Evolution and Human Behavior xxx (2016) xxx–xxx

Contents lists available at ScienceDirect

Evolution and Human Behavior

journal homepage: www.ehbonline.org

Original Article

Evidence of partner choice heuristics in a one-shot bargaining game

Adar B. Eisenbruch [a,*], Rachel L. Grillot [a], Dario Maestripieri [b], James R. Roney [a]

[a] Department of Psychological and Brain Sciences, University of California, Santa Barbara, CA 93106-9660, USA
[b] Department of Comparative Human Development, The University of Chicago, 940 E. 57th Street, Chicago, IL 60637, USA

ARTICLE INFO

Article history:
Initial receipt 3 October 2015
Final revision received 4 April 2016
Available online xxxx

Keywords:
Ultimatum game
Bargaining
Partner choice
Cooperation
Faces
Strength

ABSTRACT

Economists and psychologists have developed a variety of models to explain human behavior in the ultimatum game, but none can adequately account for all of the available data. Across two studies using a face perception paradigm, we provide evidence that people use evolved, specialized heuristics for long-term cooperative partner choice to calibrate their generosity toward ultimatum game partners. Men and women played one-shot ultimatum games for real incentives with partners represented by face photographs. Men were more generous toward partners who were stronger, and who appeared more attractive, more prosocial, more productive, healthier and higher in social status; the effect of strength was mediated by productivity, but not dangerousness, suggesting that men implemented heuristics designed for partner choice rather than the asymmetric war of attrition. Moreover, men reduced their earnings by cooperating selectively with valuable long-term partners. Women also gave better treatment to valuable-appearing partners, but appeared to prioritize partner choice less than men did, relative to game earnings and intrasexual competition. The results suggest that people treat the ultimatum game as though it were an opportunity to establish a cooperative relationship with a new partner, and implications are discussed for an evolved psychology of cooperative partner choice.

Researchers have long used the Ultimatum Game (UG) to study human cooperation and bargaining (Camerer, 2003; Güth & Kocher, 2014). In the UG, a proposer offers a specific split of a fixed sum of money, and the responder either accepts the offer – in which case the proposed split is enacted – or rejects it, in which case both players receive nothing. Behavior in the UG is typically regarded as economically "anomalous" (Thaler, 1988), because people fail to pursue the income-maximizing strategies whereby responders accept any positive offer and prescient proposers therefore make the lowest possible offer. Instead, proposers in industrial societies typically offer 40%–50% of the endowment and responders frequently reject low offers (but see Henrich et al., 2005 regarding cultural differences). To explain these results, economists have developed a variety of models suggesting that people are averse to unequal distributions between the two players (reviewed by Camerer, 2003).

Exogenous to these models, however, is a body of research showing that people are sensitive to the traits of their UG partner, not merely to the structure of the game. For example, offers are more likely to be accepted if they are from a smiling proposer (Mussel, Göritz, & Hewig, 2013) or one described as generous (Marchetti, Castelli, Harlé, & Sanfey, 2011); more symmetrical responders receive higher offers (Zaatari, Palestis, & Trivers, 2009); and more attractive individuals receive higher offers from proposers but responders also demand more from them in order to accept an offer (Solnick & Schweitzer, 1999). There is complementary evidence from other economic games as well, for example showing that attractive individuals are more likely to be trusted (Wilson & Eckel, 2006) and to have their trust reciprocated (Krupp, DeBruine, & Jones, 2011) in a trust game. These results suggest that people process economic games, including the UG, as though they are real-world social interactions, in which the biological and behavioral traits of their partners matter. Since humans have cognitive adaptations for social exchange relationships (see Cosmides & Tooby, 2005), we investigated whether behavior in the UG conforms to evolved heuristics for resource division.

We identified two adaptationist theories of how resources might be divided in the UG. First, there is evidence suggesting that people divide resources according to the logic of the asymmetric war of attrition (AWA; Hammerstein & Parker, 1982; Maynard Smith, 1979), in which resources are allocated based on the relative ability and willingness of each individual to inflict damage on the other. Physically stronger men feel more entitled to advantageous outcomes and are more willing to use force to resolve conflicts in their favor (Sell, Tooby, & Cosmides, 2009; see also Petersen, Sznycer, Sell, Cosmides, & Tooby, 2013). If resources are divided in the UG according to the logic of the AWA, then any cues of the likelihood of winning a violent conflict over resources (e.g., strength, aggressiveness) should lead to more advantageous treatment in the game.

The second theory is that people will treat the UG not as a conflict over an existing resource (in which the AWA would apply), but as an

* Corresponding author.
E-mail addresses: Eisenbruch@psych.ucsb.edu (A.B. Eisenbruch), Rachel.Grillot@psych.ucsb.edu (R.L. Grillot), Dario@uchicago.edu (D. Maestripieri), roney@psych.ucsb.edu (J.R. Roney).

http://dx.doi.org/10.1016/j.evolhumbehav.2016.04.002
1090-5138/

opportunity to initiate a long-term cooperative relationship. Humans evolved in a biological marketplace of long-term cooperative relationships, and therefore faced selection pressures to choose (and be chosen by) the most valuable available cooperators (Barclay, 2013; Baumard, André, & Sperber, 2013; Noë & Hammerstein, 1994, 1995). An individual's value in the biological market of cooperators is a function of their ability to create future benefits, their expected generosity in sharing those benefits, and their outside options for production and/or cooperation (Barclay, 2013; Baumard et al., 2013; Zaatari & Trivers, 2007). If mechanisms that evolved for partner choice (PC) govern behavior in the UG, then participants should offer advantageous treatment to partners who appear high in partner value, as a type of opening bid for the establishment of a cooperative relationship. On this account, any cues that a potential partner is more valuable than alternative possible partners should cause that potential partner to be treated better in the UG. As discussed further below, cues of health, strength, and prosociality, among other traits, likely predicted relative partner value in the ancestral environments in which PC mechanisms evolved. As such, on the PC model, players perceived to possess these traits should receive more generous treatment in the UG.

In the present research, we used face photographs that had been measured and rated for various traits as partners in the UG in order to test how perceived traits affect treatment in the game. We initially hypothesized effects consistent with the AWA – in which more threatening and formidable individuals should receive better treatment – but initial results suggested that cues of high partner value might be the stronger predictor of treatment in the game. Subsequent data collections were therefore designed to test between the AWA and PC models.

1. Study 1a

1.1. Study 1a: Introduction

Since humans form rich impressions of others based on limited exposure to faces (e.g., Willis & Todorov, 2006), we used a face-perception paradigm to test the effects of various cues on treatment in the UG. In an initial study using male participants, we predicted on the basis of the AWA that cues of the likelihood of escalating and winning a violent conflict over resources would lead to more generous treatment in the UG. Recent research suggests that men's facial-width-to-height ratio (fWHR) may be a cue of formidability. Men with greater fWHRs are judged as more aggressive (Carré, McCormick, & Mondloch, 2009), dominant (Alrajih & Ward, 2014) and intimidating (Hehman, Leitner, & Gaertner, 2013), and are in fact more aggressive both in the laboratory and in real-world settings (Carré & McCormick, 2008). Similarly, men with wider faces are trusted less and are less trustworthy in an economic task (Stirrat & Perrett, 2010). Men with wider faces are more likely to be violent (Christiansen & Winkler, 1992), but less likely to die in fights (Stirrat, Stulp, & Pollet, 2012). In sum, there is evidence to suggest that men with wider faces may be calibrated to a more aggressive, exploitative interpersonal strategy, and are perceived as such. Therefore, the logic of the AWA predicts that men with a higher fWHR will receive more generous treatment in the UG.

1.2. Study 1a: Materials and methods

1.2.1. Design

We tested this prediction using stimulus faces drawn from a sample of men who participated in a study on mating psychology and behavior. These men had been measured for physical strength, and photos of their faces were measured for fWHR and rated for health, attractiveness, dominance, and prosociality. We then used these pictures to represent UG partners (hereafter "targets") for a new set of male participants. The above measurements and ratings were initially made because of their relevance to the larger project on mating psychology, but they also allowed us to test predictors of treatment in the UG. On the basis of the AWA, we predicted that fWHR would positively predict generosity received in the UG; the other traits were also examined because prior findings suggest that facial traits may be influential in the UG (see Introduction).

We employed the strategy method of the UG (see Güth & Kocher, 2014). In the strategy method, the responder states the minimum offer they would accept from the proposer, rather than accepting or rejecting a specific offer. We refer to this as the responder's "demand." This method allows all subjects to play as both proposer and responder with all possible partners, and elicits continuous measures of UG behavior. During session 1, participants played a series of one-shot ultimatum games (with a $10 endowment) with multiple same-sex partners ("targets") who were represented by a facial photograph. Participants saw a picture of a target's face and were asked to state either an offer or a demand for that target, and this was repeated for all targets (participants were instructed to skip any targets they recognized). Participants were randomly assigned to play first as the proposer toward all targets and then as the responder toward all targets, or vice versa. Targets were presented in a random order. These targets had previously played a single, one-shot UG for real money using the strategy method with an anonymous partner (i.e., their partners were not identified to them, nor they to their partners, in any way beyond knowing that they were all participants in the same study). These recorded UG decisions allowed us to pay our study 1a participants based on the actual outcomes of their games.

Session 2 occurred a few weeks after session 1. During session 2, subjects rolled a die. If the die came up 6, one of their UG decisions from session 1 was chosen at random, and compared to the corresponding decision of their target from that round. Participants were then paid their earnings for that round in cash. As such, all participant decisions were incentive-compatible, and there was no deception. All targets, photograph raters, and participants were students at UCSB, who gave informed consent to participate or have their picture used for research.

1.2.2. Male target stimuli

Facial photographs of 83 male students were used as stimuli ("targets") in study 1a. They were 18–26 years old (mean = 20.0, s.d. = 1.85). Thirty-five self-identified as Caucasian, 20 as Asian, 16 as Hispanic, and the rest as multiracial or "Other." All gave permission for their photographs to be used for research purposes.

Photographs were taken directly facing the camera under standardized lighting conditions, and were digitally rotated so that the pupils were aligned on a horizontal axis. fWHR was measured as the distance between the left and right zygion (the outermost edge of the face, before the ear) divided by the distance from the top of the upper lip to the upper edge of the eyelids. Measurements were made independently by two research assistants; there was high agreement between the two sets of measurements ($r = .95$), and their mean was used in analysis. Photographs were then cropped with an oval around the face. Strength was measured as the composite of grip and chest strength (measured with a dynamometer) and flexed bicep circumference (see Sell et al., 2009).

1.2.3. Raters

Due to the design of the study from which these target stimuli were drawn, the target face photographs were rated in two batches. Sixty-nine students (42 female) rated 39 of the male targets; these raters were 17–22 years old (mean = 18.6 years, s.d. = 0.99). Forty-eight students (19 female) rated the other 44 male targets; these raters' ages ranged from 18 to 22 years (mean = 18.6 years, s.d. = 0.99). Target photos were rated for attractiveness (3 items; alpha = .980), health, dominance (3 items; alpha = .946), and prosociality (3 items; alpha = .974). Items were presented in a random order, and target faces were randomized within items. Full wording of all items and their intra-class correlations are presented in Appendix A.

1.2.4. Male ultimatum game participants

Ninety-nine men played the UG with the target face photographs as partners. None of these men were among the participants who had

Please cite this article as: Eisenbruch, A.B., et al., Evidence of partner choice heuristics in a one-shot bargaining game, *Evolution and Human Behavior* (2016), http://dx.doi.org/10.1016/j.evolhumbehav.2016.04.002

rated the faces. Eleven men showed no variance in their generosity index (see below), likely indicating disengagement from the task, so analysis was restricted to the other 88 participants. (Given the potential uncertainty regarding whether invariance in generosity reflects disengagement or a consistent strategy, analyses were also run including all participants, and statistical results were very similar. Generally speaking, including all participants changed zero-order correlations only in the third decimal place.) Due to experimenter error, we did not record the ages of these participants. However, they were drawn from the same subject pool as the raters used in study 1a, so we expect a similar age distribution.

1.2.5. Data analysis

Mean values for each rating dimension for each target face were computed and used in subsequent analyses. We calculated bivariate correlations in order to evaluate the zero-order effect of each of the target traits (measured fWHR, measured strength, and ratings of attractiveness, health, dominance and prosociality) on how the target faces were treated in the ultimatum game.

1.3. Study 1a: Results

Table 1 presents the correlations between fWHR, strength, attractiveness, health, dominance and prosociality for the male targets. (Note that the traits rated in study 1b are included in the same table, for efficiency of presentation.) Surprisingly, fWHR was not significantly correlated with strength or dominance, suggesting that it may not in fact be a reliable cue of formidability, at least in this sample. It was, however, negatively correlated with ratings of attractiveness, prosociality, and health, suggesting that raters had negative impressions of men with wider faces.

There was a significant negative correlation between the mean offers and mean demands received by targets (i.e., the UG partner in the photograph), $r(83) = -.45$, $p < .001$, such that targets who received higher offers also received lower demands. This indicates that participants used offers and demands in concert when responding to UG partners; therefore we used mean generosity received by a target (generosity = offer–demand) as the primary measure of treatment in the UG.

Table 2 presents the zero-order correlations of mean generosity received by targets with their fWHR, strength, and ratings of attractiveness, health, dominance and prosociality (for efficiency of presentation, the traits rated in study 1b are also included in this table). fWHR was significantly negatively correlated with generosity received, but all of the other traits positively predicted mean generosity received. Effect sizes were especially large for health and attractiveness ratings (which were highly correlated with each other; see Table 1), with these traits accounting for nearly two-thirds of the variance in how well specific targets were treated ($rs > 0.75$).

Table 2
Zero-order correlations between mean generosity received and target traits in men (study 1).

Trait	*r*	*p*
Study 1a		
fWHR	−0.33	0.002
Strength	0.25	0.022
Health	0.79	<.001
Attractiveness	0.80	<.001
Prosociality	0.56	<.001
Dominance	0.53	<.001
Study 1b		
Friend desirability	0.75	<.001
Productivity	0.70	<.001
Dangerousness	0.24	0.03
Social status	0.86	<.001

Note: *p* values are two-tailed.

1.4. Study 1a: Discussion

The results of study 1a defied our expectations: fWHR negatively predicted generosity received in the UG. This may be because fWHR in this sample did not reliably cue the likelihood of winning a violent conflict over resources, as suggested by the lack of significant correlations between fWHR and strength and dominance. The negative correlation between fWHR and prosociality suggests that fWHR was instead used as a cue that an individual was exploitative or uncooperative.

More importantly, these results suggested to us that participants may have treated the UG as an opportunity for partner choice. The large effects of health, attractiveness, and prosociality suggest that participants gave preferential treatment to the types of people who are generally in high demand as social partners. As such, these results were consistent with a PC model for explaining UG behavior. On the other hand, the positive effect of dominance is still potentially consistent with the AWA model, given that individuals are generally prone to cede resources to dominant individuals. The effect of strength is consistent with both the AWA and PC models, since male strength may have been a reliable cue of either dangerousness or productivity in ancestral environments (Apicella, 2014; von Rueden, Gurven, & Kaplan, 2008). These ambiguities led us to have the target faces rated for additional traits in order to test between the PC and AWA models (Study 1b).

2. Study 1b

2.1. Study 1b: Introduction

Study 1b used the same UG decisions as in 1a, but the target faces were rated for additional traits in order to better test the AWA and PC theories against each other. In particular, we obtained ratings of productivity in an ancestral-like environment (e.g., how good the target would be at finding food on a desert island), dangerousness in response to a

Table 1
Intercorrelations among fWHR, strength, and the rated traits in Studies 1a and 1b.

Trait	1.	2.	3.	4.	5.	6.	7.	8.	9.
1. fWHR									
2. Strength	0.12								
3. Health	−0.55**	0.13							
4. Attractiveness	−0.44**	0.18	0.88**						
5. Prosociality	−0.31**	0.18	0.68**	0.63**					
6. Dominance	−0.08	0.19	0.46**	0.59**	−0.01				
7. Friend desirability	−0.29**	0.20	0.75**	0.79**	0.70**	0.45**			
8. Productivity	−0.21	0.27*	0.59**	0.68**	0.34**	0.79**	0.70**		
9. Dangerousness	0.14	0.18	0.03	0.25*	−0.29**	0.82**	0.17	0.61**	
10. Social status	−0.45**	0.21	0.90**	0.95**	0.66**	0.56**	0.81**	0.68**	0.18

Note. Variables 1–6 were collected in study 1a, and variables 7–10 were collected in study 1b.
* $p < 0.05$, two-tailed.
** $p < 0.01$, two-tailed.

Please cite this article as: Eisenbruch, A.B., et al., Evidence of partner choice heuristics in a one-shot bargaining game, *Evolution and Human Behavior* (2016), http://dx.doi.org/10.1016/j.evolhumbehav.2016.04.002

low offer (e.g., the target's likelihood of starting a fight in response to an insulting offer), and desirability as a friend. On the PC model, partners who appear more productive should receive greater generosity, while those who appear dangerous should receive less generosity. This is because the mind will implement algorithms designed to secure cooperative relationships with productive, non-exploitative partners in a competitive marketplace of cooperators (Barclay, 2013; Baumard et al., 2013). Desirability as a friend may then serve as a summary judgment of cooperative partner value (Tooby & Cosmides, 1996; Vigil, 2007). We chose to measure cues of ancestral, rather than modern, productivity, because their effects more clearly indicate the operation of evolved heuristics. In other words, if traits that are irrelevant to productivity in modern environments nonetheless have an effect on contemporary economic decisions, this is evidence that those decisions are implemented by mechanisms that have been tailored by natural selection to the environment in which our species evolved.

On the other hand, the AWA model predicts that partners who appear more dangerous will receive more generous treatment, because men will defer to individuals who are likely to win a violent conflict over resources. In addition, the PC model predicts that the positive effect of strength on generosity observed in study 1a will be mediated by productivity, while the AWA model predicts that the effect of strength will be mediated by dangerousness.

Since perceived productivity is a relatively new addition to the partner choice literature (see Barclay & Reeve, 2012; Debove, Baumard, & André, under review for theoretical work on the importance of individual quality and productivity, respectively; see Krupp et al., 2011; Zaatari & Trivers, 2007; Zaatari et al., 2009 for effects of cues of condition), we wanted to test it against other theoretically-relevant partner choice criteria. Most existing research on partner choice focuses on dispositional cooperativeness as the criterion by which partners are chosen (e.g., Aktipis, 2004; Delton & Robertson, 2012; Fu, Hauert, Nowak, & Wang, 2008), and health is also a theoretically-important component of partner value (e.g., Barclay, 2013; Krupp et al., 2011; Zaatari & Trivers, 2007). We used multiple regression analyses to test the independent effect of productivity, controlling for these other traits.

In addition, we tested the PC model against other possible models of UG behavior. First, a "beauty premium" has been previously observed in the UG and other economic settings (see Maestripieri, Henry, & Nickels, in press), which predicts more generous treatment toward more attractive partners. Second, proposers in study 1a could have attempted to maximize their earnings in the game by matching their offer to the demand expected from the responder. Third, participants may have simply reciprocated the treatment they anticipated receiving from their partner. We statistically controlled for each of these possibilities in order to confirm that the effects of PC heuristics obtained above and beyond these other potential influences. Note that these are particularly stringent tests of the PC model, since attractiveness may contain cues of partner value (see Section 5), and the PC model actually predicts that participants will prefer partners whom they expect to be generous; the PC model, however, uniquely predicts that other cues of partner value will matter even controlling for attractiveness halo effects and desires to reciprocate expected treatment.

2.2. Study 1b: Materials and methods

2.2.1. Male target stimuli

The target stimuli were exactly the same as those used in study 1a.

2.2.2. Raters

Eight research assistants (3 female) completed the ratings of dangerousness (3 items, e.g., likelihood of starting a fight in response to a low offer; alpha = .851), productivity (2 items, e.g., skill at acquiring food while stranded on a desert island; alpha = .871), and desirability as a friend. These research assistants also estimated how the targets would behave in an ultimatum game, i.e., the offers and demands that each target would make. Raters were blind to hypotheses, the targets' actual UG behavior, and the treatment the targets received in the UG. They ranged from 19–23 years old (mean = 21.3 years, s.d. = 2.06). Eighteen students (13 female) rated the male target faces for their apparent social status (7 items; alpha = .988). These raters were 18–21 years old (mean = 18.8 years, s.d. = 0.86). (Ratings of male social status were performed after study 2, given the strong effect of social status in women.) Items were presented in a random order, and target faces were randomized within items. Full wording of all items and their intra-class correlations are presented in Appendix A.

2.2.3. Data analysis

Bivariate correlations were employed in order to evaluate the zero-order effects of perceived productivity, dangerousness, desirability as a friend, and social status on generosity received in the UG. The positive effect of target strength observed in study 1a is consistent with both the AWA and PC models. In order to test these two hypotheses against each other, we constructed a model in which ratings of dangerousness and productivity were entered as mediators of the effect of strength on generosity received, using Preacher and Hayes' (2008) INDIRECT macro for SPSS with 2000 random samplings. Multiple regression analyses tested the independent effects of perceived productivity on generosity received, controlling first for prosociality ratings, and then for prosociality and health ratings.

In order to test the effects of target traits beyond attractiveness halo effects, we calculated partial correlations, controlling for attractiveness, between the remaining target traits (from studies 1a and 1b) and generosity received in the UG. In order to control for the possibility that proposers might try to maximize their income by matching their offer to the target's expected demand, we calculated partial correlations between all of the target traits and offers received, controlling for the demands expected from the targets. We calculated partial correlations between all of the target traits and generosity received, controlling for estimates of the targets' generosity, in order to control for any possible reciprocity motivations.

Finally, we tested the effect of participants' use of partner choice heuristics on their earnings in the UG. To do this, we calculated, for each participant, the correlations between UG decisions and target traits. The absolute value of these correlations indexes each participant's sensitivity to the various target traits. We then correlated these sensitivity indexes with the participants' mean earnings across all rounds (if they were to be paid out). The correlation between sensitivity to target traits and mean earnings reveals how sensitivity to various target traits affects earnings in the UG.

2.3. Study 1b: Results

Table 1 presents the correlations between the ratings of productivity, dangerousness, desirability as a friend, and social status, as well as all of the traits rated or measured in study 1a. Of note, the productivity composite generally correlated highly and positively with other positive traits (like friend desirability) but also with dangerousness, although dangerousness did not exhibit strong correlations with the positive traits. This suggests that some cues signal both productivity and dangerousness, but that other cues differentiate between productive individuals who are desirable as opposed to undesirable social partners.

2.3.1. Zero-order correlations between perceived traits and generosity received

Table 2 presents the zero-order correlations of mean generosity received by targets with their ratings of productivity, dangerousness, desirability as a friend and social status (for convenience, the variables from study 1a are also shown in this table). Dangerousness was significantly, *positively* correlated with mean generosity received, albeit with a modest effect size; although on its face this supports the AWA model, this could be a byproduct of the positive correlation between dangerousness and

Please cite this article as: Eisenbruch, A.B., et al., Evidence of partner choice heuristics in a one-shot bargaining game, *Evolution and Human Behavior* (2016), http://dx.doi.org/10.1016/j.evolhumbehav.2016.04.002

productivity (see Section 2.3.2 below). Productivity, desirability as a friend, and social status were all very highly and positively correlated with generosity received (r's ≥ 0.7), which is consistent with the PC model.

2.3.2. Mediating the effect of strength

Fig. 1 presents the results of the model in which productivity and dangerousness were entered as mediators of the effect of strength on generosity received, and shows that apparent productivity, but not dangerousness, significantly and completely mediated the effect of strength. Importantly, when productivity was controlled for, the effect of dangerousness reversed in sign and this variable became a significant *negative* predictor of generosity received. (This same reversal also occurred when productivity ($\beta = .89$, $t(80) = 9.27$, $p < .001$) and dangerousness ($\beta = -.31$, $t(80) = -3.23$, $p = .002$) were entered as the only predictors of generosity received.) These results support the PC model over the AWA model.

2.3.3. Independent effects of productivity

In the regression model with productivity and prosociality ratings as simultaneous predictors of generosity received, productivity had a significant positive effect, $\beta = .57$, $t(80) = 7.64$, $p < .001$, as did prosociality, $\beta = .37$, $t(80) = 4.94$, $p < .001$. Adding health as a predictor improved the accuracy of the model, R^2 change = .101, $F(1,79) = 27.18$, $p < .001$. Productivity remained a significant predictor, $\beta = .37$, $t(79) = 4.90$, $p < .001$, and health had a significant positive effect, $\beta = .51$, $t(79) = 5.21$, $p < .001$, but prosociality was no longer a significant predictor of generosity received, $\beta = .09$, $t(79) = 1.10$, $p = .28$. In both models, collinearity diagnostics revealed sufficient independence of predictors (all VIFs < 2.6). These models suggest that productivity is an important independent predictor of generosity received, supporting the PC hypothesis, while prosociality has a less robust effect.

2.3.4. Effects on earnings and controlling for alternative explanations

Strength, dominance, desirability as a friend, productivity, health, and social status had significant or marginally significant positive effects above and beyond the effect of attractiveness (see Supplementary Online Materials (SOM), Table S1, available on the journal's Web site at www.ehbonline.org). Participants were more generous toward targets who were expected to be more generous, $r(83) = .43$, $p < .001$, but the effects of target traits on generosity received were virtually unchanged after controlling for expected generosity (see SOM, Table S3). Participants offered *less* to targets who looked like they would demand more to accept an offer, $r(83) = -.39$, $p < .001$, which is the opposite of an income-maximizing strategy, and sensitivity to all target traits (except productivity) had a negative effect on UG earnings (see SOM, Table S4). These results show that the effects of target traits on generosity cannot be accounted for by attractiveness halo effects, reciprocity motivations or income maximizing strategies. Further details for these variables appear in Supplementary Online Materials (available on the journal's Web site at www.ehbonline.org).

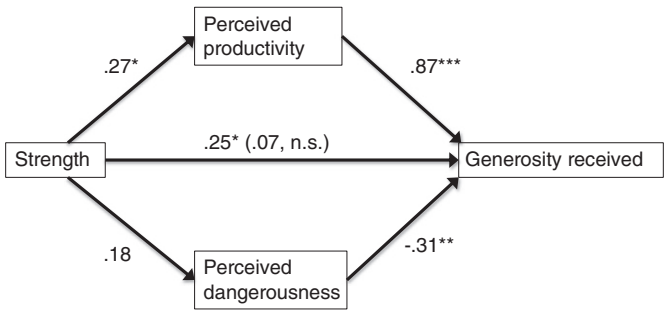

Fig. 1. The effect of strength on generosity received, with perceived dangerousness and productivity as mediators (study 1). Coefficients are standardized; model constructed with 2000 bootstrap samples using Preacher and Hayes' (2008) INDIRECT macro in SPSS. $^{*}p < .05$ $^{**}p < .01$; $^{***}p < .001$.

2.4. Study 1b: Discussion

The results of study 1b robustly supported the PC hypothesis over the AWA hypothesis. A target's apparent productivity, social status and desirability as a friend all had large positive effects on the generosity that target received in the UG. While apparent dangerousness had a positive zero-order effect on generosity received, dangerousness had a significant negative effect on generosity once productivity was controlled for, suggesting that formidability above and beyond implied productivity is actually penalized in the UG. Moreover, the positive effect of strength on generosity observed in study 1a was mediated by ratings of productivity, further supporting the partner choice model.

The existence of a market of potential cooperators likely limits the ability of even formidable individuals to coerce others into cooperative relationships over the long run, given the effectiveness of alliances (e.g., Wrangham, 1999) and social exclusion (e.g., Aktipis, 2004; Debove, Baumard, & André, 2015) in mitigating risks from exploitative individuals. This may explain why men appear to respond to apparently dangerous potential partners with aversion, rather than appeasement. However, future research should examine how individual differences (e.g., the perceiver's own formidability) and contextual variables (e.g., the cost of partner switching) moderate the effect of dangerousness on cooperative surplus divisions. In addition, it is possible that the use of target photographs in the controlled setting of the lab muted the effect of target dangerousness (and potentially other target traits), compared to what their effect would be in a spontaneous, face-to-face interaction. Testing the PC and AWA models against each other in more naturalistic settings may be a valuable avenue for future research.

Importantly, we observed effects of partner choice heuristics above and beyond attractiveness halo effects, strategies to maximize earnings, and motivations to reciprocate the target's quality of treatment. In fact, participants appeared to implement *costly* partner choice heuristics: men offered less to targets who looked like they would demand more, thereby reducing the odds of their offer being accepted, and sensitivity to target traits was negatively correlated with participant earnings. While this behavior is "anomalous" with respect to maximizing earnings in the UG, it is sensible as an output of a mechanism designed by natural selection for an ecology in which the benefits of long-term cooperative relationships may justify the costs incurred in establishing those relationships (see Delton, Krasnow, Cosmides, & Tooby, 2011).

Controlling for the target's expected generosity (i.e., controlling for reciprocity motivations) is a particularly strong test of the PC model, since the PC model actually predicts that individuals should be more generous toward partners whom they expect to be generous in turn (e.g., Barclay, 2013; Baumard et al., 2013). Our results (see Supplementary Online Materials; table S3, available on the journal's Web site at www.ehbonline.org) show that, on top of being generous toward apparently generous partners, people have additional strong preferences for partners who appear to have other components of long-term cooperative value (e.g., those who appear healthy, productive and high in social status).

The strong effect of ratings of ancestral productivity is an important addition to the partner choice literature. Previous modeling (e.g., Aktipis, 2004; Fu et al., 2008) and empirical (e.g., Delton & Robertson, 2012) research has focused on dispositional cooperativeness as the criterion by which partners are chosen or rejected. While individuals should certainly prefer partners who are cooperative, generous and value them highly, our results show that men also prefer partners who have above-average resource production capabilities. This is consistent with partner choice theory (Barclay, 2013; Debove et al., under review) and research in other species on partner choice for competence (Melis, Hare, & Tomasello, 2006;

Please cite this article as: Eisenbruch, A.B., et al., Evidence of partner choice heuristics in a one-shot bargaining game, *Evolution and Human Behavior* (2016), http://dx.doi.org/10.1016/j.evolhumbehav.2016.04.002

Vail, Manica, & Bshary, 2014; von Bayern, Clayton, & Emery, 2011). Moreover, the fact that contemporary economic decisions were strongly predicted by ratings of productivity in a hunter–gatherer-like environment (which appear irrelevant or even bizarre in a modern context) suggests that humans implement a psychology of partner choice that was designed by natural selection for an ancestral environment. The positive effect of target productivity on generosity above and beyond the effect of expected target generosity (see Supplementary Online Materials; table S3, available on the journal's Web site at www.ehbonline.org), and the robustness of the effect of productivity in comparison to prosociality (see Section 2.3.3), raises the possibility that men might be willing to trade off generosity in a partner in favor of productivity; future research will be necessary to identify the precise parameters of that trade off (see Debove et al., under review for modeling results to a similar effect).

3. Study 2

3.1. Introduction

Study 2 was designed to test whether women would also offer better treatment to same-sex UG partners who possessed indicators of high partner value. We expected replication of the study 1 findings of better treatment of partners who appeared healthier and more prosocial, since these traits should have predicted larger streams of benefits for women's cooperative partners in ancestral environments. We measured strength in women but did not expect to replicate its positive effect on UG treatment in men; since women have historically been less involved in large game hunting and coalitional violence (e.g., Marlowe, 2007; Wrangham, 1999), for which strength is beneficial (Apicella, 2014; von Rueden et al., 2008), women's perceived partner value may be less related to this variable. Relatedly, we expected that the effect of productivity might be reduced in women compared to men, since gathering has lower variance of outcomes than hunting does (Kaplan & Hill, 1985), female foraging parties tend to be larger than optimal with respect to food production (Marlowe, 2010), and female same-sex relationships tend to be less task-oriented than male same-sex relationships (Bakan, 1966; see Benenson et al., 2009 for discussion), all of which suggest that women may have faced weaker selection pressures than men for choosing partners on the basis of their ability to collaboratively create food resources. Perceived dangerousness was tested in order to evaluate whether the AWA model might account for women's behavior with same-sex partners; we predicted that it would not. Ratings of target face attractiveness were collected, allowing tests of partial effects of other variables when controlling for attractiveness, as well as allowing us to test whether more attractive individuals are treated better in the UG.

To further extend the PC model, we identified social status as another potential component of partner value, since individuals who are high in social status may be able to provide greater benefits to their partners by virtue of their social influence, and high social status may indicate high quality and quantity of outside options for cooperation. We therefore had the female target faces used in study 2 rated for social status as well, and predicted that social status would positively predict the quality of treatment received in the UG.

3.2. Materials and methods

3.2.1. Design

The design of study 2 was largely the same as the design of study 1a (see Section 1.2.1); female participants played one-shot UGs with a series of target partners represented by face photographs that had been measured and rated on various dimensions. The only difference from study 1a is that not all of the targets used as UG partners in study 2 had previously played the UG. Some of the targets had previously played a hypothetical, one-shot UG with a partner with whom they had recently had a conversation; other targets had never played the UG. Participants in study 2 were told truthfully that some of the targets they would play with had previously played the UG, but that they would be unable to tell which targets had or had not played the UG. When participants returned for session 2, they rolled a die. If they rolled a 6, one of their decisions was matched with the corresponding decision from a target who had previously played the UG, and they were paid their game earnings in cash. Therefore all participant decisions were incentive-compatible, and no deception was used.

3.2.2. Female target stimuli

Facial photographs of 100 female students that were collected in two unrelated studies were used as targets, i.e., to represent UG partners to the participants in study 2. They ranged in age from 18 to 23 years (mean = 18.6, s.d. = 0.96). Forty-two self-identified as Caucasian, 2 as African-American, 22 as Asian, 24 as Hispanic, and the rest as multiracial or "Other." All gave permission for their photographs to be used for research purposes.

Photographs were taken and processed in the same way as in study 1a. Strength was computed as the composite of hand grip and chest strength as measured by a dynamometer (bicep circumference was not available for all targets).

3.2.3. Raters

A pool of 105 students (66 female) rated the female targets on attractiveness (3 items; alpha = .979), health, prosociality (3 items; alpha = .893), dangerousness (3 items; alpha = .920), productivity (3 items; alpha = .868), and social status (7 items; alpha = .937). These same students also estimated the offer and demand that each target would make if the target were playing the UG. Each rater was randomly assigned to rate or estimate 5-6 items, and ratings on specific items continued until intra-class correlations for all rated items were at least .7. Due to experimenter error, we did not record the ages of these raters, but they were drawn from the same subject pool as the raters used for studies 1a and 1b. Ratings of attractiveness were made only by male raters, but other items were rated by both men and women. Items were presented in a random order, and target faces were randomized within items. Full wording of all items and their intra-class correlations are presented in Appendix A.

3.2.4. Ultimatum game participants

Seventy-four women played the UG with the female targets as partners. Seven women showed no variance in their generosity index (generosity = offer–demand), likely indicating disengagement from the task, so analysis was restricted to the other 67 participants (but results were very similar when all participants were included). Due to experimenter error, we did not record the ages of these participants, but they were drawn from the same subject pool as the raters used for studies 1a and 1b.

3.2.5. Data analysis

We used a data analysis strategy similar to that of study 1b (see Section 2.2.3) to evaluate the PC hypothesis, control for alternative explanations, and evaluate the effect of partner choice heuristics on UG earnings. First, we tested the zero-order effects of ratings of strength, attractiveness, health, prosociality, productivity, dangerousness and social status on treatment received in the UG.

We next computed a series of partial correlations in order to control for various alternative explanations. First, in order to control for the effect of attractiveness, we computed partial correlations, controlling for attractiveness, between UG decisions and the remaining target traits. Next, in order to control for the effect of participants' income-maximization strategies, we computed the effects of target traits on mean offers received, controlling for the targets' mean expected demands. Third, in order to control for participants' motivation to reciprocate the quality of treatment the target is expected to provide, we

Please cite this article as: Eisenbruch, A.B., et al., Evidence of partner choice heuristics in a one-shot bargaining game, *Evolution and Human Behavior* (2016), http://dx.doi.org/10.1016/j.evolhumbehav.2016.04.002

computed partial correlations between UG treatment received and target traits, controlling for the targets' expected decisions.

Finally, in order to measure the effect of partner choice heuristics on earnings in the UG, we calculated the correlations between participant earnings and sensitivity to each of the target traits tested in study 2 (see Section 2.2.3).

3.3. Study 2: Results

Table 3 presents the correlations between all of the measured and rated traits in study 2. Of note, dangerousness and strength were uncorrelated with productivity in the female targets, in contrast to the male targets for which productivity was predicted by these variables (see Table 1).

There was a significant positive correlation between the mean offers and demands received by targets, $r(100) = .20$, $p = .05$. This indicates that women deployed their offers and demands in conflict with each other, such that targets who received higher offers also received higher demands. The generosity index used in study 1 would therefore obscure effects on both offers and demands, so offers and demands were analyzed separately.

3.3.1. Zero-order correlations between target traits and UG treatment

Table 4 presents the zero-order correlations between target traits and mean offers and demands received. Targets who appeared healthier, more attractive, more prosocial, more productive and higher in social status all received significantly higher offers, although effect sizes were generally smaller than for men. As expected, strength was uncorrelated with offers received, and dangerousness was marginally, negatively correlated with the size of offers. These patterns appear to support the PC model over the AWA model. When productivity and prosociality were entered into the same regression model predicting mean offers received, prosociality had a significant positive effect, $\beta = .26$, $t(96) = 2.61$, $p = .010$, while productivity did not, $\beta = .15$, $t(96) = 1.47$, $p = .15$. This suggests that women prioritize prosociality over productivity in a partner, which stands in contrast to the results in men (see Section 2.3.3).

For mean demands received (right side of Table 4), however, traits indicative of high partner value actually predicted worse treatment in the game. Targets who appeared healthier, more attractive, and higher in social status received higher demands for their offers to be accepted. Unlike offers received, prosociality and productivity did not predict demands received.

3.3.2. Effects on earnings and controlling for alternative explanations

Controlling for attractiveness substantially reduced the effects of other target traits on offers and demands received, but social status, prosociality and dangerousness retained at least marginally significant partial correlations with offers received (see SOM, Table S5). There were significant positive correlations between mean offers received by targets and the mean offers they were expected to make, and between the mean demands received by targets and the mean demands they were expected to make (both correlations: $r(100) = .37$, $p < .001$). However, ratings of health, social status and attractiveness had significant partial correlations with offers received, controlling for expected offers, and ratings of target health, prosociality, social status, and attractiveness had significant partial correlations with demands received, controlling for expected demands (see SOM, Table S7). There was a significant positive correlation between the mean demands expected from targets and the mean offers they received, $r(100) = .22$, $p = .028$, which is consistent with an income-maximizing strategy, but there were significant effects of health, prosociality, social status, attractiveness, and dangerousness, on offers, controlling for expected demands (see SOM, Table S6). There were no effects of sensitivity to target traits on participant UG earnings (see SOM, Table S8). These results indicate that the observed relationships between target traits and behavior in the UG cannot be fully accounted for by attractiveness halo effects, reciprocity motivations, or income maximizing strategies. See Supplementary Online Materials (available on the journal's Web site at www.ehbonline.org) for further details.

3.4. Study 2: Discussion

As expected, female participants made higher offers in the UG to targets who appeared healthier, more attractive, more productive, more prosocial and higher in social status. This suggests that women also interpreted the UG as an opportunity to establish a long-term cooperative relationship, and therefore offered to divide the surplus based on partner value. However, participants also made higher demands to targets who appeared healthier, more attractive and higher in social status. There are several possible explanations for this inconsistency. Women may implement partner choice heuristics, but may also be more demanding of attractive mating rivals (contrast Table 4 with Table S5). Women face a tradeoff between forming cooperative same-sex relationships and competing with same-sex rivals (see Benenson et al., 2009), and intrasexual competition may be manifested in the UG (Lucas & Koff, 2013; Lucas, Koff, & Skeath, 2007). Alternatively, women may make high offers to apparently-valuable partners to attract them for a cooperative relationship, but then make high demands to those same partners to ensure that they will reciprocate that generosity. This view may be supported by our finding that women prioritize prosociality over productivity in a partner (Section 3.3.1), and research suggesting that equality is emphasized more in female relationships, relative to male relationships (see Benenson, 2013). Future research should disentangle these issues.

Importantly, the effects of partner choice criteria are robust to controlling for income-maximization strategies and reciprocity motivations. While social status, prosociality and dangerousness retained effects on offers after controlling for target attractiveness, controlling for attractiveness substantially reduced the effects of these and all of the other traits. This may represent more than just an attractiveness halo effect; women in ancestral environments likely derived substantial social influence from their attractiveness (see Sell et al., 2009), so attractiveness may have been an important cue of women's abilities to generate benefits for social partners.

Table 3
Intercorrelations among strength and the rated traits in study 2.

Trait	1.	2.	3.	4.	5.	6.
1. Strength						
2. Health	−0.23*					
3. Attractiveness	−0.17^	0.84**				
4. Prosociality	−0.14	0.41**	0.32**			
5. Productivity	−0.05	0.50**	0.37**	0.24*		
6. Dangerousness	0.29**	−0.12	−0.03	−0.67**	0.13	
7. Social status	−0.13	0.84**	0.88**	0.52**	0.49**	−0.05

^ $p < 0.10$, two-tailed.
* $p < 0.05$, two-tailed.
** $p < 0.01$, two-tailed.

Table 4
Zero-order correlations between female target traits and mean offers and demands received (study 2).

Trait	Offers		Demands	
	r	*p*	*r*	*p*
Strength	−0.12	0.237	−0.09	0.380
Health	0.44	<.001	0.39	<.001
Attractiveness	0.43	<.001	0.50	<.001
Prosociality	0.29	0.003	0.15	0.131
Productivity	0.21	0.038	0.16	0.107
Dangerousness	−0.17	0.084	0.07	0.522
Social status	0.48	<.001	0.48	<.001

Note: *p* values are two-tailed.

Please cite this article as: Eisenbruch, A.B., et al., Evidence of partner choice heuristics in a one-shot bargaining game, *Evolution and Human Behavior* (2016), http://dx.doi.org/10.1016/j.evolhumbehav.2016.04.002

As expected, there was no effect of targets' strength on offers or demands received, and the effect of perceived productivity on UG treatment was weaker than among men.

4. Sex differences

Fig. 2 compares the zero-order effects of strength, health, attractiveness, prosociality, productivity, dangerousness, social status and estimated UG behavior on offers received in men and women. There are statistically significant sex differences in the effects of target strength, attractiveness, dangerousness and expected demands. Descriptively, in all cases the effect size is larger among men than among women. We entered all of the variables in Fig. 2 into multiple regressions predicting mean offers separately for men and women. The overall R^2 for men was .69 and the overall R^2 for women was .30; using Fisher's *r*-to-*z* transformation, this is a significant difference in total variance predicted, $z = 3.84$, $p < .001$, suggesting that women were significantly less influenced overall by cues of partner value than men were.

5. General discussion

We found that participants' offers and demands in the ultimatum game were related to facial cues of their partner's value as a long-term cooperative partner. Men were more generous to targets who appeared more attractive, prosocial, productive, dominant, healthier, stronger, higher in social status and more desirable as a friend. Women made higher offers and higher demands to targets who appeared healthier, more attractive, and higher in social status; higher offers to targets who appeared more prosocial and productive; and lower offers to targets who appeared more dangerous. Most of the effects of perceived partner traits cannot be explained by attractiveness halo effects, income maximizing strategies, or reciprocity motivations. These findings represent the most direct empirical evidence to date of a human psychology of cooperative surplus division based on partner choice criteria, and they suggest a new interpretation of the UG as an opportunity for overtures to potential cooperative partners.

Our results suggest that behavior in the ultimatum game is generated by psychological mechanisms specialized for long-term social exchange relationships (see Cosmides & Tooby, 2005), and therefore that effects of partner traits that are outside of the structure of the game may be central to understanding the UG. Since humans likely evolved in social environments characterized by highly-valuable long-term cooperative relationships (see Delton et al., 2011), a one-shot UG may be interpreted as though it were an opening bid for an ongoing cooperative relationship within a biological market of cooperators (Barclay, 2013; Noë & Hammerstein, 1994, 1995). Therefore, offers and demands in the UG are generated by an evolved heuristic for partner choice that implements a rule like "be more generous to more valuable long-term cooperative partners." Partner choice theory suggests that a potential partner's "market value" as a long-term cooperator is a function of their ability to create future benefits, their expected generosity in sharing those benefits, and their outside options for production (Barclay, 2013; Baumard et al., 2013; Zaatari & Trivers, 2007); consistent with this, we observed that traits such as apparent health, productivity, prosociality, and social status had important effects on offers and demands in the UG.

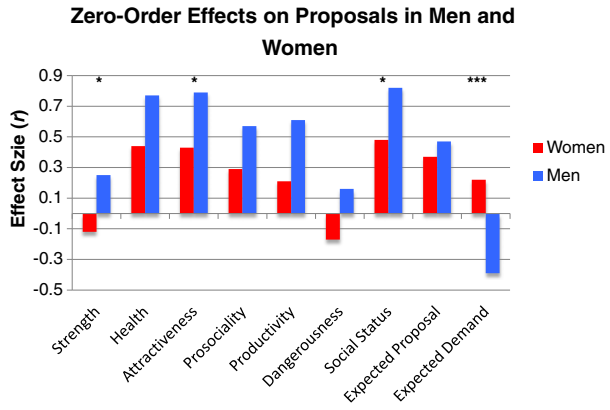

Fig. 2. Zero-order effects of target traits and estimated UG behavior on offers received in men and women (studies 1 and 2). Significant sex differences are indicated, $^{*}p < .05$, $^{***}p < .001$.

These data illustrate the close link between cooperation and selectivity regarding cooperative partners (e.g., McNamara, Barta, Fromhage, & Houston, 2008). The human psychology of partner choice appears designed to target valuable partners for relationship initiation and establish acceptable "terms of trade" with new partners, rather than establish the greatest possible number of new cooperative relationships (which would manifest as indiscriminate hypergenerosity in the UG). In addition, the system is not designed to establish a relationship at any cost, even with apparently valuable partners, because individuals who accepted worse terms of trade than they could receive from either the same or other partners would likely have faced adverse selection pressures (Trivers, 1971). While this may not maximize the number of accepted offers in the UG, a heuristic that prioritizes the quality rather than the quantity of cooperative relationships appears well-adapted to an ecology in which potential partners vary in value (e.g., Apicella, 2014; Debove et al., under review), and an individual can only have a limited number of social exchange relationships due to time constraints and the finite nature of social closeness and caring (e.g., DeScioli & Kurzban, 2009; Tooby & Cosmides, 1996).

Our results suggest that the human psychology of partner choice is specialized to an ancestral ecology. Men, but not women, were more generous toward physically stronger partners. This effect was driven by perceptions that stronger men would be more productive in an environment similar to that in which our species evolved, but not by perceptions of dangerousness, suggesting that the psychological mechanisms involved are designed to establish cooperative relationships with stronger men rather than merely to avoid violent retribution. In a modern context, this sex difference is senseless: for the types of cooperation that our participants typically engage in (e.g., group assignments for a class), physical strength is equally useless for men and women. However, men likely faced much stronger selection pressures from coalitional violence and large-game hunting (e.g., Marlowe, 2007; Wrangham, 1999), domains in which physical strength does predict productivity (Apicella, 2014; von Rueden et al., 2008). The effect of strength on men's bargaining psychology is typically framed in terms of the AWA (e.g., Petersen et al., 2013; Sell et al., 2009); however, a widespread preference for physically strong men as productive partners provides an alternative account for why strong men may receive more generous divisions of cooperative surpluses (cf. Debove et al., 2015; see also Lukaszewski, Simmons, Anderson, & Roney, 2016).

Additional sex differences suggest that the partner choice interpretation of UG behavior was more strongly supported for men than for women. Men were more sensitive to target traits overall, and only men reduced their earnings by calibrating their decisions to target traits. Women appeared to follow the income-maximizing strategy by matching their offers to the targets' expected demands, while men made lower offers to targets with higher expected demands. These results suggest that men, but not women, are willing to incur immediate costs in order to cooperate selectively with partners who display cues of long-term partner value. Women, unlike men, both offered more to and demanded more from seemingly high value partners, suggesting that women's UG behavior may have involved an element of competition with same-sex rivals or a greater insistence on reciprocity from cooperative partners (Section 3.4). Overall, these sex differences are consistent with evidence suggesting that men are more willing than women to tolerate costs in a relationship in order to maintain access to cooperative partners who can generate future benefits, likely due to selection pressures from

Please cite this article as: Eisenbruch, A.B., et al., Evidence of partner choice heuristics in a one-shot bargaining game, *Evolution and Human Behavior* (2016), http://dx.doi.org/10.1016/j.evolhumbehav.2016.04.002

coalitional violence and large game hunting (Balliet, Li, Macfarlan, & Van Vugt, 2011; Benenson et al., 2009; Vigil, 2007).

Alternative explanations for the observed sex differences include the possibility that we did not measure the target traits that are most important in female partner choice, or that male faces trigger more powerful behavioral inferences than do female faces. An additional limitation of the present research is that trait inferences from faces are confounded with each other. Alternative methods of representing targets will be important for testing the individual effects of traits and their prioritization in computations of partner value. For instance, the reported effect of social status is ambiguous. It is possible that apparently high status targets receive more generous treatment because they are capable of providing additional benefits to partners via social influence, or because they are assumed to have greater outside options.

We expect that the human psychology of partner choice will be an exciting area of research in the near future. The heuristic we suggest above ("be more generous to more valuable long-term cooperative partners") is flexible enough to be adaptively implemented in a variety of social and economic contexts. For example, the behaviors that are considered generous, and the cues that contribute to the estimation of partner value, may be different for different ecologies and types of cooperation. In addition, parameters such as the costs of searching for new partners should calibrate the prioritization of partner choice strategies relative to other behavioral strategies, such as partner control (Barclay & Raihani, 2015; Schino & Aureli, 2016). It will be important for researchers to systematically map the partner choice psychologies of men and women, including individual and contextual variation in partner choice criteria, effects of different information modalities (e.g., visual information vs. direct experience with a partner vs. communicated information on a partner), and behaviors and judgments in a variety of tasks (e.g., see McCabe, Smith, & LePore, 2000 for possible limitations of the strategy method in economic games).

Finally, our data suggest a novel explanation for the advantageous treatment that attractive individuals typically receive in economic settings. A proposed explanation for the "beauty premium" is that it is primarily the result of men attempting to court or maintain access to attractive women (reviewed by Maestripieri et al., in press). This cannot account for the strong effects of attractiveness that we observed, however, given that we conducted the UG exclusively with same-sex partners. We suggest that attractive individuals may be preferred as cooperative partners because many of the traits that made individuals desirable as mates also made them desirable as cooperators within ancestral environments (for example, apparent health, prosociality and competence), and so attractiveness may serve as a summary judgment of partner value. While this explanation is not mutually exclusive with the courtship-based explanation, it may spur new thinking and research on the topic.

5.1. Conclusion

Our findings provide direct empirical evidence that people divide the surpluses of cooperation based on estimates of long-term partner value, and that judgments of partner value incorporate the ability to create benefits, not merely dispositional cooperativeness or generosity. This psychology of surplus division based on partner choice criteria appears to be specialized for ancestral ecologies, and is likely to be distinct from heuristics that have evolved for dividing fixed resources (Petersen et al., 2013) or for choosing partners for risk-pooling relationships (Delton & Robertson, 2012). Finally, our results suggest that non-income-maximizing behavior in the UG may not be "anomalous" at all (Thaler, 1988), but may instead be an output of adaptations for long-term cooperative relationships (see Barclay, 2013; Cosmides & Tooby, 2005; Kenrick et al., 2009).

Supplementary Materials

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.evolhumbehav.2016.04.002.

Acknowledgments

This research was supported by NSF Grant BCS-1349023 to JRR. The authors would also like to thank the members of the Center for Evolutionary Psychology at UCSB for comments and advice on this project.

Appendix A

All items rated from 1 (far below average) to 7 (far above average)

Attractiveness items

How attractive is this man (woman)?
- Study 1 (first batch of target ratings) ICC = .970
- Study 1 (second batch of target ratings) ICC = .941
- Study 2 ICC = .887

How attractive is this man (woman) as a short-term mate?
- Study 1 (first batch of target ratings) ICC = .967
- Study 1 (second batch of target ratings) ICC = .935
- Study 2 ICC = .880

How attractive is this man (woman) as a long-term mate?
- Study 1 (first batch of target ratings) ICC = .967
- Study 1 (second batch of target ratings) ICC = .945
- Study 2 ICC = .878

Prosociality items

How kind does this person look?
- Study 1 (first batch of target ratings) ICC = .947
- Study 1 (second batch of target ratings) ICC = .945
- Study 2 ICC = .815

How cooperative does this person look?
- Study 1 (first batch of target ratings) ICC = .946
- Study 1 (second batch of target ratings) ICC = .940
- Study 2 ICC = .834

How trustworthy does this person look?
- Study 1 (first batch of target ratings) ICC = .951
- Study 1 (second batch of target ratings) ICC = .923
- Study 2 ICC = .774

Dominance items

How dominant does this person look?
- Study 1 (first batch of target ratings) ICC = .977
- Study 1 (second batch of target ratings) ICC = .935

How masculine does this person look?
- Study 1 (first batch of target ratings) ICC = .982
- Study 1 (second batch of target ratings) ICC = .952

How aggressive would this person be if provoked?
- Study 1 (first batch of target ratings) ICC = .960
- Study 1 (second batch of target ratings) ICC = .922

Health item

How healthy does this person look?
- Study 1 (first batch of target ratings) ICC = .981
- Study 1 (second batch of target ratings) ICC = .922
- Study 2 ICC = .761

Productivity items

If this person were stranded on a desert island, how good do you think he (she) would be at getting food (compared to the average man (woman))?
- Study 1 ICC = .679
- Study 2 ICC = .728

Please cite this article as: Eisenbruch, A.B., et al., Evidence of partner choice heuristics in a one-shot bargaining game, *Evolution and Human Behavior* (2016), http://dx.doi.org/10.1016/j.evolhumbehav.2016.04.002

Imagine that this person lived 100,000 years ago, when humans had to hunt or gather food and find or build shelter. Compared to the average man (woman), how productive a member of his (her) group would this person have been?
Study 1 ICC = .789
Study 2 ICC = .822
Imagine that this person went on a long camping trip, where they had to find their own food, make tools, etc. Compared to the average woman, how well do you think this person would do on this camping trip? (Item used for female targets only)
Study 2 ICC = .712

Dangerousness items

Imagine that this man (woman) is selling something valuable to him (her). Compared to the average man (woman), how likely would he (she) be to start a fight if he (she) received an offer that he (she) thought was too low?
Study 1 ICC = .644
Study 2 ICC = .732
If this man (woman) was in a fight, how likely do you think he'd (she'd) be to win (compared to the average man (woman))?
Study 1 ICC = .804
Study 2 ICC = .790
Imagine that this man (woman) is selling something valuable to him (her). Compared to the average man (woman), how physically dangerous would he (she) be if he (she) received an offer that he (she) thought was too low?
Study 1 ICC = .591
Study 2 ICC = .732

Desirability as a friend item

How much would you like to be friends with this man?
Study 1 ICC = .715

Social status items

How much do you think this person is respected by his (her) peers?
Study 1 ICC = .877
Study 2 ICC = .773
How often do you think this person gets what they want when they disagree with their friends?
Study 1 ICC = .894
Study 2 ICC = .758
How much do you think this person's friends look to them as a leader?
Study 1 ICC = .905
Study 2 ICC = .726
How many friends do you think this person has?
Study 1 ICC = .877
Study 2 ICC = .795
How popular do you think this person is within their peer group?
Study 1 ICC = .902
Study 2 ICC = .887
How easy do you think it would be for this person to find a partner for a cooperative project (e.g., carpooling, a roommate, starting a small business together, etc.)?
Study 1 ICC = .897
Study 2 ICC = .790
If other people were choosing partners for a cooperative project (e.g., carpooling, a roommate, starting a small business together, etc.), how in-demand would this person be?
Study 1 ICC = .899
Study 2 ICC = .774

Estimated Ultimatum Game Behavior

If this man (woman) were the Proposer in the Ultimatum Game with another man (woman), how much do you think he (she) would offer ($0-$10)?
If this man (woman) were the Responder in the Ultimatum Game with another man (woman), how much do you think he (she) would demand ($0-$10)?

References

Aktipis, C. A. (2004). Know when to walk away: Contingent movement and the evolution of cooperation. *Journal of Theoretical Biology*, *231*(2), 249–260.
Alrajih, S., & Ward, J. (2014). Increased facial width-to-height ratio and perceived dominance in the faces of the UK's leading business leaders. *British Journal of Psychology*, *105*(2), 153–161.
Apicella, C. L. (2014). Upper-body strength predicts hunting reputation and reproductive success in Hadza hunter–gatherers. *Evolution and Human Behavior*, *35*(6), 508–518.
Bakan, D. (1966). *The duality of human existence*. Chicago, IL: Rand McNally.
Balliet, D., Li, N. P., Macfarlan, S. J., & Van Vugt, M. (2011). Sex differences in cooperation: A meta-analytic review of social dilemmas. *Psychological Bulletin*, *137*(6), 881–909.
Barclay, P. (2013). Strategies for cooperation in biological markets, especially for humans. *Evolution and Human Behavior*, *34*(3), 164–175.
Barclay, P., & Raihani, N. (2015). Partner choice versus punishment in human Prisoner's Dilemmas. *Evolution and Human Behavior*. http://dx.doi.org/10.1016/j.evolhumbehav.2015.12.004.
Barclay, P., & Reeve, H. K. (2012). The varying relationship between helping and individual quality. *Behavioral Ecology*, *23*(4), 693–698.
Baumard, N., André, J. B., & Sperber, D. (2013). A mutualistic approach to morality: The evolution of fairness by partner choice. *Behavioral and Brain Sciences*, *36*(01), 59–78.
Benenson, J. F. (2013). The development of human female competition: Allies and adversaries. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, *368*(1631), 20130079.
Benenson, J. F., Markovits, H., Fitzgerald, C., Geoffroy, D., Flemming, J., Kahlenberg, S. M., & Wrangham, R. W. (2009). Males' greater tolerance of same-sex peers. *Psychological Science*, *20*(2), 184–190.
Camerer, C. (2003). *Behavioral game theory: Experiments in strategic interaction*. Princeton, NJ: Princeton University Press.
Carré, J. M., & McCormick, C. M. (2008). In your face: facial metrics predict aggressive behaviour in the laboratory and in varsity and professional hockey players. *Proceedings of the Royal Society of London B: Biological Sciences*, *275*(1651), 2651–2656.
Carré, J. M., McCormick, C. M., & Mondloch, C. J. (2009). Facial structure is a reliable cue of aggressive behavior. *Psychological Science*, *20*(10), 1194–1198.
Christiansen, K., & Winkler, E. M. (1992). Hormonal, anthropometrical, and behavioral correlates of physical aggression in !Kung San men of Namibia. *Aggressive Behavior*, *18*(4), 271–280.
Cosmides, L., & Tooby, J. (2005). Neurocognitive adaptations designed for social exchange. In D. M. Buss (Ed.), *The Handbook of Evolutionary Psychology* (pp. 584–627). Hoboken, NJ: Wiley.
Debove, S., Baumard, N., & André, J. B. (2015). Evolution of equal division among unequal partners. *Evolution*, *69*(2), 561–569.
Debove, S., Baumard, N., & André, J. B. (2015n). *On the evolutionary origin of equity*. (Manuscript submitted for publication).
Delton, A. W., Krasnow, M. M., Cosmides, L., & Tooby, J. (2011). Evolution of direct reciprocity under uncertainty can explain human generosity in one-shot encounters. *Proceedings of the National Academy of Sciences*, *108*(32), 13335–13340.
Delton, A. W., & Robertson, T. E. (2012). The social cognition of social foraging: Partner selection by underlying valuation. *Evolution and Human Behavior*, *33*(6), 715–725.
DeScioli, P., & Kurzban, R. (2009). The alliance hypothesis for human friendship. *PLoS One*, *4*(6), e5802.
Fu, F., Hauert, C., Nowak, M. A., & Wang, L. (2008). Reputation-based partner choice promotes cooperation in social networks. *Physical Review E*, *78*(2), 026117.
Güth, W., & Kocher, M. G. (2014). More than thirty years of ultimatum bargaining experiments: Motives, variations, and a survey of the recent literature. *Journal of Economic Behavior & Organization*, *108*, 396–409.
Hammerstein, P., & Parker, G. A. (1982). The asymmetric war of attrition. *Journal of Theoretical Biology*, *96*(4), 647–682.
Hehman, E., Leitner, J. B., & Gaertner, S. L. (2013). Enhancing static facial features increases intimidation. *Journal of Experimental Social Psychology*, *49*(4), 747–754.
Henrich, J., Boyd, R., Bowles, S., Camerer, C., Fehr, E., Gintis, H., ... Henrich, N. S. (2005). "Economic man" in cross-cultural perspective: Behavioral experiments in 15 small-scale societies. *Behavioral and Brain Sciences*, *28*(6), 795–815.
Kaplan, H., & Hill, K. (1985). Food sharing among Ache foragers: Tests of explanatory hypotheses. *Current Anthropology*, *26*(2), 223–246.
Kenrick, D. T., Griskevicius, V., Sundie, J. M., Li, N. P., Li, Y. J., & Neuberg, S. L. (2009). Deep rationality: The evolutionary economics of decision making. *Social Cognition*, *27*(5), 764–785.
Krupp, D. B., DeBruine, L. M., & Jones, B. C. (2011). Apparent health encourages reciprocity. *Evolution and Human Behavior*, *32*(3), 198–203.
Lucas, M., & Koff, E. (2013). How conception risk affects competition and cooperation with attractive women and men. *Evolution and Human Behavior*, *34*(1), 16–22.
Lucas, M., Koff, E., & Skeath, S. (2007). Pilot study of relationship between fertility risk and bargaining. *Psychological Reports*, *101*(1), 302–310.

Please cite this article as: Eisenbruch, A.B., et al., Evidence of partner choice heuristics in a one-shot bargaining game, *Evolution and Human Behavior* (2016), http://dx.doi.org/10.1016/j.evolhumbehav.2016.04.002

Lukaszewski, A. W., Simmons, Z. L., Anderson, C., & Roney, J. R. (2016). The role of physical formidability in human social status allocation. *Journal of Personality and Social Psychology*, *110*(3), 385–406.
Maestripieri, D., Henry, A., & Nickels, N. (in press). Explaining financial and prosocial biases in favor of attractive people: Interdisciplinary perspectives from economics, social psychology, and evolutionary psychology. Behavioral and Brain Sciences.
Marchetti, A., Castelli, I., Harlé, K. M., & Sanfey, A. G. (2011). Expectations and outcome: The role of proposer features in the Ultimatum Game. *Journal of Economic Psychology*, *32*(3), 446–449.
Marlowe, F. W. (2007). Hunting and gathering: The human sexual division of foraging labor. *Cross-Cultural Research*, *41*(2), 170–195.
Marlowe, F. W. (2010). *The Hadza: Hunter–gatherers of Tanzania*. Berkeley, CA: University of California Press.
Maynard Smith, J. (1979). Game theory and the evolution of behaviour. *Proceedings of the Royal Society of London B: Biological Sciences*, *205*(1161), 475–488.
McCabe, K. A., Smith, V. L., & LePore, M. (2000). Intentionality detection and "mindreading": Why does game form matter? *Proceedings of the National Academy of Sciences*, *97*(8), 4404–4409.
McNamara, J. M., Barta, Z., Fromhage, L., & Houston, A. I. (2008). The coevolution of choosiness and cooperation. *Nature*, *451*(7175), 189–192.
Melis, A. P., Hare, B., & Tomasello, M. (2006). Chimpanzees recruit the best collaborators. *Science*, *311*(5765), 1297–1300.
Mussel, P., Göritz, A. S., & Hewig, J. (2013). The value of a smile: Facial expression affects ultimatum-game responses. *Judgment and Decision Making*, *8*(3), 381–385.
Noë, R., & Hammerstein, P. (1994). Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behavioral Ecology And Sociobiology*, *35*(1), 1–11.
Noë, R., & Hammerstein, P. (1995). Biological markets. *Trends in Ecology & Evolution*, *10*(8), 336–339.
Petersen, M. B., Sznycer, D., Sell, A., Cosmides, L., & Tooby, J. (2013). The ancestral logic of politics upper-body strength regulates men's assertion of self-interest over economic redistribution. *Psychological Science*, *24*(7), 1098–1103.
Preacher, K. J., & Hayes, A. F. (2008). Asymptotic and resampling strategies for assessing and comparing indirect effects in multiple mediator models. *Behavior Research Methods*, *40*, 879–891.
Schino, G., & Aureli, F. (2016). Reciprocity in group-living animals: Partner control versus partner choice. *Biological Reviews*. http://dx.doi.org/10.1111/brv.12248.
Sell, A., Tooby, J., & Cosmides, L. (2009). Formidability and the logic of human anger. *Proceedings of the National Academy of Sciences*, *106*(35), 15073–15078.
Solnick, S. J., & Schweitzer, M. E. (1999). The influence of physical attractiveness and gender on ultimatum game decisions. *Organizational Behavior And Human Decision Processes*, *79*(3), 199–215.
Stirrat, M., & Perrett, D. I. (2010). Valid facial cues to cooperation and trust male facial width and trustworthiness. *Psychological Science*, *21*(3), 349–354.
Stirrat, M., Stulp, G., & Pollet, T. V. (2012). Male facial width is associated with death by contact violence: Narrow-faced males are more likely to die from contact violence. *Evolution and Human Behavior*, *33*(5), 551–556.
Thaler, R. H. (1988). Anomalies: The ultimatum game. *The Journal of Economic Perspectives*, *2*(4), 195–206.
Tooby, J., & Cosmides, L. (1996). Friendship and the Banker's Paradox: Other pathways to the evolution of adaptations for altruism. In W. G. Runciman, J. Maynard Smith, & R. I. M. Dunbar (Eds.), *Evolution of Social Behaviour Patterns in Primates and Man. Proceedings of the British Academy*, *88*. (pp. 119–143).
Trivers, R. L. (1971). The evolution of reciprocal altruism. *Quarterly Review of Biology*, 35–57.
Vail, A. L., Manica, A., & Bshary, R. (2014). Fish choose appropriately when and with whom to collaborate. *Current Biology*, *24*(17), R791–R793.
Vigil, J. M. (2007). Asymmetries in the friendship preferences and social styles of men and women. *Human Nature*, *18*(2), 143–161.
von Bayern, A. M., Clayton, N. S., & Emery, N. J. (2011). Can jackdaws (*Corvus monedula*) select individuals based on their ability to help? *Interaction Studies*, *12*(2), 262–280.
von Rueden, C., Gurven, M., & Kaplan, H. (2008). The multiple dimensions of male social status in an Amazonian society. *Evolution and Human Behavior*, *29*(6), 402–415.
Willis, J., & Todorov, A. (2006). First impressions: Making up your mind after a 100-ms exposure to a face. *Psychological Science*, *17*(7), 592–598.
Wilson, R. K., & Eckel, C. C. (2006). Judging a book by its cover: Beauty and expectations in the trust game. *Political Research Quarterly*, *59*(2), 189–202.
Wrangham, R. W. (1999). Evolution of coalitionary killing. *Yearbook of Physical Anthropology*, *42*, 1–30.
Zaatari, D., Palestis, B. G., & Trivers, R. (2009). Fluctuating asymmetry of responders affects offers in the ultimatum game oppositely according to attractiveness or need as perceived by proposers. *Ethology*, *115*(7), 627–632.
Zaatari, D., & Trivers, R. (2007). Fluctuating asymmetry and behavior in the ultimatum game in Jamaica. *Evolution and Human Behavior*, *28*(4), 223–227.

Please cite this article as: Eisenbruch, A.B., et al., Evidence of partner choice heuristics in a one-shot bargaining game, *Evolution and Human Behavior* (2016), http://dx.doi.org/10.1016/j.evolhumbehav.2016.04.002