts, uncles, nieces, cousins, nephews and blood relatives in general, also share a varying proportion of genes. This accordingly disposes them more or less altruistically to each other. Analogously, individuals can share many, few or no memes yielding a gradation of memetic kinships. And indeed, culturally based helping behaviour among genetically unrelated people that have the same beliefs or traditions is widespread. Muslims help Muslims, freemasons aid freemasons, fraternity members assist fraternity members, etc.. Both genes and memes stand to gain in fitness by this kind of convention. In advanced cultures with educational institutions such as schools and universities large numbers of memes are transmitted among unrelated persons. Paternalistic/maternalistic behaviour of teachers/professors towards their "best" pupils/students (i.e. those that have adopted many of their memes) is not uncommon. Such cultural altruism can however also be viewed as an extension of the other form of genetically induced altruism, namely reciprocal altruism. As already mentioned it comes about by a kind of unspoken contract (implying nonetheless "if you do me good, I will do you good"), by friendship between genetically unrelated individuals. Memes encoding mutual helping behaviour make such contracts quite explicit. They institutionalize fellowship.

Competition between biological kin groups can, however, also enhance strife. Howler-monkey bands composed mainly of relations, for example engage in quite war-like agression against ohter bands about trees in fruit. The same, and even more so 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 that the items provide. Megalithic stone circles, pyramids, gothic cathedrals, tulipomania, dangerous sports, fanciful fashions are some examples. Can these be compared to biological extravaganzas such as elk antlers, birds 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 kinds of organisms is closely interdependent in the sense that each kind is a selection agency that affects the evolution of the other, then there is scope for unpredictable, sometimes spectacular developments.

Males and females of one species are often involved in this kind of phylogenetic runaway. 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. That generates selection for males that have such characteristics. But this also leads to breeding for females that have ever stronger preferences. The mutual and spiralling feedback can end up giving rise to unusual features such as the peacock's tail or the bowerbird's bower. Mutualistic memes that are like extensions of genes, are bound to get caught up in this sort of game. The whole bird-song culture is as already mentioned, almost certainly an off-shoot of gene-based sexual selection. Among humans sex-differentiated dress fashions have probably originated in the same way. But both song and fashion memes have undoubtedly come under the influence of other selection pressures than purely sexual ones, some no doubt of an intrinsically cultural kind.

Is there anything in meme reproduction that could support a cultural analogue to sexual selection? Meme replication at first sight resembles the asexual reproduction by simple budding or cloning that is typical of such organisms as virus and bacteria. A meme that somebody carries often descends from just one other meme that somebody else carried. Among American college students for example the meme occasioning art museum visits appears to derive solely from the father's relevant meme. The meme that instigates listening to classical music in the same population originates from only the mother's matching meme. However, other memes are composite descendants of two or more like memes. The propagation of the meme motivating church-going among the same college students for instance, appears to require the fusion of the church-going memes born by both father and mother. This kind of "sexual" meme replication does not always need to parallel the sexual reproduction of the hosts though. A person's memes are often descendants of fusions of memes coming from non-parent persons (relations, peers, teachers). It was in fact suggested earlier that fused multisource memes may be preferred by host genomes because they promise quality. In short memes can procreate mono-, bi- and multiparentally.

It is not obvious though that meme "sexuality" by itself guarantees the operation of a sexual selection analogue in cultural evolution. Rather, cultural luxuriation are more probably produced by the same kind of coevolutionary tangles that are effective in complex biological communities occupying fancy niches like the humid tropics. There the survival and reproduction chances of any organism is 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 that characterizes such communities has lead to the evolution of freaks such as flowers that look like bees, caterpillars that look like snakes, moths that look like hummingbirds, butterflies that look like other butterflies. Analogously, how well a meme does largely depends on the cultural context it finds itself in. Once for example, 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, to fanaticism becomes a strong possibility in this instance. More generally, the selection of memes by memes is doubtlessly a major factor in cultural evolution. The fantasies that this can generate are there for everybody to see in our own culture. Understanding them, however, will be the exciting intellectual enterprise of coming years.

Concluding, the idea that the processes underlying cultural evolution have similarities with those on which biological evolution is based is quite old. A serious analysis of the analogy has however only been pursued in the last two decades or so. Much conceptual clarification is still required. A great hindrance is the lack of empirical data on cultural evolution assembled with the analogy in mind. The purpose of the present essay was to convey and develop some of the concepts that have begun to emerge. It stresses that the parallel that comes closest to cultural evolution is the biological evolution of symbionts[8].

10. Notes

1) None of the ideas or arguments presented in this essay is highly original even though the parallels between symbiontic and cultural evolution are stressed more than elsewhere. To keep the text readable it has been left free of references. The reader should be aware that many of the points, issues, problems and facts raised are more thoroughly and accurately treated in the publications listed at the end. A shorter paper in German on the same matter by the same author is included. Some issues are perhaps more clearly explained there than here.

2) It is well known that a distinction between innate and learned behaviour is difficult and even futile. The reason is that, regardless of the behaviour one has in mind (learning itself included!) there is no behaviour without genes but also there is no behaviour without environment, and probably none that does not involve some learning. In this essay the term "innate" is used to grossly characterize behavioural traits that develop without the environment having more than a supportive role and particularly without any very specific learning being required.

3) At times it is difficult to distinguish culturally and biologically transmitted behaviour at first sight. A disposition towards authoritarianism that characterizes some persons was long thought to be a trait transmitted through education until it was recently shown to be largely genetically determined. Inversely, bird song was long thought to be a typical example of innate species-specific behaviour until it was shown in the fifties to be the prime example of culturally transmitted behaviour among animals.

4) To avoid misunderstanding and even though the context should make it clear it needs stressing that genetic fitness and cultural fitness have nothing to do with right and wrong, true or false, good and bad, just and unjust, etc. A successful meme may easily gives rise to behaviour untrue, unfair and evil. Conversely meme occasioned behaviour may be true, beautiful and fair, and still unsuccessful. Gnostic and ethical values relate tortuously and/or tenuously to cultural or biological evolution parameters even though they are the joint products of both processes.

5) The general ways in which the acquisition of knowledge by individuals is under the control of genes is the subject matter of evolutionary epistemology, a currently fashionable topic. The decision whether given knowledge is going to further their fitness or not is a difficult forecasting task for mechanisms instructed by genes. By definition it is only the future, sometimes the

remote future that finally adjudicates. Meantime genes have necessarily to depend on rules of thumb due to "experience" accumulated during the evolutionary past. As weather forecasters know best, predicting the future on the basis of the past is a hazardous, error-prone undertaking.

6) The fact that besides genes and memes humans often also bequeath/inherit environmental resources such as land, houses and money (sometimes also libraries!) gives rise to a kind of evolution of material means. The process is obviously strongly influenced by memetic information. Conversely, as noted earlier in this essay goods influence the shape of culture in several ways. The coevolutionary interactions that are implied could do with a thorough analysis.

7) Computers that communicate with each other, often still needing the help of human operators, harbour communal knowledge akin to culture. Games, programs, data are passed about and multiply, often illegally. Computers sometimes get invaded by replicating information that behaves parasitically. Reports on computer viruses these days make as exciting reading as historical accounts on the black death or the potato blight epidemics of the past.

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