# **Engineering Human Cooperation**

Does Involuntary Neural Activation Increase Public Goods Contributions?

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Abstract In a laboratory experiment, we use a public goods game to examine the hypothesis that human subjects use an involuntary eye-detector mechanism for evaluating the level of privacy. Half of our subjects are "watched" by images of a robot presented on their computer screen. The robot—named Kismet and invented at MIT—is constructed from objects that are obviously not human with the exception of its eyes. In our experiment, Kismet produces a significant difference in behavior that is not consistent with existing economic models of preferences, either self- or other-regarding. Subjects who are "watched" by Kismet contribute 29% more to the public good than do subjects in the same setting without Kismet.

**Keywords** Altruism · Proximate causation · Public goods · Reciprocity · Tinbergen

Over the past several decades, evidence has accumulated that documents the divergence between human economic behavior and that predicted by mainstream economic theory (Kahneman 2003; Kahneman and Tversky 1984; Thaler 1992). One interesting class of behavioral anomaly involves voluntary actions that decrease monetary earnings. Experimental demonstrations of such costly tendencies include some behaviors that increase payoffs for other people (altruism) and other costly behaviors that decrease payoffs for other people (spite).

Examples of experimentally induced altruism include contributions in dictator games (Forsythe et al. 1994; Hoffman et al. 1994, 1996a; Kahneman et al. 1986), public goods contributions (Ledyard 1995), and reciprocation in trust games (Berg et al. 1995; McCabe et al. 1996). Experimental demonstrations of

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spite include rejections in ultimatum games (Guth et al. 1982; Guth and Tietz 1990), replicated cross-culturally (Henrich 2000; Henrich et al. 2001; Roth et al. 1991) and for high stakes (Cameron 1999; Hoffman et al. 1996b), and some forms of punishment in public goods games (Fehr and Gächter 2002; Yamagishi 1986).

Economic altruism and spite occur even under anonymous experimental conditions in which subjects cannot be rewarded for their acts in future interactions (Fehr and Fischbacher 2003). Thus these behaviors are inconsistent with economic preferences that are entirely self-regarding. Some important aspects of altruism and spite are captured in "other-regarding" preference models that incorporate observed human regularities such as inequality aversion and fairness (Bolton 1991; Bolton and Ockenfels 2000; Levine 1998; Rabin 1993). More recent work seeks to explain altruism and spite as efforts to benefit the group (Bowles and Gintis 2002; Boyd et al. 2003; Fehr and Fischbacher 2003; Fehr and Gächter 2002; Fehr and Henrich 2003; Fehr and Rockenbach 2003; Fehr et al. 2002; Gintis et al. 2003).

Where do other-regarding preferences originate? In particular, why would any organism voluntarily choose fewer resources by being altruistic or spiteful? To the contrary, one might reasonably believe that "a predominant quality to be expected in a successful gene is ruthless selfishness" (Dawkins 1976). In addressing similar questions, natural scientists have found it productive to distinguish the direct physiological and/or psychological source of behavior (proximate causation) from its evolutionary origin (ultimate causation; Mayr 1961; Tinbergen 1963, 1968). Other-regarding preferences—in forms with more parameters than current models—could accurately describe the proximate cause of altruism and spite, but they do not address the ultimate cause (Burnham 2003, 2007; Burnham and Johnson 2005).

A variety of scholars find the ultimate cause of human behavioral anomalies, including altruism and spite, in what can be labeled the "evolutionary legacy hypothesis," which suggests that the human brain reflects, in part, ancestral conditions that may vary systematically from modern environments (Bowlby 1969, 1973; Tooby and Cosmides 1989, 1990; Wilson 1975, 1978). Central to this argument is the fact that the human brain did not arise de novo (Klein 1999). Instead the human brain was shaped from existing structures in our nonhuman ancestors (Jerison 1973). This approach has been applied in a handful of recent economic works (Burnham 1997, 2001, 2003, 2007; Burnham et al. 2000; Frank 1987; McCabe 2003; McCabe and Smith 2001; McCabe et al. 1996, 1997).

The evolutionary legacy hypothesis suggests that economic behavioral anomalies are caused, in part, by a mismatch between human ancestral conditions and modern conditions (Burnham 1997, 2003, 2007; Burnham et al. 2000). Specifically, it is suggested that anomalies in human economic behavior might, in part, be due to the "misfiring" 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).

Although these proximate causes of behavior contained in the human brain may have facilitated inclusive-fitness-maximizing behavior in the ancestral environment, the evolutionary legacy hypothesis suggests that these same systems can be "fooled" in novel or artificial contexts. When operating in evolutionary equilibrium, proximate causes achieve ultimate goals, but in novel settings these same



mechanisms can produce bizarre or even self-destructive behavior (Barkow et al. 1992; Pickens and Harris 1968; Weeks 1962).

If this evolutionary legacy hypothesis is correct, it should be possible to "engineer" behavioral anomalies by the systematic manipulation of the proximate causes of human behavior (Burnham 2003). Three lines of research suggest an interesting test of the evolutionary legacy hypothesis.

- 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 between strangers in a large city
  (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 et al. 2000). This brain system is one of several that seems to have remained largely unchanged for millions of years and is shared with nonhuman primates. Included in this system are circuits which evolved to be involuntarily activated by environmental cues that previously were reliably invariant (Brothers 1990, 1996; Corballis and Lea 1999).
- 3. Neuroeconomic studies have discovered that economic games activate areas of the human brain that are outside an individual's directly controllable decision centers (McCabe et al. 2001; Rilling et al. 2002; Sanfey et al. 2003; Smith et al. 2002, 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 read words (Stroop 1935). People are considerably faster in reading when the meaning and color of words match each other. For example, subjects are faster recognizing the word "red" when the text is red rather than when it is 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 evolutionary legacy 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 evolutionary legacy 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. For example, an increase in prosociality could occur even if the artificial eyes belong to "Kismet," a robot that cannot be mistaken as being human by any normally functioning adult (Breazeal and Scassellati 2002). Furthermore, the evolutionary legacy hypothesis



predicts that an effect may exist even when the presence of eyes has no connection to either actual observation or future payoffs.

To test the evolutionary legacy hypothesis, an experiment was designed in which human subjects play a public goods game while being "watched" by images of Kismet on their computer screen. As in previous fMRI studies presenting pictures of faces (Emery 2000; Haxby et al. 2000), Kismet's human-like eyes should activate the subjects' neural architecture dedicated to eye detection. The evolutionary legacy hypothesis predicts that this activation will cause subjects to alter their behavior as if this activation had occurred while observing the eyes and face of an actual human. In particular, the evolutionary legacy hypothesis suggests the possibility of a "Kismet effect" wherein subjects watched by Kismet increase their contributions in a public goods game.

In the next section we discuss the evidence for a dedicated, human neural architecture to detect eyes. The following section explains the experimental design for activating this neural architecture in a public goods game, and the penultimate section contains results of the experiment. The paper ends with a discussion, and the subjects' instructions.

### Humans' Adaptive Neural Architecture for Eye Detection

Humans have dedicated neural architecture for detecting a variety of facial features, including the presence of eyes. This system involves brain areas that control sophisticated decision making, and brain areas that are not directly under voluntary control. In particular, the human prefrontal cortex, where our most complicated conscious decisions are made, is permanently connected to the amygdala and the superior temporal sulcus (STS), which are not in the prefrontal cortex and are activated involuntarily by objects resembling human eyes. The evidence for this architecture and its functional origin comes from a wide variety of studies of humans and nonhumans.

Dedicated neural architecture for eye detection enables animals to adjust social behavior. All animals have interactions with individuals of their own species 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 from 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 et al. 2003) and they are capable of using a human's gaze direction to find hidden food (Hare et al. 2002). Thus, eye and face detection play a critical role in social problems across a wide range of nonprimate species.

Nonhuman 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 is



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; Silk 2003; Tomasello et al. 1998). Upon the detection of another's gaze, primates typically act prosocially. When rhesus monkeys detect the 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 et al. 2001, 2006).

Neuroscientists have studied the neural architecture underlying this problemsolving in animals. This research has revealed dedicated neural architecture for the detection of both faces and eyes and their orientation. Invasive studies of facial cues in nonhumans detail the role of individual neurons in the amygdala and STS. Singleunit recording studies among primates demonstrate that individual neurons in the superior 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 et al. 1990; Heywood and Cowey 1992).

Studies of 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 when the monkeys are shown a picture of any face or any face that is positioned at a specific angle relative to the viewer (Perrett et al. 1982, 1985). Still other cells specifically fire in response to a picture of an individual with opened eyes regardless of head direction (Yamane et al. 1988). Perhaps most intriguing is the fact that single-neuron recordings from within the amygdala of stump-tailed macaques show that many cells send the strongest signal in response to pictures of another monkey making eye contact and the weakest signal when the pictured monkey's gaze is averted (Brothers 1990, 1996; Brothers et al. 1990).

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 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 on information about others' faces (Winston et al. 2002). During language development, most children 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 et al. 1995).

Such findings have led some theorists to suggest that it is our species's heavy reliance on face and eye cues that accounts for much of our 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 problem-solving, neuroscientists have also investigated the details of how human brains are designed to acquire and process information about others' faces and eyes. Using noninvasive 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 has led some to conclude that the human eye-detection system was inherited from our primate ancestors (Haxby et al. 2000). Important aspects of this system include the following:

- 1. Humans have dedicated brain structures to store and recognize human faces. Humans with prosopagnosia have no ability to recognize faces. People who suffer from this condition have focal damage to the occipitotemporal cortex (Damasio et al. 1982; Landis et al. 1986).
- 2. Human brains have specific neural architecture for monitoring gaze. fMRI studies have revealed that the inferior fusiform gyrus and superior temporal sulcus are responsible for gaze detection (Haxby et al. 2000; Hoffman and Haxby 2000; Puce et al. 1998). 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 et al. 1995). Corroborating this finding, PET scanning of adult humans showed a significant activation of the amygdala during a gaze discrimination task (Kawashima et al. 1999).
- 3. There is also evidence that activation of the 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 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 et al. 1999; Emery 2000; Hoffman and Haxby 2000). The implication of these findings is that even when subjects are not intentionally attending to gaze direction, the brain areas for such categorization are activated.

### Summary of Eye Detection in Humans

Over evolutionary time, our species has 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, a stimulus of the dedicated neural architecture in the amygdala and STS might affect human behavior, including economic decisions.



### **Experimental Design**

Goal Alter the perception of anonymity, without altering actual anonymity.

The evolutionary legacy hypothesis suggests that the mechanisms that evaluate anonymity can be fooled. In particular, stimulation of the dedicated neural architecture for eye detection may cause people to behave more prosocially even when it is obvious that the stimulus can have no effect on actual anonymity.

Nonhuman primates can be fooled in this manner. For example, rhesus monkeys perform a "lip-smack" in the presence of other monkeys as a form of communication (Mistlin and Perrett 1990). When monkeys see their own image in a mirror, they lip-smack, even though there is no other animal present, and thus no communication. Furthermore, this behavior persists even after years of exposure (Gallup et al. 1980).

Humans almost certainly have better control of involuntary neural activations than do nonhuman primates. Nevertheless, the similarity of the underlying neural circuitry suggests that it may be possible to produce a similar effect in humans. In fact, in a public goods setting, mutual eye gaze has been shown to increase contributions to a public good without any change in anonymity (Kurzban 2001).

As reviewed in the introduction, public goods game contributions are higher in non-anonymous settings (Andreoni and Petrie 2004; Rege and Telle 2004). In addition, the evolutionary legacy hypothesis suggests that activation of the human eye-detection neural architecture may influence economic behavior. This perspective creates a two-dimensional framework, as shown in Fig. 1.

The existing public goods experiments on anonymity vary both actual and perceived anonymity simultaneously. Thus, in the framework in Fig. 1, the previous experiments find a significant difference between the upper-left quadrant (condition 1) and the lower-right quadrant (condition 4).

The comparisons that differentiate the evolutionary legacy hypotheses from alternatives based in actual anonymity are condition 1 vs condition 3 and condition 2 vs condition 4. These two comparisons alter perceived anonymity while holding anonymity constant.

Actual anonymity (Evaluated by prefrontal cortex)

Perceived anonymity (Evaluated by brain areas outside the prefrontal cortex the amygdala and the STS)

	Anonymous	Public	
Anonymous	CONDITION 1 Demonstrated: Lower public goods contributions	CONDITION 2	
Public	condition 3	CONDITION 4 Demonstrated: Higher public goods contributions	

Fig. 1 Four different combinations of actual and perceived anonymity



In addition, it is important to differentiate between-subject anonymity from subject-experimenter anonymity. In the public goods setting, one study found no effect for subject-experimenter anonymity (Laury et al. 1995). In other experimental settings, there is conflicting evidence, with some studies reporting a change in behavior owing to variations in subject-experimenter anonymity (Burnham 2003; Eckel and Grossman 1996; Hoffman et al. 1996a) and another reporting no effect (Bolton and Zwick 1995).

Given these conflicting data, we sought to ensure a constant level of subject-experimenter anonymity while manipulating perceived between-subject anonymity. Accordingly, we chose the following setup. In all conditions, subjects' decisions were known to the experimenter and private with regard to other subjects. The control and test conditions seek to vary the perception of between-subject anonymity. Thus, we contrast condition 1 with condition 3 in a setting where there is no subject-experimenter anonymity.

We implement this design by having all subjects make decisions in their own private area (between-subject anonymity), but in a manner that makes it clear that the experimenter will know their decisions (no subject-experimenter anonymity). The control treatment is private with regard to other subjects, and it is built to be perceived as private (condition 1 in Fig. 1). The test treatment adds a pair of human eyes to the control environment. Because of the neural architecture discussed above, the evolutionary legacy hypothesis suggests that the test treatment, although actually still private with regard to other subjects, will be perceived as public by the eye detection neuro-architecture (condition 3 in Fig. 1).

In summary, the experimental manipulation is designed to create different information states within the subjects' brains. In both treatments, the more sophisticated cognitive areas in the prefrontal cortex of the brain "know" that the decisions will be observed by the experimenter, and not by other subjects. The experiment is designed to alter the information state in the involuntarily activated brain areas that also estimate the level of anonymity.

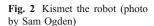
### The Eye Stimulus: Kismet the Robot

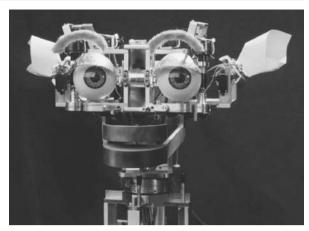
In order to test the prediction of the evolutionary legacy hypothesis a stimulus was needed that would elicit the maximum activation from the two non-prefrontal-cortex areas that detect eyes (the amygdala and STS) while creating the least amount of activation in the prefrontal cortex.

Pictures of Kismet the robot were used as the stimuli (Fig. 2). Kismet was designed at MIT with the goal of creating an embodied robotic system that could effectively interact and cooperate with humans as a social partner instead of as a tool. Therefore Kismet was carefully designed to maximize its ability to engage people through its appearance and the expressive social cues it gives off while behaving (Breazeal 2003; Breazeal and Scassellati 2002). Kismet's face has a structure resembling that of a human, with nonhuman material resembling a nose, mouth, and ears. Critically, Kismet has extremely large eyes that resemble human eyes.

What is the effect of Kismet on actual and perceived anonymity? Kismet does not change subjects' actual anonymity, but Kismet is likely to stimulate the dedicated







neural architecture for eye detection in the STS and amygdala. Thus Kismet might produce the critical combination in subjects—awareness that other subjects will not learn their choices, along with involuntary cognitive brain activation that signals someone is watching.

Because Microsoft software uses "clippy" the paperclip—an animated agent (with eyes)—we introduce Kismet to our subjects in a similar manner. The hope is that this presentation minimizes any demand effect. Accordingly, we had an image of Kismet appear on the screen at the beginning of the experiment with the text, "Hi, I'm Kismet and I'm here to help you through this experiment."

# Subjects

Subjects were recruited by email via a Harvard Business School list. Subjects were restricted to having participated in two or fewer previous experiments at the HBS laboratory. Ninety-six subjects participated in four sessions of 24 subjects each. Forty-seven of the subjects were woman and 49 were men.

The subject pool draws from local colleges and thus is subject to flux around important college dates. To minimize any between-session variability caused by differences in the subject pool, all sessions were run during the summer of 2003. For similar reasons, all sessions started between 2:30 P.M. and 3:30 P.M., mid-week (Tuesday–Thursday).

### The Experimental Setup

Subjects each received \$10 in advance for participation and then played six rounds of a public goods game. In each round, each player was given ten tokens to allocate between a public and a private account. Tokens in the private account remained with the player, while those allocated to the group account were doubled and divided up equally among four players in a group. Tokens were converted to cash at a rate of \$0.20. Subjects were paid in cash and privately at the end of the session.



Each session consisted of 24 subjects playing in six groups of four. The groups were shuffled between rounds so that subjects never played twice with the same counterpart. The design used the "perfect stranger" pairings described by Fehr and Gächter (2002).

This setup ensures that any contribution to the public good will be costly. Tokens in the private account are worth \$0.20 whereas tokens given to the public account are worth \$0.10 to each group member. Because subjects never see each other again, there is no ability to form reputations or to strategically alter other subjects' behavior. Every token allocated to the public account costs the contributor \$0.10 regardless of the behavior of other subjects. Thus, the dominant, money-maximizing strategy is to contribute nothing to the public account.

The subjects sat in four rows with six individuals per row. All decisions were made via computers, and each subject had his or her own computer. Three-sided, opaque screens separated each computer and subject. Subjects were instructed not to look at anyone else's screen and not to speak to each other.

In each round, each subject's decision was displayed graphically on her or his screen. These decisions remained on the screen for the entire time between rounds. All sessions were run on the same schedule so decisions were visible for the same amount of time in each round across all sessions.

The pace of the experiment was controlled by password. In each round, after the subject had made a decision, the screen stayed fixed, with the decisions visible, until a password was entered.

Upon arrival at the laboratory, each subject was given a tax ID form. They were told that at the end of the experiment, they would bring the completed form to the experimenter and be paid the amount that they had earned.

No deception was used in the experiment.

### Control Treatment: Kismet Is Not Watching

The control treatment is a standard setting wherein subjects make their decisions via computer and the experimenter receives the decisions over the network.

We sought to ensure that the presence of Kismet is not working through estimates of subject–experimenter anonymity. Although the experimenter does see all of the subjects' behavior in all treatments, it is not obvious that subjects understand this completely.

To check this empirically, we implemented two different versions of the control treatment.

Control 1: "Public" Treatment Throughout the rounds, the experimenters stayed in the front of the room. At the end of the time for each round, the experimenter called out a password that the subjects entered to advance to the next round. This treatment is labeled "public" because we expected that subjects would understand that their decisions were being recorded and would be known to the experimenters.

Control 2: "Double Public" Treatment Same as above, except after each decision the experimenter visits each subject to enter the password on the subject's computer. When the experimenter comes to the subject's computer, the subject's current



decision is clearly visible on the screen. This control treatment is labeled "double public" because the experimenter sees each decision twice—once while entering the password, and a second time when the computer network sends the decision to the experimenter.

If behavior in the two control conditions does not differ, this supports the hypothesis that subjects understand that there is no experimenter-subject anonymity.

Test Treatment: Kismet Is Watching

This treatment is identical to the "public" treatment with the addition of having an image of Kismet on the screen at all times. Throughout the instruction phase, a single fixed image is present. During the decision phase, two different images of Kismet alternate. The images alternate every 0–2 s based on a random process. The images alternate to make sure that the subjects will at least momentarily focus on Kismet so as to maximize the chance that at the key point in the experiment—the moment of actual decision—the presence of Kismet increases neural activation in the eye-detection system of each subject.

### Hypothesis

The evolutionary legacy hypothesis suggests that subjects will contribute more in the test treatment (with Kismet) than in the control treatment (without Kismet).

### Results

Do subjects in the standard experimental conditions understand that the experimenter will see their choices? To address this question, behavior during the two control conditions was compared. Subjects' behavior does not differ significantly between the two control treatments. The first-round contribution in the public treatment averages 4.92 tokens vs 5.58 in the double public treatment (p=0.52). Similarly, across all rounds, contribution in the public treatment averages 4.33 tokens vs 4.02 in the double public treatment (p=0.70). Thus we conclude that subjects in the standard computer-run sessions understand that the experimenter will see their decisions.

This empirical validation of the control conditions allows us to test the evolutionary legacy hypothesis of a Kismet effect without fear that the stimulus is working through changing perceptions of experimenter-subject anonymity.

As shown in Table 1 and Figs. 3 and 4, contributions when Kismet is watching are 29% higher in the first round, 29% higher in the average round, and higher in every round. These differences are statistically significant with p values below 0.05 (one-sided t test for difference in means).

Across rounds, subjects contributed a mean of 5.39 tokens in the Kismet condition while contributing 4.17 tokens in the No Kismet treatment. A two-way ANOVA (treatment  $\times$  round) was used to compare subjects' contributions in the two treatments and across rounds. There was a significant effect of condition [ $F_{1,94}$ =4.77,



Table 1 Average (± SEM) contributions (out of ten possible) to the public good by round for control treatments

	Kismet (N=48)	No Kismet ( <i>N</i> =48)	p value
First round	6.75	5.25	0.014
Avg. over all six rounds	5.39	4.17	0.016

p=0.032], with subjects contributing significantly more to the public good in the Kismet treatment. Moreover, there was no significant treatment  $\times$  round interaction, indicating that the difference between conditions was persistent across rounds.

These results do not appear to be caused by gender differences. The gender composition of sessions was not controlled, and the number of women in a session ranged from 10 to 13. The effect of controlling for gender is to increase the magnitude of the treatment effect and to increase the statistical significance. Addition of a gender variable in the regression for first-round contributions increases the magnitude of the Kismet effect from 1.5 tokens to 1.54 tokens and increases the t statistic for the Kismet effect from 2.23 to 2.28. Addition of a gender variable in the regression for the average contribution across all rounds increases the magnitude of the Kismet effect from 1.22 tokens to 1.28 tokens and increases the t statistic for the Kismet effect from 2.17 to 2.33.

Thus, we conclude that the difference between Kismet and No Kismet treatments is not caused by gender. Similarly, we can find no other subject characteristic that accounts for the Kismet effect.

#### Discussion

This study finds that subjects in a standard public goods game contribute significantly more when "watched" by Kismet the robot. In particular, subjects with an image of Kismet on their computer screen contribute 29% more to a public good in the first round, and an average of 29% more across all six rounds, than subjects without an image of Kismet on their computer screen. This Kismet effect is predicted

Fig. 3 Average (± SEM) first-round contributions (out of ten possible) to the public good, for subjects with and without Kismet watching

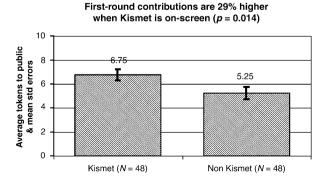
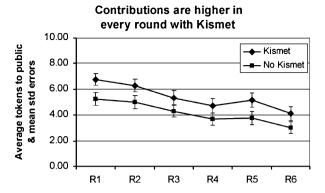




Fig. 4 Average (± SEM) contributions (out of ten possible) to the public good, by round for Kismet and No Kismet conditions



by the evolutionary legacy hypothesis; we are not aware of any other economic model, either mainstream or behavioral, that makes a similar prediction.

Mainstream economic models of human behavior that are entirely self-regarding predict no contributions to the public good either with or without Kismet. Thus, such models are not consistent with the Kismet effect nor with previous findings of public goods contributions (Ledyard 1995). Behavioral economic models of other-regarding preferences or group-selected altruistic intent (Bolton 1991; Bolton and Ockenfels 2000; Fehr and Fischbacher 2003; Fehr and Gächter 2002; Fehr and Schmidt 1999; Gintis et al. 2003; Levine 1998; Rabin 1993) predict positive contributions to public goods, but do not predict the Kismet effect. Thus, neither mainstream nor behavioral economic models of preferences predict the Kismet effect.

In contrast, the evolutionary legacy hypothesis predicts a Kismet effect based on four logical steps. First, humans have dedicated neural architecture that detects human eyes (Emery 2000; Haxby et al. 2000). Second, in ancestral human environments, the presence or absence of human eyes provided information about the level of privacy (Krebs and Dawkins 1984). Third, in the ancestral environment, humans who varied their behavior based on the presence or absence of human eyes would have an advantage over humans who did not have such a mechanism (Baron-Cohen 1995; Cosmides and Tooby 1992). Fourth, this mechanism may continue to function even in settings where the ancestral relationship between the presence of eyes and optimal behavior does not exist (e.g., anonymous and one-shot laboratory settings) (Bowlby 1969, 1973; Tooby and Cosmides 1989, 1990; Wilson 1975, 1978).

Analysis suggests that the Kismet effect in this study is not produced by gender differences or any other measured attribute of the subjects. Furthermore, the participants in all sessions were drawn from the same subject pool using an identical recruitment process, and the sessions were run under standardized conditions (computerized instructions, same period of day, same days of the week, etc.). Thus, we are not aware of any difference between the sessions that could be the source of the Kismet effect. Replication of this study, particularly in other laboratories, would further reduce the likelihood of a spurious correlation.

An alternative interpretation is that the presence of Kismet produces a demand effect whereby subjects contribute more in an effort to please the experimenter. The two control treatments of this study seem to diminish this likelihood. As compared



with a standard experimental setting, subjects in this study do not contribute more even when they know that their individual decisions will be observed directly by the experimenter. In other words, there is no demand effect when subjects in this study know that the experimenter will literally be looking over their shoulder at each and every decision. This seems to diminish the likelihood that the addition of Kismet in the same setting produces a demand effect. It is, nevertheless, impossible to rule out a demand effect in this case. One method to investigate this further would be to use a more abstract or more fleeting stimulus representing a human face or eyes. If these more subtle stimuli also increase subjects' level of prosociality, then the likelihood that the Kismet effect is a demand effect would be further reduced.

Although this experiment supports the predictions of the evolutionary legacy hypothesis, the result of this initial experiment should be replicated and, if replicated, extended. The evolutionary legacy hypothesis suggests that economic behavior might be affected in many different economic games. Further experiments could help define the exact neural mechanisms. One experimental path would be to investigate brain function with fMRI or other brain imaging technologies during the presentation of an eye stimulus.

A related fMRI investigation of the ultimatum game is suggestive (Sanfey et al. 2003). In the ultimatum game, subjects who reject positive offers voluntarily decrease their monetary earnings (Stahl 1972). Nevertheless, studies show some people reject positive ultimatum game offers in many cultures and even for high stakes (Cameron 1999; Guth et al. 1982; Henrich 2000; Henrich et al. 2001; Hoffman et al. 1996b; Roth et al. 1991). Why do some ultimatum game players walk away from "free" money? A clue may lie in the finding that fMRIs indicate that subjects with higher neural activation in the bilateral anterior insula (not part of the prefrontal cortex) were more likely to reject small offers (\$1 or \$2) (Sanfey et al. 2003).

One interpretation of these ultimatum game data is that different parts of subjects' brains conflict regarding the correct course of action (Camerer 2003). The emotional part of the brain reacts to the "unfairness" of a low offer while the cognitive portion of the brain understands that rejection leads to less money. Thus, in an ultimatum game played anonymously without repetition, there is a conflict between the goal of making money and the goal of resisting unfairness. Subjects' rejection decisions can be viewed as a function of the relative strength of neural activation towards these competing goals. Those subjects with increased brain activation outside the prefrontal cortex are more likely to reject low offers (Sanfey et al. 2003). In these subjects who reject positive offers, the fairness goal is achieved at some monetary cost.

Although there is conflict between a desire for "fairness" and a desire to make money in a one-shot, anonymous ultimatum game, there may have been no such conflict in the human ancestral environment (Burnham 2007). A careful mathematic model of the ultimatum game in an environment with some chance of observation concludes, "evolutionary dynamics tend to favor strategies that demand and offer a fair share of the prize" (Nowak et al. 2000). This suggests that the evolutionary legacy hypothesis might help explain ultimatum game behavior. Based on archaeological evidence (Renfrew and Bahn 1991) and studies of modern foragers (Chagnon 1992; Hill and Hurtado 1996; Lee 1993), it is likely that most ancestral human behavior took place in non-anonymous settings. Thus, it is possible that in the human ancestral environment "fairness" was a tool used to achieve material



rewards (Frank 1987, 1988; Schelling 1978). In the evolutionarily novel one-shot and anonymous setting, however, there is conflict between the goals of fairness and money.

Although such an evolutionary hypothesis will require further testing, the existing data do seem consistent with its predictions. An investigation in the context of the public goods game with and without eyes would enable a further test. Does Kismet activate the human neural architecture dedicated to eye detection? Additionally, is there any correlation between the strength of activity in different parts of the brain and subject behavior? For example, do subjects with higher activity in the eye-detection areas contribute more when being watched by Kismet? Conversely, do subjects with higher activation in other brain areas suppress the effect of the eye-detection mechanism and contribute less to the public good?

The Kismet results, if replicated and extended, demonstrate that the evolutionary legacy hypothesis may contribute to resolving the debate between behavioral and mainstream economics. The success of behavioral economics is driven, in part, by the ability to document "anomalies"—deviations between actual human behavior and that predicted by mainstream models (Kahneman 2003; Kahneman and Tversky 1984; Thaler 1992). Robyn Dawes and Richard Thaler define an 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" (Dawes and Thaler 1988).

One could view the Kismet effect as an anomaly within an anomaly. Not only do subjects make costly public goods contributions, but also the level of contributions is changed significantly by an unexpected and seemingly irrelevant factor. Therefore, one could view the Kismet effect as a further complication to an already complicated picture.

However, the discovery of the Kismet effect, using evolutionary predictions, can also be viewed as a step towards reconciling anomalies and optimization. The Kismet effect suggests that behavioral anomalies are themselves the result of an optimizing process. Evolution by natural selection favors maximization. The mechanisms that produce maximization, however, are reified in human physiology that changes only over evolutionary time (Tinbergen 1963).

The result is that natural selection—a potent force for optimization—can produce persistent deviations from maximizing behavior. The positive aspect is that anomalies can be predicted and modeled within a broader maximizing framework. The hope is this path may produce reconciliation between mainstream and behavioral economics, and eventually between economics and the natural sciences (Burnham 1997, 2007; Wilson 1978, 1998).

Four years have lapsed between these experiments and their publication (more than two years between acceptance of this submission and its publication). Consequently, it is important to note some of the developments that have occurred in the meantime. The first paper of which we are aware that posits a mechanistic explanation for altruism in humans was published by the senior author in 2003 (Burnham 2003). Two other studies have documented the effect of eyes on human altruism (Bateson et al. 2006; Haley and Fessler 2005). Both of those studies have features not included in the Kismet study. Haley and Fessler use a control image treatment, and the study by Bateson and colleagues presents the stimulus subliminally. Taken together, these four papers present a strong case for the suggestion that the human brain is built to detect eyes, and that humans act more



prosocially when the eye-detection neural architecture is activated. In our opinion it would be very useful to measure brain activation directly in related settings using modern imaging techniques.

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## **Appendix**

#### Instructions

### Welcome!

This is an experiment about decision-making. There are other people in this room who are also participating in this experiment. You must not talk to them or communicate with them in any way until the experiment is over. The experiment will take about an hour and a half, and at the end you will be paid in private and in cash. The amount of money you will earn depends on the decisions that you and the other participants make.

In this experiment you will perform a decision task six times. We refer to each decision task as a round. In each round you will be in a group with three other people, but you will not know which of the other people in this room are in your group. The decisions made by you and the three other people in your group will determine how much you earn.

Each round you will be matched with three new group members. You will never be matched with the same person more than once.

You have been paid \$10 to show up today. In addition to your show-up fee, you will earn money in each round. Your total earnings for the experiment today will be the show-up fee plus the sum of what you earn in all six rounds.

In each round you will have ten tokens, which you can place in your private account or in a shared group account. The other members of your group will also have ten tokens each and can place them in either their own private account or the shared group account. Your earnings depend on how much you keep in your private account and the total amount placed in the group account by you and the other three members of your group.

You will be paid based on the number of tokens that you collect throughout the experiment. Each token that you earn will convert to \$0.20 to be paid in cash at the end of the experiment.

In each round you decide how many of your ten tokens to keep in your private account and how many to place in the group account. You will retain each token that you keep in your private account. Each token that you place in the group account will be doubled and then divided equally among the four members of the group.



Likewise, each of the three other members of your group will decide on dividing their tokens between their own private account and the group account.

### References

- Andreoni, J., & Petrie, R. (2004). Public goods experiment without confidentiality: A glimpse into fundraising. *Journal of Public Economics*, 88, 1605–1623.
- Barkow, J. H., Cosmides, L., & Tooby, J. (1992). The Adapted Mind: Evolutionary Psychology and the Generation of Culture. New York: Oxford University Press.
- Baron-Cohen, S. (1995). Mindblindness: An Essay on autism and theory of mind. Cambridge, MA: MIT Press.
- Baron-Cohen, S., Campbell, R., Karmiloff-Smith, A., Grant, J., & Walker, J. (1995). Are children with autism blind to the mentalistic significance of the eyes? *British Journal of Developmental Psychology*, 13, 379–398.
- Bateson, M., Nettle, D., & Roberts, G. (2006). Cues of being watched enhance cooperation in a real world setting. *Biology Letters*, 2, 412–414. Retrieved from www.journals.royalsoc.ac.uk.
- Berg, J., Dickhaut, J., & McCabe, K. (1995). Trust, reciprocity, and social history. *Games and Economic Behavior*, 10, 122–142.
- Bolton, G. (1991). A comparative model of bargaining: theory and evidence. *American Economic Review*, 81, 1096–1136.
- Bolton, G., & Ockenfels, A. (2000). ERC: A theory of equity, reciprocity and competition. *American Economic Review*, 90, 166–193.
- Bolton, G., & Zwick, R. (1995). Anonymity versus punishment in ultimatum bargaining. *Games and Economic Behavior*, 10, 95–121.
- Bowlby, J. (1969). Attachment and loss. vol. I: Attachment. New York: Basic Books.
- Bowlby, J. (1973). Attachment and loss, vol. II: Separation, anxiety, and anger. New York: Basic Books. Bowles, S., & Gintis, H. (2002). Homo reciprocans. Nature, 415, 125–126.
- Boyd, R., Gintis, H., Bowles, S., & Richerson, P. J. (2003). The evolution of altruistic punishment. Proceedings of the National Academy of Sciences, 100, 3531–3535.
- Breazeal, C. (2003). Emotion and sociable humanoid robots. *International Journal of Human–Computer Studies*, 59, 119–155.
- Breazeal, C., & Scassellati, B. (2002). Robots that imitate humans. Trends in Cognitive Science, 6, 481-487.
- Brothers, L. (1990). The neural basis of primate social communication. Motivation & Emotion, 14, 81-91.
- Brothers, L. (1996). Brain mechanisms of social cognition. Journal of Psychopharmacology, 10, 2–8.
- Brothers, L., Ring, B., & Kling, A. (1990). Response of neurons in the macaque amygdala to complex social stimuli. *Behavioural Brain Research*, 41, 199–213.
- Burnham, T. C. (1997). Essays on genetic evolution and economics. Parkland, FL. Retrieved from www. dissertation.com.
- Burnham, T. C. (2001). Altruism and spite in a selfish gene model of endogenous preferences. *Journal of BioEconomics*, 3, 123–148.
- Burnham, T. C. (2003). Engineering altruism: A theoretical and experimental investigation of anonymity and gift giving. *Journal of Economic Behavior and Organization*, 50, 133–144.
- Burnham, T. C. (2007). High-testosterone men reject low ultimatum game offers. *Proceedings of the Royal Society B, Biological Sciences* (in press).
- Burnham, T. C., & Johnson, D. (2005). The biological and evolutionary logic of human cooperation. Analyse & Kritik, 27(2), 113–135.
- Burnham, T. C., McCabe, K., & Smith, V. L. (2000). Friend-or-Foe priming in an extensive form trust game. *Journal of Economic Behavior and Organization*, 43, 57–73.
- Byrne, R. W., & Whiten, A. (1988). Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes, and humans. Oxford: Clarendon.
- Call, J., Brauer, J., Kaminski, J., Tomasello, M. (2003). Domestic dogs (*Canis familiaris*) are sensitive to the attentional state of humans. *Journal of Comparative Psychology*, 117, 257–263.
- Camerer, C. (2003). Strategizing in the brain. Science, 300, 1673–1675.
- Cameron, L. (1999). Raising the Stakes in the ultimatum game: Experimental evidence from Indonesia. Economic Inquiry, 37, 47–59.



- Campbell, R., Heywood, C. A., Cowey, A., Regard, M., & Landis, T. (1990). Sensitivity to eye gaze in prosopagnosic patients and monkeys with superior temporal sulcus ablation. *Neuropsychologia*, 28, 1123–1142.
- Chagnon, N. (1992). Yanomamo, 4th ed. New York: Harcourt Brace Jovanovich.
- Corballis, M. C., & Lea, S. E. G. (1999). The descent of mind: Psychological perspectives on hominid evolution. Oxford: Oxford University Press.
- Corkum, V., & Moore, C. (1995). Development of joint visual attention in infants. In C. Moore, & P. Dunham (Eds.) *Joint attention: Its origins and role in development* (pp. 61–83). Hillsdale, NJ: Lawrence Erlbaum Associates.
- Cosmides, L., & Tooby, J. (1992). Cognitive adaptations for social exchange. In J. H. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 163–228). New York: Oxford University Press.
- Coss, R. G. (1978). Delayed plasticity of an instinct: Recognition and avoidance of 2 facing eyes by the jewel fish. *Developmental Psychobiology*, 12, 335–345.
- Damasio, A. D., Damasio, H., & Van Hoesen, G. W. (1982). Prosopagnosia: Anatomic basis and behavioral mechanisms. *Neurology*, 32, 331–342.
- Dawes, R., & Thaler, R. (1988). Cooperation. Journal of Economic Perspectives, 2, 187-197.
- Dawkins, R. (1976). The selfish gene. New York: Oxford University Press.
- Driver, J., Davis, G., Ricciardelli, P., Kidd, P., Maxwell, E., & Baron-Cohen, S. (1999). Gaze perception triggers reflexive visuospatial orienting. Visual Cognition, 6, 509–540.
- Eckel, C., & Grossman, P. (1996). Altruism in anonymous dictator games. *Games and Economic Behavior*, 16, 181–191.
- Emery, N. J. (2000). The eyes have it: The neuroethology, function and evolution of social gaze. Neuroscience and Biobehavioral Reviews, 24, 581–604.
- Fehr, E., & Fischbacher, U. (2003). The nature of altruism. Nature, 425, 785-791.
- Fehr, E., & Gächter, S. (2002). Altruistic punishment in humans. Nature, 415, 137-140.
- Fehr, E., & Henrich, J. (2003). Is strong reciprocity a maladaptation? On the evolutionary foundations of human altruism. In: P. Hammerstein (Ed.), The genetical and cultural evolution of cooperation (pp. 55–82). Cambridge, MA: MIT Press.
- Fehr, E., & Rockenbach, B. (2003). Detrimental effects of sanctions on human altruism. *Nature*, 422, 137–140.
- Fehr, E., & Schmidt, K. (1999). A theory of fairness, competition, and cooperation. *Quarterly Journal of Economics*, 114, 817–868.
- Fehr, E., Fischbacher, U., & Gächter, S. (2002). Strong reciprocity, human cooperation and the enforcement of social norms. *Human Nature*, 13, 1–25.
- Forsythe, R., Horowitz, J. L., Savin, N. E., & Sefton, M. (1994). Fairness in simple bargaining experiments. *Games and Economic Behavior*, 6, 347–369.
- Frank, R. H. (1987). If *Homo economicus* could choose his own utility function, would he want one with a conscience? *American Economic Review*, 77, 593–604.
- Frank, R. H. (1988). Passions within reason: The strategic role of emotions. New York: Norton.
- Gächter, S., & Fehr, E. (1999). Collective action as a social exchange. *Journal of Economic Behavior and Organization*, 39, 341–369.
- Gallup, G., Wallnau, L., & Suarez, S. (1980). Failure to find self-recognition in mother-infant and infant-infant rhesus monkey pairs. Folia Primatologica, 33, 210–219.
- Gintis, H. (2000). Strong reciprocity and human sociality. Journal of Theoretical Biology, 206, 169-179.
- Gintis, H., Bowles, S., Boyd, R., & Fehr, E. (2003). Explaining altruistic behavior in humans. Evolution and Human Behavior, 24, 153–172.
- Guth, W., & Tietz, R. (1990). Ultimatum bargaining behavior: A survey and comparison of experimental results. *Journal of Economic Psychology*, 11, 417–449.
- Guth, W., Schmittberger, R., & Schwarze, B. (1982). An experimental analysis of ultimatum bargaining. *Journal of Economic Behavior and Organization*, 3, 367–388.
- Haley, K., & Fessler, D. (2005). Nobody's watching? Subtle cues affect generosity in an anonymous economic game. Evolution and Human Behavior, 26, 245–256.
- Hampton, R. R. (1994). Sensitivity to information specifying the line of gaze of humans in sparrows (*Passer domesticus*). Behaviour, 130, 41–51.
- Hare, B., Brown, M., Williamson, C., & Tomasello, M. (2002). The domestication of social cognition in dogs. Science, 298, 1634–1636.
- Hare, B., Call, J., Tomasello, M. (2001). Do chimpanzees know what conspecifics know? Animal Behaviour, 61, 139–151.



- Hare, B., Call, J., & Tomasello, M. (2006). Chimpanzees deceive a human by hiding. Cognition, 101, 495–514.
- Haxby, J. V., Hoffman, E. A., & Gobbini, I. (2000). The distributed human neural system for face perception. Trends in Cognitive Science, 4, 223–233.
- Henrich, J. (2000). Does culture matter in economic behavior? Ultimatum game bargaining among the machiguenga of the Peruvian Amazon. American Economic Review, 90, 973–979.
- Henrich, J., Boyd, R., Bowles, S., Camerer, C., Fehr, E., Gintis, H., et al. (2001). In search of Homo economicus: Behavioral experiments in 15 small-scale societies. American Economic Review, 91, 73-78.
- Heywood, C. A., & Cowey, A. (1992). The role of the "face-cell" area in the discrimination and recognition of faces by monkeys. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 335, 31–38.
- Hill, K., & Hurtado, M. (1996) *Ache life history: The ecology and demography of a foraging people.* New York: Aline de Gruyter.
- Hoffman, E. A., & Haxby, J. V. (2000). Distinct representations of eye gaze and identity in the distributed human neural system for face perception. *Nature Neuroscience*, 3, 80–84.
- Hoffman, E., McCabe, K., Shachat, K., & Smith, V. (1994). Preferences, property rights, and anonymity in bargaining games. Games and Economic Behavior, 7, 346–380.
- Hoffman, E., McCabe, K., & Smith, V. (1996a). Social distance and other-regarding behavior in dictator games. American Economic Review, 86, 653–660.
- Hoffman, E., McCabe, K., & Smith, V. L. (1996b). On expectations and the monetary stakes in ultimatum games. *International Journal of Game Theory*, 25, 289–301.
- Jerison, H. (1973). Evolution of the brain and intelligence. New York: Academic Press.
- Kahneman, D. (2003). A psychological perspective on economics. American Economic Review, 93, 162–168.
- Kahneman, D., & Tversky, A. (1984). Choices, values, and frames. American Psychologist, 39, 341–350.
  Kahneman, D., Knetsch, J., & Thaler, R. (1986). Fairness and the assumptions of economics. Journal of Business, 59, S285–S300.
- Kawashima, R., Sugiura, M., Kato, T., Nakamura, A., Hatano, K., Ito, K., et al. (1999). The human amygdala plays an important role in gaze monitoring. A PET study. *Brain*, 122, 779–783.
- Klein, R. (1999). The human career: Human biological and cultural origins. Chicago: University of Chicago Press.
- Krebs, J. R., & Dawkins, R. (1984). Animal signals: Mind reading and manipulation. In J. R. Krebs, & N. B. Davies (Eds.), *Behavioural ecology: An evolutionary approach*, 2nd ed. (pp. 380–402). Oxford: Blackwell.
- Kurzban, R. (2001). The social psychophysics of cooperation: Nonverbal communication in a public goods game. *Journal of Nonverbal Behavior*, 25, 241–259.
- Landis, T., Cummings, J. L., Christen, L., Bogen, J. E., & Imhof, H. G. (1986). Are unilateral right posterior cerebral lesions sufficient to cause prosopagnosia? Clinical and radiological findings in six additional patients. *Cortex*, 22, 243–252.
- Laury, S. J., Walker, J. M., & Williams, A. W. (1995). Anonymity and voluntary provision of public goods. *Journal of Economic Behavior and Organization*, 27, 365–380.
- Ledyard, J. O. (1995). Public goods. In J. H. Kagel, & A. E. Roth, (Eds.), Handbook of experimental economics (pp. 111–194). Princeton, NJ: Princeton University Press.
- Lee, R. (1993). The Dobe Júhoansi. New York: Harcourt Brace.
- Levine, D. (1998). Modeling altruism and spitefulness in experiments. *Review of Economic Dynamics*, 1, 593–622.
- Mayr, E. (1961). Cause and effect in biology. Science, 134, 1501-1506.
- McCabe, K. (2003). A cognitive theory of reciprocal exchange. In E. Ostrom, J. Walker (Eds.), *Trust and reciprocity: Interdisciplinary lessons from experimental research* (pp. 147–169). New York: Sage.
- McCabe, K., Houser, D., Ryan, L., Smith, V., & Trouard, T. (2001). A functional imaging study of cooperation in two-person reciprocal exchange. *Proceedings of the National Academy of Science*, 98, 11832–11835.
- McCabe, K. A., Rassenti, S. J., & Smith, V. L. (1996). Game theory and reciprocity in some extensive form experimental games. *Proceedings of the National Academy of Science*, 93, 113421–113428.
- McCabe, K., & Smith, V. L. (2001). Goodwill accounting in economic exchange. In G. Gigerenzer, & R. Selten (Eds.), *Bounded rationality: The adaptive toolbox* (pp. 319–340). Cambridge: MIT Press.
- McCabe, K. A., Smith, V. L., & LePore, M. (1997). Intentionality detection and "Mindreading": Why does game form matter? *Proceedings of the National Academy of Science*, 97, 4404–4409.



- Mistlin, A. J., & Perrett, D. I. (1990). Visual and somatosensory processing in the macaque temporal cortex: The role of "Expectation." *Experimental Brain Research*, 82, 437–450.
- Nowak, M. A., Page, K. M., & Sigmund, K. (2000). Fairness versus reason in the ultimatum bargaining game. Science, 289, 1773–1775.
- Perrett, D. I., Rolls, E. T., & Caan, W. (1982). Visual neurones responsive to faces in the monkey temporal cortex. Experimental Brain Research, 47, 329–342.
- Perrett, D. I., Smith, P. A. J., Potter, D. D., Mistlin, A. J., Head, A. S., Milner, A. D., et al. (1985). Visual cells in the temporal cortex sensitive to face view and gaze direction. *Proceedings of the Royal Society* of London B: Biological Sciences, 223, 293–317.
- Pickens, R., & Harris, W. C. (1968). Self-administration of d-amphetamine by rats. Psychopharmacologia, 12, 158–163.
- Povinelli, D. (2000). Folk physics for apes. Oxford: Oxford University Press.
- Puce, A., Allison, T., Bentin, S., Gore, J. C., & McCarthy, G. (1998). Temporal cortex activation in humans viewing eye and mouth movements. *Journal of Neuroscience*, 18, 2188–2199.
- Rabin, M. (1993). Incorporating fairness into game theory and econometrics. American Economic Review, 83, 1281–1303.
- Rege, M., & Telle, K. (2004). The impact of social approval and framing on cooperation in public good situations. *Journal of Public Economics*, 88, 1625–1644.
- Renfrew, C., & Bahn, C. (1991). Archeology: Theories, methods, and practice. London: Thames and Hudson.
- Rilling, J. K., Gutman, D., Zeh, T., Pagnoni, G., Berns, G., & Kilts, C. (2002). A neural basis for social cooperation. *Neuron*, 35, 395–405.
- Roth, A. E., Prasnikar, V., Okuno-Fujiwara, M., & Zamir, S. (1991). Bargaining and market behavior in Jerusalem, Ljubljana, Pittsburgh, and Tokyo: An experimental study. *American Economic Review*, 81, 1068–1095.
- Sanfey, A. G., Rilling, J. K., Aronson, J. A., Nystrom, L. E., & Cohen, J. D. (2003). The neural basis of economic decision-making in the ultimatum game. *Science*, 300, 1755–1758.
- Schelling, T. (1978). Altruism, meanness and other potentially strategic behaviors. American Economic Review, 68, 229–230.
- Silk, J. (2003). Social bonds of female baboons enhance infant survival. Science, 302, 1231-1234.
- Smith, K., Dickhaut, J., McCabe, K., & Pardo, J. V. (2002). Neuronal substrates for choice under ambiguity, risk, gains and losses. *Management Science*, 48, 711–718.
- Smith, K., Dickhaut, J., McCabe, K., & Pardo, J. V. (2003). The impact of the certainty context on the process of choice. Proceedings of the National Academy of Science, 100, 3536–3541.
- Stahl, I. (1972). Bargaining theory. Stockholm: Economic Research Institute.
- Stroop, J. R. (1935) Studies of interference in serial verbal reactions. *Journal of Experimental Psychology*, 18, 643–662.
- Thaler, R. H. (1992). The Winner's curse: Paradoxes and anomalies of economic life. Princeton, NJ: Princeton University Press.
- Tinbergen, N. (1963). On aims and methods in ethology. Zeitschrift für Tierpsychologie, 20, 410-433.
- Tinbergen, N. (1968) On war and peace in animals and man. An ethologist's approach to the biology of aggression. *Science*, 160, 1411–1418.
- Tomasello, M. (2000). *The cultural origins of human cognition*. Cambridge, MA: Harvard University Press.
- Tomasello, M., Call, J., & Hare, B. (1998). Five primate species follow the visual gaze of conspecifics. Animal Behaviour, 55, 1063–1069.
- Tooby, J., & Cosmides, L. (1989). Evolutionary psychology and the generation of culture, I: Theoretical considerations. *Ethology & Sociobiology*, 10, 29–49.
- Tooby, J., & Cosmides, L. (1990). The past explains the present: Emotional adaptations and the structure of ancestral environments. *Ethology & Sociobiology*, 11, 375–424.
- Weeks, J. R. (1962). Experimental morphine addiction: Method for automatic intravenous injections in unrestrained rats. Science, 138, 143–144.
- Wilson, E. O. (1975). Sociobiology: The new synthesis. Cambridge, MA: Belknap Press of Harvard University Press.
- Wilson, E. O. (1978). On human nature. Cambridge, MA: Harvard University Press.
- Wilson, E. O. (1998). Consilience. New York: Knopf.
- Winston, J. S., Strange, B. A., O'Doherty, J., & Dolan, R. J. (2002). Automatic and intentional brain responses during evaluation of trustworthiness of faces. *Nature Neuroscience*, 5, 277–283.



Yamagishi, T. (1986). The provision of a sanctioning system as a public good. *Journal of Personality and Social Psychology*, 51, 110–116.

Yamane, S., Kaji, S., & Kawano, K. (1988). What facial features activate face neurons in the inferotemporal cortex of the monkey? *Experimental Brain Research*, 73, 209–214.

Young, A. W., Aggleton, J. P., Hellawell, D. J., Johnson, M., Broks, P., & Hanley, J. R. (1995). Face processing impairments after amygdalotomy. *Brain*, 118, 15–24.

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