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Emotions, Not Just Decision-Making Processes, Are Critical to an Evolutionary Model of Human Behavior

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subfield both within and beyond psychology take the "the brain as a decision-making organ" and "the fitness-enhancing character of the human brain" as the central starting point for their research.

There is considerable convergence in the two frameworks (on culture, evolutionary game theory, etc.), but it is illuminating to examine where they diverge. For example, EP would consider evolutionary game theory an ultimate – not a proximate – theory. More importantly, EP rests on the recognition that in cause-and-effect terms, it is the information-processing structure of our evolved neurocomputational mechanisms that is actually responsible for determining decisions. This is because selection built neural systems in order to function as computational decision-making devices. Accordingly, computational descriptions of these evolved programs (for exchange, kinship, coalitions, mating) are the genuine building blocks of behavioral science theories, because they specify their input-output relations in a scientific language that (unlike BPC) can track their operations precisely. For example, kin selection theory defines part of the adaptive problem posed by the existence of genetic relatives; but it is the architecture of the human kin detection and motivation system that controls real decision making, not an optimization function (Lieberman et al. 2007).

The design of these programs is *ecologically rational* (Cosmides & Tooby 1994) rather than classically rational either in Gintis's BPC minimalist sense or in widely accepted stronger senses. Classically, decisions are considered irrational when they depart from some normative theory drawn from mathematics, logic, or decision theory (such as choice consistency, the propositional calculus, or probability theory). Departures are indeed ubiquitous (Kahneman et al. 1982). However, these normative theories were designed to have the broadest possible scope of application by stripping them of any contentful assumptions about the world that would limit their generality (e.g., p and q can stand for anything in the propositional calculus).

Natural selection is not inhibited by such motives, however, and would favor building special assumptions, innate content, and domain-specific problem-solving strategies into the proprietary logic of neural devices whenever this increases their power to solve adaptive problems. These special strategies can exploit the long-enduring, evolutionarily recurrent ecological structure of each problem domain by applying procedures special to that domain that are successful within the domain even if problematic beyond it. These decision-making enhancements are achieved at the cost of unleashing a diverse constellation of specialized rationalities whose principles are often irrational by classical normative standards but "better than rational" by selectionist criteria (Cosmides & Tooby 1994).

Research on the Wason task, for example, indicates that humans evolved a specialized logic of exchange that is distinct from "general" logic – and so produces "faulty" choices. Its scope is limited to exchange, and its primitives are not placeholders for any propositions p and q, but rather *rationed benefit* and *requirement*. It uses procedures whose success depends on assumptions that are true for the domain of exchanges, but not outside it. Because of this, it solves reasoning problems involving exchange that the propositional calculus cannot solve. Evidence indicates that this mechanism is evolved, reliably developing, species-typical, neurally dissociable, far better than general reasoning abilities in its domain, and specialized for reasoning about exchange (Cosmides & Tooby 2005). Indeed, economists might be interested in learning that the neural foundation of trade behavior is not general rationality, but rather, rests on an ecologically rational, proprietary logic evolutionarily specialized for this function. (For comparable analyses of the ecological rationality underlying Ellsberg Paradox-like choices, and an evolutionary prospect theory to replace Kahneman and Tversky's [1979] prospect theory, see Rode et al. [1999].)

The Theory of Mind (TOM) mechanism is a specialization that causes humans to interpret behavior in terms of unobservable mental entities – beliefs and desires (Baron-Cohen et al. 1985). We think that the discipline of economics was built out of this seductive framework through its mathematical formalization, without awareness of the extrascientific reasons why its foundational primitives (beliefs, preferences) seem intuitively compelling while being scientifically misleading. Like BPC, TOM does not see the mind's many mechanisms, resists seeing that many computational elements do not fractionate into either "beliefs" or "preferences," and does not recognize that the "knowledge states" inhabiting these heterogeneous subsystems are often mutually inconsistent (Cosmides & Tooby 2000). The BPC framework is a partial, occasionally useful, ultimate theory of selection pressures that our evolved programs partly evolved to conform to. It is distant from any core model of individual behavior that could unify the behavioral sciences. For that, we need the progressively accumulating product of EP: maps of the computational procedures of the programs that constitute our evolved psychological architecture.

Emotions, not just decision-making processes, are critical to an evolutionary model of human behavior

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Abstract: An evolutionary model of human behavior should privilege emotions: essential, phylogenetically ancient behaviors that learning and decision making only subserve. Infants and non-mammals lack advanced cognitive powers but still survive. Decision making is only a means to emotional ends, which organize and prioritize behavior. The emotion of pride/shame, or dominance striving, bridges the social and biological sciences via internalization of cultural norms.

We agree wholeheartedly that evolutionary theory must serve as the basis for unifying the behavioral sciences. Other, specifically behavioral, theories apply only to some limited domain of behavior, such as personality, learning, cultural beliefs, or cognition. Another strength of Gintis's model is his emphasis on neural mechanisms. However, when he focuses on decision-making, he commits the very same error of excluding essential categories of behavior.

If we step back and view behavior from an evolutionary standpoint, it becomes apparent that fitness-enhancing behaviors themselves, rather than decision-making or other cognitive processes, are paramount. Ultimately, selection can operate only on the behavioral consequences for the individual organism. All animals must execute some basic, essential behaviors, such as feeding, respiration, excretion, defense, temperature regulation, and reproduction. This is true even of protozoans, which lack learning or cognition. Only mammals possess a cerebral cortex, seat of most behaviors of interest to Gintis.

Decision making in simple (but often very successful) animals is virtually absent. Behavior consists of responding automatically to releasers as they are encountered. Therefore, Gintis's model would not apply to these animals, or to the stereotypic behaviors of more complex organisms, such as primates' reflexes and facial expressions. Yet all these behaviors are already included in a model of behavior that is truly comparative and emphasizes naturally occurring behaviors – an ethological one.

A model of human behavior that does not easily integrate data from other species, risks excluding all the emerging information about our close genetic relationship to other species. It also risks ignoring the adaptive features of bodily systems that interact with the central nervous system, thus perpetuating the mind-body schism.

Gintis's model also neglects ontogeny. Tellingly, he states that the mainstays of his model, evolution and game theory, cover ultimate and proximate causation. But Tinbergen (1963) also included ontogeny and phylogeny in his four levels of behavioral explanation. Gintis's model does not easily incorporate the behavior of infants and children, who have inchoate cognitive capacities and yet behave successfully enough to survive. Furthermore, the unity of development and its correspondence with phylogenetic adaptation must be addressed. This means being able to describe how an evolved system emerges from precursors and the processes by which it is transformed and reorganized over the life course to meet adaptational needs.

An ethological model gives prominence to behaviors with great phylogenetic stability, namely, motivated behaviors, or *emotions.* These essential, fitness-enhancing behaviors are guided, in complex organisms, by capacities for learning and cognition. But there is no adaptive value in learning or thinking unless it leads to adaptive behavior. First there was motivation, and only later, in some species, did cognition evolve to enhance the efficiency of motivated behaviors. Phylogenetically, the limbic system, which mediates motivation and emotion, preceded the cortex. Even in humans, the limbic system sends more outputs to the cortex than it receives from it. The cortex is often said to be the servant of the hypothalamus (Wilson 1975).

A model of human behavior that revolves around the emotions would provide a framework for incorporating most essential aspects of behavior. Hunger, thirst, sexual feelings, tactile feelings, tasting, smelling, fatigue, drowsiness, anger, fear, pride and shame, love and loneliness, boredom and interest, and humor appreciation – these are universal affects that prompt our essential adaptive behaviors and have deep phylogenetic roots (Panksepp 1998). They can serve as unifying concepts for many disciplines in the sciences and humanities. Such a model would include the internal as well as external elicitors of affect, the overt behavior that the affect prompts, and the emotional expressions and visceral adjustments that accompany many emotions.

Such a model could incorporate age and sex differences in emotional behavior. The emotions change across the life span. For example, infants possess a sucking drive and a desire for rhythmic vestibular stimulation of the sort experienced when being carried. The sex drive appears at puberty. Various emotions may differ quantitatively between men and women. Emotional pathologies such as depression and conduct disorder vary across age and gender.

A model that centered on the emotions could aid us in characterizing individual and cultural differences. Differences in personality and temperament, including many psychopathologies, are essentially differences in the threshold for various affects. Cultures, economies, and political regimes might be described in terms of their success in addressing various emotional needs. Economic models that reduce human behavior to striving for material goods offer a cramped view of human nature; surely we need to incorporate into our models of well-being intangibles such as esthetic and social factors. We need a current, evolutionary model of human needs and tendencies in order to address the normative questions of the social sciences and humanities. Cognitive and economic models are insufficient.

One great strength of Gintis's model is his inclusion of pride and shame, a neglected emotion involving the orbitofrontal cortex, a limbic structure. Recognizing this emotion, ethologists have argued that striving for approval evolved from dominance striving in other primates (e.g., Mazur 2005; Omark et al. 1980; Weisfeld 1997). Unlike animals, however, humans compete for status mainly in non-combative ways, at least after childhood. Each culture, as Gintis says, socializes its children to adopt values that promote fitness in that particular environment. Individuals who fulfill these values gain fitness advantages, often by helping others and earning their trust and reciprocal help (Trivers 1971). But we also "internalize" other sorts of values, such as those concerning what foods to eat and what dangers lurk. The emotion of pride and shame is not sui generis, a superego; it competes for priority just as do other motives. We seek the approval of others and abide by social values in order to maintain our social status, but if hungry enough, we may steal.

Gintis mentions that his model can explain pathological behaviors such as drug addiction, unsafe sex, and unhealthy diet. However, evolutionists have addressed such "diseases of civilization" effectively without recourse to decision-making concepts (e.g., Nesse & Williams 1994/1996). For example, phobias seem to constitute exaggerated fears of objects that were dangerous in prehistory, such as heights and strangers.

Lastly, Gintis's model privileges laboratory research conducted on isolated individuals performing artificial tasks. This research doubtless helps us to imagine behavior that occurred under the prehistoric social conditions that shaped the human genome. However, we can gain more direct insight by studying spontaneous behavior, especially in forager cultures, given that humans evolved as a collectively foraging species arranged in extended families.

We are driven by our emotions, which are guideposts to fitness. We attend to and remember stimuli with emotional significance. We repeat behaviors that are emotionally rewarding, and avoid aversive actions. Our "errors" in reasoning are often systematic and adaptive, such as self-overrating, which apparently helps maintain self-confidence and feelings of deservedness. Rationality would have evolved only insofar as it served these pre-existing emotions and the adaptive behaviors they prompt. We have labeled ourselves *Homo sapiens*, but it is time to disabuse ourselves of the overemphasis on learning and cognition that has plagued the behavioral sciences since the time of Watson, and philosophy since Descartes.

The indeterminacy of the beliefs, preferences, and constraints framework

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Abstract: The beliefs, preferences, and constraints framework provides a language that economists, and possibly others, may largely share. However, it has got so many levels of indeterminacy that it is otherwise almost meaningless: when no evidence can ever be a problem for scientific construct Z, then there is a problem for Z, for nothing can also be considered supportive of Z.

Herbert Gintis and I share a similar language. It is (if with different emphasis) the language of an extended, socially grounded, and cognitively limited version of rational choice – the language of game theory and evolution, and that of experimental and neuroscientific evidence. An achievement of the target article is in enabling readers to see how, among the many disagreements, there is also significant cross-talk going on among different behavioural sciences. Of course, the sceptic may reply that the reason that the author and I share a similar language is because, ultimately, we are both economists.

I am less clear about what is the contribution of the target article's beliefs, preferences, and constraints (BPC) framework beyond the broad recognition of common themes and the exposition of specific views on specific points. It is natural for scientific frameworks, as opposed to specific theories, to have degrees of indeterminacy; but in order to be meaningful they still need to put restrictions on what they can explain. Take rational choice in economics. Rational choice by an individual is any choice