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Toward a neo-Darwinian synthesis of neoclassical and behavioral economics

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ABSTRACT

There is a schism within economics between the neoclassical and behavioral schools. A primary cause of the behavioral ascent is the experimental evidence of deviations between actual behavior and the neoclassical prediction of behavior. While behavioral scholars have documented these "anomalies," they have made little progress explaining the origin of such behavior. This paper proposes a biological and evolutionary foundation for the anomalies of behavioral economics by separating proximate and ultimate causation. Such a foundation may allow for a re-uniting of economics; a neo-Darwinian synthesis of neoclassical and behavioral economics.

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1. Introduction

Economics is divided into two competing schools based on divergent views of human nature. This paper argues that the two schools of economics can be re-connected by incorporating insights from the natural sciences. In particular, the concepts of proximate and ultimate causation may allow a synthesis of neoclassical and behavioral economics that reconciles and combines the competing perspectives.

Behavioral economics has made significant advances in recent decades. An important source of these successes is the documentation of divergences between neoclassical predictions of human behavior and actual human behavior. Richard Thaler labels these divergences as "anomalies."

Neoclassical economists dismiss the behavioral anomalies as interesting quirks, laboratory artifacts, or small-stakes effects that can be ignored when working on important, real-world issues. Mainstream economic textbooks, economic teaching, and applied economics are still based primarily on the neoclassical assumptions. While much of economics maintains the status quo, behavioral economists, in turn, dismiss neoclassical economics as irrelevant, applied math.

The two groups of economists do not communicate productively, and the schism is a major obstacle to improving economics. The field of economics is divided, and faces a crisis.

Biologists have faced similar issues regarding the behavior of non-human animals. Animals exhibit sophisticated behaviors, but animals can also behave in ways that appear counterproductive. While economics has fragmented over the apparent contradiction of animals as both optimizers and bumblers, biology accommodates both in a single, unified view of behavior.

Economists may benefit by incorporating the insights of natural scientists. Natural selection favors optimization, but the maximization is achieved by specific physical machinery that does not maximize in all settings (Mayr, 1961; Tinbergen,

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1963, 1968). There is no schism in biology over maximization because natural scientists differentiate between the "ultimate" and "proximate" causes of behavior.

The ultimate cause of a behavior is based in the evolutionary payoffs. The proximate cause of a behavior is based in specific machinery or "mechanism" that produces the behavior. Proximate cause can lead to behaviors that appear destructive or anomalous in the spirit of behavioral economics.

An integrated view of behavior, that combines both ultimate and proximate causation, is richer and more productive than any single idea of causation.

This paper is entitled "caveman economics" to highlight the difference between ancestral human environments and modern industrial or agricultural environments. Proximate mechanisms are more likely to lead to anomalous behavior in evolutionarily novel environments. The behaviors that puzzle economists occur primarily in two types of evolutionary novel environments: Laboratories for economic experiments, and modern industrialized societies.

The caveman economic hypothesis is that behavioral anomalies are caused, in significant part, by an "evolutionary mismatch" between human proximate decision-making machinery and specific environments. The term evolutionary mismatch describes situations when traits are out of equilibrium with important aspects of the environment (Bowlby, 1969; Crespi, 2000; Lloyd et al., 2012; Tooby and Cosmides, 1989, 1990; Wilson, 1978).

This paper focuses primarily on genetic mismatch; the notion that genes can be out of sync with the environment. If human preferences evolved by natural selection, and genetic mismatch is an important issue, then preferences were shaped in ancestral environments. Attempts to understand human economic preferences and behavior should, therefore, model the ancestral and not modern world.

The caveman economics hypothesis is that a number of important puzzles in economics, including the anomalies of behavioral economics, may be resolved by understanding proximate and ultimate causation. Many puzzles in economics disappear when we consider the world of our ancestors and the implications for behavior.

There are important caveats and uncertainties in the caveman economic approach.

First, mismatch takes place for cultural evolution in addition to genetic evolution. This paper focuses on genetic mismatch, without explicit reference to cultural mismatch. However, it should be noted that culture is implicit. For example, evolutionary mismatch is frequently the product of cultural change. Genes and culture co-evolve so that cultures have been selecting genes as much as genes have been selecting cultures for a long time (Stoelhorst and Richerson, 2013; Witt and Schwesinger, in press).

Second, humans have a unique ability to modify and control behavior; we are not lumbering robots, hard-wired to carry out genetic programs. Human genes build flexible behavior that is acutely sensitive to cultural nuances and social norms. This flexibility is greater than that found in other animals, and may even be qualitatively different. For example, our closest animal ancestors, the chimpanzees, have a harder time suppressing certain types of urges (Boysen et al., 1999) and capuchin monkeys appear to have an even harder time at delaying gratification than chimpanzees (Evans et al., 2012).

Third, human brains may be uniquely able to adapt to evolutionary mismatch, thus mitigating the negative consequences. 'Niche construction' is a process where animals alter the environment. Some scholars argue that humans are so skilled at niche construction that the negative effects of the lag between genetic evolution and environmental change are mitigated (Laland and Brown, 2006). Furthermore, while this paper argues that the proximate/ultimate distinction will help economics, there is a new literature that de-emphasizes related ideas in the natural sciences (Bolhuis et al., 2011; Dean et al., 2012; Laland et al., 2011).

These three ideas highlight human cultural transmission and human behavioral flexibility, which may limit the benefit of incorporating genetic proximate and ultimate distinctions into economics. The benefit of focusing on genetic mismatch is that the clarity of the perspective may allow insights not available with a more nuanced perspective. The risk, of course, is that the simplification is too extreme, and leads to incorrect conclusions. These ideas are revisited in the discussion.

In summary, economics is a field divided upon itself with the two main camps diverging. The specific goal of this paper is to demonstrate the utility of the distinction between proximate and ultimate causation for understanding behavioral anomalies. The longer term goal is to place economics into a consilient framework where human economic behavior is studied within the same framework as human non-economic behavior and non-human behavior.

The remainder of this paper is structured as follows. In the next section, the schism between neoclassical and behavioral economics is elaborated in more detail. Next, the proximate/ultimate framework is introduced. Using this framework, biology is able to reconcile sophisticated behavior with other behaviors that appear anomalous. The subsequent section discusses two lines of research in economics using the proximate/ultimate framework. In these cases, the biological framework produces novel, testable hypotheses that are different from neoclassical and behavioral frameworks. The empirical data in the handful of studies that have been completed support the value of the biological framework to understanding economic behavior. The final discussion section looks forward to an economics based on an evolutionary and biological foundation.

2. The schism between neoclassical and behavioral economics

2.1. Behavioral anomalies challenge core assumptions of neoclassical economics

There is a significant divide between neoclassical and behavioral economics. Over the last several decades, the behavioral school has had a significant impact on economics (Thaler, 1992; Kahneman and Tversky, 1979, #2005; Tversky and

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Kahneman, 1974). The behavioral approach has gained traction because of its ability to document deviations between actual human behavior and the neoclassical prediction of human behavior.

Richard Thaler (1988) defines a "behavioral anomaly" as follows, "An empirical result qualifies as an anomaly, if it is difficult to 'rationalize,' or if implausible assumptions are necessary to explain it within the paradigm." In contrast to lay critiques of neoclassical economics, the behavioral critique has gained traction because it works "works within the paradigm."

Every assumption in neoclassical economics now has a behavioral economic literature documenting anomalies. Some of the most famous anomalies include the use of heuristics (Tversky and Kahneman, 1974), deviations from narrow self-interest in the form of altruism and spite (Guth et al., 1982; Kahneman et al., 1986), hyperbolic discounting (Ainslie and Haslam, 1992; Frederick et al., 2002; Laibson, 1997), and non-standard attitudes toward risk (Kahneman and Tversky, 1979).

2.2. Responses to behavioral anomalies

The documentation of behavioral anomalies had transformed the field, with 50,000 academic papers citing the two seminal articles (Kahneman and Tversky, 1979; Tversky and Kahneman, 1974). Three areas of research are relevant to this paper. First, neuroeconomics has studied the neurologic bases of behavioral anomalies. Second, classic twin studies and other approaches have examined the genetic basis of anomalies. Third, behavioral scholars have developed "behavioral" utility functions. The following sections provide a relevant summary of these areas, and then we return to consider the current state of the divide between neoclassical and behavioral economics.

2.2.1. Neuroeconomics

A central goal of neuroeconomics is to understand the neural circuits that produce behavioral anomalies. An important review article expresses this goal, and some progress toward it, by stating that the research on 'desirability,' "may begin to explain, in a mechanistic way, how information is analyzed when at least one class of behavior which is not predicted by the expected utility theory is produced" (Glimcher and Rustichini, 2004, p. 452).

Thus, a significant aspect of the neuroeconomics literature correlates economic behavior in general, and behavioral anomalies in particular, with activity in distinct brain regions (Glimcher and Rustichini, 2004; Vromen, 2007; Zak, 2004). For example, specific regions of orbitofrontal cortex (OFC) are involved in decision making related to rewards and punishments (O'Doherty et al., 2001). A goal of this work is to understand the brain circuitry involved in economic decisions, "Desirability is computed and represented in the brain, and we now have the means to test, measure, and represent this activation" (Glimcher and Rustichini, 2004, p. 452).

Another important behavioral anomaly is the finding that people often cooperate in settings where neoclassical economics predicts no cooperation. A neuroeconomics study scanned brains of subjects playing a trust game (McCabe et al., 2001). As with representations of desirability, this study of trust found correlations between brain activation and behavior. Specifically, "within this group [subjects who attempted cooperation in trust games] prefrontal regions are more active when subjects are playing a human than when they are playing a computer following a fixed (and known) probabilistic strategy" (p. 11832).

Neuroeconomics continues to study the correlation between brain activity and important economic behaviors. For example, ultimatum game rejections are correlated with high activation of the anterior insula relative to the dorsolateral prefrontal cortex (dIPFC) (Sanfey et al., 2003a). Is the role of the dIPFC in the ultimatum game correlation or causal? Subsequent neuroeconomics studies investigate. A study disrupts dIPFC function by repetitive transcranial magnetic stimulation (rTMS), and reports that disruption of the right DIPFC led to increase acceptance of low ultimatum game offers (Knoch et al., 2006).

A more recent study investigates the role of the amygdala in ultimatum game rejections (Gospic et al., 2011). Subjects given the amygdala inhibitor, benzodiazepine, were less likely to reject low offers. Further insight comes from a study that looks at the neural response to inequality after some subjects are given relatively large cash gifts (Tricomi et al., 2010). Subjects who had just received large amounts of cash, showed less significant neural activation to future payments to them, but remained sensitive to relative payments to others.

In summary, neuroeconomics continues to elucidate the representation in the brain of economic decision-making. Furthermore, there has been progress in identifying the neural signature of some of the most significant behavioral anomalies.

2.2.2. Genetic heritability of behavioral anomalies

Heritability has been estimated for a number of famous behavioral anomalies using canonical twin study methodology. Additive genetic effects are reported to explain more than forty percent of ultimatum game rejection behavior (Wallace et al., 2007). Heritability estimates for behavior in a trust game are estimated at 20% in a Swedish sample, and 10% in a US sample (Cesarini et al., 2008). In the area of giving and risk taking, genetic differences are credited with explaining roughly 20% of the individual variation in the laboratory (Cesarini et al., 2009) and 25% in explaining the risk level in subjects' financial portfolios (Cesarini et al., 2010a). Finally, genetic differences are reported to explain 16–34% of the variation is levels of overconfidence (Cesarini et al., 2010b).

The ability to rapidly sequence DNA has led to genomic wide association studies (GWAS) of economic and social behaviors. A study examined single nucleotide polymorphism (SNP) data to look at the genetic contribution to some of the same behavioral anomalies examined in the twin studies (Benjamin et al., 2012). This study concludes that "the estimated fraction of phenotypic variation that could, in principle, be explained by dense SNP arrays is around one-half of the narrow heritability estimated using twin and family samples" (p. 8026).

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In summary, behavioral anomalies appear to be heritable thus indicating that variation in economic behavior is linked to variation in gene sequences.

2.2.3. Behavioral utility functions

Behavioral anomalies are often labeled as decision-making failures or mistakes. An alternative is that subjects are not making mistakes, but that the neoclassical assumptions on the form of the utility function are incorrect. Behavioral anomalies, in this view, are not caused by failures of the experimental subjects but rather by failures of neoclassical economic theory.

Working from this perspective, behavioral scholars have created new utility functions to explain the behavioral anomalies. These new utility functions alter the axioms of economics, and behavioral scholars are attempting to re-invent economics with a new set of theories consistent with the behavioral views. A primary behavioral approach to re-inventing economics is to retain the rationality assumption of neoclassical economics, but alter the form of the utility function.

For example, in the area of intertemporal choice, neoclassical economics assumes that people discount exponentially, which means that the relative value of any two adjacent periods is constant. For example, consumption in any given year might be valued at 5% more than the same consumption one year later. In this neoclassical view, today is worth more than tomorrow, and people make optimal trade-offs between time periods.

The behavioral school has documented deviations from exponential discounting (Ainslie and Haslam, 1992; Frederick et al., 2002). In many of these studies, people appear to be too impatient by putting excessive importance on today. In addition, time preferences appear to be inconsistent. Tomorrow is traded off correctly with the day after tomorrow. However, when tomorrow becomes today, people are impulsive, and they put additional, relative value on today.

Behavioral scholars have created 'hyperbolic' utility functions to explain intertemporal choice behavior. As compared with the neoclassical assumption of exponential discounting, hyperbolic discounting places an unusually high premium on today. With these hyperbolic preferences, all the related theorems are then attempted to be re-derived (Gowdy et al., in press; Laibson, 1997).

Hyperbolic discounting functions were created to be consistent with the main thrust of behavioral economic research. Thus, by definition, hyperbolic utility functions are more consistent with some behavioral data than exponential utility function. It remains to be seen, however, what novel insights will be generated from these utility functions, and work continues on ways to alter the specifics of the behavioral utility function (Benhabib et al., 2010).

A similar behavioral utility function approach is used to make sense of the anomalies regarding altruism and spite. Because this area is the focus of the two empirical examples in this paper, it is worthwhile to discuss in a bit of detail.

Most applied economics assumes that people want to make the most money for themselves and do not care about others, with the possible exception in some macroeconomic models that people are assumed to care about their direct, lineal descendants (children, grandchildren, great-grandchildren, etc.).

Among the most famous behavioral anomalies is evidence that people are willing to spend significant amounts of money to either help or hurt other people. Altruism is defined as a voluntary and costly behavior that helps other people. Spite is defined as a voluntary and costly behavior the hurts other people.

The ultimatum game is a famous demonstration of spite in economic experiments. In the ultimatum game people are faced with take it or leave it offers of a division of a fixed amount of money. Rejection of the offer fits the definition of spite because the rejecter bears the cost of the lost money, while at the same time imposing a cost on the counterpart. The first ultimatum game reports twenty percent of ultimatum game responders exhibit spite in the form of rejecting positive offers (Guth et al., 1982).

There have been many further examinations of ultimatum game behavior with over 2000 citations of the original 1982 study. The finding that some positive ultimatum game offers are routinely rejected has been replicated cross culturally (Henrich et al., 2001; Roth et al., 1991) and for larger stakes (Cameron, 1999; Hoffman et al., 1996b; van den Assem et al., 2012). In most cultures lower offers are rejected more often, and the chance of rejection approaches 50% when offer declines to about 20% of the total.

Altruism, the bearing of a cost to help others, has also been demonstrated in several different economic games. The 'dictator game' has a person divide a fixed sum of money with another person (Forsythe et al., 1994; Kahneman et al., 1986). Any donation fits the definition of altruism when these games are played under anonymous and one shot conditions. People in the role of dictators routinely display altruism by giving money to counterparts (Forsythe et al., 1994; Hoffman et al., 1996a), although there is considerable variation based on the situation (Hoffman et al., 1996a). In addition to the dictator game, altruism has been documented in public goods games (Fehr and Gachter, 2002; Ledyard, 1995) and trust games (Berg et al., 1995).

What is the explanation for altruism and spite in economic experiments? One approach is to classify these behaviors as mistakes. An alternative is to recognize that that people have a sense of fairness, and the problem is with the neoclassical assumption of self-regarding preferences.

Accordingly, behavior scholars have developed 'other-regarding' utility functions. When a subject walks away from money by rejecting a low ultimatum game offer, or voluntarily gives money away in a dictator game, he or she can be viewed as maximizing utility that is derived, in part, from caring about the impact on other people.

For example, in most cultures ultimatum games rejection rates are higher for smaller offers than for larger offers. Early other-regarding preferences models incorporate this by assuming that humans exhibit 'inequality aversion' (Bolton, 1991).

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The story is more complicated than simple inequality aversion, however, as rejection thresholds drop toward zero if a computer generates the split (Blount, 1995).

Later models of other-regarding preferences include factors beyond inequality aversion (Bolton and Ockenfels, 2000; Fehr and Schmidt, 1999; Levine, 1998; Rabin, 1993). In Rabin's fairness concept, for example, humans derive happiness from helping those who have been nice but also enjoy punishing those who have been not nice. So what a naïve observer might label as altruism or spite becomes self-interest with an other-regarding twist. The concepts of 'strong reciprocity' and 'altruistic punishment' (Fehr et al., 2002; Fehr and Gachter, 2002) are more recent efforts to capture important features of non-maximizing human behavior. Work continues on more complicated other-regarding utility functions (Maccheronia et al., 2012).

Has the work on behavioral utility functions succeeded? In one sense, yes, but in a broader sense no, or not yet. Yes, in the sense that behavioral utility functions attempt to go beyond a laundry list of anomalies. Furthermore, these utility functions are more consistent with actual human behavior. However, these behavioral utility functions have significant negative aspects as well.

First, the behavioral utility functions start with a goal to explain the relevant behavioral anomaly. Because they are constructed to explain certain facts, they cannot then be credited with explaining those facts. To be successful, they need to make novel, testable predictions. In this area, it is not clear that the models have any more predictive power than folk wisdom.

Second, the behavioral utility models are more complicated. Complexity may be required because human nature may be complex, however, all things being equal, one would prefer a simple, tractable model.

Third, the behavioral utility functions, in some case, omit important drivers of behavior. For example, there is debate on the effect of subject-experimenter anonymity. One study varied the level of 'social distance' between dictators and others and reports that self-interest increases when subjects' decisions are shielded from the experimenter (Hoffman et al., 1996a). This result has been replicated (Burnham, 2003; Eckel and Grossman, 1996), but also challenged (Bolton and Zwick, 1995).

These anonymity effects are large. The percentage of subjects giving zero in the dictator game increases from 18% to 64% as the decisions become more private (Hoffman et al., 1996a). The existing other-regarding preference models are silent of the effect of anonymity.

Thus, the critique of behavioral utility functions is that they are complicated, fail to produce novel insights, and fail to include important drivers of behavior.

Does this imply that behavioral utility functions are silly? Not necessarily. Perhaps they simply need additional refinement. None of the existing other-regarding preference models predict that subject-experimenter anonymity will affect behavior. In the event that such anonymity should prove to be important, however, it is a technical triviality to add additional parameters to the other-regarding preference structure.

Behavioral utility functions could in newer, more complex manifestations explain all the anomalies of behavioral economics. However, current models have significant negatives and it remains to be seen if this approach can replace the axioms of neoclassical economics.

These difficulties of behavioral models were anticipated as long ago as 1991, "It is in the nature of economic anomalies that they violate standard theory. The next question is what to do about it. In many cases there is no obvious way to amend the theory to fit the facts, either because too little is known, or because the changes would greatly increase the complexity of the theory and reduce its predictive yield." (Kahneman et al., 1991).

2.3. The economist's dilemma

There has been tremendous effort expended on behavioral economics in the decades since the pioneering Kahneman and Tversky studies, and a lot has been learned. The nature and extent of behavioral anomalies has been documented. The neural circuitry of behavioral anomalies has been elucidated, and there is evidence of heritability in these traits. Finally, behavioral scholars have made concerted efforts to go beyond a laundry list of behavioral anomalies by creating behavioral utility functions.

While there has been tremendous effort, and significant accomplishments, economics remains divided between neoclassical and behavioral scholars. Neoclassical models can be elegant and they are mathematically tractable. Using neoclassical models, economists are able to make unambiguous statements such as free trade is good, and rent control is bad. However, the behavioral economic movement has demonstrated the divergence between neoclassical theories of human nature and reality.

Most of economics continues to use the neoclassical foundation that ignores behavioral anomalies. There is an acknowledgment of the behavioral findings, but the neoclassical approach is still used for most teaching, and the vast majority of applied work.

Beyond the explicit denial of the relevance of behavioral findings, there is an implicit reliance on the 'as if' assumption of Milton Friedman's billiard's player (Friedman, 1953). This view argues that while people may suffer from the biases and heuristics documented by behavioral scholars, they get the big issues right using some non-conscious process.

The most forceful, direct response by neoclassical economists is the argument that behavioral phenomena are not important because the behavioral anomalies disappear with either large, real-life stakes or with learning (List, 2003, 2007; List and Levitt, 2007). Behavioral scholars disagree, arguing for more behavioral research (Falk and Heckman, 2009), and

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demonstrating, for example, that the anomalies do not disappear even with very large stakes (Burton-Chellew and West, 2012).

What about behavioral economics? The anomalies documented by behavioral economics appear to be robust and significant. Behavioral economics, however, has severe limitations. First, there is no foundation for the behavioral view of human nature. The behavioral view begins with assumptions about people, but those assumptions are not grounded in any theory. (The lack of a foundation is shared with neoclassical economics.)

Second, behavioral economic models have severe limitations. The behavioral models are more complicated than the neoclassical models, yet generate limited, testable hypotheses beyond the data used to create the models. At worst, these behavioral models are *ex-poste* rationalizations of common sense, created by over interpreting the experimental data.

Economists face a dilemma. They can choose the elegant models of neoclassical economics that are inconsistent with human behavior, or they can embrace the behavioral view that has no foundation and limited predictive power.

3. Proximate and ultimate causation in the natural sciences

The biological study of behavior has been able to deal with 'anomalous' behavior without any ideological divide. Natural scientists use more nuanced views of causation that allow them to reconcile sophisticated, goal-directed behavior with behaviors that seem to be destructive. The concepts of proximate and ultimate causation are important tools in the natural scientists view of other puzzling behavior.

While economists seek to explain all behavior through the single cause of maximization of stable preferences (Becker, 1976b), natural scientists distinguish four distinct types of causation for the morphology and behavior of organisms that arose by genetic evolution (Mayr, 1961; Tinbergen, 1963, 1968; Wilson and Gowdy, in press). Of particular importance is the distinction between the machinery that implements a particular behavior ("proximate" causation) and the evolutionary function of that behavior ("ultimate" causation).

Natural scientists are able to reconcile both maximizing and non-maximizing behavior through this framework. For example, the **proximate cause** of sweetness is a biological system that links the ingestion of certain molecular shapes to the pleasure center of the brain. This proximate explanation does not connect sweetness to its evolutionary advantage or disadvantage. The **ultimate cause** of sweetness is the caloric value of sugar. Humans are built to obtain energy from food; sugar is a source of calories.

Over evolutionary time, proximate and ultimate causation are linked. Natural selection favors proximate mechanisms that produce maximizing behavior. Animals that liked the taste of calorie-rich foods had higher reproductive success and eventually the world was filled with taste buds built to detect calories, or, more precisely, genes to build a taste for sweetness. Evolution favors genes that produce pleasure in organisms when they consume objects that are nutritious for them.

Unlike temperature or color, there is no objective attribute of sweetness in the world (Johnson, 1999); organisms have mechanisms that generate pleasure when they ingest nutritious objects. One can speculate that termites derive as much pleasure from eating maple trees as humans do from eating maple syrup. The sensation of sweetness is produced by a proximate mechanism that evolved to further the ultimate goal of genetic replication.

Careful analysis of proximate and ultimate causation clarifies the effects of technological change. Sugar substitutes such as aspartame (a.k.a. NutraSweet) taste sweet to humans but yield few or no calories. Substances that have no nutritional value, yet tickle human taste buds, might puzzle an ignorant anthropologist from Mars.

One could imagine an economist writing a behavioral anomalies paper on the preference of calorie-free NutraSweet over calorie-rich glucose. However there are no such papers in natural science journals because the apparent paradox is resolved by distinguishing proximate from ultimate causation.

Evolution by natural selection built humans to find and consume foods that yielded calories in the ancestral environment. The mechanism for evaluating foods is reified in a specific system that is activated by certain molecular shapes. Novel compounds that mimic certain attributes of sugar stimulate the sweetness pleasure pathway yet need not yield calories. Thus, the proximate mechanism built with the ultimate goal of inducing maximizing behavior, produces non-maximizing behavior in certain novel environments.

Proximate and ultimate causation are central to understanding behavior, particularly behavior that appears to lead to bad consequences. For example, rats that are given unlimited quantities of both food and drugs, choose to self-administer drugs to the point of starvation (Pickens and Harris, 1968; Weeks, 1962). This behavior does not maximize reproductive success, yet is not treated as an anomaly within biology. Rat pleasure-seeking mechanisms result in the ultimate goal of baby rats in the ancestral environment, but result in death in the evolutionary-novel, drug-rich environment of the laboratory.

In addition to helping understand preferences toward novel substances, distinguishing proximate and ultimate causation is useful in understanding behavior that results from evolutionary arms races. For example, birds of many species feed the young of other species (e.g. cuckoos) who are labeled 'brood parasites' (Payne, 1977). This interspecies 'altruism' might appear paradoxical because the feeding does not further the genetic goals of the host parents.

The puzzle of host parents that willingly feed brood parasites is resolved by distinguishing proximate and ultimate causation. Bird 'altruism' is caused by the manipulation of the hosts' proximate feeding mechanisms by the parasitic species. Thus, the proximate mechanism that evolved to maximize the host's payoff is co-opted to produce 'anomalous' behavior. (This view is consistent with the more recently documented 'mafia' behavior of cuckoos (Soler et al., 1995; Thomas et al.,

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The concepts of proximate and ultimate causation are central to understanding non-maximizing behavior. This approach is the standard methodology among natural scientists, but generally has not been used to explain the anomalies of behavioral economics.

4. Behavioral economic anomalies from an evolutionary perspective

4.1. Introduction: evolution & economics

Both neoclassical and behavior economics have no theoretical foundation. For example, neoclassical economics assumes that people exponentially discount the future, while behavioral economists assume hyperbolic discounting. Neither group has any theoretical support for their view. Evolutionary perspectives provide a theory of behavior for any organism, including humans.

This paper argues that one aspect of an evolutionary view has already provided novel insights into economic behavior, and as such, there is a promise of more significant progress by working to ground economics in evolutionary theory.

The caveman economics agenda is to use evolutionary perspectives to understand both neoclassical and behavioral perspectives. In many situations, non-human animals exhibit extremely sophisticated behavior. For example, chimpanzees (*Pan troglydytes*) are adept at selecting the best partners for cooperative tasks (Melis et al., 2006). Furthermore, sophisticated behavior is not confined to primates; small-brained dungflies (*Scatophagastercoraria*) exhibit evolutionarily stable strategies when competing for egg laying opportunities (Parker, 1970). The behavioral ecology literature contains hundreds of studies documenting subtle and sophisticated non-human animal behavior (Krebs and Davies, 1996).

4.2. Evolutionary mismatch

While optimization has support within the natural sciences, there is also support for exactly the sort of behavior documented of behavioral economics. Evolutionary mismatch is one cause of behavior that is deleterious, or anomalous.

"Evolutionary mismatch is a state of disequilibrium between an organism and its environment. It occurs when a trait evolves in one environment and then the environment changes, with the result that the trait has a deleterious effect in the latter environment that it did not have in the earlier one." (Lloyd et al., 2012)

Evolutionary mismatch may be of central importance to human behavior because the evolutionary environment is different from the modern environment (Bowlby, 1969; Tooby and Cosmides, 1989, 1990; Wilson, 1978). The logic of this argument is as follows.

For a very long time, human ancestors foraged for food. The important attributes of: (i) relatively small group size, (ii) low population density, and (iii) high likelihood of repeat interactions with both kin and non-kin, remained constant for non-human primates, and also for tens of thousands of years after the origin of genetically modern humans.

The end of the Pleistocene Epoch, marked by the domestication of plants and animals, permanently altered these features. With increased food supplies, humans began to live in large groups, at high population density, and interact more frequently with non-relatives and strangers.

Because important aspects of pre-human and human environments remained constant up until the end of the Pleistocene Epoch, approximately 10,000 years ago, genetic evolution had thousands of generations to select human genes that worked well in small groups of foragers. Therefore, it is reasonable to conclude that at the end of the Pleistocene, human genes were in equilibrium with some important aspects of the environment including key social features regarding the nature and frequency of interactions with conspecifics.

The phrase, the "environment of evolutionary adaptiveness", or EEA, was coined by John Bowlby (1969, 1973) as the environment "that man inhabited for two million years until change of the past few thousand years led to the extraordinary variety of habitats he occupies today" – Bowlby, 1969, chapter 4, p. 59.

The EEA is often used to describe a stylized Pleistocene environment that was in equilibrium with human genes. More recently, Irons (1998) argues that there was no single golden moment of equilibrium but rather a different 'adaptively relevant environment' or ARE which varies by trait. For example, the human taste for certain calorie-rich foods derives from a long primate history that predates the origin of humans. Thus, the ARE for human food preference spans more than the Pleistocene. Beyond food choice, Irons argues that the Pleistocene did not play a special role in the evolution of many human traits. The two concepts of EEA and ARE agree that ancestral environments shaped human nature; the debate is over the relevant time period for each trait.

Because humans live in an evolutionarily novel environment, however, proximate mechanisms that evolved to maximize in the ancestral world create robust and significant deviations from maximization in the modern world.

The importance of the ancestral environment lies in the significant and systematic discord between the genes adapted for that environment and modern settings. This mismatch provides the key to understanding a wide variety of human behaviors. There has been considerable progress utilizing genetic mismatch in studies of non-economic behavior. For examples of primary research see (Gigerenzer, 1993; Irons, 1998; Tooby and Cosmides, 1989), for book length treatments see (Barkow et al., 1992; Pinker, 2002; Wilson, 1975, 1978), and for the seminal critique of the adaptationist program, see (Gould and

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Lewontin, 1979) as well as the more recent criticisms (Bolhuis et al., 2011; Dean et al., 2012; Laland and Brown, 2006; Laland et al., 2011).

4.3. Caveman economics methodology

Because humans live in novel environments, behavior may deviate systematically from that which maximizes. The general method is:

- (1) Model the relevant aspects of the human ancestral environment (the ARE).
- (2) Solve for maximizing behavior in the ARE and predict the structure of preferences.
- (3) Predict how the preferences that evolved by natural selection in the ARE (step II) operate in important modern environments
- (4) Test and refine.

There is a key difference between caveman economics and other existing efforts to endogenize preferences. Other attempts (described below) to derive the ultimate cause of preferences model the current environment, not the ancestral world.

Economists do not generally differentiate proximate and ultimate causation. In the biological framework, economic preferences - selfish or other-regarding - are proximate causes of behavior. Rabin's description, for example, that "If someone is being nice to you, fairness dictates that you be nice to him" (Rabin, 1993, p. 1281) is a proximate explanation that does not connect fairness to its evolutionary advantage or disadvantage.

As early as 1976, Gary Becker (1976a) sought ultimate causation for preferences, writing "The preferences taken as given by economists and vaguely attributed to 'human nature' or something similar... may be largely explained by the selection over time of traits having greater genetic fitness and survival value." (p. 826).

There have been a relatively small number of other papers on the evolution of human preferences and thus behavior (Hirshleifer, 1987). These papers seek to understand how ultimate causation shapes the structure of proximate mechanisms regarding goods and time (Becker and Mulligan, 1997; Hansson and Stuart, 1990; Rogers, 1994). There have been several attempts to model the evolution of risk (Brennan and Lo, 2011; Robson, 2001; Rubin and Paul, 1979). Utility maximization may itself be an evolutionary product (Burnham, 1997; Robson, 2001).

In an interesting twist, an evolutionary process can create certain types of systematic deviations from utility maximization (Waldman, 1994). Frank (1987) looks for an evolutionary root to morality in an economic context as does Alexander (1987) more broadly. There are also efforts to use evolutionary approaches to understand fairness (Huck and Oechssler, 1999). Galor and Moav (2002) argue for a causal link between genetic evolution and economic growth.

The economic literature on ultimate causation for non-maximizing behavior includes (Bergstrom, 1995; Bergstrom and Stark, 1993) that show altruism can exist because of kin selection (Hamilton, 1964; Samuelson, 1983). Simon (1993) argues that some non-maximizing behavior is caused by imperfect information. Two papers seek ultimate causation for altruistic economic behavior in the concept of group selection (Boyd et al., 2003; Gintis, 2000); an idea that has been reformulated in a manner consistent with modern Darwinian theory (Wilson and Sober, 1994).

Vernon Smith (2003) argues for an ecological rationality to economic experiments very much in the spirit of this paper and Gigerenzer (2000) has created a body of work consistent with these views.

Does the caveman economic theory make specific and testable hypotheses that differentiate it from prior theories? The next two sections discuss two such findings. First, increased altruism caused by activation of neural mechanisms that monitor privacy. Second, high testosterone men are more likely to reject low ultimatum game offers.

4.4. Caveman example 1: eye-detection neural architecture and altruism

One of the best studied behavioral anomalies is 'altruism' exhibited in laboratory games. A common assumption in economics is that people will seek to make the most money possible. However, myriad studies document situations where people do not make the most money possible (Berg et al., 1995; Cameron, 1999; Fehr and Gachter, 2002; Forsythe et al., 1994; Guth et al., 1982; Guth and Tietz, 1990; Henrich, 2000; Henrich et al., 2001; Hoffman et al., 1994, 1996a, 1996b; Kahneman et al., 1986; Ledyard, 1995; McCabe et al., 1996; Roth et al., 1991; Yamagishi, 1986).

Are these behaviors altruistic? In non-experimental settings there are reputational consequences to charitable acts. Thus, isolated acts that appear altruistic might be strategic behavior to garner future benefits or avoid future punishments (Fudenberg and Maskin, 1986).

In the laboratory demonstrations of altruism cited above, however, all of the behavior labeled as altruism occurs in final and anonymous situations. For example, in the dictator game people decide how much to give to an unknown and unseen counterpart. After this donation of money the laboratory game ends, and the dictator is not identified. Thus, within the laboratory setting of an anonymous dictator game there is no way for any gift to be repaid.

Why do people behavior altruistically in these economic games? People voluntarily walk away from money – sometimes on the order of three months wages. This is a bedrock finding of behavioral economics; one of the most important anomalies.

The caveman economics hypothesis is as follows:

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Laboratory altruism is produced by mechanisms that arose for self-interest. These mechanisms were selected in evolutionary environments where behavior was likely to be repeated or observed. Thus, the human brain acts 'as if' there are reputational consequences to behavior even in laboratory environments specifically constructed to eliminate reputational effects.

An interesting test of this hypothesis lies in the prediction that people might be more "altruistic" in settings where their brains are detecting the images of eyes.

Over evolutionary time, humans and non-human primates faced different payoffs for public and private behavior. Public behavior, observed by conspecifics, is subject to indirect effects. It paid for our ancestors to be nicer when they were being observed.

The implication is that people will be nicer when in public. Furthermore, it may be possible to activate the mechanisms that evaluate the level of privacy independently from actual privacy and thus push people to act nicer even when they are in private.

A key to this view is that human brains are designed to identify eyes, and related features, in the environment. If the eye-detection machinery in the human brain is stimulated, the prediction is that people will be more "altruistic".

Three lines of research suggest that activation of the eye-detection machinery might cause people to display higher levels of altruism in class economic games.

- (1) Anonymity affects the level of altruism in economics experiments. For example, subjects donate more to a public good when they are identified than when they remain anonymous (Andreoni and Petrie, 2004). This increase in public goods contributions exists even among strangers in a large city (Rege and Telle, 2004). In a dictator game, contributions are higher the lower the 'social distance' between dictator and recipient (Hoffman et al., 1996a).
- (2) Humans are built to detect faces and eyes. Humans, and non-human primates have neurons that activate automatically upon the detection of eyes and faces including those shown in pictures (Emery, 2000; Haxby et al., 2000). Because this brain architecture appears to be very similar across a range of primate species, it is likely to be conserved for millions of years. These circuits are activated involuntarily by eyes, heads, and cues to head direction; in many settings these cues reliably signal important social information about the environment (Brothers, 1990, 1996; Corballis and Lea, 1999).
- (3) Neuroeconomic studies document activity in brain areas that are not under the individual's direct control (McCabe et al., 2001; Rilling et al., 2002; Sanfey et al., 2003b; Smith et al., 2002, 2003). These neuroeconomic studies build upon a much older literature on involuntary influences on behavior. For example, the "Stroop effect" documents an involuntary effect on the ability to identify colors (Stroop, 1935). People are significantly faster in identifying the color of letters when the meaning and color of words match each other. The Stroop effect is not eliminated by repetition, thus demonstrating a persistent effect on reading behavior.

Over evolutionary time, humans have inherited a conserved brain system that inflexibly activates in the presence of eyes and faces. This activation occurs involuntarily in brain regions that are connected to the brain areas that control sophisticated decision-making. Thus, there is a possibility that a stimulus of the human dedicated neural architecture in the amygdala and STS might affect human behavior including economic decisions.

The first paper on testing this hypothesis, "humans will exhibit more pro-social behavior when they perceive themselves to be in public," and that perceptions of anonymity would be altered by seeing eye images because, "Until the advent of cameras, the ability to see a person, particularly her or his eyes, meant that those eyes could see you." (Burnham, 2003). There is now a growing literature documenting the ability to alter economic behavior by stimulating the human eye-detection machinery (Bateson et al., 2006; Burnham, 2003; Burnham and Hare, 2007; Francey and Bergmüller, 2012; Haley and Fessler, 2005; Malinski and Rockenbach, 2007; Powell et al., 2012; Rigdon et al., 2009; but for studies that report no effect see Fehr and Schneider, 2009; Raihani and Bshary, 2012).

To be clear, these eye-detection experiments do not provide a complete explanation for why people fail to maximize their monetary payoffs in experimental economics games. There remain many possible explanations for the results. One explanation is that humans experienced both public and private settings during the EEA and evolved to perceive the difference. If this were the case, they would indeed maximize their monetary gain when eyes and comparable cues are removed. The fact that they act more altruistically in the presence of eyes does not imply that altruism is zero in the absence of eyes. In short, these findings do not end the process of understanding the anomaly. They do, however, open a new avenue of discovery.

In summary, stimulating the neural architecture for eye-detection was a novel, testable hypothesis generated by thinking that behavioral economic anomalies are caused, in part, by proximate mechanisms in particular settings. Neither the neoclassical nor the behavioral view predicts such a relationship. In this case, the caveman economics hypothesis has passed the first hurdle of a novel, testable hypothesis shown to be consistent with data gathered after the hypothesis was generated.

4.5. Caveman example 2: testosterone and spite

The ultimatum game provides a second test of the value of understanding the proximate causation of behavioral anomalies. The hormone testosterone allows an interesting test of the hypothesis that proximate mechanisms produce behavioral anomalies in particular settings. In non-anonymous, potentially repeated interactions, high testosterone men are more

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willing to be confrontational because of reputational benefits. In an anonymous, one-shot ultimatum game there are no reputational benefits (at least in the laboratory), but human proximate systems may cause high testosterone men to engage in costly behavior even when there is no benefit.

In men, high testosterone is correlated with dominance-seeking behavior (Mazur and Booth, 1998). In the context of economic theory, dominance can be viewed as part of a system to increase future benefits. Thus, a costly act to maintain dominance makes sense from an evolutionary perspective because of the future benefits afforded to a dominant position. Thus, while biologists talk about dominance as its own topic, this discussion considers dominance as a form of reputation management.

When dominance is mediated by aggression, testosterone also appears to facilitate this process. A meta-analysis, summarizing the results of 45 human studies, found a consistent, positive relationship between aggression and testosterone (Book et al., 2001). Testosterone is hypothesized to mediate status and hierarchy in an adaptive manner (Kemper, 1990; Mazur, 1973, 1983, 1985). High testosterone males are willing to be more aggressive because of lower costs of aggression and/or higher benefits to aggression.

Testosterone is part of a physiological system that is at least partially conserved across many species. The 'challenge hypothesis' is that male testosterone varies to regulate male–male competition (Wingfield, 1984; Wingfield et al., 1990). For example, exogenous addition of testosterone increases male–male competition in a number of bird species (Hegner and Wingfield, 1987; Silverin, 1980). Such competition can be extremely costly; in a study of free-living cowbirds, 6.3% of testosterone-implanted males were seen one year later vs. 40.7% of controls (Dufty, 1989).

Some apes show similar relationships between testosterone and behavior. Chimpanzees (*Pan troglodytes*) are particularly relevant because they have relatively clear dominance hierarchies and because they (along with Bonobos, *Pan paniscus*) are the closest living genetic relatives of humans. A study of wild chimpanzees reports that high-ranking males were more aggressive and produced higher levels of urinary testosterone than low-ranking males (Muller and Wrangham, 2004). Testosterone and rank were positively correlated in a study of wild mountain gorillas (Robbins and Czekala, 1997).

Testosterone levels in men are correlated with non-economic behavior in an enormous variety of settings (Dabbs and Dabbs, 2000). For example, professional football players have significantly higher testosterone levels than ministers (Dabbs et al., 1990) and trial lawyers have higher testosterone than non-litigators (Dabbs et al., 1998). Testosterone correlates with other competitive behaviors. Among male prisoners, high testosterone is associated with increasing levels of infraction including overt confrontation (Dabbs et al., 1995). High testosterone men are rated as less friendly and more dominant (Dabbs, 1997). Consistent with Wingfield's challenge hypothesis that testosterone modulates male-male competition, men in committed, romantic relationships (married or not) have lower testosterone than single men (Burnham et al., 2003; Dabbs and Booth, 1993; Gray et al., 2002).

Testosterone is correlated with behavior in a number of non-physical settings including chess (Mazur et al., 1992). In one of the most economically applicable studies, subjects injected with testosterone were more likely to reduce a fictitious opponent's payoff than subjects in a control group (Kouri et al., 1995).

Over evolutionary time, humans have inherited a conserved hormonal system that uses testosterone to modulate behavior. High testosterone animals are more willing to incur the costs of conflict because of the compensating benefits that accrue in future interactions. In short, testosterone modulates a reputation management system where high testosterone males are more willing to engage in costly conflict (Ellison, 2001). In a review article on punishment, Clutton-Brock and Parker (1995) conclude "negative reciprocity is used by dominant animals to resist subordinate members from indulging in a behavior, which threatens the fitness of the dominant members".

A testable implication of this theory is the testosterone might be positively correlated with rejections in the ultimatum game. Two papers are consistent with this view. High testosterone men are more likely to reject \$5 out of \$40 (Burnham, 2007). This first study is only a correlation. A second study exogenously alters testosterone in men to further elucidate causation. This second study reports that high testosterone men are more likely to reject low ultimatum game offers regardless of whether the high testosterone levels are endogenous or elevated experimentally (Zak et al., 2009).

Research on the role of testosterone and economic behavior has expanded. Both men and women are reported to have a similar U-shaped relationship between endogenous testosterone and risk attitudes (Stanton et al., 2011). The ability of emotional signals to influence ultimatum game rejections is studied by examining cardiovascular responses and electrodermal activity (Dunn et al., 2012). This area of looking at biological and cognitive correlates to ultimatum game has become a very active area of research (Dunn et al., 2012; Emanuele et al., 2008, 2009; Ma et al., 2012; Mancini et al., 2011; Sütterlin et al., 2011; Takagishi et al., 2009).

As with the experiments on eye-detection, these testosterone results do not explain the entire anomaly of ultimatum game rejections. Any rejection rate constitutes an anomaly as far as the neoclassical prediction is concerned. The fact that high and low testosterone males differ in their rejection rate begins to identify the proximate mechanisms, but does not entirely explain the anomaly. These results do, however, begin a novel avenue of investigation into this important phenomenon.

In summary, a relationship between testosterone and ultimatum game rejections was a novel, testable hypothesis generated by thinking that behavioral economic anomalies are caused, in part, by proximate mechanisms in particular settings. Neither the neoclassical nor the behavioral view predicts such a relationship. Thus, the caveman economics hypothesis has passed the first hurdle of a novel, testable hypothesis shown to be consistent with data gathered after the hypothesis was generated. Furthermore, this early study has contributed to a variety of new approaches to understanding an important behavioral anomaly.

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5. Discussion

The debate between behavioral and neo-classical economics can be viewed, in significant part, as a failure to understand proximate and ultimate causation. Natural selection favors maximization of fitness, but the biological mechanisms that effect behavior use specific physiologic cues. Thus, these proximate causes can produce the anomalies of behavioral economics. Let us consider altruism, risk, and intertemporal discounting.

Altruism and spite exist in laboratory situations when subjects earn less than they could either to help someone else (altruism) or to hurt someone else (spite). Outside the laboratory there are a number of situations that appear to fall into these categories, however, because of reputational effects it is much harder to document altruism and spite outside the laboratory.

Caveman economics explains altruism and spite by a combination of mechanism and environment. The mental machinery that lubricates social exchange evolved in the ancestral environment. Based on archeological and anthropological evidence, it is likely that human ancestral environments involved fewer interactions with strangers, and much less privacy. Thus, behavioral anomalies that appear to be costly in the laboratory may have been produced by mechanisms that favored maximization in the ancestral environments.

In short, altruism and spite in the laboratory are produced by the evolutionary novel feature of an interaction with no future and no reputation impact. Such settings, it is hypothesized, were sufficiently rare in the ancestral environment that the optimal decision rule, reified in human nature, is to act as if there is some substantial likelihood of repeat interaction or public disclosure of behavior (Burnham and Johnson, 2005; Fehr and Henrich, 2003; Johnson et al., 2003; Trivers, 2004).

Similar to this explanation for altruism, the caveman economic explanation for the behavioral anomalies regarding time preference is also a combination of mechanism and environment. Natural selection favors organisms that optimally trade-off behaviors between time periods. Squirrels, myriad bird species, and many other animals store food even though they earn negative interest rates in the form of retrieving less food than stored. Squirrels behave this way, presumably, because the marginal benefit of an acorn is high when the squirrel is hungry, high enough to justify the loss.

Given the proficiency of non-human animals at delaying consumption, why do many behavioral experiments document too high a level of current consumption? The caveman economic hypothesis is that up until the invention of agriculture and ceramic pots around 10,000 years ago, it was much harder for humans to save. Without food preservation technology, it pays to eat everything, or give it away, as opposed to leaving the food to rot. Modern financial instruments, that allow people to earn positive real returns, are very recent inventions.

In summary, the caveman economic explanation for so-called hyperbolic discounting is an ancestral environment with bad savings technology. In such a world, it pays to consume today (Daly and Wilson, 2005).

Finally, what about loss aversion and other behavioral anomalies regarding risk? The caveman economic hypothesis is the same in this area as in altruism and discounting; the behavioral anomaly is produced in particular settings by mechanisms that arose in an ancestral setting.

Are all the behavioral anomalies produced by proximate causes in particular environments? Natural scientists who study non-human behavior work with this assumption. Non-human behavior is studied through an integrated view of causation. There is no 'behavioral' school in biology that posits, for example, other-regarding preferences for non-human animals. Anomalous behavior that appears to be disadvantageous is the used by natural scientists as the beginning of a process of discovery.

If it is true that biology reconciles non-human animal behavior into a unified framework, will the same approach work for humans? Not necessarily, and possibly because of the caveats regarding caveman economics in the introduction. Humans may be qualitatively different in transmitting ideas through culture, and in behavioral flexibility (Gould and Lewontin, 1979; Laland and Brown, 2006; Laland et al., 2011; Bolhuis et al., 2011; Dean et al., 2012). Thus, the natural sciences approach may be more limited in explaining human behavior than non-human behavior.

Most important economic behavior takes place outside the laboratory. Much of this paper has been devoted to investigating and explaining behavioral anomalies that are documented in laboratory experiments.

Laboratory experiments play an important role because of the high-level of control. A person who makes an altruistic donation in the last stage of anonymous game cannot be repaid within the experiment. Analogous behaviors outside the laboratory, such as tipping a waiter on vacation, allow the possibility for reputation formation and are less clear evidence of deviations for neoclassical economics.

While the laboratory is important for understanding, 'real world' behavior is more significant for most people. The caveman economic view based in proximate and ultimate causation may be central to many of the most important human issues (Burnham and Phelan, 2000).

Many individuals in rich societies eat too much. This issue is easily reconciled with proximate mechanisms that arose in ancestral worlds with less food (Irons, 1998). Drug addiction is another problem where pleasure-seeking mechanisms that were good for our ancestors cause problems in modern settings. Moving more directly to financial decisions, people in some countries save very little. This can cause problems for individuals and societies. The novelty of savings instruments may lay at the foundation or our problems to use such financial instruments wisely.

Caveman economics provides a path to a modern synthesis in economics. Both neoclassical and behavioral economics find support in the natural sciences view of human nature. Preferences arose via evolution by natural selection. In equilibrium, human behavior would conform more closely to the predictions of neoclassical economics. Because human genes are not

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in equilibrium with important aspects of our environment, however, maximization of preferences leads to the anomalies of behavioral economics.

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