Brief Communication

The Mental Arms Race Amplifier

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The use of tools to obtain food is probably a long-standing hominid adaptation. Therefore, the rapid increase in hominid brain size over the last million years cannot be explained by selection for basic tool use alone. Two alternative theories, here termed the ecological adaptation hypothesis and the intraspecific competition hypothesis, are reviewed and rejected. Instead, a combination of these two theories is offered: the mental arms race amplifier hypothesis.

KEY WORDS: hominid evolution; tool use; evolutionary game theory.

INTRODUCTION

In addition to the accumulating evidence that most if not all hominids were tool users (Lancaster, 1968), as well as the discovery of tool use among nonhuman primates (Goodall, 1973), it is apparent that the mental ability of modern humans is far in advance of the minimal requirements for successful tool use in a hunting and gathering setting. Certainly tool use of itself does not require a very large brain (Washburn and Avis, 1958). This suggests that more attention must be paid to later hominid selection pressures.

Two evolutionary theories attempt to explain continued increase in hominid brain size after the establishment of the tool-use adaptation, what I will call the ecological adaptation hypothesis and the intraspecific competition hypothesis. I will argue that neither alone is correct, though a combination of the two could be.

My arguments turn on three major empirical assumptions. First, the variance of potential human mental ability between historically distinct breeding populations is assumed to be small relative to the variance within these populations.

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Second, the ancestral hominid pattern of rate of brain evolution is taken to be slow-fast-stop: that is, slow increase in mental ability as tool use was adopted, followed by rapid increase, ending with contemporary evolutionary equilibrium. Third, the functional minimum mental ability is generally assumed to have increased during this period of evolution.

THE ECOLOGICAL ADAPTATION HYPOTHESIS

The most generally credited explanation of human evolution is the hypothesis that tool use engenders a positive feedback selection mechanism, higher levels of tool use increasing the ecological selection pressures for those traits that enable hominids to use tools (e.g., Washburn, 1957, 1960, 1968; Caspari, 1963; Geertz, 1962). Such traits are of different kinds, from manual anatomy to brain size, but only the latter provides the basis of human mental ability.

It is reasonable to suppose that there could be a period of "increasing returns" to the growth of brain tissue devoted to the programming and data storage requirements for tool-use techniques. If side costs were absent, brain size and associated mental ability should have increased to become arbitrarily large. Clearly this has not happened, because there are fitness costs to increased brain size. Childbirth hazards and infant helplessness due to rapid brain growth are obvious examples of such costs (Gould, 1978).

The evolutionary effects of benefits vs. costs for such a trait are shown in Fig. 1. Evolutionary feedback notwithstanding, brain size cannot increase in-

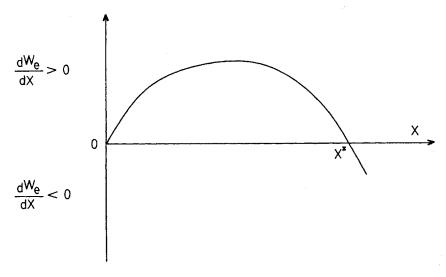


Fig. 1

definitely, since fitness costs eventually equal ecological benefits, at which point selection favoring further increases must cease. Assuming numerous loci having individually minor effects on the x of Fig. 1, evolution should ultimately come to rest at or near x^* , with some variance spreading the phenotypic distribution somewhat about this point.

The problem is that the point where costs equal benefits must depend on the environment. Even for tool users, ecological factors vary significantly from Australia to Alaska. And while the ecological adaptive equilibria must vary between populations due to geographic differences, selection will act to reduce variation about these equilibria. Were mental ability selected for because of ecological selection pressures alone, it should exhibit relatively large between-population variance compared to within-population variance, contrary to my first assumption.

THE INTRASPECIFIC COMPETITION HYPOTHESIS

The second hypothesis for human evolution is that tool use exacerbated hominid intraspecific competition, strongly selecting for greater "cunning" and/or complex forms of social cooperation, and thus mental ability. Variants of this idea have been put forward by Darwin (1901), Keith (1946), Alexander and Tinkle (1968), Bigelow (1969), Alexander (1971), Trivers (1971), Hamilton (1975), Humphrey (1976), and Pitt (1978). Each one requires a relatively specific combination of hominid selection pressures, however. In the interests of a more general theory I will try to express this hypothesis in terms of evolutionary game theory developed by Maynard Smith (1974, 1976).

Central to the intraspecific competition hypothesis is an intraspecific evolutionary game contest. In such a contest, whether violent or peaceful, between tribes or within them, the hominid brain, according to this hypothesis, was an innovatory device to "outwit" opposition.

There does not seem to have been any constraint on tool use in escalated evolutionary game contests (Bartholomew and Birdsell, 1953; Washburn and Avis, 1958). In terms of the Hawk-Dove game of Maynard Smith and Price (1973), a hominid employing its usual hunting weapons without restraint in intraspecific conflict with unarmed opponents would be a Hawk strategist with a significantly reduced risk of injury.

The use of weapons in hominid behavioral evolutionary games would have radically altered the nature of those games. Since weapons are hand-held and not built-in, new weapons could have been invented, yielding an initial advantage to the inventor. Yet this would be short-lived because any opponent would be able to imitate such successful weapon use. Since weaponry tends to equalize nonpathological physique differences, compared with unarmed combat, the

only way to "keep up" with opponents under these conditions is to adopt successful new weaponry, or tactics of weapon use, as quickly as they. To "stay ahead," a hominid would have had to invent ever more effective weapons and tactics. Finally, the most effective innovation would be to exploit other techniques, such as the use of social cooperation to form game-playing alliances, as Bigelow (1969) has suggested.

If this stage was reached, the outcome of each game conflict dependent on only four factors: (1) the particular learned techniques available to opponents, (2) their skill in using them, (3) their general strategic facility, and (4) general strategic biases built into players by natural selection due to enduring advantageousness in the overall competition. Since both (1) and (2) must depend on the specific nature of the extant techniques, natural selection could have acted effectively on factors (3) and (4) only.

It is increase in the third factor, what I have termed strategic facility, that provides the foundation of all variants of the intraspecific competition hypothesis. Increases in characters like brain size, all other things being equal, will increase strategic facility, so defined. We might call this process a "mental arms race."

The problem with this hypothesis is that the evolution of general strategic facility is taken to depend on selection pressures that cannot increase the functional minimum for characters subject to them. In a forthcoming paper, Dr. J. Haigh and myself (1980) analyze such evolutionary games under quite general conditions. Our results indicate that all such games give rise to selection pressures which cannot increase the functional minimum for characters subject to them. Indeed, if mental ability is subject to this selection mechanism, at selective equilibrium the most numerous class of individuals would be those making virtually no investment in increased mental ability. Therefore, if all increases in mean mental ability since the time of the Australopithecines are due to an intraspecific mental arms race, contemporary populations would have very large numbers with roughly Australopithecine mental abilities, contrary to my third initial assumption.

THE MENTAL ARMS RACE AMPLIFIER HYPOTHESIS

It has been argued that the ecological adaptation mechanism can explain a radical increase in the minimum functional mental ability, while the intraspecific competition model explains the contemporary spread of potential mental abilities within populations. An obvious conclusion is to explain the increase in mental ability up to the contemporary minimum in terms of the ecological adaptation mechanism, and then posit a mental arms race after that point. If this were correct, the rate of increase in mental ability should have steadily slowed, due to cultural effects obscuring environmental selection, up to the

point where the mental arms race began, when it should have surged forward. This implies a fast start to these increases, a steady slowing until the modern functional minimum was reached, and then another spurt. Yet there is no reason why a mental arms race could not have begun shortly after an early hominid species became relatively proficient in the use of weapons for hunting and predator defense, i.e., *before* the fitness costs of increased brain size had exceeded the ecological benefits.

There are two further combinations of the two mechanisms: a mental arms race followed by ecological adaptation or an initial mental arms race with a later period of ecological adaptation overlapping with it. Both presuppose that tool use was not required to initiate the hominid mental arms race, hence widespread mental arms races throughout the primates (e.g., Chance, 1962 and Humphrey, 1976). One problem with this view is that the divergent evolution of the hominids from the other primates then requires additional explanatory hypotheses. Another is that if the mental arms race ceased before hominid brain evolution finished, the final pattern of geographic variability should be like that entailed by the ecological adaptation hypothesis.

My hypothesis rests on the assumption that after an initial period of exclusively ecological adaptation, both ecological adaptation and intraspecific competition depended on learned techniques, tool use being the first among them. Thus both the positive feedback selection mechanism and the mental arms race selection mechanism are presumed to have acted in later hominid evolution.

The traits subject to selection in this complex situation can be sorted into three groups. One includes those subject almost exclusively to ecological selection pressures. These should evolve to optima dependent on particular environmental conditions and can be expected to show considerable geographic variation. While there may be some geographic variation in specific human abilities due to different environmental optima for technique-related traits, it is doubtful that it is large. So this first group must be of minor importance.

The second group includes those subject exclusively to intraspecific competition selection pressures. This probably involves only a few broad strategic biases favored in the mental arms race mentioned above.

It is the third group of traits, those subject to selection pressures in both arenas, which I contend have been the key factors in hominid evolution. High "general intelligence" and language are perhaps the foremost human adaptations that distinguish contemporary humans from tool-using primates of low intelligence and more or less upright stance. I contend that these adaptations evolved because only those traits subject to both strong ecological selection and strong intraspecific competitive selection evolved in the transition from early toolusing hominids to contemporary humans, via a selection mechanism I call the mental arms race amplifier.

Consider a general technique adaptation which increases along one dimension. In addition to ecological benefits and fitness costs, which both increase along the same dimension, x, suppose that above some threshold level the use of the technique confers an advantage in intraspecific competition, which itself increases with the other two, so that those individuals with higher values of x have an advantage over those with lower values. These are the conditions for a mental arms race.

If the arms race threshold value of x is less than the x^* of Fig. 1, then the mental arms race will accelerate the evolution of x to x^* , and then smear the distribution of x from x^* upward. The evolutionary dynamics will be those of hominid evolution, with an initial slow increase in x, a rapid middle period due to the arms race acting together with environmental selection, and then a final slowing. However, the distribution of mental ability should show considerable geographic variation as variation in the ecological fitness benefits moves x^* about, and thus changes the mental arms race equilibrium distribution, which I contend is not the contemporary human situation.

Consider a variation of Fig. 1 with the net fitness benefits of x slowly declining to zero, then remaining close to zero for an interval of x values, and finally diverging gradually. This is shown in Fig. 2. In addition, assume that a mental arms race begins before x_1 is reached. This case also entails the actual evolutionary dynamics of hominid evolution, because a cost-free arms race acts quickly to maximize arms investment. Yet this pattern of selection is insensitive to geographical variation in the ecological fitness benefits so long as there is a broad interval of x values over which the mental arms race proceeds without

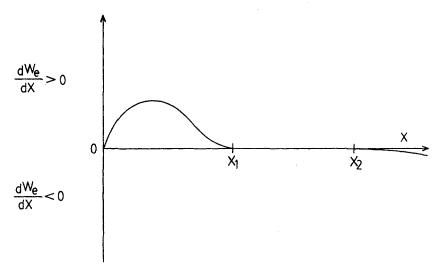


Fig. 2

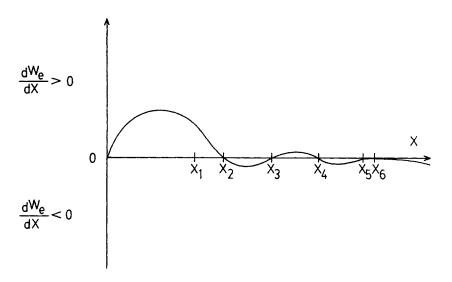


Fig. 3

cost differentials followed by a gradual increase in the arms race costs. Mental arms differences between populations in different geographical regions would be almost wholly obscured because a slow rise in armament investment costs should give rise to a very broad equilibrium distribution of investment.

Of course, the situation depicted in Fig. 2 is wholly improbable. Instead, consider the case of the fitness effects curve falling gradually to meet the zero axis, then criss-crossing several times before finally diverging gradually. This is depicted in Fig. 3.

The mental arms race amplifier mechanism can still work under these conditions. When the ecological fitness effects curve is above zero, the mental arms race will merely accelerate the rate of increase in x due to ecological adaptation. This might be called superamplification. Occasionally, the ecological fitness effects curve will be quite close to zero, allowing virtually perfect amplification, in which case the mental arms race proceeds without cost. Finally, there will be periods when the fitness effects curve falls below zero before rising again. In such instances, an unamplified mental arms race will give rise to a spread of investment levels. Assuming the cost excess does not rise too high and/or the cost excess interval is not too broad, the spread of investment levels brought about by the arms race should bridge the gap between intervals of amplification, whether super- or perfect.

As in the idealized perfect case, the effects of geographic variation should be wholly obscured because the final increase in costs is gradual.

It is apparent that the mental arms race amplifier selection mechanism predicts the evolutionary trajectory assumed at the outset. The increase to the

Australopithecine level can be attributed to the action of the ecological adaptation mechanism alone. The middle period of rapid increase in *Homo* brain sizes can be attributed to an amplified mental arms race in which armament investment costs went largely unpaid. It is important to note that the increasing importance of culture during this period would not have mitigated mental arms race amplifier selection. The final slowing and cessation of mental ability increases can be attributed to the onset of an unamplified arms race and the approach to a polymorphic equilibrium of mental abilities. (It is an interesting feature of this sort of frequency dependent equilibrium that all individuals within the range of the equilibrium distribution should have equal fitnesses if all other fitness effects are equal as well.)

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