SOMATIC PATHS TO CULTURE

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FOR the present discussion, I am going to assume that culture is a biological adaptation, with non-genetic modes of transmission, which greatly supplements somatic evolution. Viewed in this way, there is a gap between cultural behavior and non-cultural behavior. The two sides of the gap are defined in terms of symbol and lack of symbol. Also, viewed in this way, we see that the gap is bridged. The gap was crossed in the past by the human species, and it is still being crossed by babies as they learn to become human.

Now certainly the behavior we observe in all human societies is fundamentally different in some respects from the behavior we observe in societies of monkeys, apes, and insects. We all recognize the rich symbolic character of human behavior. But I want to stress the bridge —the crossing of the gap from non-symbolic to symbolic behavior—and not the gap itself. To me it appears absolutely necessary to consider

[1] Aside from minor changes, the present paper is the version presented in the American Anthropological Association symposium on the "Evolution of Man's Capacity for Culture," Chicago, 29 December 1957.

both in the history of the species and of the individual that certain conditions are prerequisites for the full acquisition of culture whether by individuals or by the species. And we find these elements in babies before they begin to use symbols and we find certain of them in the behavior of monkeys and apes. Of course the above statements refer to culture in the specific sense of that variety of culture realized by members of the genus *Homo* and not to culture in the generic sense, not to all conceivable varieties of culture.[2]

Since all agree that modern man has culture, or is cultural, the easiest way in which I could discuss the morphological paths to culture would be to summarize the evidence which supports some particular phylogeny leading to man. The argument would then be: 1) Man has culture. 2) This or that phylogenetic diagram tells us how man changed from some non-cultural stem primate in the Paleocene to what he looks like today. In one sense this would be a proper discussion of the somatic paths to culture. It is important, and perhaps lucky, that we can make such pictures of man's biological history with a considerable amount of credibility. But this approach, while valuable, in not sufficient to help us understand the historical biology of human behavior, and I am not going to give it much attention here.

In thinking about human phylogeny, I believe in using all, or nearly all, the hominoid fossils we know about, so long as they are not fragments. To argue that none of the known man-like fossils are in *the* human phylogenetic line seems to me obscurantist. To argue that the fossils we know about are "somewhat near" but not exactly on the main line seems unnecessarily cautious and hedging and may give the unknown greater weight than the known. Perhaps Weidenreich (1946) and Heberer (1950) went too far in using all known hominid specimens they considered authentic. But I prefer their use of all of them to Wood Jones' (1948) use of almost none.

There is not space here to give a review of new developments in human paleontology. In the last few years we have acquired a wealth of new specimens and new ideas and we have also been able to discard some old specimens and ideas with good cause. If additional fossils become available it may be necessary to make major revisions in what I am about to say. By taking an abstract level—the level of

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[2] In a more extended treatment it would be useful to make "society" a level of integration between biology and culture. There are a number of recognizable and important primate "social paths to culture."

the taxonomic genus—I can avoid some undecided issues on the phylogenetic placement of individual specimens. For the moment I am going to assume a human evolutionary sequence of 4 or 5 genera (Clark, 1955):

1) Leaving out the periods before the Miocene, we start with *Proconsul*, the earliest ape whose skull is known (Clark and Leakey, 1951). I assume *Proconsul* had precursors who developed the general features of a man-like thorax and arms as we know them today, but that these terrestrial apes were not highly specialized as brachiators. There is no reason to suppose that any human ancestors since the Miocene have been arboreal to the extent characteristic of living gibbons, orangutans, or chimpanzees (Leakey, 1952; Washburn, 1951).

2) We don't know what happened in the Pliocene.

3) At least by Early Pleistocene there is *Australopithecus*, now known from dozens of good, or as Broom would say, "beautiful," specimens, and the earliest evidence of man-like animals with bipedal locomotion.

4) By Early Pleistocene times, and lasting into Middle Pleistocene in parts of Asia, we have the genus *Pithecanthropus*. From the neck down they were very like the genus *Homo* and like him they were tool makes, fire users, and hunters. Their brain volume was intermediate between *Australopithecus* and *Homo*.

5) At least by Middle Pleistocene we have the genus *Homo*, represented by such forms as Swanscombe, Fontéchevade, the Neanderthals, and Upper Paleolithic man. Everyone agrees that some, if not all, members of the genus *Homo* have culture.

Now, in the context of this sequence of 4 known genera, and with comparisons from living monkeys and apes, I want to discuss 7 biological topics which are preconditions for the beginning of culture. They are:

1) Accomodative vision,
2) Bipedal locomotion,
3) Manipulation,
4) Carnivorous-omnivorous diet,
5) Cortical control of sexual behavior,
6) Vocal communication,
7) Expansion of the association areas in the cerebal cortex.

Of course, these 7 conditions alone did not make a population of apes

lacking culture into a population of men with culture. The evolution of man was not predetermined by a few conditions in a population of Miocene apes. Mutations are the fundamental genetic events in the historical process of the acquisition of the capacity for culture. Mutations are random events that do not point in an orthogenetic direction. But mutations are limited by the structure of the gene which mutates and this structure is determined by the evolutionary forces, especially selection, active in the history of the gene. In this way populations that survive accumulate genes which are favorable in the prevailing environment of the population.

To illustrate the complexity of human evolution since the Miocene as seen at the mutational level, let me do some speculative arithmetic— using figures that have fair justification and are conservative (Spuhler, 1948, 1956; Simpson, 1953). From the Miocene to now there must have been at least two million generations in the hominoid line. If the total breeding population in successful phyla was 10 thousand, we have 20 billion individuals as real or potential ancestors of modern man. If genes at the average locus mutate at a rate of 1 in 100,000, and if only 1 in 200,000 of these result in new and favorable steps (and that is a low estimate), we still could have about 20 thousand "visible," favorable mutational steps (in all loci) since the Miocene in the hominoid line.

Thus when we talk about 7 conditions we are perhaps oversimplifying the matter. But there is not time for further discussion, even if we knew what to say. And, I should add, the 7 conditions I list do not represent unit mutations, although mutation is the ultimate source of the genetic variation in each condition. Further, the order of listing is not strictly chronological. Evolutionary changes in the 7 conditions were interdependent and roughly synchronous.

1) *Accomodative vision.* Vision has been the primary sense in vertebrates as far back as we know them (Polyak, 1957). It makes possible their great mobility. The most complex vertebrates, birds and mammals, interact with their external environment predominantly *via* their eyes. Under the influence of the arboreal habitat, primate vision was perfected into a leading sense. Visual behavior is one key difference between the nocturnal, mostly solitary Prosimians, and the diurnal, more social Anthropoidea. The difference between these two is perhaps the largest gap in non-human Primate social behavior. With upright, or sitting-up posture, vision in the Anthropoidea gained strict control of

manipulation—it became super*vision*, a guide and control of fine manipulation.

The relationship between the evolution of keen vision and fine manipulation is two-directional. As Polyak (1957) says: ". . . vision itself [became] more refined and the intellectual absorption and mental utilization more complete and lasting, as the skilled movements became more complex and more efficient." We will find that this kind of both-way causation with two or more systems evolving simultaneously, where progress in each stimulates change in the other, is important to the understanding of many topics in this symposium.

Before taking up bipedal locomotion, let me mention one good thing that came out of the Piltdown affair. It was the insight given, for example in Hooton's excellent paper of 1925, on the asymmetrical character of human evolution. Hooton was right, mostly for the wrong reason (Piltdown), but he was early to stress that different regions of the human body change at different rates. Many workers today would follow Washburn's (1951) separation of the human body into three regions distinct in phylogeny, with arms and thorax the oldest, the bipedal complex of pelvis and legs later, and the head and face latest of all to reach their modern form.

2) *Bipedal locomotion.* Although functional differentiation of the front and hind limbs started with the first tetrapods where the front legs reach out and the hind legs push, *Australopithecus* is the first primate with upright bipedal locomotion (the tarsiers are bipedal hoppers). The australopithecine pelvis, sacrum, and femur resemble modern man in those features which make his upright posture possible. There are some features of full bipedalism not found in *Australopithecus*—these are fully developed in *Pithecanthropus* from Java and Peking. Australopithecine locomotion was certainly more similar to that of *Pithecanthropus* and *Homo* than to any of the quadramanus primates. We must conclude that, by the early Pleistocene, hominoids were bipedal with free hands which could be used to handle tools. We will see that this was a master adaptation that demanded other adaptations leading to man's capacity for culture.

3) *Manipulation.* A good start toward precise manipulation is seen in monkeys. When monkeys sit up their hands are temporarilly free and are used to bring objects close to the organs of touch, vision, taste, and smell. But something like a quantum jump is made when the hands

are continually free for such activity as they are in an upright, fully bipedal hominoid. Then the arms and hands—under the guidance of binocular vision with good accommodation—are principal organs for interaction with the immediate physical environment. Getting food, eating, grooming, fighting, making, using, and carrying tools, these manipulations, accompanied by a rich flow of sense data including those from the more developed proprioceptive arm-and-hand muscle sense, enlarge the flow of information to the brain which in turn fosters development of association areas for storage of past experience with the hands and guides and initiates new hand movements. The neural delay required when some extra-organic tool is interposed between stimulus and response probably had much to do with the first ability to use symbols and the start of language.[3] The co-adaptation of the hands, senses, and association areas in precise manipulation seems a first basis for the subsequent development of human intelligence.

4) *Carnivorous-omnivorous diet.* Man and the tarsier are unusual among primates in being carnivores. Many monkeys are omnivores and take small animals as prey. Man is unique among living primates in taking large animals for food and these in large numbers.

Fortunately we have some fossil evidence on the problem of diet. It is still an open question whether the Australopithecines were hunters or the hunted. But by Middle Pleistocene times the *Pithecanthropus* of Peking were hunters of large mammals as well as gathers of hackberries and other plant food.

The change to a partially carnivorous diet had extremely broad implications for the social organization of early hominoids. Carnivores get a large supply of calories at each kill. This concentrated food is more easily transported to a central, continually used shelter than is low-calorie plant food, especially before containers were available.

Whoever killed the baboons and bucks associated with the Australopithecines must have been tool carriers as well as tool users. Tool carrying implies a degree of conceptualization not required in the occasional use of tools (White, 1942; Bartholomew and Birdsell, 1953). Before starting on the hunt there must be a minding which associates the tool with an event which is to occur in the future. This type of

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[3] Probably no one today knows the exact significance of this. See C. Judson Herrick, The Evolution of Human Nature, University of Texas Press, Austin, 1956 for suggestions on the evolution of human mentation.

mentation has not been observed in captive chimpanzees or monkeys, and certainly not in wild non-human primates. The archaeological record shows it was a consistent part of *Pithcanthropus* behavior by Middle Pleistocene times.

Compact animal protein high in calories is a good basis for food sharing. Of non-human mammals it is only the carnivores that share gathered food. It is unlikely that the long dependency of human children—so important in the acquisition of culture by individuals— could develop in a society without food sharing. And the amount of information which needs to be transduced in a communication system for plant eaters like the gibbons is small compared to that needed in group-hunting of large animals. Gibbons share, by vocal communication, knowledge about the location of food collected and eaten individually on the site; hominoids share in the location, collection, and consumption of food.

5) *Cortical control of sexual behavior.* There seems little danger that modern anthropologists will overlook the importance of sex in the evolution of culture. Some of us fail to emphasize that, with regard to the physiology of sexual behavior, man is neither a) completely like most other beasts, nor b) completely different from non-human animals. Here, as in many other biological characters, the apes and man are alike and man and the apes are unlike other mammals. In the majority of mammals sexual behavior is seasonal and the sexual periods correspond to times when the female has high probability of ovulation and conception. In such mammals including the lower primates, copulation is evoked by an increase of gonadal hormones in the body fluids. In such animals we can bring about, or prevent, copulation by gonadectomy and hormonal injections. But in man and the chimpanzee, and probably also in others apes, copulation is strongly under cortical control and is not prevented by gonadectomy (Ford and Beach, 1951).

An important adaptation for culture is the change from built-in nervous pathways to neural connections over association areas (where learning and symboling can be involved) in the physiological control of activities like sleep, play, and sex. Cortical rather than gonadal control of female sexual receptivity may not be essential to the hominoid family (observations on other animals suggest not), but cortical dominance in sexual activity may have contributed to the easy transition of the family from a social unit where sex and reproduction were more important than food economy to a unit where subsistence is the dominant familial function.

6) *Vocal communication.* Human speech is an overlaid physiological function. It uses a set of body parts of quite diverse primary action. Consider the muscles used in speaking. Most of our coordinated muscular movement involves corrections and adjustments from proprioceptors. But the laryngeal muscles lack proprioceptors, and feedback control of speech comes by way of the ear and the 8th cranial nerve. When we talk, the voice box, tongue, and lips must work together smoothly and precisely. The 10th nerve controls the adjustment of the vocal cords and the 5th nerve the movement of the lips. Both of these involve branchial muscle while the 12th nerve moves the tongue with somatomotor muscle. The neurological basis of speech is not clear, but it is clear that the only place where the motor organs and steering apparatus of speech are wired together is in the cerebral cortex. Perhaps handtool manipulation in group activities like hunting coordinated by vocalization may have helped to make the connections.

Although the larynx is homologous in all primates its position in the throat differs in man. The larynx of quadrapedal primates from the lemur to the chimpanzee is in close to slight contact with the soft palate. This is why chimpanzees cannot make long, resonant sounds. As a consequence of upright posture and flexion of the craniofacial base, the larynx in man is moved down the throat away from contact with the soft palate, and an oral chamber is formed which makes possible resonant human phonation (Kelemen, 1948; von Bonin, 1955).[4]

This is not to deny a rich variety of vocal production to the chimpanzee and other primates. The position of the larynx, however, is one reason why attempts to teach chimpanzees English have failed. Unfortunately no one has tried seriously to teach a chimpanzee to learn to speak using chimpanzee "phonemes."

7) *Expansion of the cerebral cortex.* Current statements in the anthropological literature regarding the size of man's brain often involve misintepretations in one or the other of two directions. On one extreme, some investigators stress the fact that, compared with *mammals* in general, especially large mammals, man's brain is unusually large, both absolutely and relatively. For example, a 150 pound man has a three pound brain, while a 150 pound sheep has a one-quarter pound brain, and a 1500 pound cow has a one pound brain (Brody, 1945). On the other extreme, the stress is put on the conclusion that man's brain is

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[4] This was written before the publication of E. Lloyd DuBrul, Evolution of the Speech Apparatus, Charles C. Thomas Publisher, Springfield, 1958.

indeed large, but not unexpectedly so. For example, when the log of brain weight in *primates* is plotted against the log of body weight, the slope of the regression line is steeper than it is among mammals in general (proportional to the 0.79th power of body weight in primates, the 0.66th power in mammals), and on visual inspection the plot shows— as log transformations often do—remarkably little scatter (see von Bonin, 1952, Fig. 2), suggesting that brain weight in modern man is just about what would be predicted given the general regression of brain on body weight in primates and a knowledge of man's body weight alone (von Bonin, 1945, 1955). But if we take 1345 gm as a brain weight typical for modern man, say of 60 or 70 kg body weight (Bailey and von Bonin, 1951), we find man's brain is significantly larger than the value of 1095 gm of brain for 70 kg of body, predicted by von Bonin's (1955) regression formula: log brain weight $= 0.79$ log body weight $- 1.00$. A conclusion which avoids both extremes might stress at least two reasons for man's large brain weight: a) about 80% of man's brain weight may be explained because he is a primate of large body size, and b) about 20% of man's brain weight results from an evolutionary increase in the relative size of hominid brains—resulting in a total brain weight which is vast compared with mammals in general, and is significantly large compared with primates in general.[5] One reason we have overstressed the size of man's brain, even among primates, is that the chimpanzee and gorilla have relatively small brains, especially for primates. Similar arguments suggest that the frontal lobes in man, while well developed, are not of extraordinary and unexpected volume compared with other higher primates.

The distinctive feature of the human cerebral cortex is not so much in overall volume nor in relative size of the frontal lobes, but rather in the way that the projection areas are connected with association areas, especially in the temporal lobes, and in the way the whole thing works. I want only to point to these gross anatomical facts; Doctors Gerard and Washburn will take up their interpretation for cultural behavior.

Rates of human evolution. In closing let me call attention to two sets of observations about rates of human evolution, one from paleontology and one from neontology. The first has to do with the rate of hominoid evolution as measured in genera per million years. Consider

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[5] In the oral presentation of this topic, I put more emphasis than now seems justified on the thesis that man's brain is only as big as one would predict for a large and typical primate.

some sequence like this one (based on chronological data from Zeuner, 1954):

PERIOD	MILLION YEARS AGO	GENUS
Miocene	12 (25)	*Proconsul*
Lower Pleistocene	1	*Australopithecus*
Middle Pleistocene	0.5	*Pithecanthropus*
Upper Pleistocene	0.25	*Homo*

Using only known forms, without guesses about unknown ones, this sequence of 4 genera is close to a minimum one for hominoid evolution. Almost everyone would agree that these are good genera, although the taxonomic distance between *Pithecanthropus* and *Homo* is not so great as between the others. If one insists that additional genera must be put in (and probably there ought to be at least one more for the Pliocene) it will only strengthen the conclusion I want to draw. The point is that there has been an unusually rapid rate of hominoid evolution as measured in genera during the past 12 million years, and especially in the past million. This is apparent when we compare hominoid rates with those for horses, chalicotheres, and ammonites (table 1). Something has

TABLE 1

Rates of evolution in terms of genera per million years
(Data, except hominoids, from Simpson, 1953)

LINE	NUMBER OF GENERA	MILLIONS OF YEARS	GENERA PER MILLION YEARS *
Ammonites	8	160	0.05
Horses	8	60	0.13
Chalicotheres	5	38	0.13
Hominoids	4	12	0.25
Hominids	3	1	2.00

* For extant lines: Number of genera minus one per million years.

speeded up hominoid evolution. I would guess that selection (perhaps within-species or inter-group selection) for a new type of environment —a cultural environment—has a lot to do with it.[6]

[6] C. H. Waddington has suggested a non-Lamarckian mechanism whereby variations in ontogenetic pattern initially brought about by environmental influence may, if subjected to strong selection, undergo genetic assimilation. See his The Strategy of the Genes, George Allen and Unwin Ltd., London, 1957.

Ontogenetic rates. Insofar as phylogenetic information can be deduced from observations on living animals, there exists among pri-

TABLE 2

Average duration of prenatal and postnatal growth periods and of life span in different primates (Schultz, 1956)

PRIMATE SPECIES	GESTATION (WEEKS)	MENARCHE (YEARS)	ERUPTION OF FIRST AND LAST PERMANENT TEETH (YEARS)	COMPLETION OF GENERAL GROWTH (YEARS)	LIFE SPAN (YEARS)
Lemur	18	?	?	3	14
Macaque	24	2	1.8–6.4	7	24
Gibbon	30	8.5	?–8.5	9	30
Orang-utan	39	?	3.0–9.8	11	30
Chimpanzee	34	8.8	2.9–10.2	11	35
Gorilla	?	9	3.0–10.5	11	?
Man	38	13.7	6.2–20.5	20	75

mates a general evolutionary trend to increase the duration of the main periods of the life cycle. The evidence is presented in table 2. In the great apes the gestation period is lengthened to at least 34 weeks, full

growth is attained by the end of the 11th year, and animals in their 3rd decade are senile. In man the duration of the prenatal period has changed little, if any, from that characteristic of the great apes, but the duration of the period of postnatal growth has almost doubled, and the total life span has more than doubled. Man is not unique with regard to the gestation period, but he is specialized in the marked elongation of postnatal growth and the long postponement of the onset of senility. These human specializations are extremes of trends found to lesser degrees in the evolutionary history of other primates (Schultz, 1956).

Man, then, is not much different from other primates, especially the apes, in the general sequence of events from conception to birth. After birth, the ontogenetic pattern in man differs markedly from that of all non-human primates but differs in a direction forecast by the general trend of primate evolution. I would guess that this elongation of the life periods after birth is a consequence of physiological adaptation to the acquisition of culture. Culture is a biological adaptation with a non-genetic mode of inheritance depending on symbolic contact rather than fusion of gametes. It has greatly supplemented somatic evolution. In all known human societies, individuals participate in social systems whose members represent more than a single biological family in which all are connected (as the social insects are) by gametes from one parental set. No human family is a self-sufficient system of social action. Symbols rather than gametes make this so. It may be assumed that the genes controlling the growth cycle in man have been changed through selection to man's *human, cultural* environment.

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