SUBJECT AREAS:

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Human responses to unfairness with primary rewards and their biological limits

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Humans bargaining over money tend to reject unfair offers, whilst chimpanzees bargaining over primary rewards of food do not show this same motivation to reject. Whether such reciprocal fairness represents a predominantly human motivation has generated considerable recent interest. We induced either moderate or severe thirst in humans using intravenous saline, and examined responses to unfairness in an Ultimatum Game with water. We ask if humans also reject unfair offers for primary rewards. Despite the induction of even severe thirst, our subjects rejected unfair offers. Further, our data provide tentative evidence that this fairness motivation was traded-off against the value of the primary reward to the individual, a trade-off determined by the subjective value of water rather than by an objective physiological metric of value. Our data demonstrate humans care about fairness during bargaining with primary rewards, but that subjective self-interest may limit this fairness motivation.

In humans fairness has been studied extensively using games played for money¹. The paradigmatic example is the Ultimatum Game (UG)² where one player (the Proposer) is given an endowment (e.g. £10) and proposes a division (e.g. keep £6/offer £4) to a second player (the Responder), who then accepts (both get the proposed split) or rejects (both get nothing) the offer. In the UG with money humans typically reject low, “unfair”, offers even at cost to themselves¹. Here, we asked if thirsty humans in an UG instead make self-interest maximising responses to unfair offers with a primary reward of water, and attempted to maximise our power to induce such self-interested behaviour.

We sought to enhance our power to induce self-interested behaviour in two ways. Firstly, we physically presented the water, which has been recently shown to increase food's propensity to trigger appetitive responses³. Secondly, we amplified this effect by inducing thirst. Such induction of thirst in humans is a non-trivial problem experimentally, for example requiring prolonged water deprivation under supervision (e.g. over at least 24 hours⁴); or extended heating and exercise as typically employed in military research^{5–7}; or intravenous infusion of hypertonic saline, which given the careful setup needed to prevent potential health risks has previously been used to study the physiology of thirst in small numbers of subjects under clinical supervision^{8,9}. Here we used an intravenous saline infusion, as this method enabled a double-blind design allowing us to test UG choices in individuals who were not in a deprived state (infusing isotonic saline similar to normal human osmolarity, so with little impact on thirst), and also in individuals who received hypertonic saline that markedly increases blood osmolarity (and thus thirst) and that might increase our power to induce self-interested behaviours.

This manipulation with primary rewards also enabled the possibility of providing insight into the nature of the self-interested motivation in the UG, although we note that our experiment was not specifically designed to address this subsidiary issue. Specifically, we probed whether objective need, subjective need, or both are traded-off against a putative fairness motivation. Objective physiological need, for example the degree of energy depletion, powerfully influences non-social value-based choice. This is seen even in organisms as simple as the grasshopper, in which the value of stimuli is higher when learning about those stimuli originally occurred in a lower than higher state of nutritional reserve¹⁰. However, when humans choose in an UG, even an increase in the stakes equivalent to many months' salary does not necessarily increase acceptances^{1,11}. In contrast, subjective motivations in the UG have been highlighted more recently in relation to a fairness motivation, with disruption to

Figure 1 | Change in subjective thirst and responses to unfairness. (a) All participants were assigned the Responder role in an UG and faced this proposed division of water. They had received an intravenous infusion of either isotonic or hypertonic saline. (b) The change in subjective thirst induced by the saline infusion is calculated by the difference in subjective thirst at baseline and at testing. In the hypertonic group the degree to which the infusion increased subjective thirst was related to choice, such that a greater increase was seen in those who accepted (6.4 ± 1.7) relative to those who rejected (3.1 ± 1.6 ; independent samples ttest, $t_{(8)} = 3.19$, $P = 0.013$, $d = 2.02$). Error bars indicate s.e.m.

right dorsolateral Prefrontal Cortex (dlPFC) using Transcranial Magnetic Stimulation (rTMS) leading to reduced rejections but leaving subjective assessments of fairness unaffected¹².

Finally, whilst in the UG with money humans typically reject low offers¹, chimpanzees with a food primary reward behave solely as self-interested maximisers in an UG and accept unfair offers¹³. Our data help address one potential source of this discrepancy, although we note a more complex picture emerges across different primate species and tasks^{14,15}, while other potential sources for this discrepancy may relate to inter-species differences in time horizon¹⁶.

In summary, we tested the behaviour of humans in an UG with primary rewards, against the hypothesis that they would be rational self-interest maximisers who would accept any offer. We sought to maximise our chances of eliciting such self-interested behaviour by physically presenting the water, and also by examining choice not only in a non-deprived state (i.e. following isotonic infusion) but also following a manipulation that might increase self-interested choices (i.e. following hypertonic infusion). We also hoped to provide tentative evidence concerning whether objective and subjective measures of need might impact on a possible fairness motivation.

Results

Thirst manipulation. As predicted, administering hypertonic saline markedly altered objective and subjective measures relating to thirst. Subjective thirst did not differ between treatments at t_{baseline} (hypertonic 2.5 ± 1.9 and isotonic 2.5 ± 1.7 ; $t(19) = 0.057$, $P = 0.96$, $d = 0.02$), but differed at t_{UG} (7.3 ± 1.6 ; 3.5 ± 2.0 ; $t(19) = 4.68$, $P < 0.0005$, $d = 2.06$). Similarly, osmolality at t_{baseline} did not differ between treatments (hypertonic $293 \text{ mOsmL}^{-1} \pm \text{s.d. } 4$; isotonic 295 ± 7 ; $t(19) = 1.27$, $P = 0.22$, $d = 0.57$), but at t_{UG} was higher for the hypertonic (310 ± 5) than isotonic group (295 ± 5 ; $t(19) = 7.58$, $P = 3.7 \times 10^{-7}$, $d = 3.30$).

Fairness influences choice. Our data show fairness influenced responses in the UG despite the use of a primary reward. In an UG with a primary reward of food, chimpanzees in a non-deprived state accepted almost all offers, shown by only around 1 out of the 11 individuals tested rejecting a low offer similar to that presented here¹³. However, our human subjects, who were also in a non-deprived state (i.e. following isotonic infusion), showed the opposite pattern with 8 of 11 individuals rejecting the unfair offer (binomial test versus no influence of fairness, $P < 0.001$). Furthermore, even following the induction of severe thirst in the hypertonic group, we still observed an effect of fairness with 5 of 10 individuals rejecting the unfair offer (binomial test versus no influence of fairness, $P < 0.001$).

There was no difference between groups (hypertonic versus isotonic) in the proportion of rejections (likelihood ratio test between groups, $X^2 = 1.16$, $P > 0.25$), as we discuss further below. When we compare the frequency of rejections here with that previously reported for similarly low monetary offer proportions (approximately 50–60% rejections, see Methods for details), we find this was not significant for either the isotonic or hypertonic group (likelihood ratio test $P > 0.3$ in both groups).

Subjective and objective measures of self-interest. In addition to our central question of whether humans were rational self-interested maximisers with primary rewards, we next sought evidence that this fairness motivation was traded-off against self-interest. When self-interest was defined as subjective thirst, measured by a rating scale, this was the case. Subjectively thirstier individuals at t_{UG} were more likely to accept the unfair offered water, indicated by a main effect of choice in a 2 choice (accept, reject) by 2 treatment (isotonic, hypertonic) ANOVA with subjective thirst as the dependent variable (main effects of choice $F_{(1,17)} = 9.37$, $P = 0.007$, $\eta_p^2 = 0.36$; and treatment $F_{(1,17)} = 19.53$, $P < 0.0005$, $\eta_p^2 = 0.54$; with no interaction, $F_{(1,17)} = 0.15$, $P = 0.7$, $\eta_p^2 = 0.01$). Further, our data revealed that the degree to which hypertonic infusion increased subjective thirst was related to choice. This was evident in a significant interaction of choice (accept, reject) and treatment (isotonic, hypertonic) in an ANOVA with change in subjective thirst as the dependent variable (interaction $F_{(1,17)} = 7.19$, $P = 0.016$, $\eta_p^2 = 0.30$; main effect of treatment $F_{(1,17)} = 27.40$, $P < 0.0001$, $\eta_p^2 = 0.62$; no main effect of choice, $F_{(1,17)} = 3.52$, $P = 0.078$, $\eta_p^2 = 0.17$). This interaction was driven by the degree to which hypertonic saline increased subjective thirst (Fig. 1b).

However, our objective measure of thirst (blood osmolality) was not related to choice, either when used as the dependent variable or as a covariate in the previous ANOVAs. Furthermore, there was no difference between groups (hypertonic versus isotonic) in the proportion of rejections (likelihood ratio test between groups, $X^2 = 1.16$, $P > 0.25$). Thus, although our experiment was primarily designed to ask whether humans behaved as rational self-interest maximisers in an UG with primary reward, together these results present tentative evidence that the primary driver of the self-interested motivation here was subjective, rather than objective, thirst.

Discussion

Humans' closest relatives, chimpanzees, appear to be rational self-interest maximisers who do not reject unfair offers in the canonical fairness task, the UG, with primary rewards¹³. In contrast, here we

show that humans remain motivated by fairness even with primary rewards and in a deprived state. Outside such a bargaining context, capuchin monkeys have been reported to be more likely to reject a cucumber slice after seeing that another capuchin has received a more attractive grape¹⁴, although we note debate concerning these findings¹⁷; for a more general discussion of experiments on social preferences in primates see the review by¹⁵. Further, in contrast to that behaviour reported in capuchins¹⁴, humans tend not to reject inequitable distributions of money when such rejection would have no effect on the proposer's payoffs, for example in a modification of the UG where rejection does not alter the Proposer's payoff (an "Impunity game") the rate of rejections is markedly reduced¹⁸. Taken together, such work across species and tasks has begun to delineate the particular contexts in which particular species may exhibit particular fairness-related behaviours. We do not suggest that fairness-related behaviours are uniquely human, but that reciprocal fairness (i.e. punishment of others' unfair behaviours) even when bargaining with primary rewards, may be particularly prominent in humans.

In addition to our data examining responses to unfair offers with primary rewards, recent work examining proposals has also shown an influence of fairness in children making offers with sweets as rewards^{19,20}. Children given the opportunity to divide sweets between themselves and others develop more egalitarian tendencies with age, by the age of 7–8 they prefer resource allocations that remove advantageous or disadvantageous inequality¹⁹. It would be interesting to examine the response to unfair offers of sweets in children, although this may require large subject numbers, deception or other such methods. For example, in a recent study of 34 pairs of preschool children only two responders faced a non-zero offer of <4 out of 10 sweets, although none of 23 fair offers (even split or greater) were rejected²⁰.

Whilst our participants were not solely self-interested, neither were they solely motivated by fairness, and instead they exhibited a trade-off between these motivations. In terms of behavioural economic theory, such a trade-off maps conceptually onto models where choice is determined by utility functions containing both self and other regarding components^{1,21}. Previous work has suggested that a subjective aspect of the fairness motivation can be dissociated from choice, for example where TMS to right dlPFC reduces rejections but does not alter subjective assessments of fairness in the UG¹².

Whilst we acknowledge that our experiment was not designed to make strong inferences regarding the nature of the self-interested motivation, our data do provide tentative evidence that this self-interested motivation may also be subjective in nature. With thirst, objective measures of physiological need of water (e.g. blood osmolality or sodium concentration) are closely monitored peripherally and in the brain⁹ to enable homeostasis. The subjective sensation of thirst (e.g. individuals' subjective reports of their thirst) is closely related to such objective monitoring but is dissociable, for example after drinking when thirsty, and involves a wide network of brain regions^{9,22}.

This observation that this self-interested motivation may be subjective in nature helps interpret previously discrepant results between UG studies with money that tried to manipulate the self-interested motivation. In previous work that manipulated individuals' subjective feeling of entitlement by having subjects "earn" the endowment before an UG, this affected behaviour and led to lower (i.e. less fair) offers in the UG²³. However, other studies that increased the stakes of the UG relative to individuals' wealth, often in countries such as Slovakia or Indonesia where the equivalent of many month's salary may be used experimentally, did not lead to a clear cut pattern of more self-interested choices^{1,11,24}. The former manipulation may affect the subjective value of the self-interested motivation more than simply raising the absolute amount of the stake. Further, our data also shows that raising the stakes by increasing osmolality (analog-

ous to reducing wealth) can matter, but only when these stakes impact upon the individual's subjective motivational state. In addition, it is known that culture can affect UG responses²⁵, and unlike previous high-stakes games with money, our method has the advantage of operationalising changes in "wealth" within a single country and culture as a physiological need. Future work could usefully focus on these aspects concerning the nature of the self-interested motivation using more subjects, perhaps also examining whether subjectively thirsty individuals are also more likely to reject low monetary offers.

Finally, a further interesting consideration here is the concept of satisficing used in economics²⁶ and foraging theory²⁷, where because of constraints (e.g. information, time, other costs) a decision-maker attempts to meet an acceptability threshold rather than choosing optimally. Here this may have led to not bothering to drink the 62.5 ml of water (about 1/5th of a standard drink can). However, we note there was no cost difference between drinking and not drinking in the current experiment. Furthermore, individuals valued even small amounts of water, as shown here by subjectively thirstier individuals becoming more likely to consume this amount. Finally, considerable previous work has shown that in thirsty individuals very significantly smaller amounts of amounts of water than used here reduce thirst²⁸, are rated pleasantly²⁹ and modulate neural activity in reward-related brain regions^{28,29}.

In summary, our data demonstrate that humans care about being treated fairly when bargaining with primary rewards, and, together with a broader literature^{13,14}, suggest that such reciprocal altruism may be particularly prominent in humans. Our data also provide tentative evidence that subjective self-interest may limit this fairness motivation.

Methods

Participants. 21 healthy participants provided informed, written consent (11 male, mean age 25 (range 20–32) years; 2 further participants did not complete testing) for a study approved by University College London Ethics Committee. Note that including gender as a factor in our analyses with respect to fairness or subjective measures of thirst did not alter our findings below.

Thirst manipulation. On the testing day, participants were asked to refrain from drinking after 08:00 am. They arrived at 09:00 am. We manipulated thirst using saline administered via an intravenous line for 50 minutes, at a rate 0.15 ml/kg/min for males and 0.12 ml/kg/min for females. The sessions lasted four to five hours (including time for preparation beforehand and to ensure subject safety afterwards) and experienced physicians were present throughout to ensure participant safety.

In a double-blind, randomised design. 11 participants received isotonic saline (0.9% NaCl) similar to normal human osmolality, with a minimal impact on thirst; and 10 received hypertonic saline (5% NaCl) that markedly increases blood osmolality and, as a consequence, thirst⁹. After infusion subjects performed one hour of non-social tasks (not reported here); then the UG; and finally waited a further hour without water. Participants were fully informed of this timetable at the start of each testing day (only the UG was unexpected, as described below). The one hour wait post-testing without water was in order to prevent the value of water being rendered negligible if participants believed they would have immediate access to water after testing.

At pre-infusion baseline (t_{baseline}) and the time of testing (t_{UG}) we measured subjective thirst (visual analogue scale from 0–10) and blood osmolality (analysis by freezing point depression osmometer). Participants completed a similar session 5–7 days before but without the UG (and receiving the alternative infusion), and were unaware of the prospect of the UG until it was conducted.

Behavioural task. Three participants attended each session where they met and interacted with each other, and were then tested in separate rooms. At time of testing, t_{UG} , participants first received written instructions stating that two of the participants (one Proposer and one Responder) would be randomly selected to play an UG, in this case dividing 500 ml of water for immediate consumption. Next, all participants were informed they were the Responder. The experimenter then brought a covered tray, removed the cover and left the room. For all participants the tray contained two straight-sided 500 ml capacity glasses, one holding 62.5 ml (12.5%) with "they offer" written below, and the other holding 437.5 ml (87.5%) next to "they keep" (Fig. 1b). Participants had 15 seconds to circle "accept" or "reject" on a piece of paper. Participants who accepted then drank the 62.5 ml, and all participants waited one further hour without water. Note that in the current study the number of participants was limited by substantial difficulties and potential risks of IV saline administration, and thus given the typically low rate of unfair offers made by Proposers in the UG¹,

here we employed this deception to examine Responder behaviour in response to low offers. Participants were informed that they would only play the UG once (i.e. it was one-shot in nature) and would undertake no further tasks subsequently (i.e. during this last post-testing wait period).

Analysis. Statistical tests were carried out using independent-samples t-tests or independent analysis of variance (ANOVA) in SPSS 17.0; reported p-values are two-tailed. Before implementing each parametric test we applied Levene's test for inhomogeneity of variance, and in no case found even trend level significance for rejection of the null hypothesis. The Kolmogorov-Smirnov test of normality also did not reach even trend level significance for rejection of the null hypothesis in either group for either objective or subjective measures of thirst at either time point.

For the purpose of comparison with choice data from our task, we estimated an average frequency of rejections of similarly low offers of money in human studies. We used data from an extensive review of the UG literature (Table 2.3 in¹) where we averaged across all quoted rejection rates (not weighted by number of subjects and collapsing over various manipulations). This revealed for offer proportions of 11–20% a mean rejection rate of 49% (mean of 39 entries), and for offer proportions of 1–10% a mean rejection rate of 59% (mean of 24 entries). This rejection rate accords well with the author's conclusion that offers below 20% are rejected about half the time¹.

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Author contributions

NDW and SMF originated the idea. NDW, KH, MS and MG collected the data. NDW analysed the data. NDW and RJD wrote the manuscript, on which all authors commented.

Additional information

Competing financial interests: The authors declare no competing financial interests.

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