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Towards A Neo-Darwinian Synthesis Of Neoclassical And Behavioral Economics

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Towards A Neo-Darwinian Synthesis Of Neoclassical And Behavioral Economics

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CAVEMAN ECONOMICS

Towards a Biological Synthesis of
Neoclassical and Behavioral Economics.

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Abstract

There is a schism within economics between the neoclassical view that people optimize and the behavioral view that people are filled with biases and heuristics. In recent decades, the behavioral school has been on the ascent. 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.

Introduction

Economics is divided into two competing schools based on divergent views of human nature. Neoclassical economists assume that people make optimal decisions. In sharp contrast, behavioral economists believe that people make systematic mistakes.

Behavioral economics has made significant advances in recent decades. At the core of these behavioral successes is the empirical evidence of divergences between neoclassical predictions of human behavior and actual human behavior. Richard Thaler calls these divergences “anomalies.” Neoclassical economics is unique among the social sciences in deriving conclusions from a small number of underlying axioms. However, each and every neoclassical axiom now has a behavioral economic literature that documents related anomalies.

Neoclassical economists dismiss the behavioral anomalies as interesting quirks, laboratory artifacts, or small-stakes effects that can be ignored when working on important issues. Conversely, behavioral economists dismiss mainstream economics as irrelevant applied math. The two groups do not communicate productively and the schism is a major obstacle to improving economics.

At the core of the neoclassical versus behavioral debate is the notion of optimization. Are humans good at solving hard problems (neoclassical view) or are humans terrible at solving all sorts of problems, even simple ones (behavioral view)?

Biologists have faced similar issues regarding the behavior of non-human animals. Animals can be incredibly sophisticated, and animals can also behave in ways that appear counterproductive. While economics has fragmented over the apparent contradiction of animals as both optimizers and bumlbers, biology has a single, unified view of both maximization and robust failures to maximize.

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, and is very much in the spirit of neoclassical optimization. The proximate cause of a behavior is based in specific machinery or mechanism that produces the behavior. Proximate causes can lead to persistent failures to optimize 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. Why, for example, are roughly half of human babies born as girls? The ultimate cause is that an equal sex ratio is evolutionarily stable (Fisher 1930). The proximate cause is that the mechanism of cell division and reproduction creates male gametes in equal proportion to female. Both answers are correct, and yet both are incomplete without the other. By combining proximate and ultimate, we are able to obtain a better understanding of behavior.

Are animals optimizers or are they subject to behavioral errors? The answer is both, and biologists see no contradiction in a combination of incredibly sophisticated behavior in one setting and failure in other settings.

The caveman economic hypothesis suggests that behavioral anomalies are caused, in part, by a mismatch between human proximate causes and specific environments, both in the laboratory and in modern life. Specifically, human economic behavior might, in part, be due to the “mis-firing” of

conserved brain systems that activate and then motivate behavior in response to environmental cues that were once reliable, but do not remain so today (McCabe 2003).

To understand optimizing economic behavior and behavioral anomalies, economists would be well-served to understand both the ultimate and proximate causes of behavior.

The Schism between Neoclassical and Behavioral Economics

The neoclassical economic model assumes the humans are good optimizers. This view of optimal decision-making may seem inconsistent with suicide, obesity, chastity, poverty and many other human behaviors. Such behaviors, however, are technically consistent with the neoclassical view that people maximize utility, not any externally observable attribute. Historically, most critiques of the neoclassical view that came from outside of economics did not make a major impact on the field.

However, over the last several decades, the behavioral school has had a significant impact on economics (Tversky and Kahneman 1974; Thaler 1992). The behavioral economic 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) describes 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 suicide and other lay critiques of neoclassical economics, the behavioral critique has gained traction because it works “works within the paradigm.”

Economics is currently divided between neoclassical and behavioral scholars. Many neoclassical papers continue to ignore behavioral critiques. Some neoclassical scholars suggest that behavioral phenomena are not important because the anomalies go away with either large, real-life stakes or with learning (List 2003; List and Levitt 2007).

Most neoclassical work continues on a foundation that ignores behavioral anomalies. In contrast, behavioral scholars are working to alter the axioms of economics, and to re-invent the field with a new set of theories that are consistent with the behavioral views.

This behavioral attempt to re-invent economics on behavioral axioms is proving difficult. This difficulty was 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, Knetsch et al. 1991)

This paper suggests that economists can make big improvements by incorporating the insights of natural scientists. It is not to say that the current approaches by neoclassical and behavior scholars are without merit. After close to half a century of the behavioral approach, perhaps a non-incremental improvement can be achieved by looking to the natural sciences. Why should economists look outside the field?

Natural scientists study animal behavior. Humans are animals and economics is about behavior. This alone might suggest a look at how natural scientists think about behavior. However, the argument for a natural science approach goes beyond the obvious truth that economics is a subfield of animal behavior. Natural scientists have grappled with the exact same paradox – behavior that contains both sophisticated optimization and persistent failures to optimize.

Theories of animal behavior are consistent with both neoclassical and behavioral views. Natural selection favors optimization, but the maximization is achieved by specific physical machinery that does not maximize in all settings (Mayr 1961; Tinbergen 1963; Tinbergen 1968). The concepts of proximate and ultimate causation are central to natural sciences' ability to produce a cohesive theory consistent with both maximization and failures to maximize.

Proximate and Ultimate Causation in the Natural Sciences.

While economists seek to explain all behavior through the single cause of maximization of stable preferences (Becker 1976), natural scientists distinguish four distinct types of causation for the morphology and behavior of organisms that arose by genetic evolution (Mayr 1961; Tinbergen 1963; Tinbergen 1968). 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 vital 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. This is precisely the sort of question that intrigued Darwin – how does evolution produce animals adapted for their environment? In this case, over many generations, evolution selected for 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. Termites may 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.

The “tastes great, less filling” 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 non-materially maximizing behavior. For example, rats that are given unlimited quantities of both food and drugs, choose to self-administer drugs to the point of starvation (Weeks 1962; Pickens and Harris 1968). 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.

Distinguishing proximate and ultimate causation is useful in understanding non-material maximizing 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 non-maximizing behavior. (This view is consistent with the more recently documented ‘mafia’ behavior (Soler, Soler et al. 1995; Thomas, Adamo et al. 2005) of cuckoos). The arms race aspect of this interspecies conflict is revealed by looking across species at a variety of tactics used by both parasite and host (Langmore, Hunt et al. 2003).

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.

Proximate Causes of Behavioral Economic Anomalies

Why do behavioral economic anomalies exist? The hypothesis of this paper is that anomalies exist, in significant part, because the mechanisms selected for maximization produce aberrant behavior in some particular situations. This mechanistic view of anomalies is completely different from either neoclassical or behavioral economic views.

Does the new theory make specific and testable hypotheses that differentiate it from prior theories? The subsequent two sections discuss two such findings. First, is it possible to increase altruism by

stimulating human brain mechanisms that monitor the level of privacy? Second, is there a relationship between testosterone and the behavioral anomaly of rejections in the ultimatum game?

As discussed next, these two approaches have produced some evidence that mechanism is involved in behavioral economic anomalies. The implications of this research is unknown at this time; there is further discussion in concluding comments.

Eyes and Altruism: Example 1 of Proximate Causation in Economic Behavior.

Introduction

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. A large number of studies show that this assumption is violated in a wide-variety of settings (Guth, Schmittberger et al. 1982; Kahneman, Knetsch et al. 1986; Yamagishi 1986; Guth and Tietz 1990; Roth, Prasnikar et al. 1991; Forsythe, Horowitz et al. 1994; Hoffman, McCabe et al. 1994; Berg, Dickhaut et al. 1995; Ledyard 1995; Hoffman, McCabe et al. 1996; McCabe, Rassenti et al. 1996; Cameron 1999; Henrich 2000; Henrich, Boyd et al. 2001; Fehr and Gächter 2002).

The fact that people voluntarily walk away from money – sometimes on the order of three months wages – is an important finding of behavioral economics. Can we improve our understanding of this important phenomenon by investigating proximate causation?

Three lines of research suggest that activation of the eye detection machinery might play a role in altruism.

1) Anonymity affects public goods contributions. Subjects contribute significantly more to a public good when they are identified with their decisions than when they remain anonymous (Andreoni and Petrie 2004). This effect is present even in a one-shot public goods game conducted in a large city between strangers (Rege and Telle 2004). One earlier study reports that the removal of anonymity increases public goods contributions only when combined with a post-game discussion (Gächter and Fehr 1999).

2) Humans have dedicated neural architecture that activates automatically and uncontrollably upon the detection of faces and eyes-even if only represented in two dimensional pictures (Emery 2000; Haxby, Hoffman et al. 2000). This human brain system is one of several that seems to have remained largely unchanged for millions of years and is shared with non-human primates. Included in this system are circuits which evolved to be involuntarily activated by environmental cues which previously were reliably invariant (Brothers 1990; Brothers 1996; Corballis and Lea 1999). This system involves brain areas that control sophisticated decision-making, and brain areas that are not directly under voluntary control. In particular, the human pre-frontal cortex, where our most complicated conscious decisions are made, is permanently connected with the amygdala and the superior temporal sulcus (STS), which are not in the pre-frontal cortex and are activated involuntarily by objects resembling human eyes. The evidence for this architecture and its functional origin come from a wide variety of studies of human and non-humans.

3) Neuroeconomic studies have discovered that economic games activate areas of the human brain that are outside of an individual's directly controllable decision centers (McCabe, Houser et al. 2001; Rilling, Gutman et al. 2002; Smith, Dickhaut et al. 2002; Sanfey, Rilling et al. 2003; Smith, Dickhaut et al. 2003). These modern 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 considerably faster in identifying the color of letters when the meaning and color of words match each other. For example, subjects are faster at recognizing the text color as red when the red letters spell 'red' rather than 'green'. The Stroop effect does not go away with training, thus revealing persistent involuntary interference with what is typically considered a voluntary behavior enabled by sophisticated cognition.

Taken together, these findings raise the possibility of 'engineering' a Stroop-like effect in the public goods game. The caveman economics hypothesis suggests that some of the anonymity effect in existing public goods experiments may be caused by activation of the dedicated neural architecture to detect faces. In other words, individuals may alter their level of prosocial behavior in the form of public goods contributions, in part, because of involuntary neural activation caused by the presence of human eyes and faces. The third strand of the literature suggests that humans do not have complete voluntary control over their subsequent behavior.

Therefore, the caveman economics hypothesis predicts that humans will tend to act more prosocially in the presence of artificial stimuli that only resemble human faces or eyes, yet cannot be categorized as anything but fake. Furthermore, the caveman economics hypothesis predicts that an effect may exist even when the presence of eyes has no connection to either actual observation or future payoffs.

Dedicated neural architecture for eye detection allows animals to adjust social behavior.

All animals have interactions with individuals from their own species (conspecifics) and those of other species. A variety of mechanisms have been discovered across a range of species that enable individuals to adjust behavior in such social interactions (Krebs and Dawkins 1984). One such ability that represents the backbone of social problem solving in animals is the exploitation of social information provided by the faces and eyes of others (Emery 2000). Fish, for example, are more likely to flee from objects that resemble the eyes of a predator than similar-sized objects that do not resemble eyes (Coss 1978). Birds are more likely to fly away from an approaching human if the human's eyes are visible (Hampton 1994). In addition, dogs avoid stealing forbidden food if they can see their master's eyes (Call, Brauer et al. 2003) while being capable of using a human's gaze direction to find hidden food (Hare, Brown et al. 2002). Thus, eye and face detection play a critical role in social problems across a wide range of non-primate species.

Non-human primates are also highly dependent on facial and eye cues in solving social problems. The use of social cues from eyes and faces of conspecifics are especially critical to the survival of group living primates whose success is largely determined by their ability to maintain close bonds with allies while avoiding rivals (Byrne and Whiten 1988; Tomasello, Call et al. 1998; Silk 2003). Upon the detection of another's gaze, primates typically act more prosocially towards others. For example, when rhesus monkeys detect the eye-gaze of a conspecific directed at them, they rapidly smack their lips together –

an appeasement behavior – in order to signal their friendly intent (Mistlin and Perrett 1990). Among chimpanzees, our closest extant genetic relatives, subordinate individuals avoid taking prized food while in someone's view based on whether they can see another individual's face and eyes (Hare, Call et al. 2001).

Neuroscientists have studied the neural architecture underlying this problem solving in animals. This research has revealed dedicated neural architecture both for the detection of faces and eyes and for their orientation. Invasive studies of facial cues in non-humans detail the role of individual neurons in the amygdala and STS. Single unit recording studies demonstrate that individual neurons in the superior temporal sulcus and inferior temporal sulcus respond selectively to pictures of monkey faces. Monkeys with experimentally induced brain lesions in their STS are unable to recognize pictures of faces that they previously could discriminate (Campbell, Heywood et al. 1990; Heywood and Cowey 1992).

Studies on single neurons in rhesus macaques have demonstrated that specific neurons are activated depending on the category of social stimuli that is perceived. For example, some neurons in the STS only send a signal ('fire') when a picture of a specific individual's face is perceived. Other STS neurons fire at a picture of any face or a picture of any face that is positioned at a specific angle relative to the viewer (Perrett, Rolls et al. 1982; Perrett, Smith et al. 1985) while still other cells specifically fire in the presence of a picture of an individual with opened eyes regardless of head direction (Yamane, Kaji et al. 1988). Perhaps, most intriguing is that fact that single neuron recordings from within the amygdala of stump tailed macaques showed that many cells send the strongest signal to pictures of another monkey making eye contact and the weakest signal when the pictured monkey's gaze is averted (Brothers 1990; Brothers, Ring et al. 1990; Brothers 1996).

Humans inherited a dedicated neural system for the recognition of faces and eyes

Among all animals, humans are arguably the most dependent on cues provided by faces and eyes in making social decisions (Haxby, Hoffman et al. 2000). In almost every social encounter, humans monitor the gaze direction of other humans, and process information about others' facial identity and expressions. When deciding if another individual is trustworthy, for example, adult humans rely heavily upon information about others' faces (Winston, Strange et al. 2002). During development, the ability of children to acquire language is dependent on their ability to use adult face and eye orientation to learn how words are associated with things in their environment (Corkum and Moore 1995; Tomasello 2000). The ability to use face and eye cues is so fundamental to normal functioning, that the absence of this ability in children is the initial diagnostic for the detection of autism, the debilitating disorder that severely impairs the ability of its victims to interact socially with others (Baron-Cohen, Campbell et al. 1995).

Such findings have led many theorists to suggest that it is our species heavy reliance on face and eye cues that accounts for much of our species unique cognitive abilities including language acquisition, deception, and cooperation (Baron-Cohen 1995; Povinelli 2000; Tomasello 2000).

Because of the human reliance on facial cues in social problems solving, neuroscientist have also investigated the details of how human brains are designed to acquire and process information about others' faces and eyes. Using non-invasive procedures neuroscientists have demonstrated that like other

animals, humans have dedicated neural architecture designed for the sole purpose of recognizing and reacting to faces and eyes (Baron-Cohen 1995). The similarity of this system's organization to that discovered in other primates lead some to conclude that the human eye detection system was inherited from our primate ancestors (Haxby, Hoffman et al. 2000). Important aspects of this system include:

1) Humans have dedicated brain structures to store and recognize human faces. Humans with the condition of 'prosopagnosia' have no ability to recognize faces. People who suffer from prosopagnosia have focal damage to the occipitotemporal cortex (Damasio, Damasio et al. 1982; Landis, Cummings et al. 1986).

2) Human brains have specific neural architecture for monitoring gaze. fMRI studies have revealed that inferior fusiform gyrus and superior temporal sulcus are responsible for gaze detection (Puce, Allison et al. 1998; Haxby, Hoffman et al. 2000; Hoffman and Haxby 2000). The amygdala is also involved in processing cues for facial recognition and orientation; humans with brain damage to their amygdala develop difficulties in recognizing faces and gaze direction of others (Young, Aggleton et al. 1995). Corroborating this finding, PET scanning of adult humans showed a significant activation of the amygdala during a gaze discrimination task (Kawashima, Sugiura et al. 1999).

3) There is also evidence that activation of our human eye detection system is involuntary. Humans have what appear to be automatic and involuntary responses to gaze. For example, when people are asked to estimate the age of a person shown in a picture, fMRI results show that the parts of the brain that judge gaze direction and facial expression are activated (Winston, Strange et al. 2002).

In addition, it seems that involuntary brain activation can lead to behavioral responses. For example, when seeing the picture of a face, humans are unable to inhibit their gaze-orienting response even when explicitly instructed to inhibit this reaction (Driver, Davis et al. 1999; Emery 2000; Hoffman and Haxby 2000). The implication of these finding is that even when subjects are not intentionally attending to gaze direction, the brain areas for such categorization are activated.

Summary of hypothesis and experimental results

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 proposing this hypothesis, "humans will exhibit more pro-social behavior when they perceive themselves to be in public ... 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 (Burnham 2003; Haley and Fessler 2005; Bateson, Nettle et al. 2006; Burnham and Hare 2007; Rigdon, Ishii et al. 2009), and there is one published negative result (Fehr and Schneider 2009).

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. 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.

Testosterone and Spite: Example 2 of Proximate Causation in Economic Behavior.

Another famous result of behavioral economics comes in the ultimatum game. This setting provides a second test of the value of the proximate causation of behavioral anomalies.

In the ultimatum game, one person (“proposer”) makes an offer to a second (“responder”) on how to divide a sum of money. This offer is final – an ultimatum – so if the responder rejects, there is no agreement and neither person earns any money. Since rejections result in no money, standard economic theory predicts that responders will accept all positive offers.

The ultimatum game is a simple negotiation that is famous because people frequently reject offers of ‘free’ money. The first ultimatum game experiment reported that low offers were frequently rejected and 20% of all negotiations ended with no agreement (Guth, Schmittberger et al. 1982). This deviation between actual human behavior and that predicted by economic theory has been replicated in myriad studies (Roth 1995), including games played for large stakes (Cameron 1999) and cross-culturally (Roth, Prasnikar et al. 1991; Henrich 2000). Who are the rejecters in the ultimatum game and why do they prefer no money to some money?

Testosterone and behavior

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 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). 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, Starzyk et al. 2001). Testosterone is hypothesized to mediate status and hierarchy in an adaptive manner (Mazur 1973; Mazur 1983; Mazur 1985; Kemper 1990). 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, Hegner et al. 1990). For example, exogenous addition of testosterone increases male-male competition in a number of bird species (Silverin 1980; Hegner and Wingfield 1987). 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, de la Rue et al. 1990) and trial lawyers have higher testosterone than non-litigators (Dabbs, Alford 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, Carr 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 (Dabbs and Booth 1993; Gray, Kahlenberg et al. 2002; Burnham, Chapman et al. 2003).

Testosterone is correlated with behavior in a number of non-physical settings including chess (Mazur, Booth 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, Lukas et al. 1995).

Summary of hypothesis and experimental results

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 injects 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, Kurzban et al. 2009).

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.

Discussion

The debate between behavioral and neo-classical economics can be viewed as a failure to distinguish between proximate and ultimate causation. Natural selection favors maximization of fitness, and equilibrium models of animal behavior are very similar to neoclassical economic models. However, the biological mechanisms that effect behavior use specific cues. Thus, these proximate causes can produce behaviors that do not increase fitness including the anomalies of behavioral economics.

This paper is entitled Caveman Economics because industrialized, and even agricultural, societies have systematic and important characteristics that differ from ancestral human environments. Proximate mechanisms are more likely to lead to anomalous behavior in evolutionarily novel environments.

If humans were in equilibrium with our environment, there would be no behavioral anomalies and no behavioral economics. In equilibrium, humans would be predicted to act 'as if' they sought to maximize both utility and genetic fitness. 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 material maximization in the modern world. Darwin grappled with issues regarding the fit between organism and environment.

I do believe that natural selection will always act very slowly, often only at long intervals of time, and generally on only a very few of the inhabitants of the same region at the same time.

— Charles Darwin
The Origin of Species, Ch. IV

Darwin struggled to reconcile genetic evolution with the fact that many organisms seem designed for their environments. How could a myopic, slow process produce sophisticated and well-adapted morphology and behavior?

Darwin solved the puzzle with the help of Lyell's evidence (which at the time was revolutionary) that the earth is much older than several thousand years (Lyell 1830; Lyell 1832; Lyell 1833). With enough generations in a stable environment, evolution by natural selection can produce organisms whose design fits their environment. Thus, time provides the key for the Darwinian reconciliation of genetic evolution and organisms built to optimize in a particular environment. While more recent evidence suggests that evolution can be both less gradual (Eldredge and Gould 1972) and more rapid (Kettlewell

1973; Endler 1986; Grant and Grant 1989) than Darwin believed, his essential insight about the role of time and organism design remains intact.

Does evolution produce perfect animal optimizers that behavior according to neoclassical economic predictions? Some animals do exhibit extremely sophisticated behavior. For example, chimpanzees (*Pan troglodytes*) are adept at selecting the best partners for cooperative tasks (Melis, Hare et al. 2006). Furthermore, sophisticated behavior is not confined to primates; small-brained dungflies (*Scatophaga stercoraria*) 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).

If non-human animals, big- and small-brained, can optimize in computationally difficult situations, why do humans suffer from the biases and heuristics document by behavioral economists? The answer is that while optimization has support within the natural sciences, there is also support for exactly the sort of persistent non-maximization of behavioral economics.

While Darwin focused on the ability of evolution by natural selection to produce appropriate design and behavior, more recent work predicts certain types of persistently maladaptive behavior (Bowlby 1969; Wilson 1978; Tooby and Cosmides 1989; Tooby and Cosmides 1990). This literature, which includes the fields of sociobiology and evolutionary psychology, places particular importance on emergence of agriculture and the implications for human social organization.

For a very long time, human ancestors foraged for food. The important attributes of: i) small group size, ii) low population density, and iii) repeat interactions with 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 kin-based 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 including the nature and frequency of interactions with conspecifics.

The phrase, the “environment of evolutionary adaptiveness” or EEA was coined by Bowlby (1969; 1973) to describe a stylized Pleistocene environment that was in equilibrium with human genes. More recently, Irons (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.

The importance of the ancestral environment lies in the significant and systematic discord between the genes adapted for that environment and modern settings. This genetic 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 (Tooby and Cosmides 1989; Gigerenzer 1993; Irons 1998), for book length treatments see (Wilson 1975; Wilson 1978; Barkow, Cosmides et al. 1992; Pinker 2002), and for the seminal critique of the adaptationist program, see (Gould and Lewontin 1979)).

Darwin struggled with the puzzle of efficient design produced by a slow, myopic process. Conversely, economists struggle to understand how a highly intelligent animal can fail to maximize in simple settings. Time, either in abundance or shortage, provides the solution to both mysteries.

Caveman economics provides a path forward for reconciling behavioral and mainstream 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 to the predictions of standard economic theory. Because human genes are not in equilibrium with important aspects of our environment, however, maximization of preferences leads to robust and significant deviations from material maximization.

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