Anderson, Clare. and David L. Dickinson (2010) “Bargaining and Trust: The Effects of 36hr Sleep Deprivation on Socially Interactive Decisions.” **Journal of Sleep Research**, vo. 19, no. 1 part 1: 54-63. DOI: 10.1111/j.1365-2869.2009.00767.x Published by Wiley-Blackwell. The definitive version is available at www3.interscience.wiley.com (ISSN: 0962-1105) March 2010.

Bargaining and Trust: The Effects of 36-H Total Sleep Deprivation on Socially Interactive Decisions

Clare Anderson and David L. Dickinson

ABSTRACT

Although it is well known that sleep loss results in poor judgement and decisions, little is known about the influence of social context in these processes. Sixteen healthy young adults underwent three games involving bargaining (‘Ultimatum’ and ‘Dictator’) and trust, following total sleep deprivation (TSD) and during rested wakefulness (RW), in a repeated-measures, counterbalanced design. To control for repeatability, a second group (n = 16) was tested twice under RW conditions. Paired anonymously with another individual, participants made their simple social interaction decisions facing real monetary incentives. For bargaining, following TSD participants were more likely to reject unequal-split offers made by their partner, despite the rejection resulting in a zero monetary payoff for both participants. For the trust game, participants were less likely to place full trust in their anonymous partner. Overall, we provide novel evidence that following TSD, the conflict between personal financial gain and payoff equality is focused upon avoidance of unfavourable inequality (i.e. unfairness). This results in the rejection of unfair offers at personal monetary cost, and the lack of full trust which would expose one to being exploited in the interaction. As such, we suggest that within a social domain decisions may be more influenced by emotion following TSD, which has fundamental consequences for real-world decision-making involving social exchange.

ARTICLE

Introduction

It is well established that sleep deprivation (SD) is associated with decrements in basic cognitive function, such as alertness, vigilance and sustained attention (Dorrian et al., 2005; Lim and Dinges, 2008; Van Dongen et al., 2003). What is less well known is the impact of SD on higher-level cognitive functions (Killgore et al., 2006), referred to collectively as the ‘executive functions’. Research findings of total sleep deprivation (TSD) have revealed more understanding of links between TSD and aspects of prefrontal function (executive function), such as planning (Horne, 1988), working memory (Chee and Chuah, 2008; Turner et al., 2007), inhibition (Harrison and Horne, 1998), generation of speech (Harrison and Horne, 1997, 1998) and novel goal-directed behaviour (Horne, 1993). Given the vulnerability of these functions to TSD, it is understandable that TSD affects the ability to make decisions per se (Harrison and Horne, 2000; Killgore et al., 2006; McKenna et al., 2007), as effective decision-making relies on the ability to appreciate future events (planning), update strategies (working memory), avoid distractions/irrelevant information (inhibition), think laterally and innovatively (novel, goal-directed behaviour) and to communicate effectively (generation of speech) (c.f. Harrison and Horne, 2000). While error in any of these TSD vulnerable behaviours may cause a poor decision judgement, what is lacking in our understanding of TSD and decision-making, and fundamental to the decision-making process in the real world, is the influence of our social environment.

Much of our current understanding of TSD effects on decision-making results from different aspects of individual decision-making (e.g. Harrison and Horne, 2000; Killgore et al., 2006). However, many important occupations rely on people working together cooperatively for extended periods and under conditions of sleep loss (e.g. emergency services, military personnel, trade union leaders). While some research has looked at the impact of TSD on decision-making in team versus individual performance (Baranski et al., 2007), to our knowledge, there remains an important gap in the literature describing TSD effects in interactive environments, especially those involving social preference domains. In behavioural economics, ‘social preference’ refers to how people rank different allocations of material payoffs to themselves and others (Fehr and Camerer, 2007). Environments of basic social interaction, such as those involving simple bargaining behaviour or trust decisions between two or more people, have yet to be explored in the wealth of TSD research. However, such environments form the building blocks of many more complicated real-world decision environments that hold particular interest because of their pitting of rational versus emotional response mechanisms in weighing decision costs and benefits.

The ability to regulate emotions is integral to any decision-making process, and given that most real-world decisions are not made individually, emotional response mechanisms may play a greater role in social dilemmas of various sorts. A recent study involving subject viewings of aversive pictures showed a weakened functional connectivity between the amygdala and the medial prefrontal cortex (PFC) following 35 h of TSD (Yoo et al., 2007). Thus, existing research suggests an important hypothesis for how TSD might affect decisions involving more emotion-based domains, such as social interaction environments. Specifically, the mediation of emotion-based responses (by the PFC) may be weakened, which would lead to more irrational decision-making (i.e. ruled by emotion) than would otherwise occur. Although decisions will not automatically be worse if more emotion-based, as the quality of the decision outcome will depend on the context of the decision, there may be an important shift in the engine driving social dilemma decisions following TSD.

A large body of literature surrounds three often-studied social preference environments in experimental and behavioural economics: the 'Ultimatum', 'Dictator' and 'Trust' games. Simple bargaining is examined with the classic Ultimatum game introduced by Guth et al. (1982). In this game, two players are given a pie of $X to divide. The player assigned as the proposer suggests a division of the pie to the other player (the responder). If the responder accepts the proposed division, then the pie is divided in the proposed way to yield the players' payoffs in the game. However, should the responder reject the proposal, both players earn zero. The game is over after the responder's accept/reject decision. While simplistic, the game captures the important tension between selfish behaviour versus fairness or other-regarding behaviour. A variation of the game, called the 'Dictator' game (Forsythe et al., 1994), removes the option of rejection by the responder. This additional simplification was examined to help distinguish the extent to which proposals in the Ultimatum game were really driven by fairness consideration rather than a simple fear of rejection. Average offers in $10.00 Ultimatum games are approximately $4.00, with offers lower than $2.50 often being rejected (see summary in Holt, 2007). Dictator offers are typically lower (average of $2.33 in Forsythe et al., 1994), although average Dictator offers still average above zero (modal offer is typically zero, however); thus strategic considerations seem to play a role in these simple bargaining environments.

The Trust game (Berg et al., 1995) allows an examination of trust and trustworthiness in an environment that is not zero sum (i.e. zero sum being where one player's gain is necessarily the other's loss), as are the Ultimatum and Dictator games. In this game, the first mover decides how much of an initial sum, for instance $10.00, to pass to the second mover. Whatever amount is passed is then tripled by the experimenter, and the second mover may then decide how much, if any, of the tripled amount to return to the first mover. Thus, the first mover's 'pass' decision can be regarded as a measure of trust, whereas the second mover's pass decision is a measure of trustworthiness. [Although more recent research has highlighted the fact that first movers in the Trust game may pass money out of altruism as well as trust, this recent evidence still indicates that trust is a probable component of the first-mover decisions in this game (see Cox, 2004).] In Berg et al. (1995), the average amount passed was $5.16, and after tripling, about $2.79 (18% of the tripled amount) was returned. An important difference in the Trust game is the risk the first mover takes in deciding to pass money. Fear of betrayal or being taken advantage of may be aroused in making the trust decision in a way that is magnified over the fear of rejection in the Ultimatum game.

While no study currently exists that assesses TSD in relation to these social preference games, clues from neurological evidence suggest that TSD may modify behaviour choices. In a pioneering imaging study assessing the neural basis of the Ultimatum game, Sanfey and colleagues demonstrated that unfair offers elicit anterior insula and dorsolateral activation (Sanfey et al., 2003), the former region being linked to specific negative states, such as anger or disgust (Damasio et al., 2000), and the latter in the control of cognitive processes (i.e. Miller and Cohen, 2001; Wagner et al., 2001). Moreover, in Sanfey et al.'s (2003) study, while rejected unfair offers activated the anterior insula, acceptance of unfair offers exhibited greater dorsolateral prefrontal cortex (DLPFC) activation, which may signify an induced 'conflict in the responder between cognitive ('accept') and emotional ('reject') motives' (Sanfey et al., 2003, pg;. 1757) following an unfair proposal. Given the disruption of the PFC during sleep loss, we hypothesize that TSD will alter the rejection of offers perceived as unfair. While this has yet to be examined with disruption to the PFC because of sleep loss, Koenigs and Tranel (2007) examined subjects with ventromedial PFC lesions, and reported that simple bargaining offers were rejected more frequently by these subjects. As such, these subjects sacrificed monetary gain to reject unfair treatment. The extent to which this may be mirrored in subjects following 36-h TSD is unknown, and forms the basis of our study.

Methodology

Participants

Thirty-two young healthy participants (16 males, 16 females, aged 20.2–24.1 years) who were good sleepers [determined via actiwatch (Cambridge Neurotechnology Ltd, Cambridge, UK) and sleep diaries] and with no complaint of daytime sleepiness (Epworth Sleepiness Scale ≤ 10; Johns, 1991) were recruited following interviews and subsequent screening to exclude those who smoked and had an average intake of alcohol more than 4 U day^{-1} [1 U = 10 mL of ethanol. For any given drink, unit = volume (mL) × % alcohol by volume (ABV)/1000, i.e. A 250-mL glass of wine (14%) = 3.5 U] and/or caffeine more than 300 mg day^{-1}; had any sleep or medical problems (other than minor illnesses); or were on any medication liable to cause daytime sleepiness. In addition, those who took daytime naps more than twice per month were excluded from the study. To check for stable sleep patterns actiwatches (Cambridge Neurotechnology) were worn for an initial screening week. Those who slept 8 ± 1 h per night, and with consistent bed/rise times, were included in the study. The study was approved by Loughborough University's Ethical Advisory Committee. All procedures were explained fully, informed consent given and participants were paid for their involvement.

Participants were assigned randomly to either the experimental group (n = 16, eight males; eight females; average age 22.6 ± 1.2 years) or control group (n = 16, eight males; eight females; average age 22.3 ± 2.1 years). Using a repeated-measures design, the experimental group underwent three social preference tasks twice, once following 36 h of TSD and another following normal sleep (rested wakefulness: RW). While these were counterbalanced, we repeated the tests twice with the control group as a check on consistency. Groups were matched for age, sex, IQ, anxiety and personality.

Design and Procedure

In a repeated-measures design, the experimental group arose at 08:00 h, following a night of 'normal' sleep at home, as determined by actiwatch (Cambridge Neurotechnology) and timed telephone calls to the laboratory. For both conditions, participants arrived at the laboratory at 14:00 h (actigraphy verified non-napping), where actiwatches were checked for compliance and questionnaires completed. For the RW condition, they were given a small meal at 16:00 h and began testing at 19:00 h on (see below). For the TSD condition, they were kept under constant supervision for a further 25 h to ensure that they remained awake, adhered to study protocol and for reasons of safety. They began testing at 19:00 h on day 2 following 35–36 h TSD.

During TSD, participants consumed only non-caffeinated drinks and were given food opportunities at 3-h intervals, where they ate ad libitum. Foods with high sugar content were omitted, because of bolus amounts of sugar having an initial alerting effect followed by a sleepiness rebound (Anderson and Horne, 2006). During the 25-h laboratory period, they engaged in conversation, light reading, watched TV or played board games. At the end of the trial, they were escorted home and consented to undertake recovery sleep before driving, riding a bicycle or operating machinery.

Conditions were counterbalanced, so eight subjects underwent TSD followed by RW and eight subjects underwent RW followed by TSD. Each session was separated by 1 week to allow for adequate recovery sleep. Control participants were tested twice under the same protocol as the experimental RW condition and, again, each test session was separated by 1 week.

Test Sessions

Four participants made up each test trial. Each participant was paired randomly with one other participant in a single-blind manner (i.e. paired anonymously). They were given the following standard information: 'We have matched you with another member of the group and between you, you will play a series of short, simple games. You should be aware that any financial payoff from the game is real and so you should make your decisions carefully'.

Each game required a first mover and a second mover. We employed a particular procedure known as the 'strategy' method to elicit a maximum amount of data from the subjects. Using this method in the Ultimatum and Trust games, the second responder enters a response for any possible contingency of money passed from the first mover (as opposed to just responding to one particular first-mover decision). Additionally, subjects are asked to make decisions for both the first-mover and second-mover subject-roles in the Ultimatum and Trust games (as well as a first-mover decision in the Dictator game). *Ex poste* role assignment was random and, after all decisions were made, was used to calculate payoffs. This method places subjects in a position to think through the social dilemma from both players' perspectives, realizing that there is an equal chance that they may be assigned to either role; their randomly assigned role may vary for each test. Finally, after role assignments were made, subjects were paired up (one first mover assigned to one second mover) randomly and anonymously, such that subjects were never aware of with whom they were paired for the decision experiments. This way of eliciting decisions does not alter play in the Ultimatum game (cf. Oxoby and McLeish, 2004).

Anonymity is accomplished by recruiting subjects in groups of four. Thus, while subjects were aware that they were matched randomly with one of the other subjects in their group, the identity of the pairings was never revealed. A key feature in this design is that subjects were keenly aware that their decisions were not hypothetical, and that a real bargaining and trust payoff would be received based on the decisions made in the random and anonymous role assignments and pairings. Thus, subjects stood to gain or lose real money based on their own and their anonymous counterpart's decisions, which enhanced the validity of their decisions.

There were three games in total and these were counterbalanced to avoid order effects. Each test was approximately 5 min in duration, and there was a 5-min gap between tests. Total test duration was less than 30 min.

Bargaining games: Ultimatum and Dictator

The Ultimatum game (see Fig. 1) (Guth et al., 1982) has been used extensively in experimental and behavioural economics research (see references in Holt, 2007), as well as in the nascent field of neuroeconomics (e.g. Koenigs and Tranel, 2007; Sanfeyet al., 2003). In this game, two players were allocated £5. The proposer proposed how to split this money and the responder chose whether to accept or reject the offer. If the offer is rejected, both players earn zero. The purely self-interested rationale, therefore, is for the proposer to offer the smallest amount possible for the responder to accept. The most frequent offer is approximately 40–50% of the sum, and about half the responders reject offers below 30% (Nowak et al., 2000). This would suggest that humans consider fairness in their decisions.

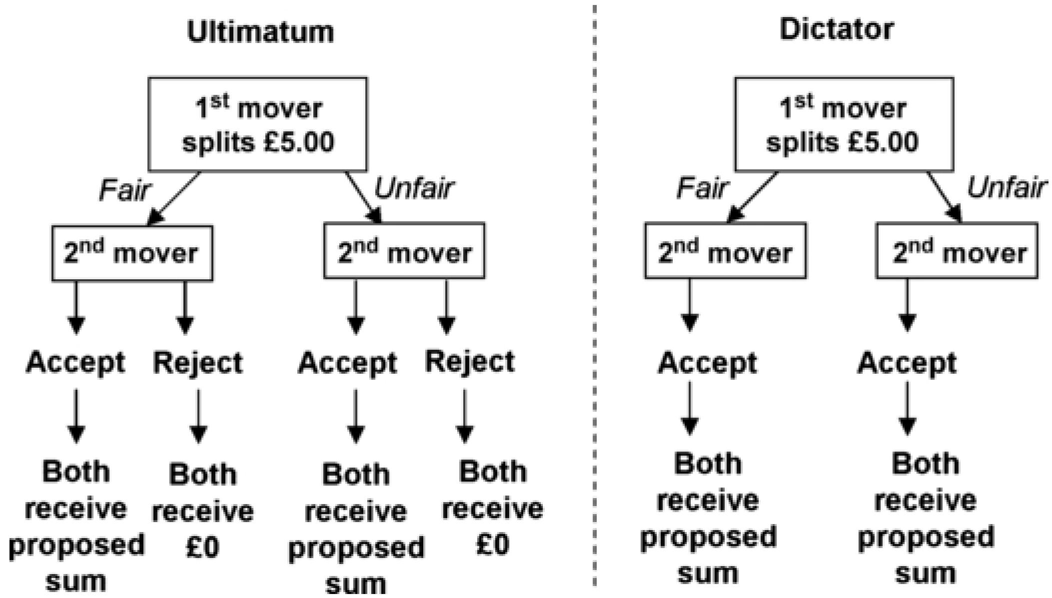

Figure 1. A graphical depiction of the Ultimatum and Dictator games. In the Ultimatum game, the first mover proposes any division of the £5.00 in 50-p increments. For simplicity, we show only a ‘fair’ and ‘unfair’ proposal branches above, where any offer of less than half the pie is probably considered unfair, to some degree. The second mover then chooses to accept or reject the proposal, with rejection implying a zero payoff for both players. The Dictator game is the same as the Ultimatum game, except that the second mover has no option to reject. Using the strategy method, the second mover was required to make an accept/reject decision for all possible proposals (£0.50, £1.00, £1.50, etc.) for the Ultimatum game.

In cubicle 1, the ‘proposer’ was given the following instruction: ‘We have matched you with another member of the group and between you, you will play a short, simple game. There is £5 and you as first mover must decide how much of the £5 (in 50-p increments) you want to pass to your partner or keep. However, we must warn you that your partner has the choice to accept your offer or reject it. If they reject it, you will both receive nothing’. Once the participant understood, they made their offer and posted it on the offer card and handed this to the experimenter in a sealed envelope.

The experimenter went to cubicle 2 (to second mover) and gave the following instruction: ‘You are the second mover and your partner has made their first move as to how much of the £5 they have chosen to give you. However, we cannot tell you the amount they have proposed but ask you to make a decision for each eventuality. Again, it is important you answer honestly, as this could be real money'. The participant was given a recording sheet of every eventuality (50 p, £1, £1.50 and so on) and was told: 'In front of you is the response sheet for you to record your decision. You can see the amount your partner has kept for themselves and how much they choose to give you. Please indicate whether you wish to accept or reject this offer. Remember, if you reject you both receive nothing'. The responder gave their decisions to the experimenter in a sealed envelope.

By not revealing the actual amount given, we were able to assess response for each eventuality for data analysis purposes. Importantly, this game was then repeated but with the roles reversed, so each participant played both the proposer (first mover) and the responder (second mover).

The 'Dictator' game (see Fig. 1) is much the same as before, the main difference being that the responder must accept *any* offer. Previous research suggests that offers made by the proposer are much lower than the Ultimatum game (although still above zero) (Forsythe *et al.*, 1994), suggesting that the 40–50% offer in the Ultimatum game is due to both an element of fairness as well as a fear of rejection (loss).

For the Dictator game, the proposer was given the following instruction: 'You have another £5 which you can split with your partner in whichever way you choose in increments of 50 p. However, this time they have no choice whether to accept or reject and so you can give them what you like. However, do remember this is real money and will be a decision used to calculate both your earnings. Please make your decision now'.

Trust Game

Here, the first mover receives £5 and then decides whether to invest in a trustee (second mover) or not. Any money invested and passed to the second mover is tripled, and the second mover then decides how much to retain or pass back to the first mover (see Fig. 2).

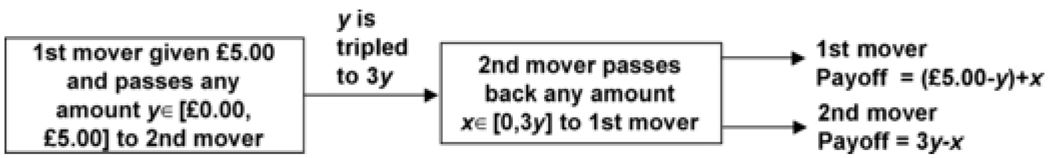

Figure 2. A graphical depiction of the Trust game. The first mover has the choice to split £5.00 between himself and player 2. Anything he/she choose to pass will be tripled. The second mover then has the option of giving some money back to the first mover. The amount passed by the first mover y, is a measure of TRUST (the extent of trust proxied by how much he/she chooses to pass). The amount, x, the second mover returns is an indication of trustworthiness. Using the strategy method, the second mover is required to make a decision for all outcomes (£0.50, £1.00, £1.50,…, £15.00).

The first mover was given the following instruction: 'We have matched you with another member of the group and between you, you will play a short, simple game. There is £5 and as first mover you must decide how much of the £5 (in 50-p increments) you want to pass or keep. Whatever you choose to pass will be multiplied by 3 and given to your partner. Your partner will then have a choice of how much to pass back to you. Remember to answer honestly as you and your partner could receive this amount. Please indicate how much you would like to pass or keep'. The first mover recorded their response and placed in a sealed envelope.

The second mover (in cubicle 2) was then given the following instruction: 'You are the second mover. Your partner has opted to give you a certain portion of their £5 and we have multiplied that by 3. However, we cannot tell you the amount they have proposed but ask you to make a decision for each eventuality. Again, it is important you answer honestly, as this could be real money. Please indicate for each amount how much (if any) you would like to give back to your partner. Again, remember this is real money and may count towards your final payoff'. The second mover made their decisions and placed them in a sealed envelope.

Roles were then reversed, so each participant made a first-mover and second-mover decision. In both simple bargaining and trust, it was explained clearly to the subjects that roles would be assigned randomly after all decisions were made, and each subject would earn the payoff associated with their decision matched with that of their randomly assigned counterpart.

Overview of test variables

In the bargaining games, for each subject we have three test variables: (1) an Ultimatum proposer decision (i.e. a proposal); (2) an Ultimatum responder decision coded as a minimum acceptable offer (MAO) from the subjects' menu of accept/reject decisions made ex ante for all possible proposal contingencies and (3) a Dictator proposal. For the Trust game, each subject makes a first-mover (trust) decision, as well as a second-mover (trustworthiness) decision for every possible first-mover choice.

Data analysis

Given our repeated-measures design, with counterbalanced ordering of TSD and RW conditions, we analyze the data as matched pairs. This allows us to examine causal changes in subject choice as a result TSD. Given the relatively small sample size and possible non-normality of the data, in most instances we employ non-parametric statistical methods. Our analysis assumes that decisions across experiments are independent, and adjustments are made for ties in the matched-pairs data (i.e. when a subject's decision is identical in the TSD and RW conditions).

While our counterbalancing of the condition order in our sleep group helps to remove any ordering effects in the matched-pairs data, as noted earlier we also administered the experiment to a group of 16 control subjects. Thus, the control subject data allow us to examine the pure effect of repeat administration or learning in the data. As will be seen, control subject decisions were never significantly different across the two administrations of the tasks.

For examining our TSD hypotheses from our repeated-measures design, we report results from the sign test on the bivariate random sample of each pair of decisions made by a subject (unless noted otherwise). This non-parametric test places no assumption of normality on the distribution of the sample data, although it does assume that the data across subjects are independent. In most cases, we reject the null hypothesis of normality of the relevant matched-pairs data distribution for our various tests (Shapiro–Wilk test, $P < 0.10$), and so do not utilize the (parametric) matched-pairs t-test. The Wilcoxon signed-rank test is another potentially more powerful non-parametric test that could be used on matched-pairs data. However, the Wilcoxon signed-rank test places the additional assumption of symmetry on the data. Given that our matched-pairs data violate this assumption (as confirmed by symmetry plots), we analyze our matched-pairs data with the more simple but appropriate sign test.

Results

Ultimatum and Dictator Results

As seen in Fig. 3, first-mover proposals from the Ultimatum and Dictator games reveal that Dictator offers were significantly lower than Ultimatum offers (P ≤ 0.01). This was also evident in the control group (P = 0.05). However, treating each subject's pair of Ultimatum offers as matched-pairs data, we conclude that ultimatum offers are not affected by the sleep condition (RW versus TSD, P > 0.10) or repeat administration for the control group (P > 0.10).

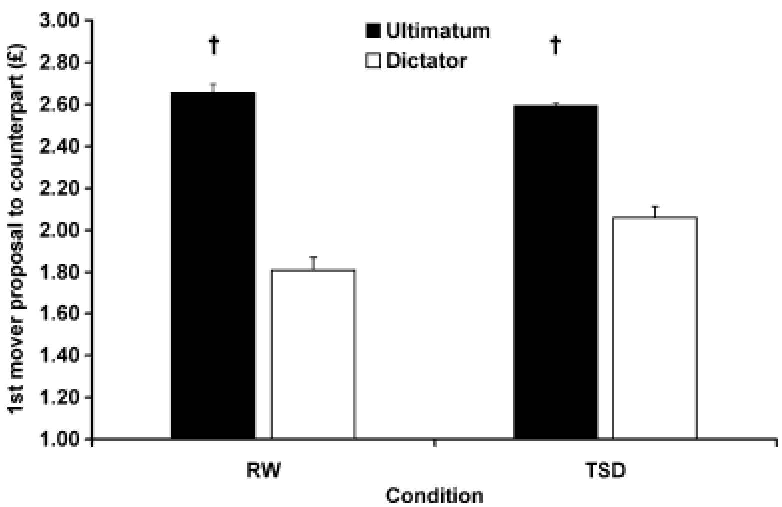

Figure 3. Average proposal decisions on the Ultimatum (black bars) and Dictator (white bars) games. Standard error bars are shown. All proposals were reduced on the Dictator game. †P < 0.01. There was no main effect of total sleep deprivation (TSD) on either decision. RW, rested wakefulness.

Figs 4 and 5 show the summarized data on the Ultimatum game responder decisions. From these data, we calculate MAO for each subject for each condition (sleep group) or administration (control group). Mean and standard deviation for MAO for the sleep condition are £0.84 ± 0.85 for well-rested subjects and £1.34 ± 1.09 following 36-h TSD. For control subjects, MAO is £1.22 ± 0.88 and £1.28 ± 0.97 on first and second administrations of the task, respectively. Figs 4 and 5 also highlight the 50 : 50 equal-split outcome at £2.50, which is an offer rarely rejected in the Ultimatum game. Examining the matched-pairs data of MAO from each subject, we find that the difference in MAO was not significant across administrations in the control treatment (P > 0.10); see Fig. 4. However, we find that MAOs are significantly higher following TSD than in the RW condition of our sleep group (P = 0.05); see Fig. 5. Thus, we conclude that 36 h of TSD leads subjects to bargain more aggressively in this simple Ultimatum game, although the effect manifests itself only in responder decisions and not in first-mover proposals.

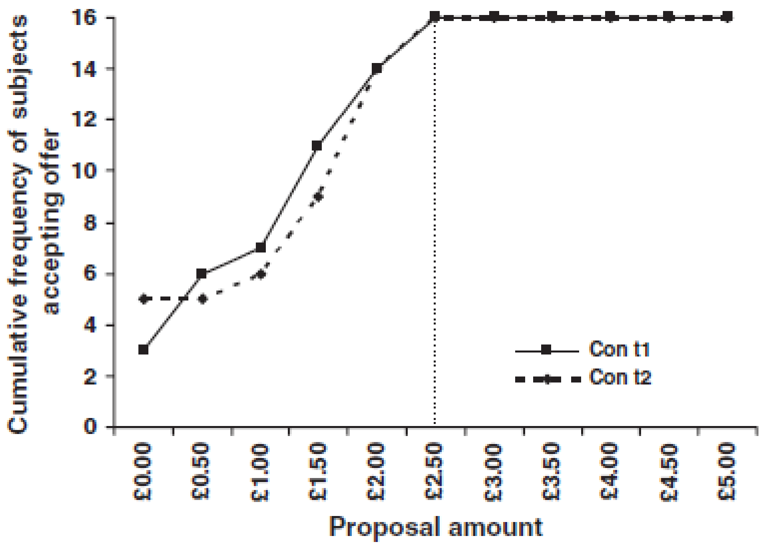

Figure 4. Cumulative frequency of participants accepting the proposer offer for the control group. The dotted vertical line marks the 50 : 50 equal split of the pie, which is normally accepted in this game. There were no differences in the matched-pairs control. NB: where only one line is evident, the dotted line runs parallel with the black line.

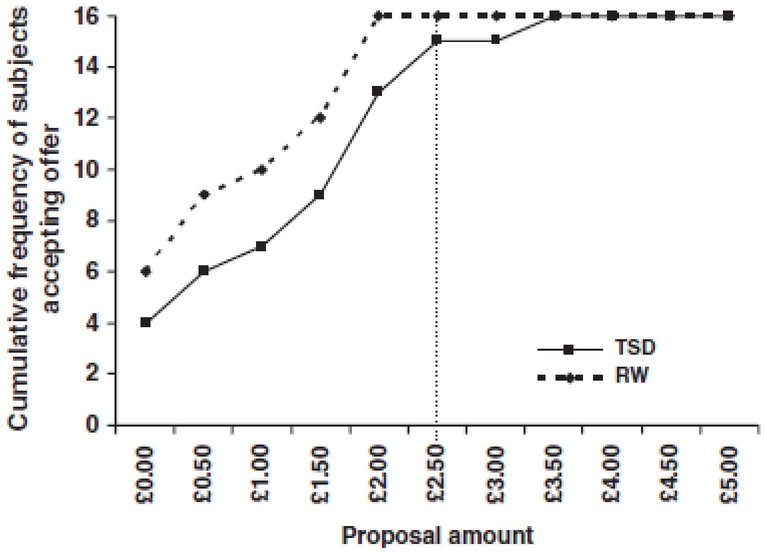

Figure 5. Cumulative frequency of participant accepting the proposer offer for the experimental group [total sleep deprivation (TSD) versus rested wakefulness (RW)]. The dotted vertical line marks the 50 : 50 equal portion size, which is normally accepted in this game. There was a significant effect of TSD ($P < 0.05$) on the minimum acceptable offer (MAO). NB: where only one line is evident, the dotted line runs parallel with the black line.

Trust game results

Fig. 6 highlights the results for TSD versus RW in the trust game. Here, data indicate that well-rested subjects may keep less and pass more (i.e. trust more) than TSD subjects. The main amount kept following TSD is £2.06 ± 1.59 SD compared with £1.41 ± 1.49 for RW (see Fig. 4). For the first and second administrations of the task for the control group, mean amounts kept were £2.25 ± 1.03 and £2.53 ± 1.31, respectively. Sign-test analysis of the matched-pairs data did not reveal any statistically significant differences, either across sleep conditions or control group administrations ($P > 0.10$).

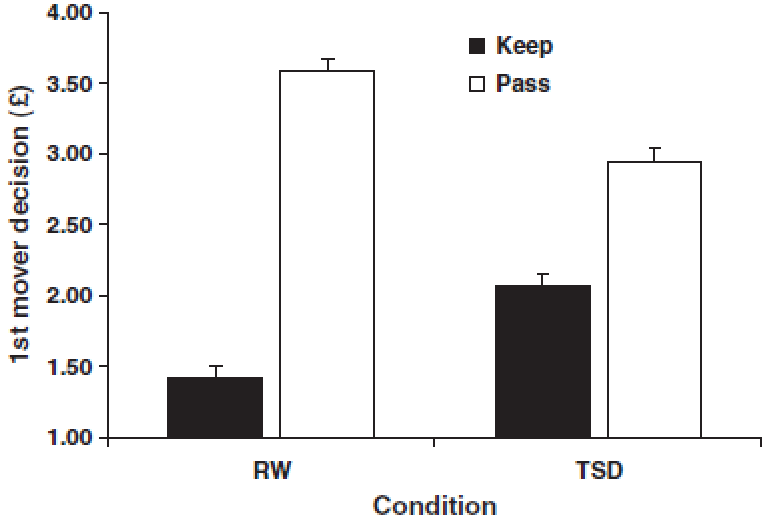

Figure 6. Average amount passed and kept by the first mover in the Trust game. Black bars refer to money kept, white bars to money given. While it appears that the subjects in the rested wakefulness (RW) group pass (trust) more, this falls below the acceptable level of significance. Standard error bars are shown. TSD, total sleep deprivation.

Upon further examination of first-mover trust decisions, Fig. 7 highlights that although sleep condition may not affect average trust levels, the difference in sleep conditions may be largest at the extreme trust end of the distribution. If we define extreme trust arbitrarily as those instances when the first mover passed at least £4.00 of the possible £5.00 (80% of possible trust amount), then we find that 5 of 16 subjects exhibit extreme trust amount during TSD, compared with 9 of 16 subjects when well-rested. Defining extreme trust as occurring in either subject condition with probability P, we then use the binomial test to examine the differences in probability of extreme trust in the TSD and RW sleep conditions. A baseline P could be generated from the control subject data, but such data may have group-specific effects, so we proceed by utilizing the experimental group's RW $P_{rw} = 0.5625$ (9 of 16) as the hypothesized probability of extreme trust for the binomial tests. In so doing, we reject the null hypothesis that the TSD subjects have a similar probability of extreme trust against the one-sided alternative that their probability $P_{tsd} < P_{rw}$ (P-value of 0.04 for the one-sided binomial test). Had we chosen $P_{tsd} = 0.3125$ (5 of 16) as the hypothesized probability of extreme trust, we reject the null hypothesis that $P_{tsd} = P_{rw}$ in favour of one-sided alternative that $P_{tsd} < P_{rw}$ (P-value = 0.01 in this instance). Thus, there is evidence consistent with the hypothesis that subjects trust less following TSD, although the effect is concentrated at the extreme trust end of the continuum of trust possibilities.

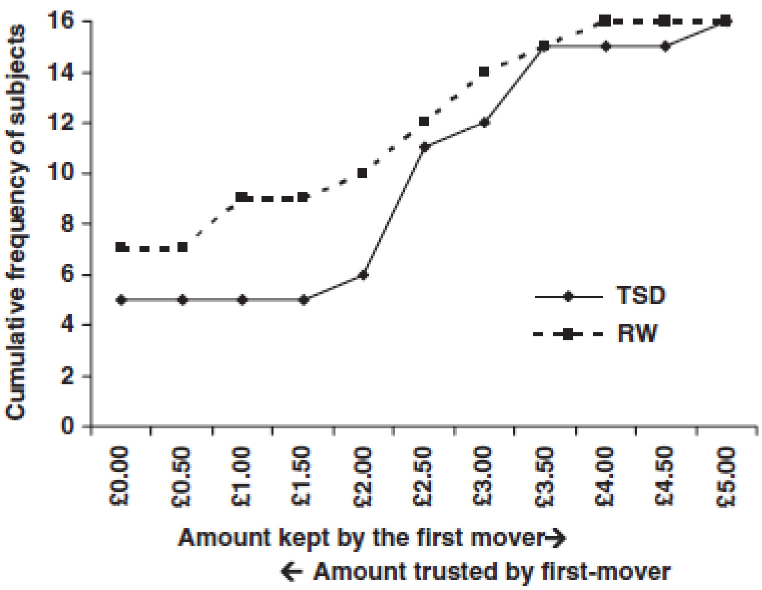

Figure 7. Cumulative distribution function (CDF) of amount kept by first mover in the Trust game. Sixteen subjects (vertical axis) from the experimental group make up the entirety of the CDF. The larger difference between the total sleep deprivation (TSD) and rested wakefulness (RW) distributions at lesser amounts kept indicates that the highest trust levels occur among significantly fewer TSD subjects compared with RW.

For second-mover decisions, while some group difference exist in the RW versus TSD group, the effects of sleep condition or repeat administration do not affect a subject's trustworthiness significantly (Kolmogorov–Smirnov full distribution test, $P > 0.10$). Interestingly, while the significant result in the bargaining experiments was localized to second-mover (responder) decisions in the Ultimatum game, in the Trust game the interesting result is with respect to first-mover (trust) decisions. We examine this in more detail in 'Discussion' section.

Discussion

Our results highlight the important effects of SD on simple two-person social interactions that may be relevant in a real-world setting. Across two related social preference environments, we find that individuals interact more aggressively following

TSD. As responders in the Ultimatum game, subjects increased their MAOs following TSD, perhaps indicating an increased resistance to offers perceived as unfair. In the simple trust environment, although the evidence is not uniform across all trust levels, we find that extreme levels of trust among first movers in the trust experiment are less likely following TSD. It is noteworthy that trusting one's counterpart by passing along money in this environment puts one at risk to being taken advantage of.

Recent advances in behavioural economics research suggest that the issue of equality may be an important factor in these decisions. Fehr and Schmidt (1999), for example, introduce a theory that models how people care about payoff inequity (i.e. fairness) in social interactions, and not just their own payoff. Thus, any deviation from equal payoffs is assumed to lower one's value or utility function over outcomes. Other theories introduce notions of fairness into individual preference functions (e.g. Bolton and Ockenfels, 2000; Rabin, 1993). Fehr and Schmidt (1999) assume that individuals are inequity-averse, but also that individuals would still rather have inequity in their favour than vice versa. In other words, there is a stronger aversion to unfavourable inequity (i.e. your payoff is higher than mine) than favourable inequity (i.e. my payoff is higher than yours). For our TSD group, subject behaviour is consistent with increased aversion to unfavourable inequity in the Ultimatum game compared with RW. That is, subjects were more willing to sacrifice personal monetary payoff and reject offers perceived as unfair. This increased tendency to reject Ultimatum offers is also present in those with ventromedial PFC damage (Koenigs and Tranel, 2007; see below).

While decision-making is seen and measured typically as a rational cognitive process, emotional experiences play a key role in guiding that process (Camerer, 2003). A plausible hypothesis based on neural evidence is a dual system approach, whereby decisions within the Ultimatum game are guided by cognition and emotion. For our TSD group, participants were less willing to accept unfair offers, even though they generated a positive monetary payoff. When viewed from a cognitive perspective, this would appear to be a poor decision to reject money over perceived unfairness. Fairness concerns are, of course, important even in RW decisions, but our results indicate that decisions following TSD may be guided more by emotion than would otherwise be the case. The data presented here adhere to this dual-hypothesis approach. SD is known to disrupt PFC function (e.g. Chee and Chuah, 2008) and as such the contribution of the cognitively orientated DLPFC to the decision-making process is potentially compromised. As a result, the emotionally orientated contribution may become dominant in the decision-making process, which will lead in turn to an increased likelihood of rejecting an unfair offer. However, the extent to which this may be reflected in imaging data during TSD is unknown. Koenigs and Tranel (2007) examine Ultimatum game play in subjects with ventromedial PFC brain lesions, and find that such subjects reject Ultimatum offers with higher frequency, similarly to our TSD group. While it is well known that behaviours mediated by the PFC are affected by sleep loss (c.f. Horne, 1993), the extent to which the cost of rejection is given less weight in the brain's cost–benefit analysis of the decision scenario (Fehr and Camerer, 2007), and whether the emotional reaction dominates the decision to reject unfair offers during TSD is unknown but warrants further research. While Knoch et al. (2006) show that disruption to the right DLPFC via repetitive transcranial magnetic stimulation (rTMS) increases the likelihood of accepting unfair offers, the extent to which disruption of the PFC via rTMS acts as a robust model of sleep loss is unknown. However, the paper does support a fundamental role of emotion in decision-making which is currently unexamined in a sleep loss context.

While we are not looking at emotion per se in our studies, the Ultimatum game does elicit an emotional response when playing against another person. Studies have shown repeatedly a stronger emotional reaction to unfair offers made by a person rather than by a computer (McCabe et al., 2001; Rilling et al., 2008; Sanfey et al., 2003; van't Wout et al., 2006), resulting in an increased rejection of unfair offers. While we suggest that our findings may point to a potential conflict between emotive and cognitive processes, it is unknown whether rejections were made because of an overt emotional expression. However, while Pillutla and Murnighan (1996) suggested that anger was more likely to invoke a rejection of an unfair offer, Crockett et al. (2008) suggested that this was unrelated to mood. While our results may also be explained, in part, by inhibition, a known consequence of sleep loss (Drummond et al., 2006), we would expect inhibition to manifest itself by TSD subjects accepting or rejecting 'all' offers because of the inability to inhibit a reject/accept response for all options. This was not the case in our study. Moreover, SD-induced inhibition does not explain the altered response for the second mover in the Ultimatum game and the first mover in the Trust game. The only commonality these two decisions share is a risk of being taken advantage of.

While the Ultimatum game is designed to assess decision-making with an emotive element (fair versus unfair decision), the findings here may also be attributable to decision-making per se, but in a social context. While we believe that the social component of this task influences the decision-making process, based on neural evidence from the literature for both Ultimatum games and sleep loss, one could assess this directly by repeating the experiment but controlling for decision-making under less social context with less emotive consequences, i.e. making a decision versus a computer. Nevertheless, if TSD affects decision-making per se (and the social context is a confound), again this would not explain the unusual result we find in that only responders in the Ultimatum game show TSD effects, but in the Trust game it is the first movers showing behavioural effects. Here, we find that extreme levels of trust among first movers in the Trust experiment are less likely following TSD. Second movers in the Trust game who still make a decision (how much money to pass back) are unaffected (they are not at risk at being taken advantage of), just as Ultimatum proposers are unaffected.

The present evidence is thus consistent with the hypothesis that SD increases one's aversion to unfavourable payoff inequity, as if one becomes more sensitized to the threat of being 'outdone' in the social interaction (although the threat may exist in some sense in the Dictator game, there is no response option). This threat may be more salient to an Ultimatum responder who can choose what level of payoff inequity he/she accepts, compared with the proposer who either gains more than half the pie (typically) or an equal-payoff outcome of zero in the event of rejection. On the contrary, in the trust environment, it becomes the first mover who faces the largest threat of being exploited. A second mover in the Trust experiment is less likely to feel exploited given that he/she can choose to always pass zero of whatever amount the first-mover trusts. Thus, it seems that the threat of exploitation looms largest for Ultimatum responders (second mover) and first-move trusters and, if TSD leads to a heightened fear of being taken advantage of, this may generate the data patterns we observe.

Some related research on the Trust game may help to shed further light on our findings, hypothesis and interpretation. Subjects playing the same Trust game were infused intranasally with the synthetic neuropeptide oxytocin (OT) in the Kosfeld et al. (2005) and Baumgartner et al. (2008) studies. In both studies, the OT-infused subjects were more trusting than the control (placebo) group, even when their trust had been breached several times (i.e. post-feedback –Baumgartner et al., 2008). This finding is of particular interest not just because we administer the same Trust game, but primarily because OT has been shown to decrease amygdala activity (Kirsch et al., 2005). Under conditions of TSD (35 h), Yoo et al. (2007) reported that subjects displayed a larger amygdala response to emotive pictures than those viewing them well-rested. Furthermore, they also reported a decreased functional connectivity between the amygdala and the medial PFC following TSD. Despite coming from different tasks, these findings suggest that emotion-related centres (i.e. the amygdala) may be more dominant in the decision-making of TSD subjects resulting in less trusting behaviours. Together, these studies suggest that TSD would lead to less trusting social choices given that it enhances amygdala activity, which appears detrimental towards exhibition of trust. Insel and Young (2001) provide corroborative (animal) data showing that OT may reduce defensive behaviour (e.g. fear of betrayal reduced). Thus, the hypothesis that increased amygdala dominance in the social decision process will increase fear of betrayal and thereby lower trust is consistent with our evidence. While no study currently exists assessing TSD and neural responses to trust, our findings remain speculative, yet beckon future work on this research agenda.

Our results suggest that individuals' social preferences are more concerned with avoiding betrayal of different sorts following TSD, even by anonymous counterparts. In both simple bargaining and trust experiments, significant behavioural effects are found on only one side of the interaction, but in both environments the result is consistent with an increased defensiveness following TSD. If trust is an important component of a well-functioning modern society, then reduction of trust in an increasingly sleep-deprived society holds significant implications. Indeed, many important institutions function on a certain level of trust (e.g. banks for solvency, informal credit markets, marriage). Clearly, the full cost of TSD effects on the quality of social interactions is beyond the scope of this study, but our results are suggestive of behaviours that have been unexamined in a TSD context. They indicate that mistrust and defensiveness may become more prevalent as our social preference decisions become more controlled by the emotional part of the brain that has heightened awareness of possible exploitation when under TSD.

These experiments are a first step in examining social preferences (allocation of resources between self and others) and TSD. While our discussion is speculative, further research addressing neural correlates of behavioural responses to these economic decision-making games is key to enhancing our understanding of decision-making under periods of sleep loss. Although our TSD results are consistent with those of frontal dysfunction, our findings were based on small sample sizes. Although we report statistical significance across the tasks on important outcome variables, further research may attempt to replicate our findings using a larger sample size to increase power, thus promoting less speculation on the results found, especially if coupled with imaging techniques. Nevertheless, this area of study is in its infancy and our results highlight the necessity to examine other aspects of SD beyond vigilance, attention, human–computer interactions, etc. to reflect real-world behaviours. Although real-world sleep loss may not be as extensive as 36 h [although medical residents work in excess of 30 h (e.g. Lockley et al., 2004) and, interestingly, have been reported to have amplified reactions to negative stimuli (Zohar et al., 2005)], further work may address the extent to which one must be sleep-deprived before such behavioural effects set in. Furthermore, we do not examine the importance of the actual face-to-face interaction present in real-world negotiations and many trust environments. Here, we do this explicitly in order to reduce the potential confounds of unquantifiable aspects of face-to-face interactions (e.g. body language), yet recognize that these are clearly interesting components of real-world social interactions. In short, there is a wealth of important aspects of social interactions that remain unexplored by sleep researchers. Nevertheless, these experiments are a first step towards a more comprehensive examination of decision-making within a social domain, and are the first indicators that a rational decision may not prevail over more emotional options following one night of sleep loss.

References

- Anderson, C. and Horne, J. A. A high sugar content, low caffeine drink does not alleviate sleepiness but may worsen it. *Hum. Psychopharmacol.*, 2006, 21: 299–303.
- Baranski, J. V., Thompson, M. M., Lichacz, F. M. J. *et al.* Effects of sleep loss on team decision making: motivational loss or motivational gain? *Hum. Factors*, 2007, 49: 646–660.
- Baumgartner, T., Heinrichs, M., Vonlanthan, A., Fischbacher, U. and Fehr, E. Oxytocin shapes the neural circuitry of trust and trust adaptation in humans. *Neuron*, 2008, 58: 639–650.
- Berg, J., Dickhaut, J. and McCabe, K. Trust, reciprocity, and social history. *Games Econ. Behav.*, 1995, 10: 122–142.
- Bolton, G. and Ockenfels, A. ERC – a theory of equity, reciprocity and competition. *Am. Econ. Rev.*, 2000, 90: 166–193.
- Camerer, C. F. Strategizing in the brain. *Science*, 2003, 300: 1673–1675.
- Chee, M. W. and Chuah, L. Y. Functional neuroimaging insights into how sleep and sleep deprivation affect memory and cognition. *Curr. Opin. Neurol.*, 2008, 21: 417–423.
- Cox, J. C. How to identify trust and reciprocity. *Games Econ. Behav.*, 2004, 46: 260–281.

- Crockett, M. J., Clark, L., Tabibnia, G., Lieberman, M. D. and Robbins, T. W. Serotonin modulates behavioral reactions to unfairness. *Science*, 2008, 320: 1739.
- Damasio, A. R., Grabowski, T. J., Bechara, A. *et al.* Subcortical and cortical brain activity during the feeling of self-generated emotions. *Nat. Neurosci.*, 2000, 3: 1049–1056.
- Dorrian, J., Rogers, N. L. and Dinges, D. F. Psychomotor vigilance performance: a neurocognitive assay sensitive to sleep loss. In: C. A.Kushida (Ed.) *Sleep Deprivation: Clinical Issues, Pharmacology and Sleep Loss Effects*. Marcel Dekker, Inc., New York, 2005: 39–70.
- Drummond, S. P., Paulus, M. P. and Tapert, S. F. Effects of two nights sleep deprivation and two nights recovery sleep on response inhibition. *J. Sleep Res.*, 2006, 15: 261–265.
- Fehr, E. and Camerer, C. F. Social neuroeconomics: the neural circuitry of social preferences. *Trends Cogn. Sci.*, 2007, 11: 419–427.
- Fehr, E. and Schmidt, K. M. A theory of fairness, competition, and cooperation. *Q. J. Econ.*, 1999, 114: 817–868.
- Forsythe, R., Horowitz, J. L., Savin, N. E. and Sefton, M. Fairness in simple bargaining games. *Games Econ. Behav.*, 1994, 6: 347–369.
- Guth, W., Schmittberger, R. and Schwarze, B. An experimental analysis of ultimatum bargaining. *J. Econ. Behav. Organ.*, 1982, 3: 367–388.
- Harrison, Y. and Horne, J. A. Sleep deprivation affects speech. *Sleep*, 1997, 20: 871–877.
- Harrison, Y. and Horne, J. A. Sleep loss impairs short and novel language tasks having a prefrontal focus. *J. Sleep Res.*, 1998, 7: 95–100.
- Harrison, Y. and Horne, J. A. The impact of sleep deprivation on decision making: a review. *J. Exp. Psychol. Appl.*, 2000, 6: 236–249.
- Holt, C. *Markets, Games, and Strategic Behavior*. Pearson Education, Inc., Boston, 2007.
- Horne, J. A. Sleep loss and ‘divergent’ thinking ability. *Sleep*, 1988, 11: 528–536.
- Horne, J. A. Human sleep, sleep loss and behaviour. Implications for the prefrontal cortex and psychiatric behaviour. *Br. J. Psychiatry*, 1993, 162: 413–419.

- Insel, T. R. and Young, L. J. The neurobiology of attachment. *Nat. Rev. Neurosci.*, 2001, 2: 129–136.
- Johns, M. W. A new method for measuring daytime sleepiness: the Epworth Sleepiness Scale. *Sleep*, 1991, 14: 540–545.
- Killgore, W. D. S., Balkin, T. J. and Wesensten, N. J. Impaired decision making following 49 h of sleep deprivation. *J. Sleep Res.*, 2006, 15: 7–13.
- Kirsch, P., Esslinger, C., Chen, Q. *et al.* Oxytocin modulates neural circuitry for social cognition and fear in humans, *J. Neurosci.*, 2005, 25: 11489–11493.
- Knoch, D., Pascual-Leone, A., Meyer, K., Treyer, V. and Fehr, E. Diminishing reciprocal fairness by disrupting the right prefrontal cortex. *Science*, 2006, 314: 829–832.
- Koenigs, M. and Tranel, D. Irrational economic decision-making after ventromedial prefrontal damage: evidence from the ultimatum game. *J. Neurosci.*, 2007, 27: 951–956.
- Kosfeld, M., Heinrichs, M., Zak, P. J., Fischbacher, U. and Fehr, E. Oxytocin increases trust in humans. *Nature*, 2005, 435: 673–676.
- Lim, J. and Dinges, D. F. Sleep deprivation and vigilant attention. *Ann. N. Y. Acad. Sci.*, 2008, 1129: 305–322.
- Lockley, S. W., Cronin, J. W., Evans, E. E. *et al.* Effect of reducing interns' weekly work hours on sleep and attentional failures. *N. Engl. J. Med.*, 2004, 351: 1829–1837.
- McCabe, K., Houser, D., Ryan, L., Smith, V. and Trouard, T. A functional imaging study of cooperation in two-person reciprocal exchange. *Proc. Natl Acad. Sci. USA*, 2001, 98: 11832–11835.
- McKenna, B. S., Dickinson, D. L., Orff, H. J. and Drummond, S. P. A. The effects of one night of sleep deprivation on known-risk and ambiguous-risk decisions. *J. Sleep Res.*, 2007, 16: 245–252.
- Miller, E. K. and Cohen, J. D. An integrative theory of prefrontal cortex function. *Annu. Rev. Neurosci.*, 2001, 24: 167–202.
- Nowak, M. A., Page, K. M. and Sigmund, K. Fairness versus reason in the ultimatum game. *Science*, 2000, 289: 1773–1775.

- Oxoby, R. J. and McLeish, K. N. Specific decision and strategy vector methods in ultimatum bargaining: evidence on the strength of other-regarding behavior. *Econ. Lett.*, 2004, 84: 399–405.
- Pillutla, M. M. and Murnighan, J. K. Unfairness, anger, and spite: emotional rejections of Ultimatum offers. *Organ. Behav. Hum. Decis. Process*, 1996, 68: 208–224.
- Rabin, M. Incorporating fairness into game theory and economics. *Am. Econ. Rev.*, 1993, 83: 1281–1302.
- Rilling, J. K., King-Casas, B. and Sanfey, A. G. The neurobiology of social decision-making. *Curr. Opin. Neurobiol.*, 2008, 18: 159–165.
- Sanfey, A. G., Rilling, J. K., Aronson, J. A., Nystrom, L. E. and Cohen, J. D. The neural basis of economic decision-making in the Ultimatum game. *Science*, 2003, 300: 1755–1758.
- Turner, T. H., Drummond, S. P. A., Salamat, J. S. and Brown, G. G. Effects of 42 h total sleep deprivation on component processes of working memory. *Neuropsychology*, 2007, 21: 787–795.
- Van Dongen, H. P. A., Maislin, G., Mullington, J. M. and Dinges, D. F. The cumulative cost of additional wakefulness: dose–response effects on neurobehavioral functions and sleep physiology from chronic sleep restriction and total sleep deprivation. *Sleep*, 2003, 26: 117–126.
- Wagner, A. D., Maril, A., Bjork, A. and Schacter, D. L. Prefrontal contributions to executive control: fMRI evidence for functional distinctions with lateral prefrontal cortex. *Neuroimage*, 2001, 14: 1337–1347.
- Van't Wout, M., Kahn, R. S., Sanfey, A. G. and Aleman, A. Affective state and decision-making in the Ultimatum game. *Exp. Brain Res.*, 2006, 169: 564–568.
- Yoo, S.-S., Gujar, N., Hu, P., Jolesz, F. A. and Walker, M. P. The human emotional brain without sleep – a prefrontal amygdale disconnect. *Curr. Biol.*, 2007, 17: 877–878.
- Zohar, D., Tzischinsky, O., Epstein, R. and Lavie, P. The effects of sleep loss on medical residents' emotional reactions to work events: a cognitive-energy model. *Sleep*, 2005, 28: 47–54.