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ARE WE STALLED PART WAY THROUGH A MAJOR EVOLUTIONARY TRANSITION FROM INDIVIDUAL TO GROUP?

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This commentary poses an evolutionary hypothesis about the nature of the human condition: that we are stalled part way through a major evolutionary transition from individuals to groups, a transition that may never be completed but that has already shaped our history, politics, psychology, and social life. The conditions causing the transition to stall include the decreasing congruence of group boundaries with kinship boundaries, growth in group size, increasing interdependence of groups, membership of individuals in several types of groups, divided loyalties of individuals among groups, and the emergence of institutions as novel entities uncoupled from the individuals who temporarily belong to them. Those conditions combine to decrease the ability of cultural group selection to effect genetic change in group-oriented traits.

The theory supporting this hypothesis deals with major transitions (e.g., Maynard Smith and Szathmáry 1995), hierarchical selection (e.g., Price 1970, 1972; Frank 1995, 2003; Rice 2004), conflicts and conflict resolution (e.g., Burt and Trivers 2006), and gene-culture coevolution (e.g., Boyd and Richerson 2005; Richerson and Boyd 2005). The evidence is diverse. It comes from biological anthropology (e.g., Hill and Hurtado 1995), behavioral economics (e.g., Hammerstein 2003; Bowles 2004; Henrich et al. 2004), evolutionary psychology (e.g., Barkow et al. 1992), and history. The research programs it suggests are at least in anthropology, history, and political science.

Brief Survey of Major Transitions

There have been fewer than 10 major evolutionary transitions (Maynard Smith and Szathmáry 1995). They include the origins of life (≈3500 million years ago [mya]), of chromosomes and of the genetic code (≈3–3500 mya), of meiosis (≈1500 mya), of multicellularity (≈1000 mya), of the full capacity for language (≈0.1 mya), and of writing (≈0.005 mya).

These are their defining characteristics:

- There is a change in the way information is transmitted from one generation to the next: the nature of the replicator changes.
- A new unit of selection—a new interactor—emerges at a higher level.
- For that to happen, conflicts within lower levels and between lower and higher levels must be suppressed or otherwise resolved. Conflicts may be resolved by brute force, by realignment of information transmission into similar pathways so that partners in conflict come to share common stakes, and by the evolution of mutualism from parasitism.
- As the new unit of selection starts to emerge at the higher level, there is a division of labor with specialization of parts. When the reproductive performance of the higher-level unit starts to depend strongly on the degree to which it has become well integrated–when it has recognizable physiology and development–we call it an organism or individual (Buss 1987).

The major transition in which we appear to be stalled is a transition from the individual to the group: if it were completed, our individuality would be submerged in a group superorganism. Some models of a more advanced—but still far from complete—stage in the transition are the utopian state Plato described in *The Republic* (modeled on the myth of Sparta), the repressive dictatorship described by Orwell in 1984, and the utopian communities of the early Christians, the first idealistic communists, and contemporary religious sects such as the Hutterites. All

are viewed here as unstable and likely to disappear in the long term, but history suggests that something like them emerges repeatedly, just as asex emerges repeatedly from sex and goes more rapidly extinct.

The History that Suggests the Hypothesis

In our lineage the transition from a solitary to a group lifestyle had begun at least by the time that primates began to live in family groups, possibly 50 mya in the Eocene. There followed tens of millions of years in which individuals acquired adaptations to social life through in-group interactions with closely related individuals and out-group interactions with distantly related individuals. At this stage evolution was primarily biological rather than cultural. Psychological predilections and susceptibilities were shaped both by kin selection and by the differential survival of groups that varied in the degree of social cohesion that promotes efficacy in competition among groups. The partitioning of genetic variation within and among groups was such that kin and group selection often worked together to shape group-oriented behavior and were at times formally indistinguishable when viewed as components of a hierarchical selection process (Hamilton 1975; Queller 1992a,b; Frank 1998; Michod 1999).

Eventually social evolution arrived at a stage of the transition that can be observed today in chimpanzees, whose fission–fusion bands hold territories that they defend against neighboring groups in warlike interactions. Chimpanzees react quite differently to encounters with in-group and out-group individuals: they can seek individually to dampen conflict within the group and exhibit behavior that can be interpreted as consoling, reconciling, or pacifying (Boehm 2000).

Chimpanzees are hunter-gatherers, and our ancestors were hunter-gatherers (Marlowe 2005) until some of them domesticated animals and became nomadic herders, a shift that did not make a large difference to in-group versus out-group dynamics. Cooperation remained important within groups, as did aggression between groups. More importantly for the hypothesis advanced here, the origin of language and the accompanying increase in cognitive capacity and tool use led to a huge expansion in the role of cultural evolution. The performance of groups in intergroup competition started to depend both on cultural and on biological characteristics, and cultural group selection began to operate on cultural variation (Boyd and Richerson 1985, 2005).

Cultural group selection increased the representation of groups whose greater social cohesion endowed them with greater efficiency in defense and aggression. Part of the increased cohesion came from biological changes in social psychology; part came from cultural inheritance of social norms biased by innate predispositions that had evolved earlier. Biological evolution provided psychological handles on which culture could pull, and cultural evolution generated selective pressures that could change the biological bases of psychology. Through gene-culture coevolution, individuals became more cooperative with members of the in-group, more willing to sacrifice themselves to defend its interests, more deferential to the authorities that emerged to lead the group in intergroup conflicts, and more susceptible to manipulation by authority. These tendencies were both cultural and genetic in a mix whose components remain hard to estimate.

The identification of individuals with the interests of the group, however, was partial, not complete, and its intensity remained variable among individuals. Some identified more strongly with group interests than others, and despite the emerging group-oriented cultural norms, many individuals retained a strong sense of self-interest. Groups needed leaders to function effectively in intergroup competition, but when leaders emerged, they often used their position to promote their own interests as well as those of the group, sometimes cheating the individuals whom they claimed to serve by exploiting their evolved deference to authority. Thus group members needed leadership but were often in conflict with it. And within the group, individuals continued to experience conflicts of ancient origin over mates, resources, access to power, and other things.

Because such conflicts could have debilitating consequences for group performance, groups in which altruistic punishment emerged had greater social cohesion because punishment repressed conflict (Boyd et al. 2003). Altruistic punishment is defined as punishment of others seen committing an infraction against any group member, related or unrelated, with no direct reward to the individual engaged in punishing. The benefit is to the group, not to the individual, who bears the cost of enforcement but gets no more than her average share of the group benefit. Individuals who responded to punishment with improvements in group-oriented behavior—or who reduced the costs of being punished by avoiding it because they had evolved the capacity for anticipatory internalizations such as shame and guilt—formed groups that were more cohesive and competitive than those in which individuals were less capable of shame or guilt, insensitive to punishment, which they resisted or ignored, and acted in pure self-interest.

(We now call those insensitive to group interest and incapable of shame or guilt sociopaths, a word that is interesting because it implies that the group has become a super-organism—it can get sick.)

Out of this process emerged the striking predilections, sensitivities, and susceptibilities of our group psychology: empathy and sympathy; sin, guilt, and shame; honor, duty, and other precursors of patriotism; the importance we place on our social reputations; and our unusual willingness—incomplete but nonetheless

striking—to wage a war and to die for nonrelatives in a war. Those features of our psychology are seen here as having been shaped in populations with the kind of hierarchical structure in which selection could operate strongly among groups for a long time (Bowles 2006).

From Hunter-Gatherers to Nation-States

The origin of agriculture caused a major reorganization of the selection pressures operating on both biological and cultural evolution. With agriculture, a significant part of humanity began to exist in settlements in which the average coefficient of relationship of those involved in social interactions dropped significantly. Much of life was now mediated by interactions with nonrelatives, many of them strangers, and the need for cultural mechanisms to reduce conflict and to increase cooperation intensified (Seabright 2004).

Ethical ideas about how to mediate social interactions, doubtless long present in oral traditions, were formalized and written down. The social role of religions as givers of laws and sources of social norms became more important. The first written legal codes were already complex: the Sumerian code of Hammurabi (about 1750 BCE) has about 230 dicta, 56 of which refer to marriage or inheritance and 80 of which refer to stealing or cheating; the Hittite code of Nesilim (about 1650 BCE) has about 150 dicta, 11 of which refer to marriage or inheritance and 20 of which refer to cheating or stealing (plus several remarkable dicta on bestiality). They contain strong emphasis on the punishment of those who break social norms, suggesting a prior oral tradition consistent with altruistic punishment.

At the same time, the food surpluses made possible by agriculture enabled populations to expand dramatically, bringing local groups into conflict over space, water, and other resources. Groups organized at a larger scale for self-defense, forming city-states that often warred with neighbors.

Up to this point, before the emergence of the first empires—roughly 3500 BCE in Egypt, Mesopotamia, and the Indus Valley, 2000 BCE in Anatolia, 1500 BCE in Greece and China, 500 BCE in the Andean highlands, later elsewhere—the conditions of cultural and biological selection on human psychology continued and intensified the trends that had started in hunter-gatherer bands. The trends toward a transition from individual to group continued.

Then, roughly when written history begins, small, warring city-states started to condense into local "empires" as particularly strong city-states conquered their neighbors and powerful military leaders forged larger political units. They were often successful in the short term but unstable in the longer term, brought down by internal conflicts driven by warlords and local militias. Weakened, they fell victim to outside enemies. Some vanished. Others passed through a sequence of reorganizations out of which modern nation-states, some of them smaller than the previous empires, emerged. Rome followed by modern Europe is one example; the quite different repeated series of larger empires and smaller, more numerous kingdoms in China and India are others. There has been some opportunity for selection at the level of the state.

The Transition Stalls . . . or Does It?

It is during the period of written history that processes start to develop, which could stall a transition from individual to group, including the following:

- The boundaries of biological populations—especially kinship groups—and the major components of cultural groups—such as language, religion, and citizenship—were often no longer congruent.
- As a result, the boundaries of higher-level groups became diffuse, cultural markers of group identity became less reliable, and loyalties became divided.
- As communication improved and trade expanded, both involved the individual in a network of relationships that extended increasingly outward from the local group, complicating the cultural selection pressures operating on in-group versus out-group psychology and reducing their net effect.
- Within the group, individuals started to belong to a variety of emerging institutions. Economic units (guilds, landowners, peasants), social units (castes, classes), religious identifications, and political affiliations did not overlap precisely. Because one individual often belonged to several different groupings, each with a different membership, the potential for divided loyalties became greater as societies grew more complex. The definition of the in-group became multidimensional; the recognition of the out-group became more difficult; group boundaries became fuzzy.
- Because groups grew larger—villages are larger than foraging groups, city-states are larger than villages, nation-states are larger than city-states, and empires are larger than nation-states—and sometimes endured longer, the frequency of selective events involving groups decreased and with it the opportunity for cultural group selection to shape group performance.

People, however, did not rapidly lose the innate psychological predispositions and susceptibilities toward group-beneficial behavior that they had previously acquired. One reason was that there was still some selection to maintain them, averaged over the new cultural complexities. Another was that genetic change occurs much more slowly than cultural change. For both reasons innate biases on social interactions remained and helped to shape politics

and history. These biases included the in-group versus out-group distinction with cooperation with insiders and aggression toward outsiders, a general sense of "fairness" towards members of the local group and sometimes beyond it, a deference to authority, a willingness to sacrifice—up to a point—for group interest, and a general sensitivity to and tendency to punish those seen violating social norms ("cheaters") (Cosmides and Tooby 1992). Originally produced by biological evolution, these innate handles were readily grasped, reinforced, and transformed by cultural processes.

Others have also seen the tension between the individual and the group as defining an important feature of the human condition (e.g., Eibl-Eibesfeldt 1979; Boehm 1996; Eibl-Eibesfeldt and Salter 1998; Bowles 2004). Bertrand Russell used it as one of the issues around which he organized his history of western philosophy:

> From 600 B.C. to the present day, philosophers have been divided into those who wished to tighten social bonds [disciplinarians—e.g. Plato, Nietzsche] and those who wished to relax them [libertarians- e.g. Democritus, Popper]. . . Every community is exposed to two opposite dangers: ossification through too much discipline and reverence for tradition, on the one hand; dissolution, or subjection to foreign conquest, through the growth of an individualism and personal independence that makes cooperation impossible, on the other hand. (Russell 1984, pp. xii-xiii)

Russell noted that history could be understood as the replacement of poorly coordinated individualistic societies by competitors that drew their power from social cohesion, and cited the absorption of the Greek city-states by Rome as an example.

Logical Status

The scenario sketched above is not yet up to the standards used in evolutionary biology. In drawing on both the natural and the social sciences, it pulls together ideas from fields that have different standards for the admission of evidence and different definitions of the point at which an argument is judged to have become reliable.

As a natural scientist, I am comfortable with situations in which theories make quantitative predictions, well-controlled experiments test those theories, alternatives are ruled out, and causation is established. In contrast, most of the evidence on which this scenario is based is descriptive, not experimental. It is consistent with the ideas advanced but can only render the conclusions plausible—not necessary. Many of the authors whom I have read seek to confirm hypotheses, not to test them in situations in which they are at real risk (there are some notable and praiseworthy exceptions). Even the most self-critical discussions are often couched in terms of concepts that are difficult to reduce to concrete mechanisms that can be observed and measured.

Thus this might seem to be a hypothesis not yet worth pursuing, one not yet part of Medawar's (1967) "art of the soluble." But I would not want work on it to be suspended without letting it have a good shot at attaining rigor, for if it does capture a significant piece of reality, it would tell us something very important about what we are, and it might help to explain major features of our history and politics. In such a case it can be better to get approximate answers to important questions than precise answers to trivial ones. And there are reasons to be optimistic, one being the work of experimental behavioral economists: elements of the logic are becoming stronger and are being tested (cf. Hammerstein 2003; Bowles 2004; Fehr and Rockenbach 2004; Henrich et al. 2004; Boyd and Richerson 2005).

Key Issues

Attaining the rigor that would satisfy natural scientists will require further work on many issues, among them these:

1. In what sense does evolution create biological "handles" on which culture can "pull?" The metaphor is plausible but fuzzy. Can it be made precise and measurable? The "handles" refer to our innate predilections, susceptibilities, motivations and biases, investigated by the cognitive scientists, evolutionary psychologists, and philosophers who accept the hypothesis that important features of our minds are innate. A recent summary of their progress can be found in Carruthers et al. (2005, 2006), a reading of which indicates that the field is quite lively but a long way from achieving consensus by eliminating alternatives, discovering mechanisms, and exporting conclusions that can be used as reliable tools in other contexts. Its initial exploratory phase has not yet settled down.

   Given the difficulty that mainstream evolutionary biology is having in discovering the major features of the genotype–phenotype map for traits with much less-complex causation than psychological ones, this is not surprising. The causal path from genes to mind is complex, long, full of environmental influences, shaped by learning, and as yet poorly understood and ill defined.
2. What is meant by "pull" and how can its strength be measured? This is the bailiwick of gene-culture coevolution (Boyd and Richerson 2005; Richerson and Boyd 2005), where substantial progress has been made in establishing the plausibility of the idea. But—to invoke a standard criterion of evolutionary genetics—can we identify any genes whose allelic variation is associated with variation in group-oriented predilections, susceptibilities, motivations, and biases? And are the frequencies of such alleles responding to cultural change in a consistent fashion that is moving us further in the transition from individual to group? We do not know the answers to either of those two important questions.

It is one thing to assert that our culture is evolving stronger social norms and making moral progress, even if with strikingly tragic fits and starts. It is quite another thing to demonstrate that our evolving culture is changing the frequencies of genes that indirectly influence the innate component of behaviors that promote group integration. There is some evidence for moral progress in the history of the last three millennia—the horrors of the 20th century notwithstanding—but no evidence that I know of for culture changing the frequencies of genes that influence group-oriented behavior. As the example of Darwin shows, considerable progress can be made without genetics, but the discussion within evolutionary biology will not be concluded until the genetic issues have been dealt with. If we had adequate phenotyping in a sufficiently large case-control or multigeneration study with whole-genome sampling, some answers might be attainable (cf. The Wellcome Trust Case Control Consortium 2007).

3. Are we actually stalled, or are we continuing to change? If our individualistic and kin-oriented biology is in conflict with our group-oriented culture, and our culture but not our biology is changing in the direction of greater group integration, then innate conflicts between individual interest and group interest are not disappearing—they are growing. If we think of this process as a hierarchical selection model formalized in the covariance mathematics of the Price equation (Price 1970, 1972), then to judge the ability in principle of cultural group selection to continue to change the frequencies of genes associated with group-oriented behavior we must measure how variation in the innate component of group-oriented behavior covaries with individual and group reproductive success. How strong are those two correlations? Do they have the same or opposite sign? Are such behaviors heritable? It is one thing to assert that hunter-gatherers, for example, were sufficiently genetically differentiated for group selection to produce a response in alleles at loci whose function is unknown (Bowles 2006). It is quite another to demonstrate the connections between allelic variation, behavioral variation, individual reproductive success, and group performance.

Leaving the difficult genetic issues aside for the moment, how should we define groups and measure their performance in modern cultures? Large modern groups can have an existence independent of the individuals that temporarily belong to them and then move on to other groups, leaving the group intact and functioning. Think of the turnover of minerals in bone or of cells in skin: "in everything alive form is more persistent than matter" (E. Szathmáry, pers. comm., recalling Aristotle). That statement needs qualification, for it appears that large groups are more stable when they have high individual turnover, whereas small groups are more stable when individuals persist in them (Palla et al. 2007).

That individuals can move among groups, belong to several at once, and have divided loyalties thus does not necessarily impede the cultural evolution of groups. But it does complicate the relationship between cultural and genetic evolution and may increase rather than decrease the conflicts felt by biologically evolved individuals encountering culturally evolved groups. Whether such conflicts have or will become strong enough for biology to put the brakes on cultural evolution is an important open question.

Conclusion

Human evolution and history suggest a hypothesis: we are stalled partway through a major evolutionary transition from individual to group. I think this hypothesis is plausible and consistent with the evidence, but consistency is a weak criterion—necessity and sufficiency are much stronger. Can the logic be strengthened? Doing so will take not just a lot of work; it will take the maturation of entire fields still in their infancy. But if the hypothesis does turn out to be even partially true, it will be very important, for it says a great deal about the major issues that frame our lives.

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