CULTURAL EVOLUTION: A BIOLOGIST'S VIEW

John Tyler Bonner

Department of Ecology and Evolutionary Biology
Princeton University, Princeton, New Jersey 08544-1003

Received June 26, 1990

Abstract. Culture is defined here as information transmitted from one individual to another by behavioral means. The evolution of culture is discussed in terms of selection of units of behavioral information defined as memes. The relationships of genes, memes, behavior and the role of individual and collective memory in cultural evolution are explored. Changes obtained via human cultural evolution are comparable in magnitude to changes resulting from millions of years of genetical evolution.
KEYWORDS: behavior, culture, genes, evolution, memes, memory.

I. Introduction.

For most people, "cultural evolution" means the changes in the cultural activities, the cultural heritage of human societies. To put the matter on a large scale if we think of the culture of stone age man, and compare it with that of modern western culture, there clearly are enormous differences and the course of changes that lead to those differences over time would certainly be a prime example of cultural evolution. In the discussion that follows, I will spend some time on this aspect of the topic, but much greater emphasis will be put on analyzing the nature and origin of cultural evolution.

The best way to understand the nature of cultural evolution, the passing down of customs and traditions from one generation to another, is to contrast it to Darwinian evolution. Both forms of evolution have a system of inheritance, but as we shall see, those systems are, in some important ways, totally unlike. By such a comparison it will be possible to have a deeper appreciation of the nature of cultural evolution.

Not surprisingly, it is the convention of anthropologists to concentrate entirely on human culture. The idea that animals, with inferior mental powers, could have anything approaching culture has been dismissed out of hand. However, in order to understand cultural evolution and how it differs from biological evolution, there is a great advantage in considering culture in both man and other animals. Because the culture of non-human animals is relatively so simple, it is possible to see the basic elements of culture and how they might lead to an evolutionary change. Furthermore, as we shall see, there are many extraordinarily interesting examples of animal culture which show how culture might have arisen in the first place during the grand course of organic evolution.

a) *Definition of culture.*

Culture is a word that has a large number of definitions. Most of them are designed specifically for human culture, but here we must seek one that is simple and includes all animals. This is not done with the thought of excluding proper anthropological definitions, but rather of finding a definition that would encompass all the more specifically man-directed definitions. Also I will define it in such a way so as to contrast cultural evolution with Darwinian evolution.

Culture will be defined here as information transmitted from one individual to another by behavioral means. Such a definition would include the gamut from the complex information passed from one human being to another, to the relatively simple learning of one animal by imitating the activities of another.

A term devised by Richard Dawkins (1976) is especially useful in understanding cultural evolution. It is the word "meme" for which he gives a very general definition: a meme is any bit of behavioral information; it could be an idea, a belief, a custom, or a lesson. Therefore we can say that cultural evolution involves the transmission of memes.

b) *The differences between memes and genes.*

In contrast to cultural evolution, biological evolution involves the transmission of genes, rather that memes. Genes are in the DNA in the chromosomes of the cells of an organism and they carry instructions on how organisms are to be built each generation; they largely control the morphology of the organism so that it is consistent from one life cycle to the next. Beginning with the work of Gregor Mendel in the last century, and followed by the work of many others right up to modern molecular genetics, we now have a wealth of information on how genes code for specific proteins which in turn are responsible for directing the structure and organizations of the growing animal. In sexual organisms half of the genes come from one parent and half from the other. Changes in the genetic make-up of any individual can come from a reshuffling of existing genes in the sperm and egg of the parents, and from a change in the structure of any one gene by mutation. Although he knew nothing about Mendel's work or genes, Charles Darwin was one of the first to recognize that variation could be the basis of evolution, and those individuals with variations which lead to success in reproduction (more offspring) would

 1049-6335/90/0100-024 $3.00

be favored. In this way, by what he called "natural selection", some genes would be promulgated and others would disappear. Nowadays the concept of natural selection is generally accepted by biologists as the means for the change in structure of animals and plants over geological time. This kind of biological evolution is often called Darwinian evolution, or evolution by natural selection. It could also be called genetical evolution, for it involves the transfer of genes from one generation to the next.

We are now in a position to see that genes and memes are very different things and therefore their mode of evolution is bound to be different as well. This point cannot be overemphasized, and let me explain why.

Gene transmission can take place only from parent to offspring; this is the sole way genetic information can pass from one individual to another. One's genes come half from one's mother and half from one's father and that is the only way they can be transmitted. They go through the germ line (reproductive cells) from one generation to another. Memes, on the other hand, can pass freely from any individual to another, whether related or not. This difference has two major consequences: One is that memes can appear (or disappear) in a population with enormous speed. One need only think of some new fad or fashion that will spread with amazing rapidity, such as a new style of dress, or a new word or phrase, or a new game, and those new memes may disappear with equal suddenness. It is also possible that such a meme will have a relatively long life span, and the dress of certain stone age tribes that exist today no doubt persisted many hundreds of years, while skirt length in the western society will jump up or down annually. Some of the colloquialisms of our children have been invented by their generation and are new to us, yet other expressions go back to our Greek and Latin ancestors. The yo-yo and the hula hoop had short life spans as games, but flying kites has a long history. In sum, the shortest duration of memes can be measured in days, while the longest last hundreds of years.

Gene changes, on the other hand, at a minimum, must be counted in generations. The change in one gene by mutation in one individual is not enough; that gene must spread in a population to give a significant change, which obviously requires many generations. Even animals with short generations such as mice or rats will take from five to ten thousand years to produce a new species. It takes this long for individuals in isolation to accumulate enough gene changes to provide sufficient genetic differences to become a separate species. The time span for elephants, with their very long generations would be correspondingly extended.

The other difference between memes and genes is at a more fundamental level of generalization. All organisms have genes, but only some animals have memes. Memes are the product of genes, but the reverse is not so. One cannot have an organism having memes without genes.

To show in more detail the relation between the two, genes are primarily responsible for the development of the morphology of the animal, and part of that morphology is the complex structure of the brain. We do not yet fully understand how the shape of the neuronal networks produces behavior, but this continues to be an area of intensively active research. In any event genes can produce a structure, the brain, which is capable of transmitting and receiving or learning memes.

Considering the large differences between cultural and genetical evolution it is not surprising that one differs radically from the other. Genetic changes have produced evolution from lowly bacteria to complex mammals over a span of a few billion years. *Homo sapiens*, the most prolific animal in the transmission of memes, has a cultural evolution of staggering changes that have taken place in the last few thousand years.

c) *The selection of genes and memes.*

It is an interesting, but sometimes a dangerously confusing fact that not only genes, but also memes can undergo selection. It is quite obvious that all these ideas, fads, fashions, customs and traditions can either be harmful to individuals within a social group or can be beneficial. With characteristic rapidity, those memes that are detrimental will be stopped, and those that are beneficial will be preserved. In this respect memes are very much like genes, and the general laws which apply to the selection of genes will apply to memes as well; many authors have made analogies between the two to point out these similarities. To give one example, if a medieval monk makes a mistake in copying a manuscript, and this error is then copied by other monks, the whole process closely resembles the appearance of a genetic mutation by a change in one nucleotide in the DNA which is then repeated in subsequent generations. Even in this one example we could extend the analogy, for both the manuscript and the DNA sequence can be proof read with a change that the errors may be rectified before their further replication. However, I shall not dwell on the multitudinous parallels between the selection of memes and genes, but rather on the difficulties of such analogies.

There is the danger of forgetting that the method of transmission of memes is so radically different from that of genes, a matter I have already stressed. Their appearance, their maintenance, and their elimination are achieved by unrelated mechanisms and therefore the laws of selection of genes have only a superficial resemblance to the selection of memes. To illustrate the point, if an environmental change induces a change in behavior of an animal that makes it more capable of existing and competing effectively, the behavioral change, or meme, will remain as long as the environment keeps its new character. If the change were genetic the whole process would be so slow that it would select only for new genes if the environmental shift were a steady, long-term one. So again we come back to the importance of the time scale for the two modes of the passing of information from one animal to another.

d) *The interaction of genes and memes.*

In the last ten to twenty years, numerous authors have become interested in the idea that these two modes of transmission might in some way be related to one another, especially in animals with an elaborate behavior, of which man is the prime example. There is a large and somewhat difficult literature on the subject, much of it making use of mathematical models. (For an excellent review of the literature, especially the work of Cavalli-Sforza and Feldman, Cloak, Durham, Wilson and Lumsden and for contributions in their own right see Boyd and Richerson, 1985).

Let us first examine the problem at the simplest level by giving two examples. The religious sect known as the Shakers, which was prominent at the end of the last century in a region of the United States, had many rules and customs (memes) which they followed and one of these was total abstinence from sexual intercourse. The result was that since they were without children, the sect slowly became extinct, for they were unable to meet the loss by death with new recruits. Since genetic evolution is measured in reproductive success, obviously their gene transmission was zero, all because they possessed a meme that blocked reproduction.

A slightly less radical example is given by Cavalli-Sforza and Feldman (1978) who point out different dialects and languages may have the effect of isolating groups of humans into separate reproductive units, which in turn will effect the respective gene pools of the groups and allow genetic differences to arise.

In both these cases it is the memes that affect the gene pool, but examples of the reverse could easily be found. For instance certain genes might produce brains which are capable of learning more effectively than others, and if learning turns out to be a crucial behavior for survival or competition for food, or escape from predators, then genes will first affect the ability to transmit information by memes, which in turn will affect gene frequency. Note that in all the cases given here genetically determined natural selection is the ultimate effect of evolution, even when initially there has been a selection for memes. The few examples above show that genetical and cultural evolution do and can interact and the outcome can be the result of both.

As I said earlier, these meme-gene coevolutionary problems have been examined by many of the authors cited above in terms of mathematical models. These show, in a theoretical manner, how the two kinds of transmission could interact. The models are useful in showing what might be possible, but in this particular case it is unusually difficult to know where it will lead, and what one can do next. I have a somewhat pessimistic view, that, like the nature-nurture problem, to which it is obviously closely related, the analysis of meme-gene interactions will always remain in an unsatisfactory state. The difficulties of testing the theories are enormous, perhaps insurmountable, and therefore the best we can hope for is that the models become progressively refined and sufficiently simple and clear so that they can guide our intuition.

II. The Evolution of Memes.

Before we can discuss the evolution of culture itself, we must first look at the origin and evolution of the whole apparatus which is capable of behavioral transmission. One wants to know not only how cultural evolution works, but how and why it arose. To answer these questions we will look for the early origins of behavior that could have led to the ability to transmit behavioral information.

a) *The evolution of the nervous system.*

We begin at the very elementary level of the origin of the nervous system which is the foundation of cultural evolution. In the most primitive protozoa there are clearly two kinds of responses to external stimuli. One is a slow response to chemical signals, and the other is a relatively rapid response to all sorts of stimuli, mechanical as well as chemical. The slow response may involve growth or differentiation; the fast responses involve movement away from potential danger signals, or towards food. These rapid responses became increasingly specialized in the evolution of invertebrates so that some cells became well adapted to receive signals (receptor cells) while others specialized in transmitting the impulse from the activated receptor cell to an effector to produce movement, such as muscle or a flagellum. Such transmitting cells are the neurons, and with increasing complexity of the organism they in turn became increasingly efficient (i.e. could transmit with greater speed), and more numerous, and able to control the information from receptor to effector with greater precision. One assumes a selection pressure for control and speed because there arose masses of interconnecting neurons in the form of ganglia and especially a brain which processed information efficiently in a central clearing house.

Even more important from the point of view of the evolution of culture is the possibility the nervous system could provide a flexible response, that is, a variety of possible responses depending upon the conditions. Such flexibility would obviously have selective advantages.

b) *Genes and behavior.*

As I pointed out earlier the structure of the nervous system including that of the brain is largely specified in the genes, so that each generation, during the course of development of the entire nervous system is somehow laid down in a pattern derived ultimately from genetic information which resides in the fertilized egg. Therefore, we may consider that like all other bodily structures, the nervous system has to some degree a determinate structure.

Let us now consider a second level where the genes, perhaps very indirectly, are responsible for a fixed behavior pattern. A good example would be the case of a solitary wasp that will emerge from its isolated nest as an adult, and without any direction or demonstration from other wasps, will hunt the right prey, kill and eat it, mate, and make a nest furnished with food for its offspring which it never sees. Clearly these wasps not only inherit the structure of their neuronal network, but also specific, rigid activities of those neurons. The wasp example is a good one because it shows how extensive inherited or instructive behavior can be in terms of the amount of information stored. All animals have some rigid behaviors, including ourselves, even though in the case of man they are more difficult to isolate and identify because of all the other influences that affect our behavior.

The third and highest level is where an animal is capable of learning and profiting from the lessons. The learning may be imitation, although it may even be via teaching, but what is transmitted are memes. To relate this to the genetic activities I have described for the other two levels, note that during development genes direct the construction of a brain that has the capability to transmit memes. The ability to learn is something that can be achieved only by certain kinds of gene-determined brains.

c) *Behavior and natural selection.*

If one asks the evolutionary question of "Why has learning been selected; what are its selective advantages?", one can make the reasonable guess that such behavioral flexibility gives advantages in escaping predation, or capturing elusive prey, or coping in innumerable ways with a sudden and unpredictable environment.

To return to the three levels, they can be written in the following diagrammatic form:

Level 1 Non-behavioral genes, i.e. structure

A ↑↓

Level 2 Rigid, gene controlled behavior

B ↑↓

Level 3 Learning and meme transmission

The next step is to show that at both the connecting points marked A and B above, there is evidence for evolution in both directions. There is a natural tendency to think of all evolution as going from the simple to the complex, but this is not necessarily the case. It may be true for overall trends, but if one looks at the record closely one can see that each step in a sequence is probably adaptive in its own right, and for this reason natural selection will, as we shall see, pull in both directions, up and down in the three level model outlined above.

d) *Structure ⇔ rigid behavior.*

If we look at the first step (marked A above) it seems elementary and obvious that behavior, however rigid, could be useful for the survival of an organism. One need not start with the elaborate fixed behavior of a wasp, but can imagine an extremely simple beginning. Consider an escape reaction where an animal flees from danger. This clearly has enormous survival value for the individual and it is not hard to see, at least in principal, how a fixed structure of the neuron network, could produce consistently from generation to generation such a fixed behavior. All those individuals lacking it would quickly be eaten, perhaps even before they reproduce.

Having established the principle that behavior may be an advantageous advance over pure morphology, let me now cite a particularly interesting example that illustrates the point. The bower birds of Australia and New Guinea are closely related to the birds of paradise and their geographic distribution overlap considerably. The birds of paradise are a well known example of extreme sexual selection in which the males have extraordinarily elaborate plumage. Following the ideas of Darwin (1871), it is generally accepted that in this case it is the female that chooses the males with conspicuous plumage, leading ultimately to the extreme patterns of the male birds of paradise. These birds are thought to be ancestral to bower birds, which in general have relatively dull plumage, but apparently have developed an equally extraordinary behavior pattern. During courtship, male bower birds build, depending upon the species, either simple avenues, or remarkably complex houses made up of sticks piled up around a small sapling. In some of the more elaborate ones, the bower is decorated by colored objects such as shells, fruits, or flowers and there are some species that paint the inside of their bower with the colored juice of a fruit, which may be purple or green. These bowers are on display for the female to admire, and there is evidence that the more experienced males with the best furbished bower are most successful in attracting females for mating.

The point has been made by Gaillard (1963) that if one compares the ancestral birds of paradise with the more recent bower birds, not only is the plumage less conspicuous, but among the various species of bower birds, there is an inverse relation between the splendor of the bower and the coloration of the male: the birds with spectacular bowers have virtually no fancy plumage, while those with a colorful crest or some such adornment have a much simpler bower. Therefore Gaillard suggests that as the bower birds evolved from birds of paradise, their plumage morphology changed, and progressively was replaced by a a behavioral phenomenon: the construction of the bower. The need to attract females has in no way diminished in this transition, it is simply that the basis of attraction has shifted from morphology to behavior. The presumption is that such a shift makes the male less conspicuous and therefore less subject to predation, but at the same time he avoids losing his sex appeal.

Let us now consider the possibility that this transition from morphology to behavior can be reversed, that is, where a behavior pattern has been lost and is replaced by a purely morphological pattern. An example of this may be found among the social insects. In primitive social wasps there may be little or no morphological difference between the functional queen of a colony and other fertile females. The true queen retains her dominant status entirely by behavioral means. She is exceedingly aggressive, and for instance should any of the other females lay an egg in a cell, the queen will immediately retrieve it and eat it, after which she will substitute her own egg. In more advanced insect societies, one finds, for instance, the true queen is morphologically different from the other females and this is accompanied by a disappearance of her aggressive behavior. Such is found in numerous species of social wasps and the example best known to us is that of honey bees.

27

Morphological specialization is particularly evident in the large and complex societies of some species of ants and termites where the workers may be of different sizes and shapes. Some tasks are most efficiently performed by small individuals (e.g. brood care), while others are best done by large individuals (e.g. colony defense). There is even a case of an Australian ant where one worker is extremely large, with huge mandibles and seems to carry out the specialized task of crushing a very large and abundant seed, a food upon which the colony is dependent (Oster and Wilson, 1978). These giant workers are the only means of the colony to take advantage of this rich source of food. In some instances in ant societies, the behavior of a particular caste is rigid, and if that caste is removed, the colony will have a deficiency in one or more of its activities. But in other species, as Calabi (1987) shows clearly in a recent review, behavioral flexibility is not lost and if a size class is removed by experiment, workers from other size classes will perform the duties of the missing workers. It might be presumed that this illustrates how closely behavioral and morphological traits are linked, and that behavior in these social insects provides flexibility, while morphology has the advantage of permitting some tasks to be performed with marked efficiency.

The main point from all these interesting facts is that not only did fixed behavior evolve from the structure of the nervous system, but the reverse has occurred also: behavior has been converted back into morphology in these social insects. In both cases, we can make the reasonable assumption that the shifts arose by natural selection, for in each case, we can see obvious advantages to the final outcome.

e) *Rigid behavior ⇔ meme transmission.*

The same arguments for changes due to natural selection can be made between the second and third level. Again, we will show examples where the evolution of learning and meme transmission can only be interpreted as adaptively advantageous, and then cite an instance where this seems to be equally true for the reverse evolution.

i) Bird song and recognition.

Let me begin with a discussion of bird song for it gives the best examples of both learned and rigid behavior. Bird song is generally associated with mating, although it has many other functions as well. It is used in territory maintenance, in mate recognition, in communication between parent and offspring, and raising alarm in the presence of danger. It is an ancient fact that some birds imitate, and captive canaries or bullfinches will imitate master singers, or even musical instruments played by people. That captive parrots can imitate human speech must also have been recognized since the earliest times, and other birds, for instance, mynah birds and even starlings can do the same with different degrees of facility.

All these examples are for birds in captivity, but there is much evidence that imitation of song is also found in the wild to produce dialects in different geographical regions. And indeed it is clear that these regional differences in bird song are cases of meme exchange and therefore of culture in the sense I defined the word. Let me give some specific instances. Many studies have been done on such birds as the chaffinch, white-crowned sparrow, indigo buntings, the New Zealand saddleback, and many others (for reviews see Slater and Tuce, 1979; Payne, 1981; Mundinger, 1982). In some instances new song innovations will appear with considerable frequency so that the dialects are constantly undergoing some modification, while in other cases, a particular song tradition will remain relatively stable for long periods of time. Both the means of transmission (i.e. memes) and the general *character* of the changes in many ways resembles dialect differences of human beings in different geographic regions. It is a clear example of cultural change in animals.

What is less clear is the nature of the adaptive value of such song imitation. There is always the possibility that it has no selective advantage, and that it is a by-product of some other circumstance, such as the passive change due to geographical isolation. Needless to say, this is not a favored view, and there is evidence in some species the ability to imitate is somehow associated with breeding success. Those individuals that master the local dialect will be more successful in attracting females than will stranger. In the case of the New Zealand saddleback, Jenkins (1978) showed that the males tended to migrate to outlying colonies, and could be successful in finding mates only after they learned the new local dialect. Therefore in this case the transmission of memes favors a mechanism of outbreeding. In all these instances, there is not only the production of dialects, but also their recognition by members of the breeding population. In this way it is possible to recognize kin, neighbors, and even individual birds including one's mate. It has been argued that the birds that are so exceptionally good at imitation, such as parrots and mynah birds, might do so to strengthen the pair bond, by inventing a special song that can produce more subtle recognition. However, all these hypotheses are tentative and difficult to prove. Unfortunately, plausibility does not mean certainty.

There are some examples of fixed song pattern which do have an obvious explanation. We might assume that the ancestors of the birds in question had cultural song transmission, but, through natural selection, this was replaced by rigid, genetically inherited song for a very good reason. The examples are the parasitic birds such as the European cuckoo or the North American cowbird. They lay their eggs in the nests of other birds, and their offspring never see their true parents, but only their foster parents. This also means they never hear the song of their own species, yet the following spring they must find mates. Simple isolation experiments have been done with the cowbird, where a female raised in total isolation will respond by assuming a precopulatory position upon hearing a recording of a male, and the isolated male will sing the cowbird song perfectly, without any lessons whatsoever. Obviously, this kind of song emission-and-response mechanism has been dictated by and must have arisen with, the evolution of the parasitic existence of the bird. Therefore, we have again here an instance where evolution seems to be going in reverse: a system of song capable of memes has reverted to a rigid, genetically controlled system of behavior with no learning involved.

ii) Feeding (and drinking).

We can find much more obvious and easy to understand instances of animal culture if we look to feeding mechanisms in animals. Unlike bird song, in each case the advantage is clear for the animal gets more food. Food and water seeking has also another important element which is especially pertinent to cultural evolution; animals often invent new techniques of feeding or drinking which are then passed on culturally. When we come to discuss human cultural evolution, we will see that there too, invention is the key aspect of cultural evolution.

Many of the examples I shall give are well known and have been described many times in the literature, yet they are of such key importance that they will be retold here as succinctly as possible. In each case, we will either see a behavior which is clearly passed on from one individual to another, or in some of the cases, the meme will be a new invention.

In the case of the opening of milk bottles by blue tits in Great Britain, there is both invention as well as cultural transmission. In Britain, the milk bottles are capped with aluminum foil, and apparently some clever individual blue tit in Northern England discovered that if one pecks through the foil one can reach the cream that has risen to the top. This trick was soon imitated by other tits, and Hinde and Fisher (1951) were able to trace the spread of the invention that today is found all over the British Isles. This is clearly the beginning of a cultural evolution.

There are two well known examples among the finches in the Galapagos Islands, which were first described by Charles Darwin in his Voyage of the Beagle. One species of these finches eat the ectoparasites (ticks, etc.) found on the backs of boobies, a large sea bird, which nests in colonies. This in itself may have been culturally transmitted, but also in pecking for the ticks, the finches sometimes cause bleeding in the larger bird, and they have learned to eat the blood of the booby, an innovation that has now become widespread, and apparently non-lethal to the booby (Bowman and Billeb, 1965). Even better known is the species of Darwin's finch that uses a thorn as a tool to tease out grubs from trees. It is reasonable to assume here also that this was one invention that spread by cultural means to other members of the species.

To continue with examples among birds, the work of Norton-Griffiths (1969) deserves special mention. Oystercatchers feed on worms of various sorts, and in regions where worms are sparse, they concentrate on mussels. But mussels are difficult to open and oystercatchers have devised two methods: they either hammer the shell open at its weakest point, or they insert their beak between the two valves to sever the adductor muscle which holds them together. These are difficult maneuvers which is illustrated by the fact that in a region plentiful in worms, the young stay with their parents six to seven weeks, but if they feed solely on mussels, the period of parental care lasts eighteen to twenty-eight weeks. It takes that much longer for the young to learn the skill of getting the meat out of mussels.

An especially interesting bit of cultural evolution is found in the case of the green heron. It has been known for some time that they have developed a clever method of fishing: they will put out a piece of floating material, such as a feather, or a small piece of stick, and wait patiently for a fish to come and seize it. The phenomenon has been recently studied in some detail by Higuchi (1986) in Japan where it is particularly prevalent in ornamental parks. One might presume that the herons learn the trick from watching visitors throwing bread to the carp, but Higuchi was unable to teach one bird who was quite content to endlessly grab the fish that went to Higuchi's bait, but would not try the whole process on its own. Regardless of who invented this first, man or bird, it is clearly a meme that is passed on among the birds.

If we turn to mammals, especially primates, there are many examples of culture. Again one of the well known examples is chimpanzees' obtaining termites by inserting a stick or a blade of grass into a termitarium, and extracting the termites that adhere to it (Goodall, 1986). This invention involves a tool and is plainly passed on by imitation of others.

Even more frequently cited is the example of Imo, a young female Japanese macaque that invented two methods of cleaning food. These monkeys were kept on an island and fed by throwing their food from a boat onto the beach. When yams were thrown, Imo devised the idea of taking the yam into the ocean and washing off the sand. Even more remarkable was her invention of dealing with kernels of wheat. She would scoop them up along with the sand, throw them into the water and skim the wheat off the surface, letting the sand sink. (Review: Tsumori, 1967). In these studies they also found that the young macaques were the first to learn Imo's invention and the older members of the colony took much longer to adopt them.

In this case, we come closer to human cultural evolution than any other, for the colony of macaques not only accumulated one invention, but two. I shall return to this point later.

There are a number of good examples of food and drink seeking memes in observations and experiments of animals in captivity. For instance, Yerkes (1943) noticed that once a chimpanzee had mastered the method of turning on a drinking fountain it was passed on to other individuals without human help.

In an interesting review of many such cases, Mainardi (1980) describes a similar one for mice. An experienced mouse was placed with naive ones, and only then did they learn how to obtain water from a drinking bottle with a special valve that had to be manipulated with their tongues. Without the knowledgeable guide who could show them the magic trick, they were unable to obtain water. In another set of experiments, house mice were enclosed in a maze, and they could escape relatively rapidly if one mouse was introduced with them who knew the geography of the escape route. Again the other mice learned from the one who had the key; without him they took a long time to escape and find food.

iii) Predator Avoidance.

Most wild animals as we know them are exceedingly shy and flee when approached, but in some regions of the earth where man has rarely penetrated, this is not so. Darwin (1845) found the terrestrial birds in the Galapagos, mocking birds, wrens, finches, doves, and even a buzzard so tame that they could be approached and killed with a switch. He cites Cowley who in 1684 found that "the turtle doves were so tame, that they would often alight upon our hats and arms, so as that we could take them alive; they not fearing man, until such time as some of our company did fire at them, whereby they were rendered more shy."

That this shyness can be passed on culturally is shown well in an example of Douglas-Hamilton (1975). In 1919 the elephants were hunted without remorse by the citrus growers, but they could not eliminate them all and the survivors were enclosed in a fenced-in park in 1930. As a result of this attempt at extermination, their behavior has been permanently altered. "Even today they remain mainly nocturnal and respond extremely aggressively to any human presence. They are reputed to be among the most dangerous elephants in Africa. Few if any of those shot at in 1919 can still be alive, so it seems that their defensive behavior has been transmitted to their offspring, now adult, and even to calves of the third and fourth generations, not one of which itself suffered attack from man".

One of the methods of predator avoidance, especially among birds, is mobbing. By making a great noise and flutter around a predator, a small bird will not only draw attention to the danger which forewarns the other birds, but it may even be successful in chasing the predator away. In some important experiments, Curio and his coworkers (1978) showed that the information as to the nature of the dangerous object to be mobbed could be passed on culturally from one individual to another. For these experiments, they used European blackbirds; two individuals were in separate cages, between them a box was placed with partitions showing stuffed birds. As one bird saw an owl, and another a harmless Australian honeyeater, the first bird would start a great commotion with calls and wing flapping at the owl. The other bird could observe this mobbing, and apparently it soon began to mob the honeyeater, although it never would do this of its own accord in isolation. Now the first bird was replaced by a naive bird and the honeyeater was placed between them so they both could see it. The second bird, which had learned to mob it, did so immediately, and soon the third, naive bird followed suit. They continued this cultural exchange through six naive birds, each teaching the next the supposed dangers of a stuffed Australian honeyeater.

This example is instructive because it seems obvious that there must be some advantages in quickly identifying new dangers. If an unfamiliar predator appears, its identification can be quickly passed on to other members of the species. If the information were transmitted genetically, it would take many years before all the members of a population would be safe from the danger.

There is another lesson here, for besides predator recognition by memes there are also examples where the recognition is inherited through genes. In some early experiments in classical ethology it was shown that young goslings rushed under cover when a hawk-like silhouette was drawn over them on a high wire. This may be another case of the substitution of gene transmission for meme transmission through the aegis of natural selection. Hawks present a danger to young birds from the moment they are hatched before they have a chance to learn and therefore, those individuals with an instinctive hiding reaction from hawks will be safer.

iv) Geographical Information.

Another phenomenon which fits under the general category of animal culture involves memorizing geographic information. If an animal can memorize a nest location, or even better a migration route, and at the same time lead others over that route who will in turn memorize it, it will demonstrate in a partial way, meme transmission. The naive individuals will follow and imitate the knowledgeable guide; therein lies the meme. But perhaps the most important component is the ability to learn the geography, which is done by each individual separately.

The ability of animals to memorize landscape is quite remarkable. This has been shown for insects returning to nest sites, and especially in the case of bees for finding food. Once a bee learns a route to nectar, it can not only find the food again, unerringly, but also identify correctly its own hive.

From the famous experiments of von Frisch we know that honey bees have a very sophisticated system of meme transmission. By means of their dances, a scout can tell the other bees the distance or the direction of a new source of nectar. Once they find it, they navigate by means of their memory of geography. The sophistication of the behavior of bees is truly extraordinary; there is increasing evidence for this, and Gould (1986) has shown recently that they understand local geography so well that they can immediately relocate themselves if they are released from some place away from a known source of food.

In the case of migrating animals, especially ducks and geese (but even monarch butterflies) there is evidence that they follow the same fly routes in their annual migrations. They do this with the young following the older individuals, and by always having an overlap of generations, the route tradition can be maintained.

f) *Conclusion: Why are there memes at all?*

We presume that primitive invertebrates are incapable of meme transmission and all their behavior is "hard wired", that is, fixed and innate. Somewhere during the course of evolution of animals behavioral transmission arose, and again we assume that, in a strict Darwinian sense, it did so because it was adaptively advantageous. Here we ask the question why, and the answers to this question are implicit in all the examples I have just given. They can be summarized in two categories of advantage: 1) one has to do with the far greater speed of transmission of memes over genes, and 2) the other has to do with the fact that more elaborate and complicated information can be transmitted by memes than by genes. Let us consider both of these in more detail.

1) I have already made the point in the case of mobbing that if the features of a new predator can be quickly conveyed to other members of a population, it will be enormously advantageous for survival. This is equally the case for the eating of new kinds of food, or finding ways how to eat those foods efficiently, or even to obtain them so they can be eaten. In all the examples we have given for feeding and drinking, it is obvious that speed is an advantage in spreading new information on the nature of new foods, and how to get the food most efficiently.

2) In the case of geographic information, it is clear that memorizing a landscape using fixed gene determined behavior would be an impossibility. The landscape varies too much from one place to another, and even in one place from one year to another, and a landscape contains so much information that the complexity of the genetic instructions would be beyond possibility. But memory of images of the outside world brought in through the eyes (or the other senses) can be extraordinarily detailed,

since memories can constantly be relearned or added to so that they can adapt to new locations and changes in familiar locations. As we have seen, it is possible by imitation, or by following, to use memes in such a way that one individual will efficiently learn the great mass of geographical information that the other, the leader, possesses. By means of such a system of geographic detail, it is possible to have seasonal migrations, and to forage for food large distances away from the nest. Therefore, with the help of behavioral transmission, it is possible to pass on complex geographical information. And again in this case, the speed with which the information can be transmitted is essential. Considering the advantages of these meme related strategies, it is not unreasonable to assume they arose by natural selection.

III. Cultural Evolution.

So far we have discussed the very general nature of culture and shown how it may have arisen during the course of evolution of the animal kingdom. We now come to the crucial question of how culture evolved. That is to say we want to know how, through memes, it is possible to change the history of animals over the course of time. In doing this, we again want to make a clear distinction from genetic evolution for now we are not concerned with how genes have become altered to change organisms through the course of time, but only how memes have made changes and what effect these changes have had on the organism. Earlier, I pointed out that many authors are concerned with how genes and memes interact, but here I will not stress such an interaction at all, but instead concentrate on meme induced evolution in a pure form. I do not do this to obscure the interesting possibilities that interactions can and do exist but rather to emphasize the distinctive character of the two kinds of evolution. The fact that meme evolution is very different than gene evolution seems to me the point of special importance. Perhaps the biggest consequence of this difference is seen in the fact that we are the only species of animal which has really undergone any continuing and cumulative cultural evolution.

a) *Seriatim Cultural Evolution.*

Cultural evolution is the change of memes over time. One way that memes can change is simply by one behavior substituting for another. Suppose one were dealing with a simple meme such as bird song. Then a particular song may be invented (or happen by chance or error) and this is passed on to other individuals, but later a variation of that song arises in the same way so that over time there are a succession of songs. If one followed the song of a population of singing birds, one could trace the changes in considerable detail and this seriatim sequence would be a cultural evolution.

b) *Memory and Cultural Evolution.*

It is quite obvious, however, that such an evolution would in every sense be trivial for there would be no significant change, but quite literally minor variations on a theme. In order to have a more consequential cultural evolution, another element must be added, and that is significant memory. We have already shown that memory plays an important role in some forms of animal culture. This was particularly the case with migrations and other instances where geographic locations are memorized. As we pointed out, the amount learned can be extensive so that entire routes, in the case of bird migrations, can be followed from year to year.

Clearly all memes involve memory to some extent, for if a meme is learned and then immediately forgotten, it cannot be imitated. The important point with respect to cultural evolution is that with memory, an animal can learn more than one meme, and this accumulation represents another, and an especially important facet of cultural evolution. To remind the reader of an example I have already given, the Japanese macaques accumulated two innovations involving the cleaning of food; the appearance and then retention of those customs in the colony represent a clear case of cultural evolution.

This means that in order to make significant cultural changes, one must not only have innovations, and ways of passing on those means to other individuals, but also a series of such changes can be accumulated by the collective memory of the individuals. In this way, by virtue of memory, it is possible to accumulate a whole series of memes that can be passed on, and now they assume the proportions of traditions or customs.

Among non-human animals, while the kinds of memory we have described are impressive, the number of separate memes that are invented or somehow acquired and then accumulated into the collective memory must be relatively small. This has never been properly estimated for any animal, but if we were to make rough guesses most social insects and the birds that provided so many of our examples probably have from one to five (at the most) of such memes memorized, although it is conceivable that some birds might have a few more.

If one turns to mammals, the numbers will rise. For instance, an Indian elephant may follow up to 21 to 24 different commands from their mahout. Not only that, but the retention of these commands can last a long time in the memory of any one individual; an elephant never forgets! In these cases, the innovations are supplied by human beings, and the capacity of the animal is being tested; this does not tell us how many traditions have accumulated in an elephant society in the wild. Yet the teaching by humans gives some measure of the animal's capacity.

The same point can be made for primates where so much recent work has been done on teaching gorillas, and especially chimpanzees how to communicate in some form of signs that can also be understood by human beings. These great apes will accumulate a vocabulary of more than 200 signs, and furthermore will not just use them to respond to their teacher, but will express wants and needs spontaneously. Therefore, their memory capacity appears to be even greater, but as before we are less certain about their repertoire in the wild, and how they communicate with one another. According to Goodall (1986) they have a variety of different calls which seem to form somewhat of a continuum and therefore it is difficult to know how many meanings they can foster, that are remembered. I do not want to enter quite yet into the subject of language, but merely wish to stress

31

that the response to signals is an index of the capacity of an animal to accumulate traditions. Those traditions can be sound signals or some rudimentary equivalent to words in that they bear some meaning, and in this sense the repertoire of grunts and hoots in wild chimpanzees or gorillas could conceivably be the result of cultural evolution of those learned and remembered signals. If we add to those signals various other kinds of learned behavior among wild great apes, it is easy to imagine that we have a sizable number of accumulated bits of culture. Since it is so difficult for us to identify these different signals and customs, there is no knowing how slow or fast is the rate of cultural evolution among these primates. All we can do is observe if some custom is lost or a new one appears, or compare two different populations for cultural difference [as McGrew and Tutin (1984) have shown for grooming postures of chimpanzees in two different parts of Africa.]

c) *Early Man.*

There is every reason to assume the *Homo erectus* and other human ancestors must have come very close to the kinds of culture we have assumed for the great apes. Somewhere during the course of their biological evolution, there must have developed a progressive sophistication of the signalling system between individuals so that ultimately the signals became a language. Undoubtedly, this further increased the amount of cultural change, for with improved communication more information can be passed from one individual to another. The result is the processing of more memes, and provided they remain within the bounds of the memory bank of the individual, they will be retained.

What are the differences between early man, apes, and modern man? The ancestors of man were capable of using tools; in this they resemble apes and other animals. The difference no doubt was one of degree, the increase being helped by improved communication between individuals. It is also possible, although this is a gratuitous assumption, that the capacity for memory has increased. We certainly are capable of remarkable feats of memory, and actors can memorize whole plays of Shakespeare, something we can hardly compare in any reasonable way with the memory of apes, or still less with fossil *Homo erectus*! During the evolution of the homonid line, there has been a great increase in relative brain size and perhaps that increase might be correlated with an increase in the ability to memorize as well as other things, such as an increase in signalling in the form of language.

In any event, the brain capacity of our ancestors was such that it could accumulate by memory a large number of memes. This includes the expanding number of signals associated with the evolution of a true language. The language of modern man could not have arisen full blown from the grunts and growls of apes, but must have followed a slow course of accumulation of new words and new syntax, and each advance would represent the invention and accumulation of new memes. Besides language, there were other inventions that went through the same evolution, such as improved ways of making hunting instruments which followed a progression from stone through bronze through iron for the manufacture of hunting and war weapons. The invention of the controlled use of fire was another, and undoubtedly there were a myriad of others of less dramatic significance.

As these memes increased in number, in order to be retained they had to be stored in the collective memory of a social group or a population. Not every individual need have all the knowledge and skills of the group. In other words, there could arise a division of labor in which some individuals became skilled in cooking, some in making weapons and so forth, and different individuals became repositories of different skills. Such a parcelling out of tasks would have led to an increased total memory of the society or tribe, so no one individual would have to store all the skills and knowledge of the group.

There is yet another way in which collective memory is fostered. It is often argued that *Homo sapiens* differs from non-human animals in that the elders are cared for and maintained during years beyond their ability to reproduce, and that they serve as a memory bank for the customs and the lore of the tribe. If this is so, we see one more instance where specialization helps toward preserving memes in the most comprehensive and efficient manner.

d) *Modern Man.*

The greatest difference between modern man and early man is the quantity of memes that have accumulated in our history and continue to accumulate today. If this is expressed in terms of the rate of increase of inventions in recent times (from 1300 A.D. to 1900 A.D.). Blum (1978) has shown by bringing the data of various authors together that the increase is exponential and rises at the rate of 25 per cent per century, while the population only increases 2.4 per cent for a century (Fig. 1).

This increase is one way of looking at the phenomenal cultural evolution of man. The reasons for it are not hard to see; they are directly related to the rise of new means of improving the collective memory, that is the invention of additional ways of storing information, which then can be retrieved at any time. The most obvious first step in such a direction was the invention of writing. By transforming spoken language into some form of written or drawn set of symbols on clay or papyrus or parchment, it is possible to preserve a set of memes so that even if individual human beings forget the facts, or die, or emigrate, those facts will be available and retrievable to any other members of the group, as long as the writing is preserved. At first the symbols may have been crude and not very comprehensive reflections of the spoken word, but with improvements that was solved, as was the convenience of the writing materials in the evolution from clay tablets to modern paper made from wood pulp. Next came the invention of printing, the filing of information in the form of books, and the formation of libraries to store the books. Consider the amazing volume of information in even a small library, and a large one such as any of the great national libraries, the quantity of memes they contain is so large, it is almost beyond our comprehension.

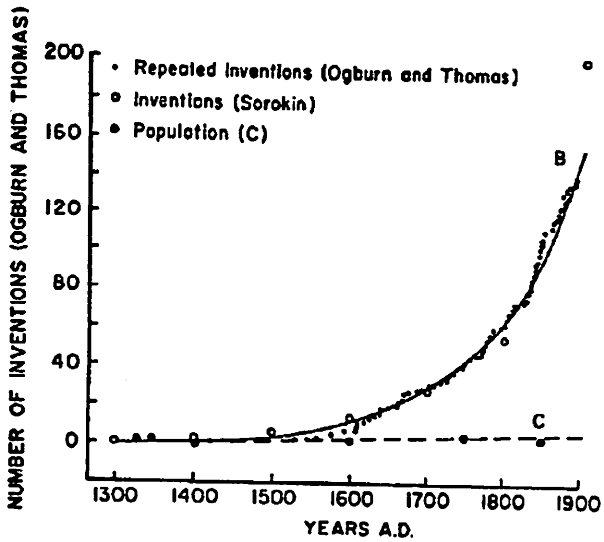

Figure 1. - The number of innovations plotted cumulatively against time. The data of Ogburn and Thomas are for the repetition of inventions, while Sorokin's data are for original inventions. (In order to bring the two curves to the same level, the data of Sorokin have been multiplied by an appropriate constant.) Both the invention curve (B) and the population curve (C) rise exponentially, the former at the rate of 25 per cent per century, while population during the same period rises only 2.4 per cent per century. (From H. F. Blum, 1978.)

To continue along the same line of thought, consider our most modern methods of fast and efficient storage of information. Today, the computer holds the fore, but it was preceded by progressively faster methods of typesetting and typewriting, and even storage and retrieval of paper files. Now all these things can be done in milliseconds by computers and instead of filing paper, one need only file tapes and discs. Besides computer banks of written information, we can also store pictures and even moving pictures in the form of film and video tape. Our methods of increasing the size of our memory bank have become so efficient that often one wonders if they have not exceeded today's needs. However this may be, it is easy to understand that the exponential increase shown in Figure 1 continues right up to the present.

Therefore, one of the most significant aspects of human cultural evolution, and one that places it on a far more prolific and successful level than the cultural evolution of any animal, is the invention of methods of improving memory storage and retrieval. This is at the root of all the great cultural changes that have occurred in modern times. It means that the total bank of memes at our disposal is enormous and all our other inventions, innovations, and even changes in style or custom are likely to rest in this great repository. But even then it is not just the size of the bank, but the efficiency of retrieval and the efficiency of transmission for we have numerous remarkable methods of passing on or communicating memes: from letters and the postal system to newspapers, telephone, radio and television.

IV. Conclusion.

We began by defining culture as the passing of behavioral information (memes) from one individual animal to another, and stressed the great differences between this kind of transmission and genetic transmission, or the transmission of genes which is responsible for organic evolution (biological evolution, or Darwinian evolution, or genetical evolution by natural selection). In a survey of non-human animals, we found many evidences of transmission by memes, however for different animals there were differences in the number of memes that are transmitted. In insects and birds there are few; mammals, and especially primates have more, and *Homo sapiens* have an incomparably larger number. Along with this increase there is also another major component and that is an increase in the storage of memes in the form of memory.

Cultural evolution involves both behavioral transmission and memory of the information transmitted. Therefore, the amount of culture accumulated in the form of customs and traditions is not significant in birds and insects, just recognizable in many mammals, significantly more important in primates, and of explosive and dominant importance for human beings. The latter is so because transmission has been greatly increased though the invention of language and more recently through the invention of writing, and in this century through the invention of electronic methods of sending messages. It is also so because not only is the human brain capable of a large memory, it has devised ways, by a division of labor, of increasing the total memory storage of a social group. Finally, there has also been a progressive increase in mechanical and electronic methods of storing information, beginning with writing and evolving to the computers of today. As a result we have a history, which is our cultural evolution; in a matter of a few thousand years we have made evolutionary changes comparable in magnitude to those of genetical evolution that took many millions of years.

Acknowledgement. I would like to thank Professor Mariou J. Levy, Jr. for his helpful comments on the first draft of this paper.

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* This is an article prepared for the *Enciclopedia Italiana* and will appear there (in Italian).

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