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Risk and Rationality: Decision-Making in the Brain

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Introduction

Our lives consist of a constant stream of decisions and choices, from the everyday (will I respond to this –email?) to they highly consequential (will I have a child?). Essentially, the study of decision-making attempts to understand our fundamental ability to process multiple alternatives and to choose an optimal course of action, an ability that has been studied by various disciplines with different theoretical assumption and measurements techniques, although with relatively little integration of findings (Sanfey, 2007). A kind of decisions that have been the subject of an increasing research interest is economic decision. Classically, economists have provided normative models that posit as people should behave for a rational decision-making. Rationality is a pivotal aspect of these models, which theorized the so-called Homo Economicus, a sort rational maximizer, unemotional and insensitive to the surrounding context.

In most part of real situations, people decisions are affected by emotions, contexts, the way alternatives are presented and other apparently irrelevant features that, in fact, have a heavy impact in choice behavior. The most popular and direct evidence in favor of the influence of these aspects has been reported by Kahneman and Tversky (1979), who demonstrated as simply changing the way the option are presented, people change their decisions. One paradigm employed is the “Asian Disease” dilemma. In the Asian disease problem, participants are told that the US is preparing for the outbreak of an unusual Asian disease, which is expected to kill 600 people. They are then presented with two options to combat the disease, and asked to choose between them. When framed in terms of gains, the two options consist of: (a) 200 people will be saved for certain (risk-free option) contrasted with (b) a 1/3 chance that 600 people will be saved and a 2/3 chance that no one will be saved (risk-seeking option). When framed in terms of losses, the two options consist of: (c) 400 people will die for certain (risk-free option) contrasted with (d) a 1/3 chance that no one will die and a 2/3 chance that 600 people will die (risk-seeking option). As a variety of different studies have shown, (see Kuhberger, 1998 for a review) participants tend to choose the risk-safe option

(200 saved for certain) when the problem is framed in terms of gains and the risky option (1/3 chance that no one will die and a 2/3 chance that 600 will die) when the problem is framed in terms of losses. The propensity for decision-makers to choose risk-averse options, when Asian disease type problems are framed in terms of gains, and risk-seeking options when framed in terms of losses, is inconsistent with the rational predictions of expected utility theory (von Neumann & Morgenstein, 1947). According to this view, the way in which the decision is framed should not change the expected utility of either the risk-seeking or risk-averse options. Recently, a study has demonstrated as the percentage of risky choices in the Asian disease dilemma is affected by finger movement (McElroy & Seta, 2004).

Classical research on decision-making has explored several aspects which has highlighted as economic decisions can be heavily affected by non-economic factors. The main aspects are listed below:

- *Framing Effect*: As already explained above, behavioural research has shown that simply changing the way options are presented, people changes their risk-attitude.
- *Joint and Separate Evaluation*: When two goods (A and B) are evaluated separately people can attribute an higher value to good A. By contrast, when the two goods are presented together, people can prefer good B.
- *Temporal Delay*: Generally the option that offers immediate reward is preferred, even if the alternative offers larger reward but delayed in time.
- *Social Contexts*: When people are offered some money, they can reject some offers because of the subjective impression of unfairness.

The newest frontier, in this research area, is the effort to understand the ways in which neural processes mediates risk-taking behavior. Recent studies applied modern neurophysiology methods (animal models, fMRI, TMS and ERPs) to economic decision making (Trepel et al., 2005). Neuroscience provides a novel point of view through which economical decision-making can be

studied, with the aim of filling the gap between formal theories and real choice behaviour. An animal study, on mallard ducks, provides evidence in favor of the rationality of decision-making (Harper, 1982). In this study 33 mallard ducks were employed. These birds eat continuously because they need energy but cannot accumulate reserve otherwise they would increase their weights, creating problems in flying. Their brain is relatively simple, compared to those of humans and it weighs about 5 grams. On one side of a pond, experimenter 1 threw a piece of bread (2 grams) every 5 seconds, while, on the opposite side of the pond, experimenter 2 threw a piece of bread (2 grams) every 10 seconds. Obviously, mallard ducks try to eat as much as they can. The best and rational behavior would be that $\frac{2}{3}$ of ducks are in front of experimenter 1 and $\frac{1}{3}$ in front of experimenter 2. In formal terms, this is Nash's equilibrium. Surprisingly, mallard ducks reached Nash's equilibrium in 60 seconds. However, Harper (1982) underlines as not every single duck eat the same quantity of food, therefore what is the best solution for the group, it is not necessary also the best solution for individual. By an economic point of view, this aspect highlights differences between microeconomics and macroeconomics (Glimcher et al., 2005). Despite this example of rational behavior in animals, the most part of the studies have shown as the rational Homo Economicus is very far from real people. In this line of research, De Martino and colleagues (2006) replicated framing effect while subjects' brain activity was scanned with fMRI, They found that the framing effect was specifically associated with amygdala activity, suggesting a key role for an emotional system in mediating decision biases. Moreover, across individuals, orbital and medial prefrontal cortex activity predicted a reduced susceptibility to the framing effect. This finding highlights the importance of incorporating emotional processes within models of human choice and suggests how the brain may modulate the effect of these biasing influences to approximate rationality. Another neuroscience study that provides additional knowledge about economic decision-making is reported by McClure and colleagues (2004). They show as when an option is immediately available is usually preferred even if the alternative ensures larger gains, while when the rewards are both delayed people prefer, rationally, the greater gain. The experiment demonstrates

that two separate systems are involved in such decisions. Parts of the limbic system associated with the midbrain dopamine system, including paralimbic cortex, are preferentially activated by decisions involving immediately available rewards. In contrast, regions of the lateral prefrontal cortex and posterior parietal cortex are engaged uniformly by intertemporal choices irrespective of delay. Furthermore, the relative engagement of the two systems is directly associated with subjects' choices, with greater relative fronto-parietal activity when subjects choose longer-term options. These reported are just examples of how neuroscience can enrich knowledge about decision-making.

However, some aspects that are particularly important in economic decision-making have been relatively understudied. One of this aspects is risk-taking that involves many economic decisions, such as investing money or choosing a kind of mortgage. Recent studies focused on assessment of outcomes of decision-making, reporting that they are essentially classified in terms of good and bad (Hajcak et al., 2006). However it is still unclear whether these binary distinction holds when outcomes have different predictability. Experiment 1 answers to this question trying to clarify this point as well as to identify the corresponding neural correlates of outcome evaluation. Another important aspect is outcomes assessment changes across contexts. Kahneman and Tversky (1979) reported consistent preference shift, when context is changed. Is this due to different outcomes evaluation depending from the context? Experiment 2 answers this question, reporting data about neural activity during risk-taking in different contexts.

Most experimental studies of decision-making to date have examined choices, with clearly defined probabilities and outcomes, such as choosing between monetary gambles. Given that we live in highly complex social environment, however, many of our most important decisions are made in the context of social interaction, which are additionally dependent on decisions of the others- for example, when we are deciding whether to ask someone on a date or entering on a business negotiation. Although relatively understudied, these social situation offer a useful window into a more complex forms of decisions, which may better approximate, many of our real life-

choices (Sanfey, 2007). The nature of decision-making changes fundamentally when individuals begin to interact in a social setting, because choices are also dependent on the decisions of others. The present research programme merges methods from neuroscience and economics with the aim to better understand how the human brain generates financial decisions in social context. Grounding social decisions in the biological substrate of the brain can provide a more fundamental (i.e., a neural-level) conceptualization of the underlying processes, and explain inconsistencies in human behaviour and forms of behaviour that some have deemed irrational.

A central conjecture of standard economic theory is that people make decisions that maximize their utility. This assumption holds that individuals (1) are rational decision-makers and (2) have purely self-regarding preferences, that is, they care only for their own material interest. Challenging the standard economic model, however, a large body of experimental evidence indicates that in social context people do not always choose what seems to be in their best interest, and that concerns for fairness and reciprocity strongly motivate social agents (Camerer, Loewenstein, & Prelec, 2005; Fehr & Camerer, 2007; Gintis, Bowles, Boyd, & Fehr, 2005). Recent research, for example, has demonstrated that individuals are willing to sacrifice resources for rewarding fair and punishing unfair behaviour, even if this is costly and provides neither present nor future material rewards (Fehr, Fischbacher, & Gächter, 2002). Experiment 3 and Experiment 4 followed this line of research. In Experiment 3 the interaction during economic decision-making is stressed, while brain activity has been recorded using ERPs, with the aim of clarify how monetary offers are perceived during social interaction. The following experiment 4 stressed the fairness of the offers, to clarify whether the kind of offers affect partner perception.

Experiment 1

Risk-Taking and Predictability

Making decisions which are of advantage for the individual is a skill that humans and animals have developed to make use of the opportunities the environment has to offer. In most situations it is unclear which response option represents the best one. With respect to mortgages, for instance, choosing fixed rates entails the precise prediction of a future financial scenario. Choosing floating rates may offer greater benefits, but also potential greater costs, features which cannot be estimated with certainty at the time of making the decision. Such “decision under uncertainty” situations are characterised by knowledge about the outcomes, but not about their precise probabilities (Knight, 1921). In everyday life, the precise probability associated with different outcomes is generally not known. Hence, decisions under uncertainty situations adequately represent an ecologically valid condition.

The normative Expected Utility (EU) model posits that outcomes must be considered in the light of their probabilities. The EU associated to an option is the sum of each probability-weighted value. The model assumes that the option with the greater EU should be chosen for a rational decision (von Neumann & Morgenstein, 1944). For example, if one option yields a gain of 10 with a probability of 20% and a second option yields a gain of 5€ with a probability of 80%, the first option has an EU of 2€ while the second has an EU of 4. In accordance with The EU model the second option should be preferred. However, when different options have the same EU, the certainty of predicting an outcome might be a salient feature of the decision. Honeybees clearly opt for the certain option (Real, 1999), while monkeys strongly opt for the uncertain one (McCoy & Platt, 2005). Humans show a tendency towards avoiding uncertainty (Ellsberg, 1961).

The brain mechanisms underlying decision making have been in the focus of current neuroscience research (Lee, 2005). Neuronal processing of outcomes has recently been reviewed by

Sanfey et al. (2006). In monkeys (Tremblay & Schultz, 1999) as well as in humans (O'Doherty et al., 2001), orbitofrontal cortex (OFC) activity has been found to correlate with the magnitude of outcomes. Coding of outcomes may, however, depend on the context and, in particular, on the evaluation of the most salient features of the context (Tobler et al., 2005). OFC activity, for instance, correlates with the subjective value attributed to the outcomes rather than their objective value in monkeys (Padoa-Schioppa & Assad, 2006), and dopamine neurons of the reward system code both outcome magnitude as well as the outcome probability (Tobler et al., 2005).

In humans, outcome processing has been investigated using the feedback related negativity (FRN), an event-related potential which reflects the activity of the medial frontal region in or near the anterior cingulate cortex (Miltner et al., 1997). The reinforcement learning theory (Holroyd & Coles, 2002) posits that the impact of the dopamine signals on anterior cingulate cortex modulates the amplitude of the FRN. In particular, a phasic decrease in dopamine activity is associated with a large FRN, while a phasic increase in dopamine activity is reflected by a small FRN. This activity is thought to code the ongoing evaluation of events and prediction of future events in terms of favourable or unfavourable outcomes (Holroyd & Coles, 2002). The reinforcement learning theory holds that the FRN amplitude depends both on valence and on expectancy (Holroyd & Coles, 2002). The idea that FRN amplitude reflects a binary evaluation in terms of gains and losses is well supported (Gehring & Willoughby, 2002; Hajcak et al., 2006) and also FRN modulation by outcome expectation has been reported. The FRN difference between expected and unexpected has generally been observed for the major distinction between gains and losses. Hajcak et al. (2005) did not find FRN differences between expected and unexpected negative outcomes, and Cohen et al. (2007) reported that FRN is modulated by probability for gains, but not for losses. Moreover, FRN amplitude has been reported to correlate with risk-taking (Yeung & Sanfey, 2004). Focusing on decisions under uncertainty, the present study aims: *i*) to clarify whether the binary evaluation of outcomes in terms of gains and losses is the most distinctive feature when outcomes differ in predictability, and *ii*) to identify the corresponding neural correlates of outcome evaluation.

Materials and Method

Participants

Twenty undergraduate students of the University of Padova (age range 22 to 26 years) participated in this study. They received course credit for participation. All subjects were healthy, had normal or corrected-to-normal vision and were debriefed at the end of the experiment.

Procedure

The experimental task was a modified version of the procedure used by McCoy and Platt (2005). On each trial, two coloured circles, one blue and one yellow, appeared on a black computer screen. The circles were located to the left and the right of the center of the screen, positions changed across trials in random order. Blue represented the certain option and yellow the uncertain option in half of the subjects, for the other half the opposite pattern applied. Participants were instructed to press a left-sided (“A”) or a right-sided (“L”) key, depending upon the option they chose for this particular trial. Although the response options had the same expected utility¹, the options led to different outcomes: The *certain option* always yielded the same outcome (10€), while the *uncertain option*, with a probability of 50%, yielded a larger gain than the certain option (30€), and with a probability of 50% a loss of 10€, and therefore a less favourable outcome than the certain option . Ideally, a more complete experimental design would be desirable with includes a predictable loss, but in practise people do not would choose options in which they systematically lose money and there would thus not be a sufficient number of trials for analysis. On individual trials, after the choice had been made, the corresponding outcome was displayed in the centre of the screen.

¹ The certain option has 10€ as possible outcome with a probability of 100%. This means that the expected utility for this option is 10€. Differently, the uncertain option has -10€ with a probability of 50% (utility: -5€) and 30 €with a probability of 50% (utility: 15€). Hence, the expected utility for the uncertain option is again 10€.

Participants completed 120 trials, divided into three blocks of 40 trials each. Within each block, the expected utility was the same for both options. There were no breaks between blocks, leaving subjects unaware of the subdivision into blocks. The division into three blocks has been introduced to allow analysis on behavioural changes in preferences across time. A single trial entailed the following sequence: Initially, the two circles (yellow and blue) were displayed on the screen until the participant had made his/her choice; then, a blank screen appeared for 1000 ms; followed by presentation of the corresponding outcome in the center of the screen for 1500 ms (see Fig. 1). After an interval of 1500 ms another trial started. E-prime software was used for stimuli presentation, markers sending, and response recording.

The instructions were presented in written form, and subjects completed an informed consent form. Participants were only told that they have to choose between one of the two options, try to earn as much as possible. They were informed in advance that they would not receive the remuneration corresponding to the total sum accumulated in the experiment, but were encouraged to try to perform well, in accordance with the procedure adopted by O’Doherty et al. (2001). EEG electrodes were then applied, using an electrocap (see below). The experimental session lasted about 45 minutes.

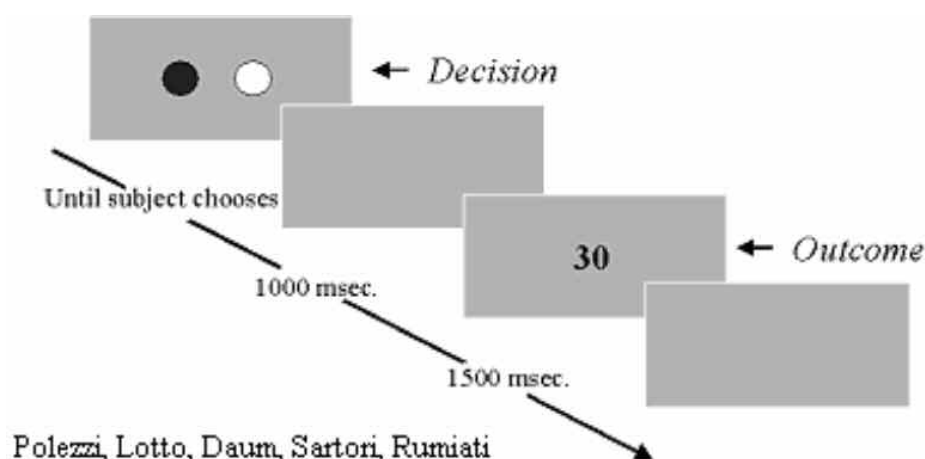


Figure 1. **Task-** The participant selects the preferred option. After this decision, the corresponding outcome is displayed and the task continues with the next trial.

ERPs recording

Scalp voltages were recorded using a 59-channel electrocap with Ag/AgCL electrodes. A frontal electrode (AFz) was connected to the ground. Electrode impedance was kept under 10 K Ω for all recordings. Vertical and horizontal ocular movements were also recorded. The EEG was digitized at a sampling rate of 500 Hz. The signal was off-line filtered using a *low pass filter* for 30 Hz, 24 dB/octave attenuation. Ocular movements' artifacts were corrected using the algorithm provided by Neuroscan 4.3 software. The EEG was segmented in *epochs* starting 200 ms before presentation of the outcome and lasting until 1000 ms after its onset. The epochs were aligned to the 200 ms baseline before onset of outcome presentation. Approximately, 5% of the trials were excluded from averaging because of movements artefacts. The average voltage across all electrodes was used as reference. In our experiment, this procedure is appropriate since more than 32 electrodes distributed across the whole scalp surface were used, as suggested by Junghöfer et al. (1999). The procedure has the advantage of reference-independent data (Junghöfer et al., 1999), without affecting source analysis which is unaffected by choice of the reference, as pointed out by Pasqual-Marqui and Lehmann (1993).

Source analysis

The P200, FRN, and N500 components recorded from all 59 electrodes entered source analysis using LORETA (Low Resolution Brain electromagnetic tomography) (Pasqual-Marqui et al., 1994; Pasqual-Marqui, 1999). LORETA is an inverse solution technique that estimates the distribution of the electrical neuronal activity in three-dimensional space. The estimation is based on information acquired from the electrodes positioned over the entire scalp (Congedo et al., 2004). This method is based on the assumption that neighboring neurons are simultaneously and synchronously activated, and it computes the current density at each gray matter voxel of a reference brain as a linear, weighted sum of the scalp electrical potentials. It provides an inverse problem solution by choosing

the smoothest of all possible current density configurations (Pasqual-Marqui et al., 1994; Pasqual-Marqui, 1999). LORETA-images represent brain activity through 2394 voxels which includes gray matter as well as hippocampus and cingulate gyrus (Congedo et al., 2004). For source analysis, we followed the procedure adopted by Bellebaum and Daum (2006). For all participants, LORETA-images were generated for the possible 3 outcomes (-10€, 10€, 30€). The images were converted (http://www.ihb.spb.ru/~pet_lab/L2S/L2Smain.htm) and further analyzed using SPM99 (<http://www.fil.ion.ucl.ac.uk/spm/>). A PET/SPECT design with multi-subjects: conditions and covariates was performed with the following parameters: Global Normalization with a proportional scaling to a mean of 50, no absolute threshold masking and global calculation of mean voxel value (within per image). The level of significance was set to $p=.05$, corrected for multiple comparisons. The coordinates of the foci of significant differences between conditions were transformed into Talaraich coordinates (Talairach & Tournoux, 1988) with the algorithm suggested by Brett (<http://www.mrc-cbu.cam.ac.uk/Imaging/Common/mnispac.shtml>). The Talaraich Daemon was then used to identify the brain structures involved (Lancaster et al., 2000).

Results

Behavioral Results

To assess preference for one of the two options, we performed one-sample *t*-tests to analyze whether the rates of choosing the certain option differed significantly from random choice behaviour (i.e., 50%) based on all trials (120 trials), and in terms of a change across the 3 blocks of 40 trials. Considering all trials, the frequency of choosing the certain options is significantly above chance ($t(19)=-2.303$, $p<.05$). The preference for the certain option increased from 56.4% for the first to 61.9% for the third block.

ERP Results

Inspection of ERPs indicates three distinct components related to the three outcomes. The first component is an early positive wave with a peak latency of about 200 ms, which has been measured over frontal areas and is referred to as P200 (Carretiè et al., 2001). Its amplitude is determined as the difference between the most negative deflection in the 100-160 ms time window and the most positive deflection in the 160-240 ms time window following the onset of outcome presentation.

The second wave is the Feedback Related Negativity (FRN), a potential peaking within 350 ms, with a maximum over frontal areas (Gehring & Willoughby, 2002; Hajcak et al., 2005; Holroyd et al., 2005; Yeung & Sanfey, 2004). To prevent possible confounding with the P200, FRN amplitude was defined as the difference between the most positive peak within 160-240 ms time window and the most negative potential within 240-350 ms time window, in accordance with the procedure suggested by Hajcak et al.(2006).

The third component of interest is a negative potential peaking at a latency of approximately 500 ms (N500) which is most prominent over frontal areas (De Pascalis et al., 1999). This potential is linked to posterior cingulate cortex and visual association cortex (Carretiè et al., 2006). Its amplitude is determined as the mean amplitude in the 400-600 time window with respect to the pre-stimulus baseline.

The ERP components were analysed for the F1, Fz and F2 electrodes in accordance with previous studies (Carretiè et al., 2001; Carretiè et al., 2005; Cohen et al., 2007; De Pascalis et al., 1999; Gehring & Willoughby, 2002; Hajcak et al., 2006).

Repeated measures analyses of variance (ANOVA) with Outcome (-10€; 10€; 30 €) and Laterality (F1; Fz; F2) as within-subjects factors were performed for the three potentials. In all analyses paired comparison were performed using Bonferroni correction.

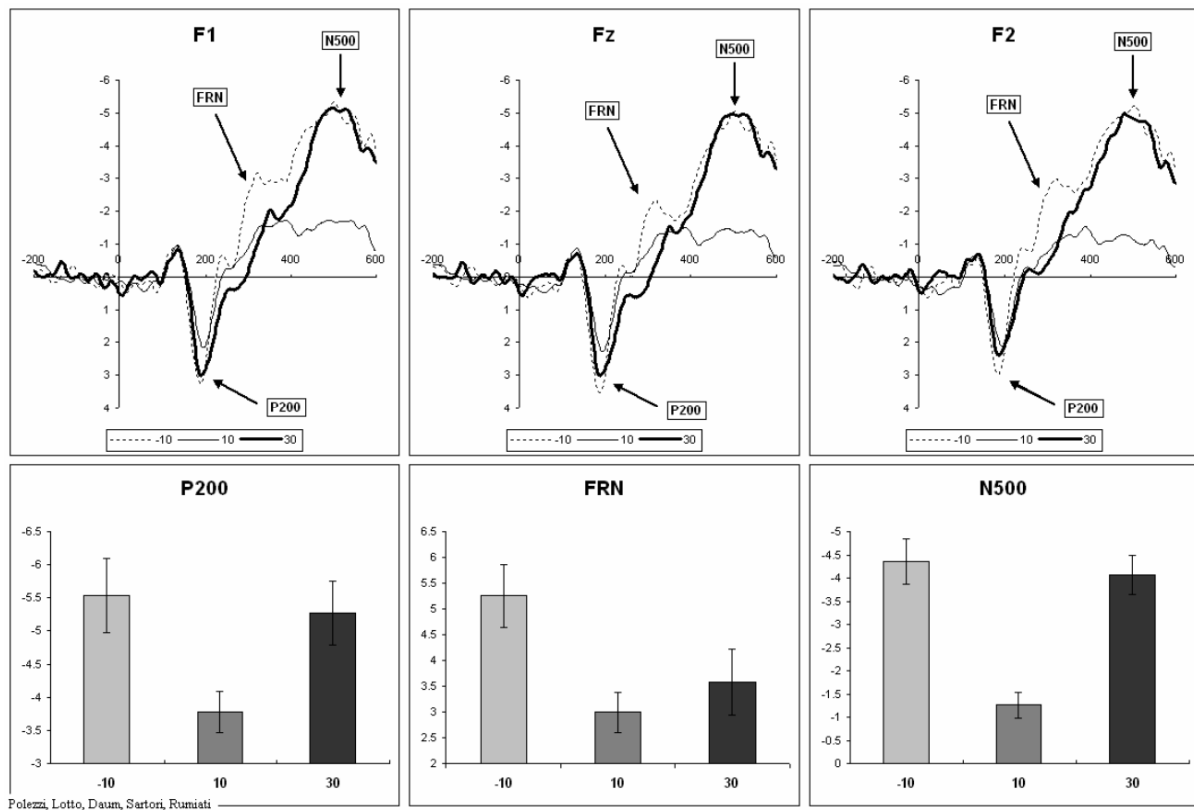


Figure 2. ERPs- The reported P200, FRN and N500 reflecting three steps of outcomes processing.

P200

ANOVA yielded a significant main effect of Outcome ($F(2,38)=7.947, p<.01; \eta^2_{\text{partial}}=.295$). Paired comparisons yielded larger P200 amplitudes for the -10€ outcome compared to the 10 € outcome ($t(19)=-3.148, p<.05$), and for the 30€ outcome compared to the 10€ outcome ($t(19)=3.546, p<.01$), while there was not significant difference between the P200 amplitude associated with the -10€ and 30€ outcomes ($t(19)=-.594; p=.99$).

The Laterality factor was also significant ($F(2,38)=11.762, p<.001, \eta^2_{\text{partial}}=.382$), with larger P200 amplitude at the central and left compared to the right position (F1 vs. F2, $t(19)=-2.842; p<.05$; Fz vs. F2, $t(19)=-4.756, p<.001$), comparison of the left and central positions did not reach significance (F1 vs. Fz, $t(19)=1.728, p=.300$). The interaction was not significant ($F(4,76)=.876; p=.482, \eta^2_{\text{partial}}=.044$).

FRN

ANOVA yielded a main Outcome effect ($F(2,38)=7.221, p<.01; \eta^2_{\text{partial}}=.275$). Paired comparisons yielded larger FRN amplitudes for the -10€ outcome compared to the 10€ outcome ($t(19)=3.314, p<.05$) and to the 30€ outcome ($t(19)=3.751, p<.01$), while there was not significant FRN difference between the 10€ and 30€ outcomes ($t(19)=-.849; p=.99$).

The Laterality factor was also significant ($F(2,38)=3.913, p<.05, \eta^2_{\text{partial}}=.171$), with larger FRNs at the lateral compared to the central position (F1 vs. Fz, $t(19)=2.598; p=.053$; F2 vs. Fz, $t(19)=-3.126, p<.05$), comparison of the left and right positions was not significant (F1 vs. F2, $t(19)=.188, p=.99$).

The interaction was also significant ($F(4,76)=3.754; p<.05, \eta^2_{\text{partial}}=.165$), reflecting a larger difference between the gains and the losses for the central and left electrodes compared to the right electrode .

N500

ANOVA yielded a main Outcome effect ($F(2,38)=28.108, p<.001; \eta^2_{\text{partial}}=.597$). Paired comparisons yielded larger N500 amplitudes for the -10€ outcome compared to the 10 € outcome ($t(19)=-6.963, p<.001$), and for the 30€ outcome compared to the 10 € outcome ($t(19)=5.876, p<.001$), while there was not significant difference between the -10€ and 30 € outcomes ($t(19)=-.636; p=.99$).

Neither the main Laterality effect ($F(2,38)=1.601, p=2.15, \eta^2_{\text{partial}}=.078$) nor the interaction reached significance ($F(4,76)=1.611; p=.180, \eta^2_{\text{partial}}=.078$).

Linear Regression Analysis: Behavioural results and ERPs data integrated

Previous studies have reported associations of P200 amplitude with stimulus valence (Carretiè et al., 2001; Carretiè et al., 2005) and of FRN with outcome evaluation and motivational aspects

(Gehring & Willoughby, 2002). To assess whether choice behaviour can be explained by the processes reflected by the ERPs components in question, linear regression analyses were run in accordance with Gehring and Willoughby (2002).

Separate linear regression analyses, for each ERP components, were performed, with ERP amplitudes for each of the possible outcomes (-10€; 10€; 30€) serving as independent variables and the proportion of choosing uncertain options as dependent variable.

P200

The results indicate that P200 amplitude associated with the -10€ condition explains 21.4% of variance in individual behaviour ($F(1,19)=6.169, p<.05$), with higher P200 amplitudes being associated with a lower number of uncertain choices. Similarly, P200 amplitude related to the 30€ outcome explains 23.9% of variance in individual behaviour ($F(1,19)=6.985, p<.05$) and, again, the higher the amplitude, the lower the number of uncertain choices. P200 amplitude for the 10€ condition, on the other hand, was not significantly related to subjects' behaviour, explaining only 4.2% of variance in individual behaviour ($F(1,19)=.235, p=.633$).

FRN

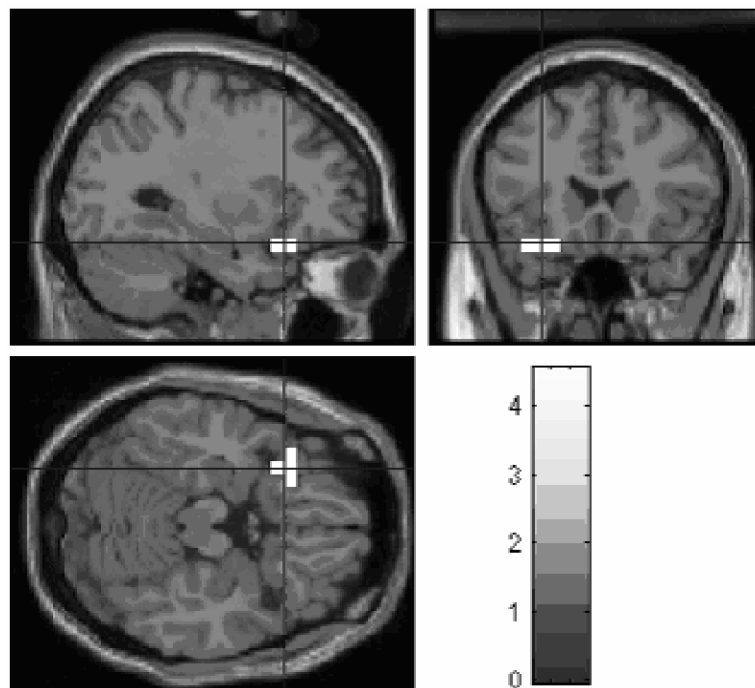
FRN amplitude was not significantly related with individual behaviour. FRN explains 4.4%, 3.9%, and only 2.7% of variance in individual behaviour for -10€, 30€, and 10 €outcomes, respectively [$(F(1,19)=.196, p=.663)$, $(F(1,19)=.279, p=.603)$, $(F(1,19)=1.545, p=.229)$].

N500

N500 amplitude was not significantly related with individual behaviour. N500 explains 0.8%, 4.4%, and only 9.3% of variance in individual behaviour for -10€, 30€, and 10 €outcomes, respectively [$(F(1,19)=1.16, p=.295)$, $(F(1,19)=.189, p=.669)$, $(F(1,19)=2.95, p=.103)$].

Source analysis

To investigate whether neural activity differed between the three outcomes, three contrasts (-10€ vs. 10€; 10€ vs. 30€; -10€ vs. 30€) were analysed. For the P200, voxels survived the significance level only for the 10€ vs. 30€ contrast, the area in question being the left inferior frontal gyrus (Brodmann area 47) ($F(1,38)=20.66, p<.05, [-24\ 24\ -20]$)², with higher activity for the 30€ than the 10€ outcome ($t(38)=4.55, p<.05$). No other contrasts yielded significant activation differences.



Polezzi, Lotto, Daum, Sartori, Rumiati

Figure 3. **Source Analysis-** The left inferior frontal gyrus (Brodmann area 47) [*MNI*: -24 24 -20] being most active for high gains.

² The coordinates reported follows the Montreal Neurological Institute system. In the Talairach system the same areas are indicated as [-24 22 -18], [-25 35 -14] and [-31 3 -30], respectively.

Discussion

The brain mechanisms underlying decision making have been the subject of increasing research interest in recent years. Within this context, the present study aimed to investigate the effect of predictability of outcomes on electrophysiological indicators of information processing. Subjects had to choose between one of two response options and outcomes: The predictable condition (certain response option) or the unpredictable condition (uncertain response option). Subjects showed a clear preference for the option associated with a predictable outcome, although the expected utility of both options was identical. This preference for the certain option suggests that subjects are clearly motivated to play the task similarly to a real gambling task although they did not receive real money, otherwise their choices for the options would be random; Moreover, in study by Gehring and Willoughby (2002), in which real money was paid depending on the participants' decisions, subjects showed a preference for the less uncertain option, similarly to our participants' decisions.

This is also in line with classical research (Ellsberg, 1961), indicating that participants preferred the option which led to a certain and known gain over the option which entailed a potentially large but unpredictable gain, or a small loss.

On an electrophysiological level, analysis of decisions between certain and uncertain options yielded three potentials which reflected different steps of outcomes processing. An early positive potential, the P200 has previously been related to subjective negative valence of emotional images: The more negative the valence, the larger the P200 amplitude (Carretié et al., 2001; Carretié et al., 2005). Outcome processing has so far centred on analysis of the FRN, which is thought to reflect the main distinction between gains and losses (Cohen et al., 2007; Gehring & Willoughby, 2002; Hajcak et al., 2005; Hajcak et al., 2006). Our data suggest an earlier processing of outcomes, reflected in the P200. First, the P200 was similar in amplitude for both unpredictable outcomes (-10 €; 30 €), and second, it was smaller for the predictable (10 €) compared to the unpredictable outcomes (-10 €, 30 €). This pattern indicates that P200 amplitude did not vary with outcome

magnitude neither did it reflect binary coding of gains and losses. Instead, P200 amplitude seems to reflect a distinction between predictable and unpredictable outcomes.

The second issue concerns the larger P200 amplitude for unpredictable compared to predictable outcomes. In previous studies, P200 was larger for stimuli with negative valence (Carretié et al., 2001; Carretié et al., 2005). In the current study, unpredictability appears to be evaluated more negatively than predictability. The behavioural data support this idea, as they indicate a clear preference for the certain option, a strategy became even more pronounced during the course of the experiment. In addition, regression analyses also suggested an association between uncertainty-avoidance behaviour and outcome processing reflected by P200. As outlined above, the larger the P200 amplitude for unpredictable outcomes, the lower the number of choices of the uncertain option, supporting the idea that P200 reflects a subjectively negative assessment.

Differential processing of outcomes was also reflected in FRN amplitude. The FRN is typically seen within 350 ms after the feedback presentation about a decision is presented (Hajcak et al., 2006). It is similar to the error-related negativity (Botvinick et al., 2004) and thought to be generated by the medial-frontal region in or near the anterior cingulate cortex (Botvinick et al., 2004; Gehring & Willoughby, 2002). The FRN generally reflects a binary evaluation of the valence of an outcome in terms of gains and losses, with larger FRN amplitudes for losses (Gehring & Willoughby, 2002; Hajcak et al., 2005). Our data confirmed the well-known distinction between gains and losses (Cohen et al., 2007; Gehring & Willoughby, 2002; Hajcak et al., 2005; Hajcak et al., 2006). FRN amplitude is larger for the 10€ loss compared to both types of gains (10 €30 €). In previous studies, the gain/loss distinction was described for conditions in which all outcomes were essentially unpredictable. In the study by Gehring and Willoughby (2002), participants had to choose between winning or losing a larger or a smaller sum, the probability for gain/loss was 50% for each outcome and thus unpredictable for all options. Along similar lines, in the Hajcak et al. (2006) study, outcomes (gain/loss) of a specific response were determined randomly. Similarly, Hajcak et al. (2005) manipulated expectancies, presenting cues for the probability of a negative

feedback, but the feedbacks were delivered randomly. In a recent study by Cohen et al. (2007), the probability of gains and losses varied across the task, the outcomes of decisions could not be predicted and the expected utility changed across the task. All studies reported the FRN-related distinction between gains and losses, but no earlier outcome-related ERP component. This pattern suggests that in case of unpredictable outcomes, the main feature is a general distinction between gains and losses. In the context of the present study, this type of outcome processing was preceded by an earlier processing stage which reflected processing in terms of predictability of outcomes.

The third component in the sequence of processing stages is the N500, which is generally larger for unpleasant stimuli (Carretié et al., 2006; De Pascalis et al., 1999; Mack et al., 2005) and thought to be generated by posterior cingulate cortex and visual association cortex (Carretié et al., 2006). Consistently with previous findings, N500 amplitude was larger for unpredictable outcomes which – as outlined above - are subjectively perceived more negative than predictable outcomes. It is also of interest in this context that activity in the posterior cingulate cortex has been found to correlate with uncertain decisions in monkeys (McCoy & Platt, 2005).

Despite the known limitations in terms of spatial resolution, source localisation of ERPs may allow an approximation of localisation of neuronal activity within short time windows and therefore during a specific stage of cognitive processing (Pasqual-Marqui et al., 1994; Pasqual-Marqui, 1999). P200 LORETA analysis suggested an involvement of the left inferior frontal gyrus which appeared to be particularly active during the processing of gains. According to recent functional neuroimaging evidence, the lateral OFC is activated in association with losses, while the medial OFC area is activated in association with gains, in particular in the left hemisphere (O'Doherty et al., 2001). In our study, using source localisation of the P200, the left inferior frontal gyrus was more active for processing 30€ (the largest gain) relative to 10 (the small gain).

Although the limited spatial resolution of the LORETA technique may allow tentative suggestion as to whether the activation in Fig. 3 unequivocally represents medial PFC, it is interesting to note that a recent fMRI study reported medial PFC activation in association with particularly large gains

(Knutson et al., 2005), which would be consistent with our source localization data. In addition, a recent ERP study reported that P200 is generated by the VMPFC (Carretiè et al., 2005).

In conclusion, the findings of the present study indicate that the processes underlying human decision making are significantly affected by predictability of outcomes when the options do not differ in EU, and that unpredictability appears to be a negative state. These results are consistent with the hypothesis by Tobler et al. (2005), suggesting that the brain codes the most relevant and informative features of a context (rather than all features) when decisions have to be made, raising the idea of a flexible evaluative system. The P200 appears to code predictability of an outcome and it is the only potential that is related to a subject's individual decision behaviour, in line with the proposal that predictability represents the most informative feature in the present context. Finally, the negative evaluation and avoidance of unpredictable outcomes relates to the ability to plan ahead: Knowing exactly what is going to happen enables us to develop efficient and successful plans.

Experiment 2

Risk-Taking between contexts and individual differences

In many daily decisions, we are faced with some degree of risk. In the financial field, savings could be invested in stocks or the safer treasury bills; for mortgages there is a choice between floating or fixed rates. Understanding the conditions in which people are more likely to accept risk is important to predict their decisions.

According to the normative Expected Utility (EU) model, when decisions under risk are being made each possible outcome should be considered in the light of its probability. The sum of each probability-weighted outcome is the EU of an option and, as a consequence, the option with the highest EU should be chosen as a rational decision (von Neumann & Morgenstein, 1947). For example, if one option yields a gain of 10€ with a probability of 20% and a second option yields a gain of 5€ with a probability of 80%, the first option has an EU of 2€ while the second has an EU of 4€. The EU model would thus suggest a preference of the second option. When people are faced with two options with the same EU, they should choose randomly. Another example entails option A (10€ or 0€, both with 50% probability) and option B (6 € or 4 €, both with 50% probability). The options have the same EU, but they entail a different degree of risk. The choice of option B is associated with certain gains, while option A involves the possibility of higher gains together with the risk of no gain at all. The EU model does not consider the risk variable, i.e. whether a person might prefer a certain gain over a risky condition of equal or higher EU (*Risk-averse*) or a risky condition to a certain gain of equal or higher EU (*Risk-seeker*). An important limitation of the EU model is the assumption that people are risk-neutral (Trepel, Fox, & Poldrack, 2005) and makes rational decisions (Kuhnen & Knutson, 2005). However, depending on the context people can be prone or averse to risk (Kahneman & Tversky, 1979) and individual differences play a crucial role in risk-taking (Lee, 2005).

In recent neurocognitive studies of economic decision making (Trepel et al., 2005), animal models yielded evidence for certain food options in bumblebees (Real, 1995) and a bias towards risky options in monkey (McCoy & Platt, 2005). The preference of monkeys for risky decision-making, even when it led to unfavorable outcomes was associated with posterior cingulate activations.

Risk taking associated with reward processing has been comprehensively studied in human subjects (Paulus, Rogalsky, Simmons, Feinstein, & Stein, 2003; Kuhnen & Knutson, 2005; Knoch, Gianotti, Pascual-Leone, Treyer, Regard, Hohmann, & Brugger, 2006; Tobler, Fiorillo, & Schultz, 2007; Tom, Fox, Trepel, & Poldrack, 2007). Taken together, these functional neuroimaging studies indicate that frontolimbic circuits involving ventromedial prefrontal cortex (vmPFC), amygdala and insula, and structures linked to reward and conflict processing, i.e. the ventral striatum and anterior and posterior cingulate cortex, are implicated in risk-taking behavior (Li, Chao, & Lee, 2008). In electrophysiological studies, the feedback-related negativity (FRN) reflects the activity of medial frontal/anterior cingulate activity (Miltner, Braun, & Coles, 1997) and its amplitude codes the ongoing evaluation of events and prediction of future events in terms of favourable or unfavourable outcomes (Holroyd & Coles, 2002). The idea that FRN amplitude reflects a binary evaluation in terms of gains and losses (Miltner et al., 1997; Gehring & Willoughby, 2002; Holroyd & Coles, 2002; Nieuwenhuis, Aston-Jones, & Cohen, 2004; Yeung & Sanfey, 2004; Hajcak, Moser, Holroyd, & Simons, 2006) and its link to outcome expectation are well supported (Hajcak, Holroyd, Moser, & Simons 2005; Cohen, Elger, & Ranganath, 2007). FRN amplitude has also been found to correlate with risk-taking behaviour (Gehring & Willoughby, 2002; Yeung & Sanfey, 2004).

The P300 has also been reported to reflect decision making (Yeung & Sanfey, 2004; Ma, Wang, Shu & Dai, 2008). According to Nieuwenhuis and colleagues (2005), the P300 is linked to the noradrenergic system and locus coeruleus activity, and its amplitude is thought to reflect the outcome of stimulus evaluation and decision making. The P300 amplitude varies with variables such as event probability, motivational significance of stimuli and magnitude of feedback outcome,

regardless of whether the outcome is a gain or a loss (Yeung & Sanfey, 2004). In economic decision-making, FRN and P300 seem to reflect different aspects of reward processing: Valence and magnitude, respectively (Yeung & Sanfey, 2004). A third component potentially linked to risky decision making is the N500 (Yang, Li, Zhang, Qiu, & Zhang, 2007; Polezzi, Lotto, Daum, Sartori, & Rumiati, 2008). The N500 is generally larger for unpredictable outcomes (Polezzi et al., 2008) and it is thought to be generated by posterior cingulate cortex and visual association cortex (Carretié, Hinojosa, & Mercado, 2006).

As outlined above, risk-taking behavior is modulated by context. Kahneman and Tversky (1979) have shown that for positive EU, people tend to be risk-averse while the majority of people are risk-seeker for negative EU. Studies of neurocognitive processes of decision making have focused on choices between options with zero EU (Gehring & Willoughby, 2002; Hajcak et al., 2006), or positive EU (Polezzi et al., 2008) or different EU (McCoy & Platt, 2005; Yeung & Sanfey, 2004), but, to our knowledge, there are no studies which directly compare decision-making across the different EU contexts. The first aim of the current study was to assess changes in risk-taking across different EU contexts and its neuronal correlates. Given the considerable interindividual variability in risk-taking behavior (Gehring & Willoughby, 2003; Yeung & Sanfey, 2004) and differences in subjective perception of options depending on attitudes to risk (Lee, 2005), individual differences in risk-taking (i.e. risk prone vs. risk averse) were also considered. To study the electrophysiological correlates of risk-taking behavior, a gambling task was administered which involved two contexts with different EU (zero and positive), which should induce a change in risk tendency. The options within each context had the same EU, with behavioral differences therefore reflecting personal preferences. Participants were informed in advance that they would receive a remuneration proportional to the amount of money won in the gambling task, for both motivational purposes and for ecological validity. EEG was recorded during performance of the gambling task and analyses focused on the ERP components known to reflect cognitive processes linked to decision making (FRN, P300 and N500).

Materials and Method

Participants

Twenty-four undergraduate students from the University of Bochum (17 females and 7 males with age ranged 19 to 41 years, mean= 23.5) participated in this study. All subjects were healthy and had normal or corrected-to-normal vision. They were recruited by advertisements, signed an informed consent form and were debriefed at the end of the experiment, after they received the money they earned during the gambling task.

Task

We employed a gambling task, which involved choices between *Risky* and *Safer* options. To ensure ecological validity of the task, subjects were informed that they would receive a remuneration corresponding to what they won in the game. They were instructed that on each trial they had to choose between two options and they should try to earn as much money as possible. Subjects did not know *a priori* either the outcomes or their probabilities, but they had to make the relevant inferences during the task. On each trial, two coloured circles, one blue and one yellow, appeared on a black computer screen. The circles were located to the left and the right of the centre of the screen; positions changed across trials in random order and were counterbalanced within the task. Blue represented the *Risky* option and yellow the *Safer* option in half of the subjects, for the other half the opposite pattern applied. Participants were instructed to press a left-sided (“A”) or a right-sided (“L”) key, depending upon the option they chose for this particular trial. Both options had zero EU but led to different outcomes and, in accordance with the task employed by Gehring and Willoughby (2003), the option with the larger outcomes is termed *Risky* and the other option is termed *Safer*. The *Safer* option yielded a gain of 5 cents or a loss of 5 cents while the *Risky* option

yielded a larger gain of 25 cents or a larger loss of 25 cents. The probability of each outcome was 50 %. This part of the task comprised 120 trials and it is referred to as “*Zero Utility*” condition.

In a second part, termed “*Positive Utility*” condition, both options had a positive EU of 5 cents but they led to different outcomes: The *Safer* option yielded a gain of 10 cents or a loss of 5 cents while the *Risky* option yielded a larger gain of 25 cents or a larger loss of 20 cents. The probability of each outcome was 50%, and there were 120 trials. Half of the subjects performed the “*Zero Utility*” condition first, followed by the “*Positive Utility*” condition, the remainder performed the tasks in the reverse order.

Ideally, a full experimental design which would also include a “*Negative Utility*” condition would be desirable. This condition might, however, require subjects to pay money at the end of the experiment and is thus not feasible for ethical reasons. Therefore, while the zero and Positive Utility are real conditions, the Negative Utility would be only a dummy condition.

On individual trials, the corresponding outcome was displayed in the centre of the screen after the choice had been made. A single trial entailed the following sequence: Initially, a fixation cross appeared in the screen centre for 1000 ms, then the two circles (yellow and blue) appeared until the participant had made his/her choice (with a time limit of 2000 ms). Then the screen went blank for 500 ms; followed by presentation of the outcome in the screen centre for 2000 ms (see Fig. 1). After an interval of 3000 ms, the next trial started. Presentation software was used for stimuli presentation, markers and response recording.

The instructions were presented in written form, and subjects completed an informed consent form. EEG electrodes were then applied, using an electrocap (see below). The experimental session lasted about 45 minutes.

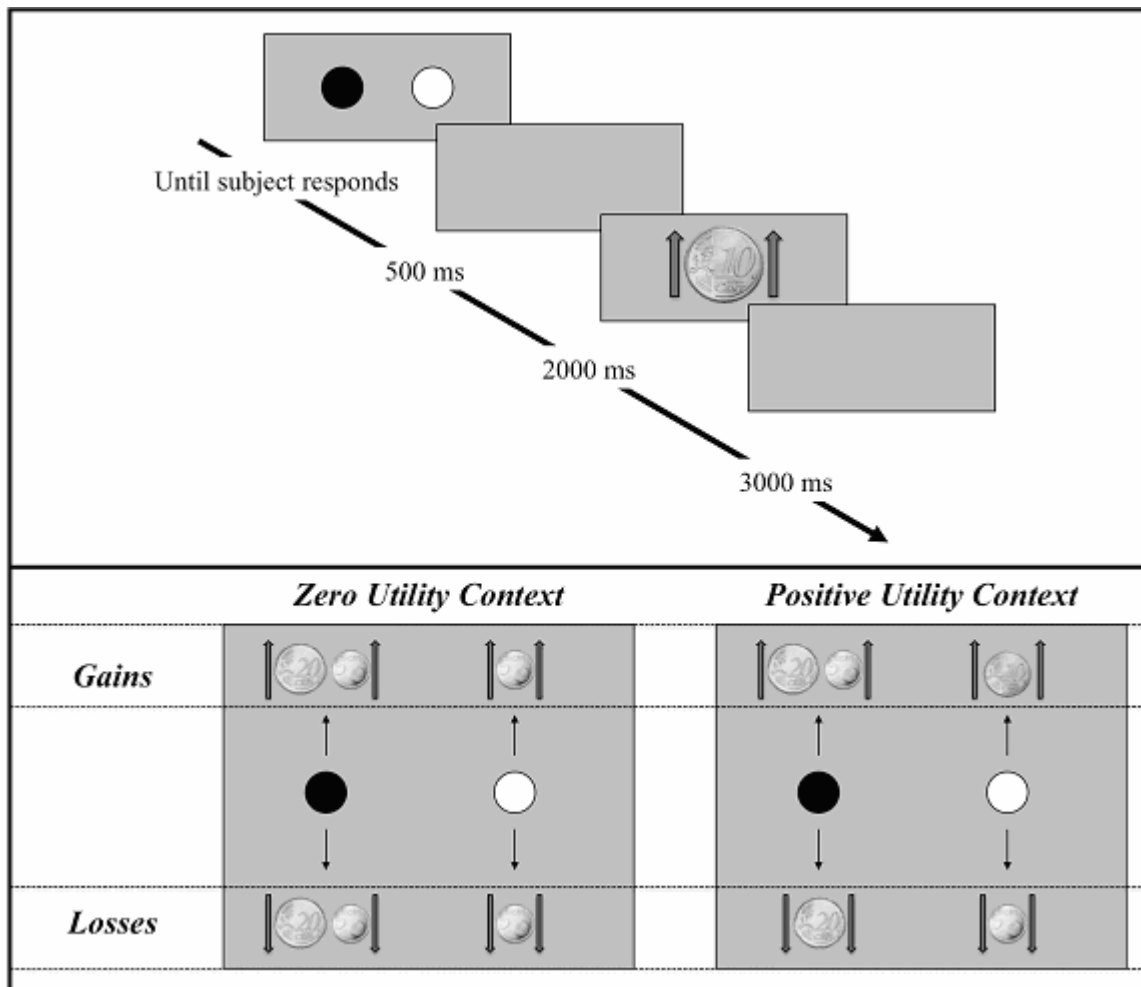


Figure 4. Participants choose between one of the two circles yielding different outcomes. After the decision, the outcome was displayed. In the lower part, the two contexts and their relative outcomes are shown.

ERP recording

Scalp voltages were recorded using 32 Ag/AgCl electrodes in a cap according to the 10-20 international system: F7, F3, Fz, F4, F8, FT7, FC3, FCz, FC4, FT8, T7, C3, Cz, C4, T8, TP7, CP3, CPz, CP4, TP8, P7, P3, Pz, P4, P8, PO7, PO3, POz, PO4, PO8. Mastoids served as reference and electrode impedance was kept under 10 KΩ for all recordings. Vertical and horizontal ocular movements were also recorded. The EEG was recorded continuously, digitized at a sampling rate of 500 Hz, and stored on hard disk for off-line analyses. Electrical signals were amplified with Synamps amplifier. The signal was off-line filtered using a 0.5-30 Hz *band pass filter*. Ocular

movements' artifacts were corrected using the algorithm provided by Brain Vision Analyzer 2004. The EEG was segmented for 1000 ms in *epochs* starting 100 ms before presentation of the offer. The epochs were aligned to the 100 ms baseline before onset of the offer stimuli. Trials affected by ocular or movements artifacts were excluded from averaging.

Source analysis

ERP amplitudes from all 32 electrodes entered source analysis with LORETA (Low Resolution Brain electromagnetic tomography) (Pascual-Marqui, Michel, & Lehman, 1994; Pascual-Marqui, 1999). LORETA is an inverse solution technique that estimates the distribution of the electrical neuronal activity in three-dimensional space. The estimation is based on information acquired from the electrodes positioned over the entire scalp (Congedo, Lubar, & Joffe, 2004). This method assumes that neighboring neurons are simultaneously and synchronously activated, and it computes the current density at each gray matter voxel of a reference brain as a linear, weighted sum of the scalp electrical potentials. It provides an inverse problem solution by choosing the smoothest of all possible current density configurations (Pascual-Marqui et al., 1994; Pascual-Marqui, 1999). LORETA-images represent brain activity through 2394 voxels, which include gray matter as well as hippocampus, amygdala, and cingulate gyrus (Congedo et al., 2004).

For source analysis, we followed the procedure suggested by Bellebaum and Daum (2006). For all subjects, LORETA-images were generated for contrast of interest relating to risk attitude (see below results section). The images were converted (http://www.ihb.spb.ru/~pet_lab/L2S/L2Smain.htm) and further analyzed using SPM99 (<http://www.fil.ion.ucl.ac.uk/spm/>). A PET/SPECT design with multi-subjects, conditions and covariates was performed with the following parameters: Global Normalization with a proportional scaling to a mean of 50, no absolute threshold masking and global calculation of mean voxel value (within per image). The level of significance was set to $p=.001$, uncorrected for multiple

comparison. The coordinates of the foci of significant differences between conditions were transformed into Talaraich coordinates (Talairach & Tournoux, 1988) with the algorithm suggested by Brett (<http://www.mrc-cbu.cam.ac.uk/Imaging/Common/mnispac.html>). The Talaraich Daemon was then used to identify the brain structures involved (Lancaster, Woldorff, Parsons, Liotti, Freitas, Rainey, Kochunov, Nickerson, Mikiten, & Fox, 2000).

Results

Behavioural Results

In order to assess whether there was a shift in risk-taking between the “Zero Utility” and the “Positive Utility” condition, the percentage of risky choices was determined for the two conditions. Two groups of subjects were identified on the basis of the pattern of behavioral change across the two conditions: *Zero-Oriented* and *Positive-Oriented*. *Zero-Oriented* participants (N=11) made more risky choices in the Zero Utility condition and fewer in the Positive Utility condition. *Positive-oriented* participants (N=13) showed the opposite pattern (see Figure 2, c and f). Repeated measures ANOVA with Group (*Zero-Oriented* vs. *Positive-Oriented*), Order (*Zero-Positive* vs. *Positive-Zero*) and Utility (*Zero* vs. *Positive*) did not yield significant differences in percent risky choices between the two groups ($F(1,20)=.01, p=.95 \eta^2_{\text{partial}}=.00$) and no significant order effects ($F(1,20)=.01, p=.93 \eta^2_{\text{partial}}=.00$) or utility effects of ($F(1,20)=.31, p=.58 \eta^2_{\text{partial}}=.02$). Analysis yielded however a significant Group x Utility interaction ($F(1,20)=22.39, p<.001 \eta^2_{\text{partial}}=.53$), indicating higher rate of risky choice of the *Positive-Oriented* group in the Positive Utility condition ($t(10)=-5.10, p<.001$) and of the *Zero-Oriented* group in the Zero Utility condition ($t(12)=4.17, p<.01$), confirming the subdivision of the two groups based on their behavioral results.

In addition, the risky choices of the *Positive-Oriented* group did not differ from random distribution in the Zero Utility condition (50.3%, $t(12)=.09, p=.93$), while they were clearly risk prone in the Positive Utility condition (62.2%, $t(12)= 4.78, p<.001$). By contrast, the *Zero-Oriented* group was risk-seeking in the Zero Utility condition (61.9%, $t(10)= 3.17, p<.05$) and showed

random choice behaviour in the Positive Utility condition (50.1%, $t(10) = .04$, $p = .970$) (see Fig. 2). No other significant effects emerged ($p > .1$).

Event Related Potentials

As outlined above, processing of outcomes of decisions are mainly reflected in the FRN, P300 and N500 (Gehring & Willoughby, 2002; Yeung & Sanfey, 2004; Hajcak et al., 2006; Yang et al., 2007). All following analyses refer to brain activity following outcomes presentation. FRN amplitude was assessed as the mean amplitude in the 200-300 ms time window, P300 amplitude as the mean amplitude within the 300-500 ms time window and N500 amplitude as the mean amplitude within 500-700 ms time window, relative to the baseline preceding presentation of the outcomes.

ANOVA were performed with Group (*Zero-Oriented* vs. *Positive-Oriented*), Utility (*Zero* vs. *Positive*), Valence (*Gains* vs. *Losses*) and Magnitude (*Small* vs. *Large*) as factors and the respective ERP amplitudes as dependent measures.

FRN

Given that the maximum FRN amplitudes are observed at frontal sites (e.g. Gehring & Willoughby, 2002; Hajcak et al., 2006; Holroyd et al., 2002), data from electrode sites F3, Fz and F4 were pooled.

The main Utility effect was not significant ($F(1,22) = .10$, $p = .75$, $\eta^2_{\text{partial}} = .01$). FRN amplitude was significantly modulated by Valence ($F(1,22) = 7.51$, $p < .05$, $\eta^2_{\text{partial}} = .26$), with large FRN for losses than for gains. Magnitude effects did not reach significance ($F(1,22) = 3.52$, $p = .08$, $\eta^2_{\text{partial}} = .14$). The significant interaction of Group x Utility x Magnitude interaction ($F(1,22) = 8.55$, $p < .01$, $\eta^2_{\text{partial}} = .28$) indicated that Magnitude affected the behaviour of the Zero-Oriented subjects in the Positive Utility condition ($t(10) = 2.01$, $p = .07$) but not in the Zero Utility condition ($t(10) = .02$, $p = .98$). The Positive-Oriented group, on the other hand, showed a tendency towards behavioral differences depending upon Magnitude in the Zero Utility condition ($t(12) = 2.05$, $p = .06$), but not in

the Positive Utility condition ($t(12)=.20$, $p=.84$). The highest order interaction (Group \times Utility \times Valence \times Magnitude) was also significant ($F(1,22)=11.63$, $p<.01$ $\eta^2_{\text{partial}}=.35$), showing that the behaviour of the zero-oriented group is sensitive to magnitude of gains in the Positive Utility context ($t(10)=3.20$, $p<.01$) but not in the Zero Utility context ($t(10)=-1.04$, $p=.33$). In the positive-oriented group the opposite pattern emerged ($t(12)= -.63$, $p=.54$; $t(12)=2.70$, $p<.05$). No effects reached or approached significance ($p>.1$).

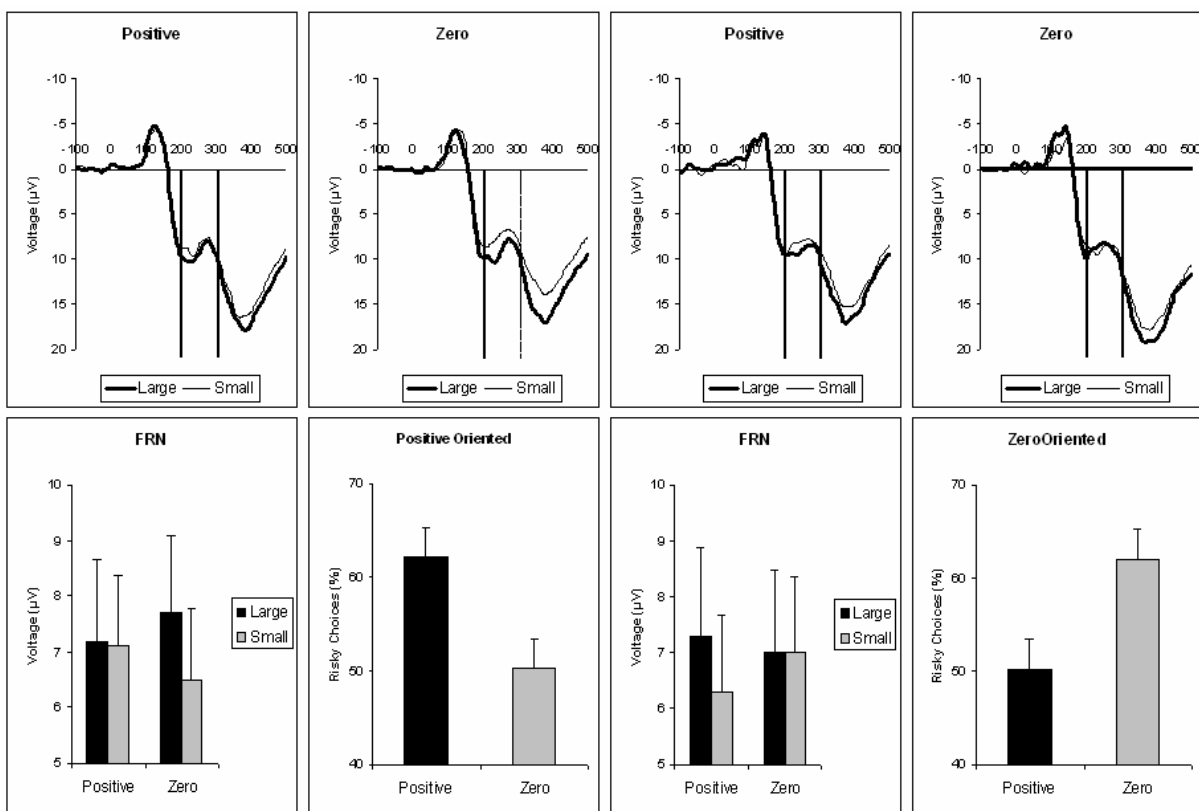


Figure 5. Group x Utility x Magnitude interaction.

P300

The P300 is observed at parietal and frontal sites (Nieuwenhuis et al., 2005); findings are therefore reported for pooled frontal (F3, Fz and F4) and parietal electrodes (CP3, CPz and CP4).

Frontal Sites. The main Utility effect was not significant ($F(1,22)=.57$, $p=.46$ $\eta^2_{\text{partial}}=.02$) but yielded a Group x Utility interaction ($F(1,22)=14.09$, $p<.01$ $\eta^2_{\text{partial}}=.39$) reflected a larger P300

amplitude in the *Zero-Oriented* group P300 in the Zero compared to the Positive Utility conditions ($t(10)=-2.81$, $p<.05$), whereas the *Positive-Oriented* group showed the opposite pattern ($t(12)=2.41$, $p<.05$) (see Fig.2). The main Valence effect was significant ($F(1,22)=35.59$, $p<.001$ $\eta^2_{\text{partial}}=.62$), reflecting a larger P300 amplitude for gains compared to losses. The significant Group x Valence interaction ($F(1,22)=5.00$, $p<.05$ $\eta^2_{\text{partial}}=.19$) mirrored a larger P300 amplitude difference between gains and losses in the Zero-Oriented compared to the Positive-oriented group. The P300 amplitude was affected by Magnitude ($F(1,22)=14.34$, $p<.01$ $\eta^2_{\text{partial}}=.40$), with higher amplitudes for large compared to the smaller magnitude. The interaction of Utility with Valence, Magnitude and Group approached significance ($F(1,22)=3.77$, $p=.07$ $\eta^2_{\text{partial}}=.15$). No other effects reached or approached significance ($p>.1$).

Parietal Sites. The main Utility effect was not significant ($F(1,22)=.30$, $p=.59$ $\eta^2_{\text{partial}}=.01$). The significant Group x Utility interaction ($F(1,22)=10.75$, $p<.01$ $\eta^2_{\text{partial}}=.33$), reflected larger P300 amplitudes in the Zero Utility compared to the Positive Utility condition in the Zero-Oriented Group ($t(10)=-1.98$, $p=.08$), while the Positive-Oriented group showed the opposite pattern ($t(12)=3.20$, $p<.01$). The main Valence effect was significant ($F(1,22)=29.05$, $p<.001$ $\eta^2_{\text{partial}}=.57$), with higher amplitudes for gains compared to losses. The Group x Valence interaction approached significance ($F(1,22)=3.34$, $p=.08$ $\eta^2_{\text{partial}}=.14$). P300 amplitude was significantly affected by Magnitude ($F(1,22)=8.03$, $p<.05$ $\eta^2_{\text{partial}}=.27$), with higher P300 amplitudes for larger than for smaller magnitude. The highest order interaction (Group x Utility x Valence x Magnitude) approached significance ($F(1,22)=3.46$, $p=.08$ $\eta^2_{\text{partial}}=.14$). No other factor nor interaction reached or approached significance ($p>.1$).

N500

In accordance with Yang et al. (2007), N500 was analyzed over frontal sites (pooled across F3, Fz and F4).

The main Utility effect did not reach significance ($F(1,22)=3.27, p=.08 \eta^2_{\text{partial}}=.13$). The significant Group x Utility interaction ($F(1,22)=11.22, p<.01 \eta^2_{\text{partial}}=.34$), showed that while N500 amplitudes were higher for Positive Utility rather than for Zero Utility in the Zero-Oriented group ($t(10)=-2.94, p<.05$), there were no significant differences in the *Positive-Oriented* ($t(12)=1.42, p=.18$). N500 amplitude was modulated by Valence ($F(1,22)=15.69, p<.01 \eta^2_{\text{partial}}=.42$), with higher amplitudes for losses than for gains. The main Magnitude effect was significant ($F(1,22)=14.56, p<.01 \eta^2_{\text{partial}}=.40$). The Group x Utility x Valence interaction ($F(1,22)=4.01 p=.06 \eta^2_{\text{partial}}=.15$) and the Group x Utility x Magnitude interaction ($F(1,22)=3.59 p=.08 \eta^2_{\text{partial}}=.14$) approached significance, as did the main Group effect ($F(1,22)=4.31, p=.05 \eta^2_{\text{partial}}=.16$). No other effects reached or approached significance ($p>.1$).

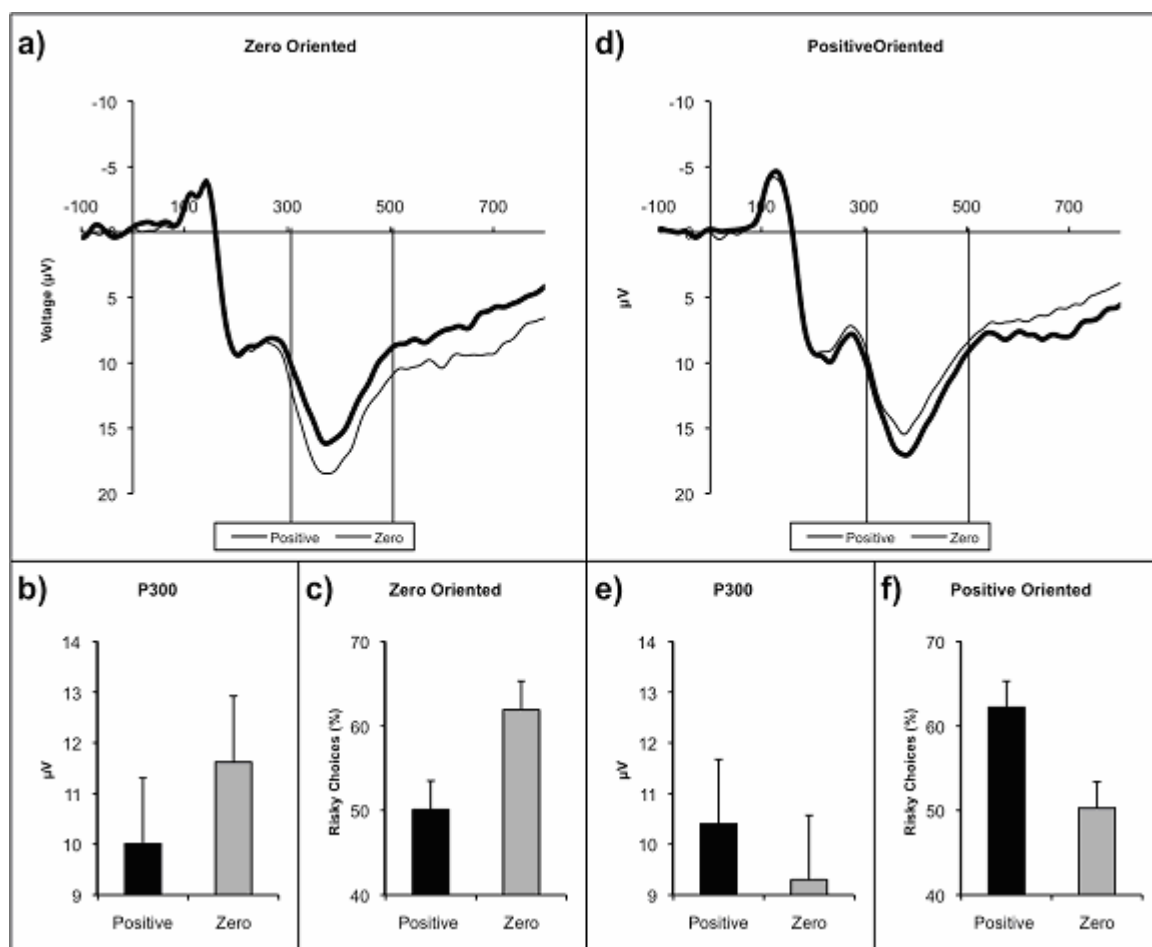


Figure 6. Zero-Oriented group was more likely to risk in the Zero Utility condition (c) in association with larger P300 (b). By contrast, Positive-Oriented group showed the opposite pattern (f) mirrored by a reverse pattern in P300 (e).

Source analysis

In order to investigate the brain correlates of the ERP effects, source analyses were performed for each main effect and for each interaction, which reached significance. The coordinates reported follow the Montreal Neurological Institute system.

FRN

For the FRN, voxels survived the significance level only for the Valence factor (Gains vs. Losses contrast), the critical area being the anterior cingulate cortex (see Figure 3, section a) ($F(1,161)=16.77, p<.001, [-3\ 31\ -5]$). This result is consistent with the frequently reported FRN sources (Gehring & Willoughby, 2002). No other contrasts yielded significant activation differences.

P300

No voxels survived the level of significance.

N500

For the N500, voxels survived the significance level only for the Utility effect (Positive vs. Zero contrast), the critical area being the posterior cingulate gyrus (see figure 3, section b) ($F(1,161)=14.41, p<.001, [-3\ -18\ 36]$), which showed higher activity for the Zero than for the Positive Utility condition ($t(161)=3.80, p<.001$). In addition, within the Positive-Oriented group, the comparison between Positive and Zero Utility conditions revealed differential activation patterns of the posterior cingulate gyrus ($F(1,84)=14.89, p<.001, [-3\ -11\ 29]$), with higher activation for the Zero compared to the Positive Utility condition ($t(84)=3.86, p<.001$). No other contrasts yielded significant activation differences.

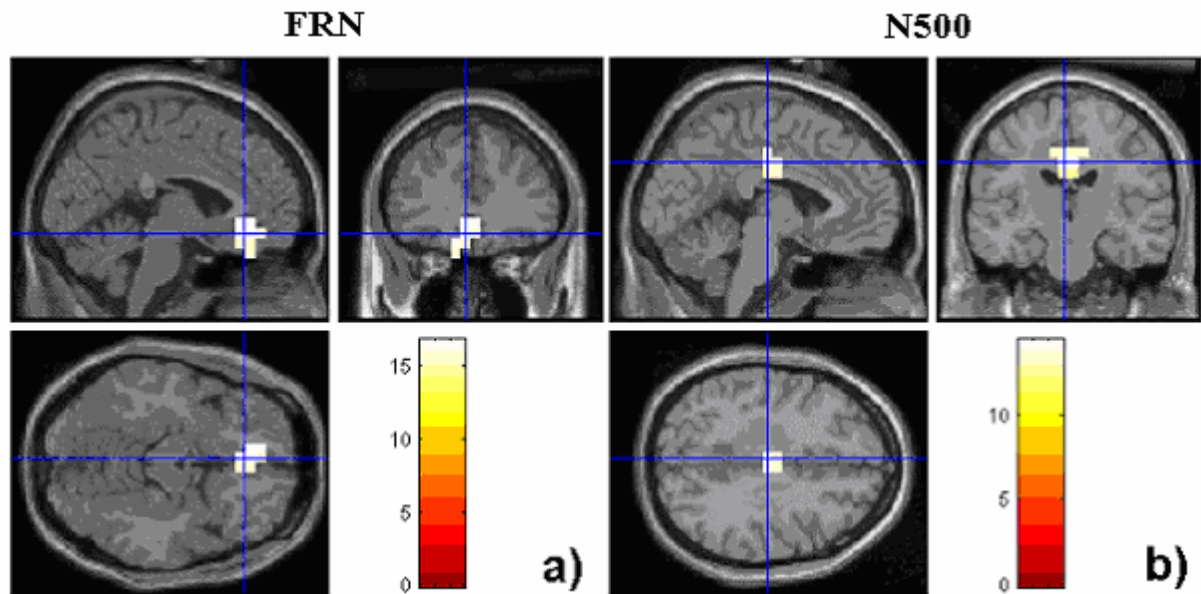


Figure 7. FRN is generated by Anterior Cingulate Cortex (a), while N500 is generated by Posterior Cingulate Cortex (b).

Discussion

Neural mechanisms underlying risky decision-making have been the subject of rising research interest in recent years. Risk-taking behaviour was found to be modulated by the decision context as well as by interindividual differences. Previous studies have investigated risky decision making in zero EU (Gehring & Willoughby, 2002) or positive EU contexts (Polezzi et al., 2008), but to our knowledge this study is the first which directly compares decision making across different contexts and associated changes in the neurocognitive correlates of decision making. A further aim addressed interindividual differences, by subdividing participants depending upon their decision strategies in our gambling task performed in two contexts: Zero Utility and Positive Utility.

Consistent with previous reports (Kahneman & Tversky, 1979), subjects show a shift in risky choices with change of context, regardless of the order in which the different contexts were introduced. Analysis of individual decision patterns yielded two different subgroups: Subjects who risked more in the Positive Utility condition (termed *Positive-Oriented* group) and subjects who showed more risk-taking behaviour in the zero-utility condition (termed *Zero-Oriented* group).

Thus both groups are risk-seekers in one context and show random choices in the other. As outlined in the introduction, when two options have the same EU, rational behaviour would imply random choices. Risk-seeking behaviour represents an interesting deviation from rationality, as outlined by Kuhnen and Knutson (2005), and we will address below the electrophysiological correlates of this behavioural tendency.

As already specified above, we investigated brain activity following outcomes onset, therefore the three potentials in question reflected different stages of outcomes processing. The FRN amplitudes were modulated by the well-known binary distinction between gains and losses (Gehring & Willoughby, 2002; Hajcak et al., 2006), and by early differences in processing of outcomes between the two groups. FRN amplitudes in the Positive-Oriented group were modulated by outcome magnitude in the zero EU condition, where risky choices did not exceed the chance level, whereas there were no magnitude effects in the positive EU condition, where the subjects adopted a risk seeking strategy. By contrast, FRN amplitudes of Zero-Oriented subjects were affected by outcome magnitude in the positive EU condition, where their decision-making behaviour followed a random pattern, but not in the Zero condition, where they showed risk-prone behaviour. These findings are consistent with the idea that risk-taking behaviour partly relies on a very early evaluation (within 300 ms) of the outcomes (Gehring & Willoughby, 2002; Yeung & Sanfey, 2004). In addition, the evaluation of response options also is not only related to payoffs, but changes in risk-taking are also affected by interindividual differences. As a note of caution, it has to be pointed out that, even in case of significant interactions, the comparisons only yielded trends towards significance. Source analysis relating to FRN yielded the expected findings, with FRN being linked to anterior cingulate cortex activity.

P300 amplitudes were generally higher for gains compared to losses, which is in line with previous findings (Yeung and Sanfey, 2004). P300 amplitudes also reflected the distinction between large and small outcomes, regardless their valence. Taken together, these data further support the idea of the independent coding of outcome magnitude and valence in FRN and P300, respectively,

as previously reported by Yeung and Sanfey (2004). Interestingly, P300 amplitude also mirrored changes in risk-taking behaviour across contexts in both subgroups of subjects, the P300 was larger in the context in which participants were more likely to show risk-prone decision behaviour. The Zero-Oriented group was more risk-prone in the Zero Utility condition in which P300 amplitudes were increased, while reduced P300 amplitudes were observed in the Positive Utility condition in which they showed random choice behaviour. The Positive-Oriented group, on the other hand, was risk-prone in the Positive Utility condition in which they also showed larger P300 amplitude, while reduced P300 amplitudes and low risk seeking behaviour characterised the Zero Utility condition. A possible interpretation of these effects is that P300 amplitudes reflect high motivation. First, P300 amplitudes are higher for target stimuli (i.e. gains), which generally have a higher motivational significance than non-target stimuli (Duncan-Johnson & Donchin, 1977). Second, P300 amplitudes are higher for larger compared to smaller outcomes, as previously reported by Yeung and Sanfey (2004), who also suggested that P300 amplitude varies with outcomes magnitude because of the increased motivational significance of larger reward and penalties (Yeung & Sanfey, 2004). Third, emotionally significant stimuli are associated with higher P300 amplitudes than emotionally neutral stimuli (Johnston, Miller, & Burleson, 1986; Keil, Bradley, Hauk, Rockstroh, Elbert & Lang, 2002). The current findings are consistent with the idea that subjects tend to risk more and show increased P300 amplitudes if their motivation is enhanced. By contrast, with lower motivational status, their decisions were random and the P300 was reduced. This pattern is consistent with the hypothesis that the P300 reflects the activity of a neuromodulatory and motivational system as suggested by Nieuwenhuis and colleagues (2005).

The third component related to outcome processing is the N500, which has been linked to the subjective pleasantness of stimuli (Carretié et al., 2006; De Pascalis, Strelau, & Zawadzki, 1999; Mack, Birbaumer, Kaps, Badke, & Kaiser, 2005) and to decision-making processes (Polezzi et al., 2008). N500 is thought to be generated by posterior cingulate cortex and visual association cortex (Carretié et al., 2006). Consistently with previously reported data, the N500 amplitude is higher for

losses than for gains. In addition, in the Zero-Oriented group, the N500 was higher for the Positive Utility context, in which they risked less compared to the Zero Utility context in which they showed more risk-seeking behaviour. Interestingly, source analyses yielded an involvement of posterior cingulate cortex in the generation of the N500. Activity in this region was found to correlate with risky decisions in monkeys (McCoy and Platt, 2005). In this study, the utility of each target was estimated on a trial-by-trial basis based on the sum of reward size and risk and utility was more reliably reflected in the posterior cingulate cortex activity (McCoy and Platt, 2005). This area might thus represent utility rather than risk itself, as outlined by Lee (2005). Our data findings would support this interpretation, since in the Zero-Oriented group, the posterior cingulate cortex showed higher activation during the Zero Utility context compared to the Positive Utility context. The Zero Utility context is, however, also the condition in which these subjects are more likely to make risky decision, therefore the relative contributions of risk and utility cannot be separated. A recent fMRI study has linked posterior cingulate cortex activation to changes in risk-taking (Li et al., 2008), and the current data thus provide converging evidence from electrophysiology.

Risky behaviour has also been related to dorsolateral prefrontal cortex (DLPFC) (Knoch and colleagues, 2006). Kuhnen and Knutson (2005) have pointed out that the adoption of risk, in preference to rational behavior, is linked to the involvement of the nucleus accumbens which anticipates possible gains, while, risk avoidance is correlated with insula activation and the anticipation of possible losses. ERP studies, on the other hand, have consistently related the ACC to risky behaviour (Gehring & Willoughby, 2002; Yeung & Sanfey, 2004), and the functional implications of the involvement of the posterior cingulate cortex, which emerged in the current study needs to be clarified by, further studies.

In conclusion, the current study highlights the idea that economic decision-making is not exclusively determined by payoffs but strongly affected by contextual cues. Economic decisions are known to depend upon reward contingences (McClure, Laibson, Loewenstein, Cohen, 2004) and social context (Sanfey, Rilling, Aronson, Nystrom, Cohen., 2003; Moretti, Dragone, & di

Pellegrino, *in press*; Polezzi, Daum, Rubaltelli, Lotto, Civai, Sartori, Rumiati, 2008). Cognitive neuroscience can offer important insights into the neurocognitive mechanisms, which may help to reduce the gap between formal theories and real choice behavior.

Experiment 3

Mentalizing in Economic Decision Making

The classical theory of economic decision-making assumes that people should behave rationally, maximizing gains and minimizing losses (von Neumann & Morgenstein, 1944). However, in the Ultimatum Game, as well as in other economic contexts, this assumption is systematically violated (Bolton & Zwick, 1995; Camerer, Loewenstein, & Prelec, 2005). In this game, two players have to split a sum of money. One person acts as proposer, who suggests how the money should be divided between the proposer and the responder. The second person - playing as the responder - has to decide whether to accept or reject the offer. If the responder accepts the offer, both players gain the amount agreed upon. If the responder rejects the offer, neither participant receives anything.

A perfectly rational proposer should make the smallest possible offer to maximize his/her gain, while a perfectly rational responder should accept any offer since – in economic terms - even a small amount is better than gaining nothing. In reality, however, players systematically do not conform to these predictions: Proposers make equal/fair offers (such as 50:50 or 60:40) because they are more likely to be accepted, and responders reject unequal/unfair offers (such as 90:10 or 80:20) to punish the proposer and to motivate him/her to make fairer offers (Bolton & Zwick, 1995).

Recently, research interest has focused on the neural correlates of the underlying decision making processes (Camerer et al., 2005; Lee, 2005; Lee, 2006; Sanfey et al., 2003; Sanfey et al., 2006). In the functional neuroimaging study by Sanfey and colleagues (2003) which focused on the brain processes in responders in the Ultimatum game, the insula, the dorso-lateral prefrontal cortex (DLPFC) and the anterior cingulate cortex (ACC) were activated during the decision making process. Insula cortex activity is known to be related to autonomic responses in decision making (Critchely et al., 2000) and, more interestingly, it seems to be involved in coding negative

emotional state, such as negative mood (Mayberg et al., 1999) and pain (Schrekenberger et al., 2005). Insula activation was consistently higher for unfair compared to fair offers, suggesting negative affect and presumably affect-driven rejection of unfair offers (Sanfey et al., 2003). This interpretation is supported by findings of increased skin conductance responses associated with the rejection of unfair offers (van't Wout et al., 2006).

The second area involved in decision making in the Ultimatum Game, the DLPFC, is known to be involved in goal maintenance (Miller & Cohen, 2001) and executive functions (Wagner et al., 2001). According to Sanfey et al. (2003), DLPFC activity reflects inhibition of affect-driven rejections linked to the insula which leads to a more rational acceptance of unfair offers and an increase in gains. Two recent TMS studies shed further light on this interpretation (Knoch et al., 2006; van't Wout et al., 2005). Contrary to prediction, disruption of DLPFC activity did not lead to an increase, but to a decrease of the rejection rates of unfair offers, without affecting the subjective ratings of fairness of the offers. In light of these findings, Knoch et al. (2006) suggested that the DLPFC inhibits selfish behaviour in favour of social communication in which rejection serves as a feedback signal to the other player. Consistent with this idea, patients with DLPFC damage tend to show inappropriate social behaviour in spite of preserved knowledge about adequate behaviour (Damasio, 1995).

The anterior cingulate cortex (ACC) is involved in conflict monitoring (Botvinick et al., 2004; Bush et al., 2000; Suchan et al., 2003), in monitoring action outcomes and guiding decision making (Botvinick, 2007) and in self-regulation (Posner et al., 2007). Within the context of the Ultimatum Game, ACC activity has been interpreted as reflecting the conflict associated with the rejection of unfair offers, i.e. the rejection of an economically advantageous situation because of a subjective impression of unfairness (Sanfey et al., 2003). Koenigs et al. (2007) hypothesized that the ventromedial prefrontal cortex (VMPFC) might also be involved in the critical decision making process. Patients with VMPFC lesions showed low acceptance rate of unfair offers, thereby exhibiting "hyper-irrational" behaviour. Since the VMPFC is, however, generally activated during

processing of monetary gains (O'Doherty et al., 2001), it is unclear whether the patients' behaviour is linked to changes in affect processing or to processing of the monetary offers in the game.

As outlined above, social interaction seems to play a relevant role in the type of economic decisions involved in the Ultimatum game. To further elucidate the underlying neurocognitive processes, we employed a modified version of the Ultimatum Game. While in the traditional task, only one offer is made by the proposer, the modified version entails a series of offers made by the same proposer. This modification allows the application of ERP methodology and because of its high temporal resolution, the on-line assessment of the neurocognitive mechanisms during decision making. In addition, in contrast to previous approaches (Knoch et al., 2006; Koenigs & Tranel, 2007; Sanfey et al., 2003), the mid-value offer was not analysed as part of unfair offers, but as a separate condition, since it presumably entails a higher degree of uncertainty with potentially distinct processing correlates. On the behavioural level, we expected the usual pattern of high acceptance rates for fair and high rejection rates for unfair offers was expected and an acceptance rate of around 50 % for mid-value offers, together with longer decision latencies. The neuronal correlates of decision making for mid-value offers should reflect decision uncertainty to a larger degree than the two other types of offers.

Materials and Method

Participants

Thirteen undergraduate students from the University of Padova (age ranged 19 to 25 years) participated in this study. All subjects were healthy and had normal or corrected-to-normal vision. They signed an informed consent form and were debriefed at the end of the experiment.

Task

A modified version of the Ultimatum Game was administered as follows. Subjects played as responders. They were told that they played with another participant, the proposer, who was located in a second laboratory. Unknown to them, they played against the computer, and the offers they received did not depend on their own decisions. Participants were told that on each trial, the proposer made an offer of how to split 10 € between them, and that they had to decide either to accept or to reject the offer. The offers appeared on a monitor. For example, if “2 €” appeared on the screen, acceptance would imply that the subject received 2 € while the proposer kept 8 €. Decisions were made by key presses (left key for rejection, right key for acceptance of the offers). There were 5 different offer conditions (1 €, 2 €, 3 €, 4 € and 5 €), and each offer was repeated 40 times, yielding a total of 200 trials. Analysis was based on the trials representing the very unfair offers (1 €), the mid-value offers (3 €) and the very fair offers (5 €).

A single trial (see Fig. 1) was made up by the following sequence: First, the words “You are offered” (in Italian) appeared sequentially on the centre of the screen against a blank background; each word was presented for 800 ms with ISIs of 100 ms. The offer was then shown in the centre of the screen until the participant responded. After an interval of 2000 ms the next trial started. E-prime software was used for stimulus presentation, markers, and response recording.

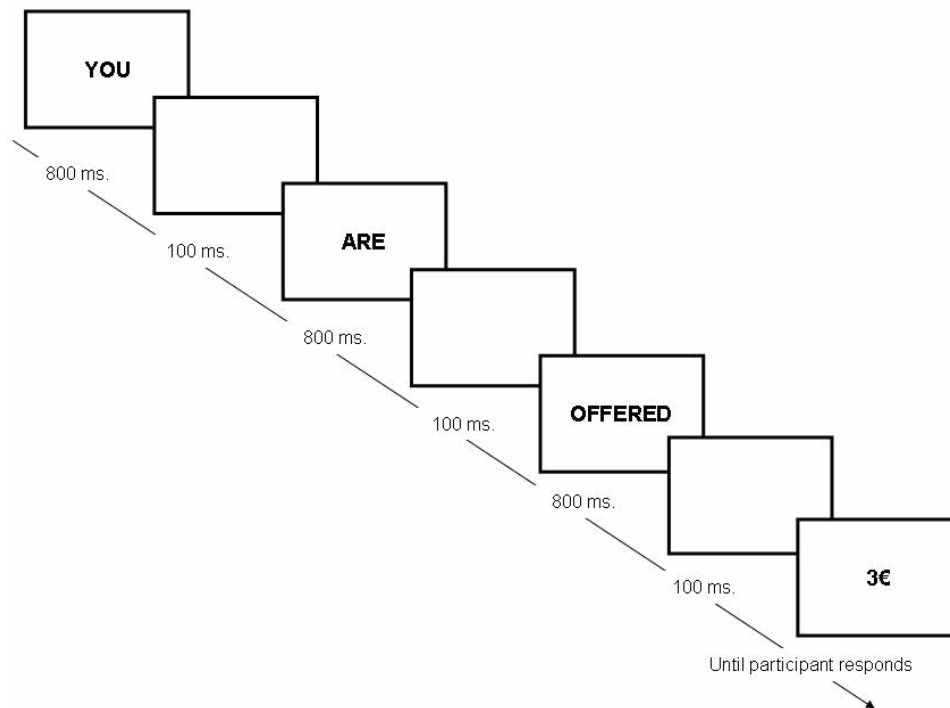


Figure 8. Sequence of stimuli on an individual trial. Each trial showed the offer made by the proposer.

Procedure

Participants performed the task in a quiet laboratory. The instructions were presented in written form. Subjects were informed that they would receive a remuneration for participation after having completed the experiment (standard amount provided by the Department of General Psychology (13 €)). EEG and EOG electrodes were then applied, using an electrocap (see below). The recording session lasted about 30 minutes.

ERPs recording

Scalp voltages were recorded using a 59-channel electrocap with Ag/AgCl electrodes. A frontal electrode (AFZ) was connected to the ground. Electrode impedance was kept under 10 K Ω for all recordings. Vertical and horizontal ocular movements were also recorded. The EEG was recorded continuously, digitized at a sampling rate of 500 Hz, and stored on hard disk for off-line analyses.

Electrical signals were amplified with Synamps amplifier (on-line filter: high pass=0.10 Hz, 24-dB/octave attenuation; low pass=1000 Hz, 24-dB/octave attenuation; 50 Hz notch filter). The signal was off-line filtered using a 30 Hz *low pass filter*, 24 dB/octave attenuation. Ocular movements' artifacts were corrected using the algorithm provided by Neuroscan 4.3 software. The EEG was segmented for 1000 ms in *epochs* starting 200 ms before presentation of the offer. The epochs were aligned to the 200 ms baseline before onset of the offer stimuli. Approximately 5 % of the trials were excluded from averaging because of ocular and movements artefacts. The average voltage across all electrodes served as reference.

Source analysis

ERPs amplitudes from all 59 electrodes entered source analysis with LORETA (Low Resolution Brain electromagnetic tomography) (Pasqual-Marqui & Lehman, 1993; Pasqual-Marqui et al., 1994). LORETA is an inverse solution technique that estimates the distribution of the electrical neuronal activity in three-dimensional space. The estimation is based on information acquired from the electrodes positioned over the entire scalp (Congedo et al., 2004). This method assumes that neighboring neurons are simultaneously and synchronously activated, and it computes the current density at each gray matter voxel of a reference brain as a linear, weighted sum of the scalp electrical potentials. It provides an inverse problem solution by choosing the smoothest of all possible current density configurations (Pasqual-Marqui & Lehman, 1993; Pasqual-Marqui et al., 1994). LORETA-images represent brain activity through 2394 voxels which include gray matter as well as hippocampus, amygdala, and cingulate gyrus (Congedo et al., 2004).

For source analysis, we followed the procedure suggested by Bellebaum and Daum (2006). For all participants, LORETA-images were generated for each of the three types of offers (Unfair, Mid-value and Fair offers). The images were converted (http://www.ihb.spb.ru/~pet_lab/L2S/L2Smain.htm) and further analyzed using SPM99

(<http://www.fil.ion.ucl.ac.uk/spm/>). A PET/SPECT design with multi-subjects, conditions and covariates was performed with the following parameters: Global Normalization with a proportional scaling to a mean of 50, no absolute threshold masking and global calculation of mean voxel value (within per image). The level of significance was set to $p=.001$, uncorrected for multiple comparisons. The coordinates of the foci of significant differences between conditions were transformed into Talaraich coordinates (Talairach & Tournoux, 1988) with the algorithm suggested by Brett (<http://www.mrc-cbu.cam.ac.uk/Imaging/Common/mnispace.shtml>). The Talaraich Daemon was then used to identify the brain structures involved (Lancaster et al., 2000).

Results

Behavioural Results

ANOVAs were performed with Type of Offer (Unfair, Mid-value, Fair) as independent variable and Acceptance Rate and Reaction Times (RTs) as dependent measures. For each comparison, Bonferroni corrections were used.

Acceptance Rate

Acceptance rate (see Fig. 2) was significantly affected by Type of Offer ($F(2,24)=47.42$, $p<.001$ $\eta^2_{\text{partial}}=.80$), and, as expected, paired comparisons yielded higher acceptance rates for fair [97%] compared to unfair [8%] offers ($t(12)=-17.99$, $p<.001$). Mid-value offer acceptance rate [48%] was significantly different from both fair and unfair offers (Mid-value vs. Fair: $t(12)= -4.55$ $p<.01$; Mid-value vs. Unfair: $t(12)=-3.380$, $p<.01$), and did not differ from random choice ($t(12)=-.24$, $p=.82$).

Reaction Times

In accordance with the procedure suggested by Knutson et al. (2007), RTs were transformed using a logarithmic function. As illustrated in Figure 2, RTs differed significantly between Type of Offer

($F(2,24)=7,679$, $p<.01$ $\eta^2_{\text{partial}}=.39$). Decisions about mid-value offers [1073 ms] took longer compared to fair offers [889 ms] (Mid-value vs. fair: $t(12)=3.59$, $p<.05$); the difference between mid-value and unfair offers [947 ms] approached significance (Mid-value vs unfair: $t(12)=-2,63$, $p=.07$). RTs for fair and unfair offers did not differ significantly ($t(12)=1.60$, $p=.41$).

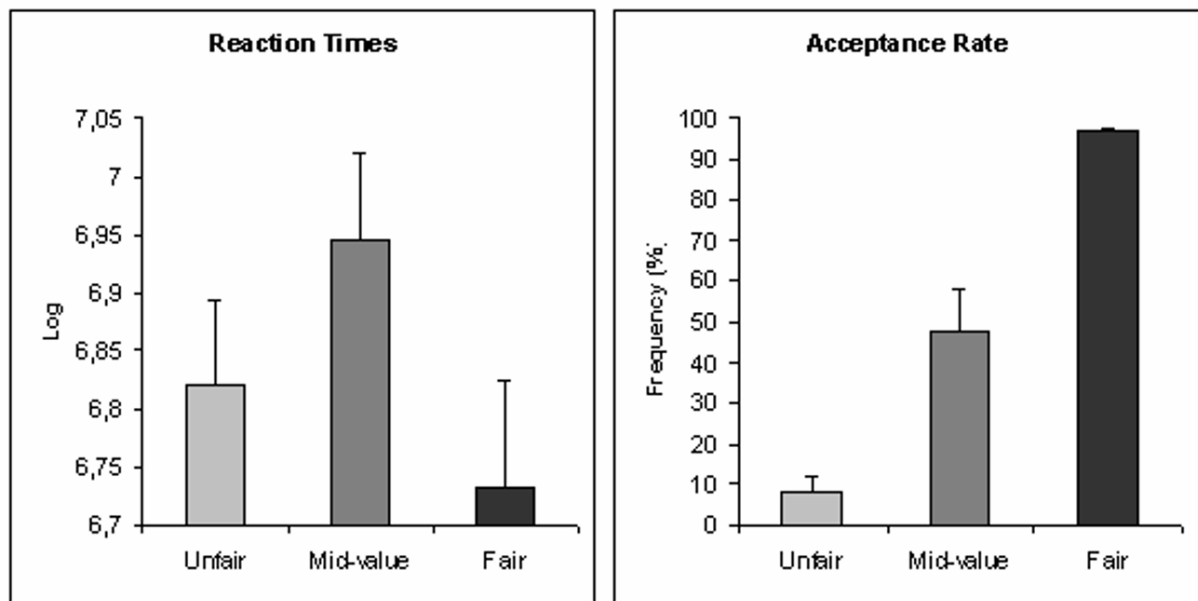


Figure 9. Acceptance rate and RTs for the different types of offers. .

Event Related Potentials

Variations in processing offers were reflected in the Feedback Related Negativity (FRN), in the N350 and in the later N500. Consistently with previous findings, these potentials were most prominent over the frontal areas as illustrated by topographical distributions (see Figure 3) (De Pascalis et al., 1999; Gehring & Willoughby, 2002; Kiehl et al., 1999; Schendan & Kutas, 2003). Following established procedures (Hajcak et al., 2006; Holroyd et al., 2005), FRN amplitude is assessed as the difference between the most positive peak in the 160-240 ms time window and the following negative peak up to 320 ms after stimulus onset. Peak detection was performed using the

algorithm provided by Brain Vision Analyzer 1.05. The N350 and the N500 were determined in terms of the mean ERP amplitude within the 320-400 ms and 400-600 ms time windows respectively, relative to the pre-stimulus baseline. Separate ANOVAs were performed for the three potentials, with Type of Offer (Unfair, Mid-value, Fair), Median Line (Frontal vs Fronto-Central electrodes) and Laterality (Left vs. Central vs. Right electrodes) as independent variables and the respective ERP as the dependent measure. For each comparison, Bonferroni corrections were used.

FRN

FRN amplitudes differed significantly between the different Types of Offers ($F(2,24)=4.87, p<.05$ $\eta^2_{\text{partial}}=.29$). The FRN was smaller for fair compared to mid-value offers (Mid-value vs fair: $t(12)=2.96, p<.05$); the difference between fair and unfair offers approached significance (fair vs. unfair: $t(12)=2.733.01, p=.054$). Furthermore, unfair and mid-value offers did not show significant amplitude differences ($t(12)=-.34, p=.99$).

The interaction between Median Line and Laterality also reached significance ($F(2,24)=4.69, p<.05$ $\eta^2_{\text{partial}}=.28$), reflecting reduced FRN amplitudes over right fronto-central sites, as illustrated in Fig. 3. None of the other effects approached significance.

N350

N350 amplitudes were significantly different for the different Types of Offers ($F(2,24)=8.285, p<.01$ $\eta^2_{\text{partial}}=.41$). The N350 was larger for mid-value compared to the other two types of offers (Mid-value vs. fair: $t(12)=-3.87, p<.01$; Mid-value vs. unfair: $t(12)=3.01, p<.05$), while fair and unfair offers did not yield significant amplitude differences ($t(12)=-.47, p=.99$). None of the other effects reached significance.

N500

There were no significant N500 amplitude differences between the different Types of Offers ($F(2,24)=1.50, p=.24, \eta^2_{\text{partial}}=.11$). The other effects did not reach significance either.

Linear Regression Analyses: Behavioural results and ERPs data integrated

To assess the degree to which decision making behaviour can be explained by the FRN and the N350, three linear regression analyses were performed, with each of the three offer types as independent variables and acceptance rate of the corresponding offer as dependent variable.

For the FRN, amplitudes associated with mid-value offers explained 40.7 % of variance in individual acceptance behaviour ($F(1,12)=7.55, p<.05$), with higher FRN amplitudes being associated with lower acceptance rates. FRN amplitudes associated with unfair and fair offers, on the other hand, were not significantly related to subjects' behaviour, explaining only 4.7 % and 3.3 % of variance in individual decision making behaviour ($F(1,12)=.55, p=.48; F(1,12)=.38, p=.55$, respectively).

N350 amplitudes associated with mid-value offers explained 54.0 % of variance in acceptance rates ($F(1,12)=12.92, p<.01$), with higher N350 amplitudes being associated with lower acceptance rates. N350 amplitudes associated with fair offers were also significantly related to acceptance rates, explaining 39.7 % of variance in individual behaviour ($F(1,12)=7.23, p<.05$). N350 amplitudes associated with unfair offers, on the other hand, were not significantly related to subjects' behaviour (13.3 % of variance, $F(1,12)=1.69, p=.22$).

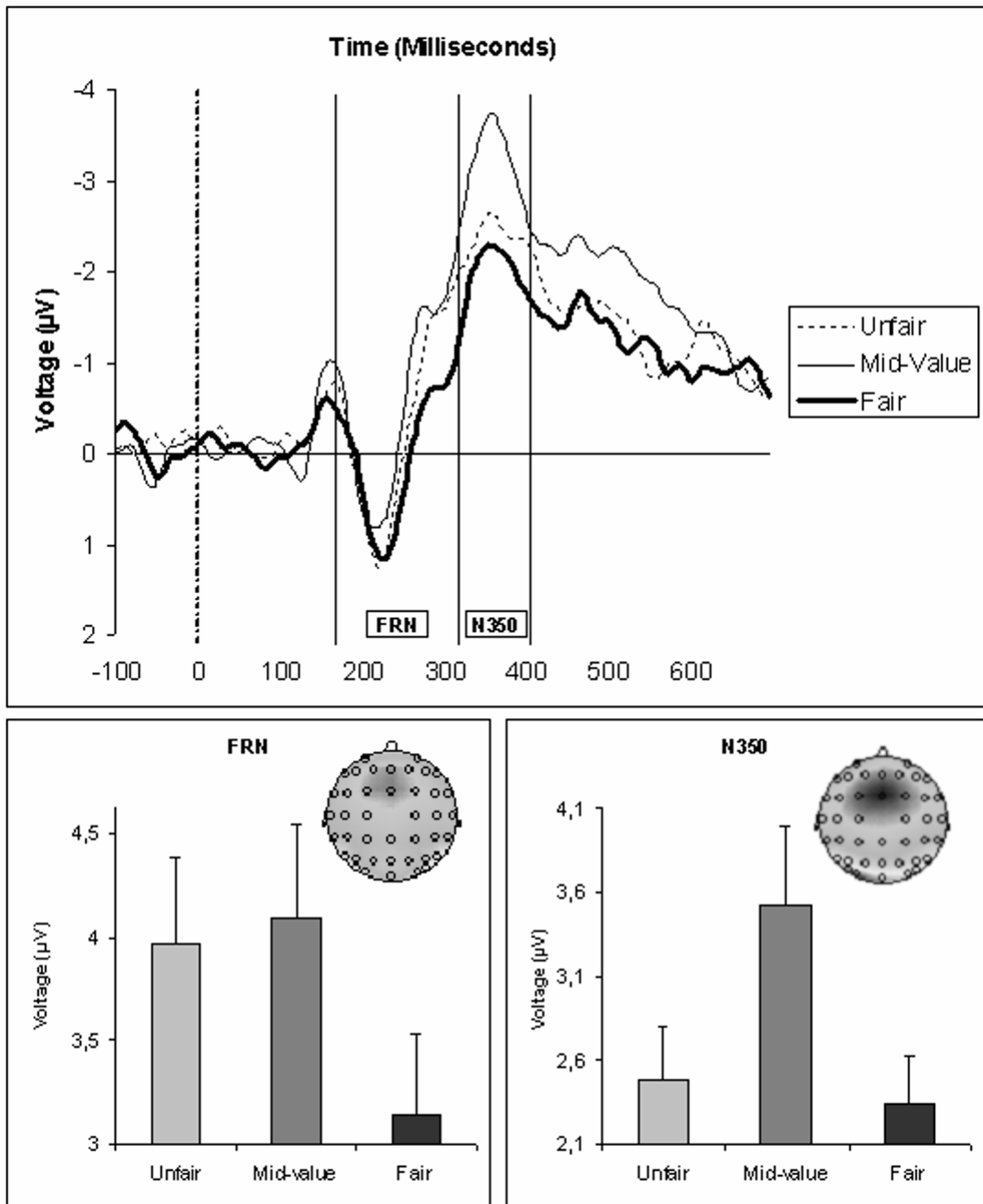


Figure 10. FRN and N350 reflect differences in offers processing. In the upper part ERPs waves are shown, while in the lower part mean amplitude as well as error bars are illustrated.

Source analysis results

To investigate the neural sources of FRN and N350 differences between the offers, three contrasts (unfair vs. mid-value; mid-value vs. fair; fair vs. unfair) entered source analysis.

Voxels survived the significance level in the mid-value vs. fair contrast, the areas in question being the left superior temporal gyrus (Brodmann Area 22) ($t(24)=5.84$, $p_{uncorrected}<.001$, $[-52 -11 -6]$ ³) and the left inferior parietal lobule ($t(24)=5.16$, $p_{uncorrected}<.001$, $[-38 -60 43]$)¹, both showing higher activation for the mid-value compared to the fair offers. No other contrast yielded significant results.

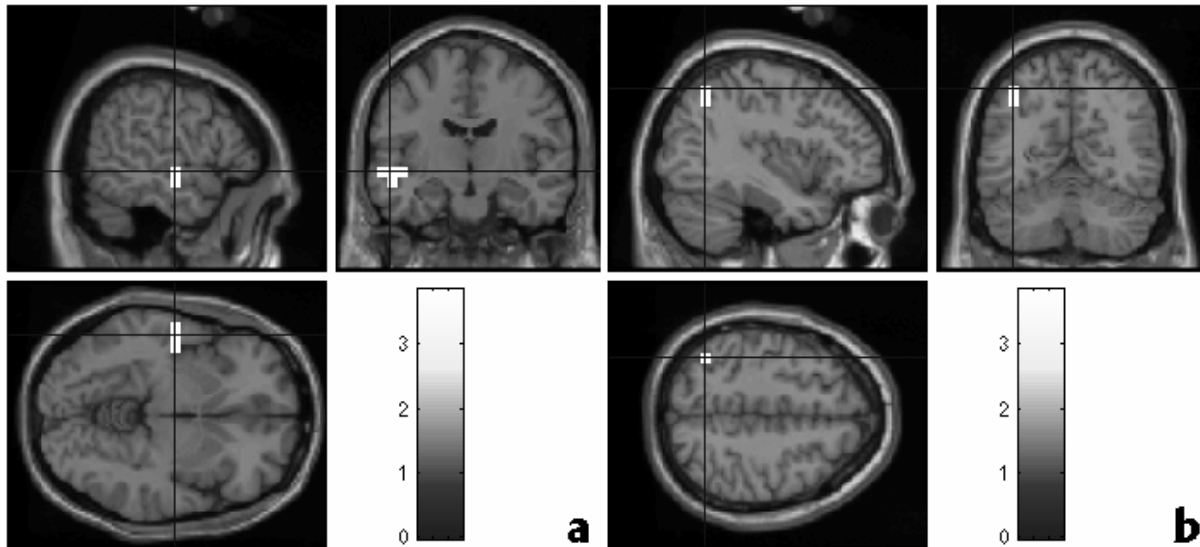


Figure 11. Higher activity in left superior temporal gyrus (a) and left inferior parietal lobule (b) for the mid-value compared to the fair offers.

Discussion

This study aimed to further investigate the neural basis of economic decision making within the context of the Ultimatum Game. In this game, people systematically violate the principle of economic rationality, which posits that responders should accept any offer in order to maximize gains (von Neumann & Morgenstein, 1944). As pointed out by Bolton and Zwick (1995), real players tend to accept only the offers which they judge as fair (e.g. 50:50 or 60:40), and they reject offer which they judge as unfair (e.g. 90:10 or 80:20).

³ The reported coordinates refer to the Montreal Neurological Institute system. The corresponding coordinates in Talairach are $[-51 -11 -5]$ and $[-38 -56 42]$, respectively.

To emphasize the interactive nature of this game, the present study introduced a long sequence of offers made the same proposer. Both behavioural and ERP data were analyzed to explore processing differences between very fair (5 €), very unfair (1 €) and mid-value (3 €) offers. Despite the modification compared to the traditional version of the ultimatum game, the well-documented acceptance rate pattern for ecological contexts in which subjects were paid based on the acceptance of the offers was replicated, with – as a general rule – fair offers being accepted and unfair offers being rejected. For the mid-value condition, acceptance rates were close to 50 %. Together with the finding of longer RTs for mid-value compared to the other conditions, this pattern implies that for both fair and unfair offers participants seem to have a clearly defined strategy or action plan, while mid-value offers involve more complex decision making mechanisms with less predictable outcomes. As a note of caution for RT interpretation, fair offers were accepted by pressing the right button and unfair offers were rejected by pressing the left button. This set-up could have produced shorter RTs for acceptance compared to rejection. However, it does not explain why RTs were longer for mid-value offers.

On the electrophysiological level, the fast and initial distinction between processing of the different offers is reflected by a negative potential peaking at about 270 ms. The fronto-central negative component peaking around 250 ms, elicited in gambling tasks and larger for unfavorable than for favorable outcomes is referred to as FRN (Folstein & Van Petten, 2008). The FRN reflects assessment as well as motivational aspects of the feedback that are critical for subsequent decisions (Gehring & Willoughby, 2002). Although the present task does not explicitly provide feedback, it is possible that the interactive nature of the game might lead to the hypothesis that decisions of the responder influence subsequent offers of the proposer. It is also noteworthy that both latency and scalp distribution correspond to previously reported FRN data (Gehring & Willoughby, 2002; Hajcak et al., 2006). In the context of the present study, FRN amplitude reflects a distinction between fair offers on one side, and mid-value and unfair offers on the other side, with smaller

amplitudes for fair offers. This is consistent with previous findings of larger FRN amplitudes for the least favorable outcomes, e.g. losses (Hajcak et al., 2006).

Although source analyses of the current data did not yield any significant activations, it should be noted that the FRN has consistently been reported to be generated by the ACC (Gehring & Willoughby, 2002; Holroyd & Coles, 2002), with larger amplitudes being associated with stronger ACC activity. The observed higher FRN amplitudes for unfair and mid-value offers are in accordance with findings by Sanfey and colleagues (2003) who reported enhanced ACC activity for offers in the range of 10 % to 30 % of the total sum.

A further distinction in processing the different types of offers was reflected in the N350, a negative potential which peaks around 350 ms with maxima over frontal electrodes (De Pascalis et al., 1999; Kiehl et al., 1999; Schendan & Kutas, 2003). The N350 amplitudes clearly mirrored the behavioural data, with mid-value offers eliciting a higher potential compared to fair and unfair offers, while the N350 for fair and unfair offers did not differ significantly. The N350 was previously described by Schendan and Kutas (2003) in an object recognition task, in which subjects viewed objects shown from usual and unusual perspectives. Unusual perspectives were associated with longer RTs and higher N350 amplitudes. In other words, the N350 was found to be larger for those conditions in which objects were harder to identify. Consistent with expectation, the mid-value offer appears to induce conflicting responses tendencies (i.e. acceptance and rejection), therefore making the decision more difficult. However, as shown by regression analyses, the strong association between N350 amplitude and the later behavioural decision suggests that this potential does not only reflect decision complexity but also the way by which the uncertainty is resolved.

Source analyses provided additional information about the underlying processes, yielding a significant difference between mid-value and fair offers, with enhanced activity in the superior temporal gyrus associated with the mid-value offers. This area is known to be involved in theory of mind or mentalizing (Brunet et al., 2000; Fletcher et al., 1995), i.e., the ability to understand the mental states of other people. The enhanced superior temporal gyrus activity associated with mid-

value offers might also mirror attempts of the responder to understand the proposer's strategy, and activity in this region has also previously been reported to be involved in non-economic decision making (Paulus et al., 2005). In addition, an fMRI study (Rilling et al., 2004) which also employed the Ultimatum game reported higher activations in the superior temporal gyrus when subjects thought they played against a human partner compared to a condition when they thought they played against a computer. This pattern of results was interpreted in terms of an involvement of mentalizing in this type of economic decisions, and our data can thus be seen as converging evidence for this issue (Rilling et al., 2004).

The left inferior parietal lobule was also found to be more active for mid-value compared to fair offers. The left parietal region has been linked to perception of social cues, such as facial expression directed toward someone else (Schilbach et al., 2005) or taking a third-person perspective (Ruby & Decety, 2001). In the context of the Ultimatum game, activity in this region might reflect attempts to take the perspective of the proposer, presumably to hypothesize about his/her strategy. It is important to note that these areas are recruited for making decisions in the mid-value situation which suggests that in addition to cognitive processes such as reasoning, non-cognitive factors unrelated to the economic facts come into play. In addition, the larger N350 amplitude for mid-value offers, presumably related to enhanced activity in the superior temporal gyrus and the parietal lobule, was linked to acceptance rates of these offers. This finding might suggest an implication of these regions in driving the decisional process towards rejection.

In summary, the present results indicate that within the context of the Ultimatum Game people consistently make fast decisions about offers which appear clearly fair or unfair. Mid-value offers which do not readily fall into one of the two categories, induce a conflict and require more time for completion of the decisional process. In addition, hypotheses about the presumed strategy of other player appear to affect decision making. The ACC, the insula and the DLPFC have previously been described as key components of the neuronal network implicated in decision making during the Ultimatum Game. The present findings suggest an additional involvement of the superior temporal

gyrus and the inferior parietal lobule, presumably reflecting the social interaction component of the Ultimatum Game itself. This is consistent with recent findings on the neural basis of decision making, which suggest that decisions during social interaction are affected by factors not directly related to the money offered (Lee, 2006). The data should make a significant contribution to efforts aimed at reducing the gap between formal theories and real choice behaviour.

Experiment 4

Offers as communications

As shown by several experiments, economic decision-making is not strictly related to payoffs when it occurs within social interaction. Ultimatum Game is a paradigm that adequately represents this behavior in which people usually reject unfair offers because of the subjective impression of unfairness even if the alternative is gaining no money at all. Knoch and colleagues (2006) interpreted this behavior in terms of social communication. The rejection is considered a message for the other player, to induce a fairer behavior. This interpretation is in line with the general model of Fehr et al. (2002) in which rejection of unfair offers is considered an punishment altruistic, because human society cannot tolerate not-cooperative behaviours. Therefore, rejections would be the expression of a natural attitude, that human developed, to punishment to induce cooperation. Altruistic punishment has been shown to be peculiar of humans, given that non-humans primates behaved rationally, accepting every possible offers (Jensen et al., 2007). In accordance with this idea, we asked to a group of people to perform Ultimatum Game as responders, playing with a fair partner or with an hyper-fair partner which sometimes offered more than he kept (for example, 70%). While players performed Ultimatum Game, brain activity was scanned with fMRI. Our interest is focused on hyper-fair offers. If these offers are perceived as possible gains, they will activate brain areas traditionally connected with reward (such as orbitofrontal cortex). By contrast, if they are perceived as communication signals, they will presumably induce also activation of the areas linked to theory of mind. After receiving a hyper-fair offer people will presumably try to image the reason for such a cooperative behavior. We also asked to people to play rounds with computer as partner, who also generates some hyper-fair offers.

Materials and Method

Participants

Fifteen undergraduate students from the University of Bochum participated in this study. All subjects were healthy and had normal or corrected-to-normal vision. They were recruited by advertisements, signed an informed consent form and were debriefed at the end of the experiment, after they received 10 % of what they accepted during Ultimatum Game.

Task

A modified version of the Ultimatum Game was administered as follows. Subjects played as responders. They were told that they played with the experimenter, the proposer, who was located in a close room or with the computer. Unknown to them, they played all rounds against the computer, and the offers they received did not depend on their own decisions. Participants were told that on each trial, the proposer made an offer of how to split 10 € between them, and that they had to decide either to accept or to reject the offer. The offers appeared on a monitor. For example, if “2 €” appeared on the screen, acceptance would imply that the subject received 2 € while the proposer kept 8 €. Decisions were made by key presses (left key for rejection, right key for acceptance of the offers). There were 6 different offer conditions (1 €, 2 €, 3 €, 4 €, 5 € and 7 €). Analysis was based on the trials representing the unfair offers (1 €, 2 € and 3 €), fair offers (4 € and 5 €) and the hyper- fair offers (7 €).

A single trial is represented in figure (see Fig. 1).

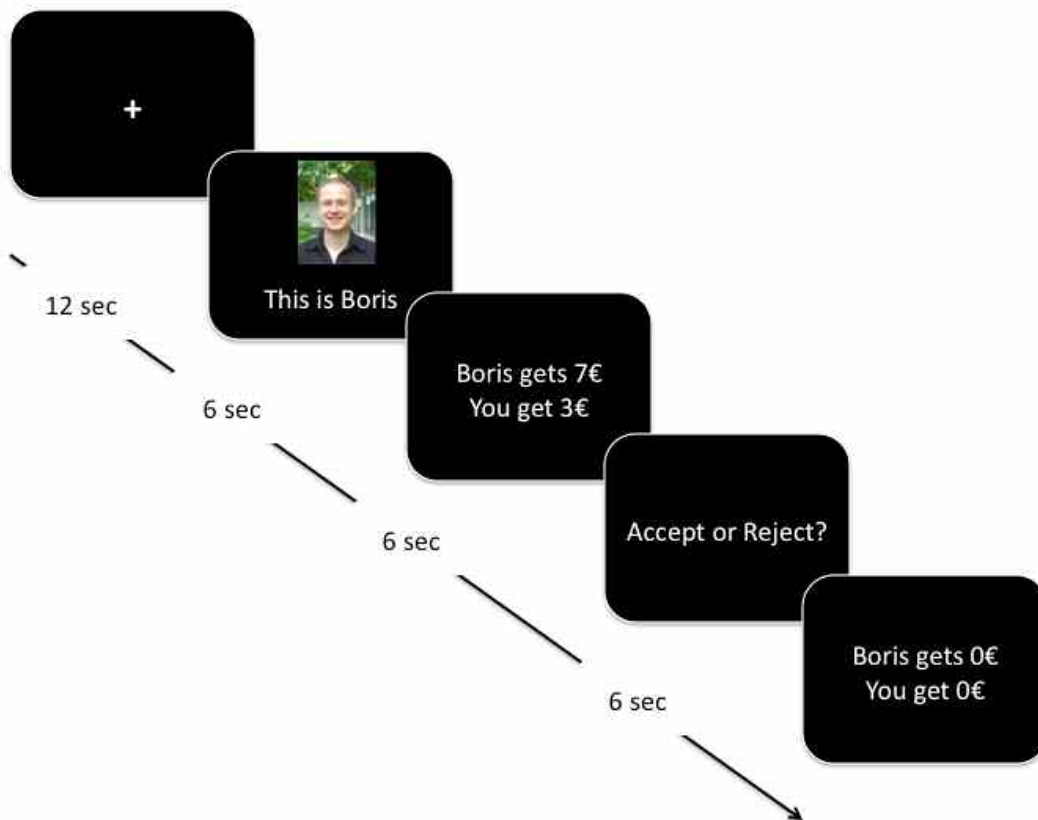


Figure 12. Sequence of stimuli on an individual trial. Each trial showed the offer made by the proposer.

Procedure

Participants performed inside of the fMRI scanner. The instructions were presented in written form. Subjects were informed that they would receive remuneration for participation after having completed the experiment, corresponding to 10% of what they accepted. The recording session lasted about 45 minutes.

fMRI recording

520 scans consisting of 25 slices with TR = 2000ms (TE = 40ms, FOV= 192mm, flip angle = 90°) and a 1mm gap were acquired for each subject on a Siemens (www.siemens.de) Symphony 1.5 T

scanner. The voxel size was 3mm×3mm×3.6mm. A high resolution T1 image (MP-RAGE sequence) of 112 slices was additionally acquired for anatomical labeling (TR = 1990 ms, TE = 4.18ms, FOV= 250mm, flip angle = 15°). The voxel size was 1.4mm×1mm×1.5mm. Functional images were analysed using SPM 5 (<http://www.fil.ion.ucl.ac.uk/spm>). Images were normalised to the stereotactic space of the Montreal Neurological Institute (MNI) brain provided by SPM 5, and smoothed with a Gaussian kernel of 8mm. A GLM was applied to the data separating them according to the stimulus category. Data were high-pass filtered to eliminate low-frequency components (a cut-off value of 128 s was used). Statistical threshold has been set at $p < .001$ (uncorrected).

Results

Below are reported the main contrasts between the different conditions.

Human Partner- UnFair > Fair

T	<i>p</i>	x,y,z {mm}	
3.89	0.000	34 -30 16	<i>Insula</i>

Human Partner- Fair>UnFair

T	<i>p</i>	x,y,z {mm}	
5.02	0.000	-16 32 26	<i>Anterior Cingulate Cortex</i>
4.79	0.000	38 36 20	<i>Middle Frontal Gyrus</i>
4.48	0.000	-40 -36 -18	<i>ParaHippocampal Gyrus</i>
4.06	0.000	62 -18 -10	<i>Middle Temporal Gyrus</i>
3.69	0.000	-10 -24 52	<i>Medial Frontal Gyrus</i>

Human Partner- HyperFair >Fair

T	<i>p</i>	x,y,z {mm}
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4.23	0.000	-20 14 8	<i>Putamen</i>
3.99	0.000	-52 12 -4	<i>Superior Temporal Gyrus</i>
3.89	0.000	-52 -62 28	<i>Superior Temporal Gyrus</i>
3.54	0.000	20 38 32	<i>Medial Frontal Gyrus</i>

Human Partner- Fair > HyperFair

T	<i>p</i>	x,y,z {mm}	
4.23	0.000	4 22 -12	<i>Subcallosal Gyrus</i>

Computer Partner- UnFair > Fair

T	<i>p</i>	x,y,z {mm}	
4.66	0.000	20 42 16	<i>Medial Frontal Gyrus</i>
4.33	0.000	-34 40 36	<i>Superior Frontal Gyrus</i>

Computer Partner- Fair>UnFair

T	<i>p</i>	x,y,z {mm}	
No voxels survived level of significance			

Computer Partner- HyperFair >Fair

T	<i>p</i>	x,y,z {mm}	
No voxels survived level of significance.			

Computer Partner- Fair > HyperFair

T	<i>p</i>	x,y,z {mm}	
No voxels survived level of significance.			

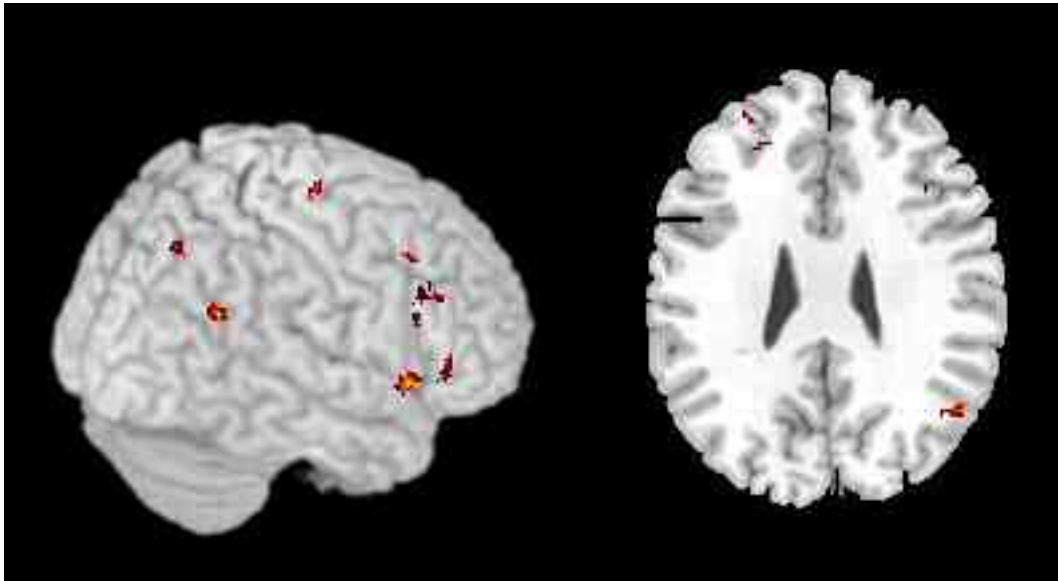


Figure 13. Contrast between Hyper-Fair and Fair offers in the Human Partner condition. When an hyper-fair offer is displayed superior temporal gyrus is selectively more activated.

Discussion

Ultimatum Game is a task that requires making economic decisions in an interactive context. The peculiar aspect of this task is that it highlights an apparently irrational behavior, in which people rejects unfair offers even if the alternative is to gain no money at all. Model provided by Fehr and colleagues (2002) posits that rejections are considered a punishment of the other player in order to induce him to behave fairer. According to this view, Knoch and her colleagues (2006) showed as disruption of dorso-lateral prefrontal cortex diminished rejection inducing selfish behavior in players that just try to accumulate as more money as they can without trying to modulate not-cooperative behavior of the other player. In order to stress the social meaning of offers in Ultimatum Game, we asked to a group of participants to perform the Ultimatum Game as responders, presenting them some hyper-fair offers (such as 70% of the total amount). Hyper-Fair offers can selectively activates superior temporal gyrus, which is known to be involved in theory of mind or mentalizing (Brunet et al., 2000; Fletcher et al., 1995), i.e., the ability to understand the mental states of other people. The enhanced superior temporal gyrus activity associated with hyper-fair offers might also mirror attempts of the responder to understand the proposer's strategy, and

activity in this region has also previously been reported to be involved in non-economic decision making (Paulus et al., 2005). In addition, an fMRI study (Rilling et al., 2004) which also employed the Ultimatum game reported higher activations in the superior temporal gyrus when subjects thought they played against a human partner compared to a condition when they thought they played against a computer. This pattern of results was interpreted in terms of an involvement of mentalizing in this type of economic decisions, and our data can thus be seen as converging evidence for this issue (Rilling et al., 2004).

Here is important to note as superior temporal gyrus is activated when people thought that they were playing with human partner, while no different activation of this area has been found in the conditions in which people were explicitly told that offers were randomly generated by the computer.

Concluding, this data underline as hyper-fair offers not only activates area traditionally involved with reward, but also those connected with theory of mind, providing converging evidences that offers are perceived as signals from the other player.

Conclusions

Classical economic model see men as rational maximizers who make decisions taking in account outcomes of decisions and their probabilities. In formal terms, the expected utility model posits that every possible outcome should be weighted by its probability and the option with the highest expected utility should be chosen (von Neuman & Morgenstein, 1947). A growing body of evidences is highlighting as economic decision-making can be heavily affected by factor not directly related to payoffs. The reported four experiments are in line with this view. In the first experiment, predictability of outcomes is a crucial aspect in regulating risk-taking behaviour. Previous experiment reported that decision outcomes are assessed in terms of good and bad. This binary distinction is mirrored by the FRN, occurring within 350 ms. However, prior and important assessment of outcomes is reflected by P200, in terms of predictable and unpredictable outcomes. Therefore, even if this binary distinction holds, predictability affects risk-attitude. Also in the second experiment, where the context is changed the binary distinction reflected by FRN is still present, but in this case what appears to be crucial is P300, which reflects changes in risk-attitude when the context is changed. FRN still reflected binary distinction in terms of good and bad, also economic decision-making within social context. Experiment 3 showed the involvement of theory of mind in this kind of decisions, suggesting that apparently irrational behaviour can be logic in the light of social interaction. Similar results are obtained by Experiment 4 who employed fMRI to study economic decision-making in social context, showing as monetary offers are perceived as social communications rather than mere economic divisions. Taken together these studies tried to narrow the gap between formal theory and real economic choice behaviour.

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