universität wien

Diplomarbeit

Titel der Arbeit

Facial cues affect the feedback negativity to offers in the Ultimatum Game. An EEG investigation.

Verfasser

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Angestrebter akademischer Grad

Magister der Naturwissenschaften (Mag. rer. nat.)

Wien, im Dezember 2009

Studienkennzahl:	298
Studienrichtung:	Psychologie
Betreuer:	PD. Dr. Uta Sailer

Danksagung

An dieser Stelle möchte ich mich bei allen Personen bedanken, die zum Gelingen dieser Arbeit beigetragen haben:

Magª. Johanna Alexopoulos, Magª. Daniela Pfabigan und PD. Drª. Uta Sailer für die kompetente sowie geduldige Betreuung.

Meiner Freundin Bettina Weixler und meinen Eltern Gertraud und Werner Schreiner für die durchgängige moralische (und im Falle meiner Eltern auch finanzielle) Unterstützung.

Meinem Kollegen Florian Göschl für die in jeder Hinsicht erfreuliche Zusammenarbeit.

Zu guter Letzt möchte ich mich bei den Versuchspersonen die an der Studie teilgenommen haben bedanken.

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Abstract

The feedback negativity, a component of the event-related brain potential, is elicited by feedback stimuli indicating unfavorable outcomes. The feedback negativity has been regarded to reflect a process of performance monitoring and/or learning about recently executed actions, since it has been primarily investigated using experimental paradigms where outcomes seemed to be contingent upon the behavior of the participants. Recently several studies demonstrated that the feedback negativity can be elicited as well by outcomes that are not contingent on preceding actions or choices. These findings led to the suggestion that the feedback negativity might additionally reflect the evaluation of expectations about environmental contingencies. The present study attempted to test this suggestion by evaluating the feedback negativity while participants‘ expectations about contingencies in the Ultimatum Game, a commonly-used bargaining task, were manipulated. Participants were confronted with proposers, displaying either a smile or an angry face, who provided differential fair offers. The displayed facial expressions were meant to affect expectations about succeeding offers. Larger feedback negativity amplitudes were elicited following unfavorable outcomes, more precisely after unfair and midfair offers, compared to fair offers. Furthermore a happy proposer offering an amount of money perceived as unfair elicited a more pronounced feedback negativity amplitude compared to angry proposers offering the same amount of money. Thus, violated expectations about contingencies in the Ultimatum Game (happy proposers providing unfair offers) led to more pronounced feedback negativity amplitudes.

Theoretical Part

1. Homo Oeconomicus and Behavioral Economy

Standard economic models traditionally base upon the homo oeconomicus concept. The homo oeconomicus is guided by his individual preferences, seeks to achieve his objectives with minimal costs, (Faber, Petersen, & Schiller, 2001) and behaves in an opportunistic, rational and calculating manner (Gray, 1987). He is always trying to maximize his own utility, based on his stable preferences.

The notion that people alway try to obtain the highest possible level of utility results from the assumption, that economic decision making follows careful deliberation, a balancing of costs and benefits of different options. The process of decision making takes place at a stage, where further deliberation, reflection and computation would not alter the choice (Camerer, Loewenstein, & Prelec, 2005). It is assumed that humans have the cognitive ability and time to weigh every choice against each other.

Economical research, grounded on the concept of homo oeconomicus, turns its focus on observable external behavior. Economic models are achieved by measuring input and output information and eliminating the assumption of intermediating feelings. Emotions and feelings, as not directly measurable, are regarded as useless intervening constructs. Assuming that the human brain, underlying behavior, and its functioning cannot be fully understood, it is sidelined as the ultimate „black box".

For instance, the revealed preference theory, assuming that humans behave as suggested by the homo oeconomicus concept, equates unobserved preferences with observed choices. To evade circularity it is assumed that people behave consistently. If a person has once revealed that she prefers A to B, she should not choose B over A afterwards (Camerer et al., 2005). Related „as-if" tools were later provided by extensions of the revealed preference theory, such as expected, subjective expected, and discounted utility.

However various studies repeatedly revealed theoretically predicted behavior deviating from real human behavior (Camerer & Thaler, 1995). These anomalies and the emerging of cognitive psychology around 1960, perceiving the human brain as a metaphor for an information-processing device, enabled a new research of ignored topics like decision-making and problem-solving, guiding the way to the development of behavioral economics (Camerer & Loewenstein, 2004).

1.1 Behavioral Economics

Behavioral economics approach is defined by integrating more realistic psychological concepts about the human nature and decision-making into economic research and thus, to increase the explanatory power of economics.

According to Mullainathan and Thaler (2001) behavioral economic research consists of two components:

1. Identifying the ways in which behavior differs from the standard model.
2. Showing how this behavior matters in economic contexts.

Psychological ideas are formalized and translated into testable predictions, to broaden models of economic behavior. Instead of ignoring non-rational-behavior, behavioral economists perceive economic behavior as influenced by emotions and subconscious processes as demonstrated in concepts like bounded rationality, bounded willpower or bounded self-interest (Kenning & Plassmann, 2005). Bounded rationality applies to the limited cognitive abilities that narrows human problem solving. Bounded willpower refers to the fact that people sometimes make choices that are not in their long-run interest. Bounded self-interest implicates the circumstance that humans are often willing to give up their own interests to help others (Mullainathan & Thaler, 2001).

Integration of psychology led to several new models on decision making. The realization that conditions occur under which humans behave in an irrational way as well as that conditions exist under which humans behave rationally resulted in the growing conviction that human decision making can be viewed as product of two underlying processes: a bounded rational process and an irrational process (Glimcher, Dorris, & Bayer, 2005). According to Glimcher (2005) irrational behavior is often attributed to limited neural architecture while rational behavior is seen as a product of a conscious faculty exceeding these limitations. Kahneman (2002) distinguishes in his well known dual-process model between reasoning and intuition. According to Kahneman one function of System 2 (reasoning) is to monitor the quality of both mental operations and overt behavior. This monitor function allows many intuitive judgements to be expressed, including erroneous ones.

Kahnemans‘ dual-process model:

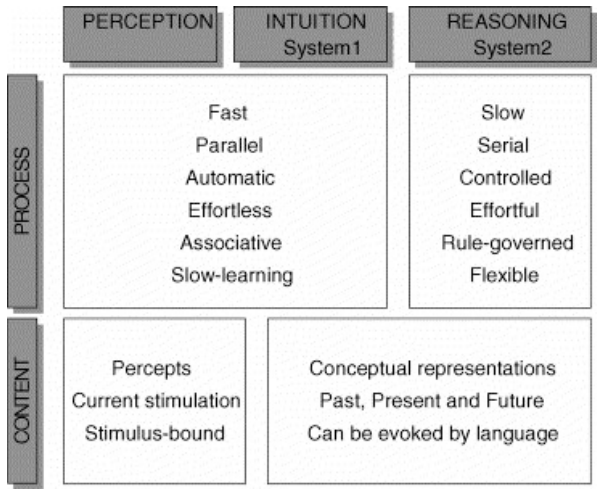


Fig.1:Dual process model (taken from Kahneman, 2002)

The assumption of underlying cognitive systems, guiding behavior and being responsible for observed deviations from standard economical models is postulated due to the observation and analysis of behavior, which in turn is used to explain behavior. Criticism from the traditional economics point of view relates to this circular reasoning as well as to the fact, that these theoretical constructs are neither observable, nor objectively measurable (Kenning & Plassmann, 2005). According to Kenning and Plassmann (2005) the answer to these problems would be the usage of new tools or methods, permitting a more objective way of investigating behavior. The requested methodical repertoire to investigate behavior in a more objective way is provided by neuroscience, since neuroscientific tools are used to directly analyze the brain operations underlying human behavior.

2. Neuroeconomics and Game-Theory

Neuroeconomics is the study of how the embodied brain interacts with its external environment to produce economic behavior. Research in this field will allow social scientists to better understand individuals' decision making, and consequently to better predict economic behavior (McCabe, 2003).

Neuroeconomics is defined as the application of neuroscientific methods to analyze and understand economically relevant behavior (Kenning & Plassmann, 2005). Its aim is to investigate and analyze brain processes related to economical behavior. Neureconomics provides the extension of economic research to brain processes, opening the „black box“, traditionally ignored in standard economic models.
See below a short description of the three most popular methods used in neuroeconomics (for a detailed description, see Schandry, 2006):

- Electroencephalography (EEG): electrodes are attached to the head in order to measure electrical activity. This activity is synchronized to behavioral responses or stimulus events.
- Positron-emission-topography (PET): detects the location and concentration of small amounts of radioactive substances to examine the metabolic activity in the brain relating to experimental manipulation.
- Functional magnetic resonance tomography (fMRI): measures the change in blood flow related to neural activity in the human brain.
- Transcranial magnetic stimulation (TMS): noninvasive method to excite or inhibit neurons in the brain, by induction of weak electric currents in the tissue through rapidly changing magnetic fields.

The investigation of psychological and neuronal correlates of social decisions is becoming increasingly popular as part of the neuroeconomic approach. Neuroeconomics aims at a fundamental comprehension of decision-making, regarding neural and cognitive constraints, as known from neuroscience and psychology, while mathematical decision models serve as a basis. Neuroscientific techniques are used to investigate the relative contributions of cognitive and emotional processes to social decision-making (Sanfey, Rilling, Aronson, Nystrom, & Cohen, 2003). Tasks used to investigate social decision-making are commonly out of a branch of experimental economics, named Game Theory.

2.1 Game Theory

Game theory is a theory of decision making. Developed in the middle of the twentieth century from Neumann and Morgenstern (1944) and Nash (1950), the theory of games defines individual, rational decision-making in social situations of conflict (Güth, 1998). Social situations of conflict (the game) are characterized as two agents (players), who have partly countervailing objectives, may behave in an unrestricted way and are in opposition to each other. Game Theory demands to explain situations in which decision-makers must interact with one another (Sanfey, 2009).
According to Camerer et al. (2005) the theory of games acts on the following assumptions:

1. Players have accurate beliefs about what others will do.
2. Players have no emotions or concern about how much others earn.
3. Players plan ahead,
4. and learn from experience.

Widespread criticism refers to these assumptions, since observed behavior deviates from the models‘ predictions (Camerer, 2003). Decision-makers seem to be less strategic and selfish then predicted. The Ultimatum Game, a common game theoretical application, illustrates the limitations of the classical game theoretic approach in a simple and effective way.

2.2 Ultimatum Game

The Ultimatum Game is used to examine strategic bargaining behavior and to investigate responses to fairness. In this game one player, the proposer, has to split a sum of money (in general $10) with another player (responder). The responder has the opportunity to reject or accept the offer provided by the proposer. If the responder accepts the offer, the sum gets split as proposed, otherwise neither of the two players receives anything.

The responder should accept the smallest offer, if the responder has no emotional reaction to the fact that the proposer is earning more than she is (as predicted by game theory). The proposer should offer the lowest possible amount, if the proposer has no emotional reaction to earning more and is able to anticipate correctly the forthcoming actions of the responder (Camerer et al., 2005). In summary, the smallest sum should be offered as well as accepted. Behavioral results are at odds with these predictions (Güth, Schmittberger, & Schwarze, 1982). The modal sum offered by proposers is a 50/50 split. Low offers (less than 20% of the total amount) get rejected by half of the responders. In connection with low offers responders seem to prefer gaining nothing. According to Pillutla and Murnighan (1996) low offers, perceived as unfair, cause angry reactions, leading to the rejection of low offer. These negative feelings seem to motivate people to actively refuse monetary reward and to penalize their opponent. A responder, rejecting an offer spends money to punish somebody who has behaved unfairly (Camerer & Loewenstein, 2004). Anticipating the possibility of low offers getting rejected, proposers generally avoid low offers.

2.3 Ultimatum Game and Neuroeconomics

One of the most prominent neuroscientific findings about the Ultimatum Game comes from Sanfey et al. (2003). This fMRI study compares neural activity responding to unfair and fair offers. Unfair offers differentially activated three regions of the human brain:

- the anterior insula,
- the dorsolateral prefrontal cortex (dlPFC),
- and the anterior cingulate cortex (ACC).

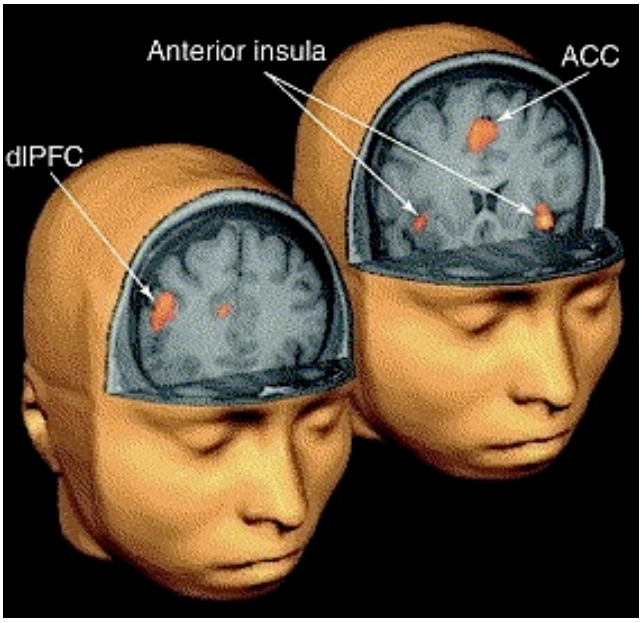


Fig.2: Activated brain regions in response to receiving an unfair (vs. fair) offer in the Ultimatum Game (adapted from Rilling et al.,2008)

Bilateral anterior insula activation is commonly associated with negative emotional states. This region seems to participate in the evaluation and representation of specific negative emotional states (Damasio, Grabowski, Bechara, Damasio, Ponto, Parvizi et al., 2000). According to Sanfey et al. (2003) participants with stronger anterior insula activation to unfair offers rejected a higher proportion of these offers. This result might underpin the assumption of neural representations of emotional states guiding human behavior.

Dorsolateral prefrontal cortex has generally been implicated in executive control and goal maintenance, thus, cognitive processes. Sanfey et al. (2003) associate stronger activation of this region to unfair offers with the representation and active maintenance of the cognitive demands of the task, achieving the maximum amount of money. To resolve emotional tendencies to reject unfair offers might be a bigger cognitive challenge and would result in stronger activations of the dlPFC.

One function, amongst others, of the anterior cingulate cortex has been linked to the detection of cognitive conflict (Botvinick, Braver, Barch, Carter, & Cohen, 1999). According to Sanfey et al. (2003) activation of the ACC might reflect the conflict between emotional and cognitive motives in the Ultimatum Game.

In summary, evidence that unfair offers engage neural structures involved in cognitive and emotional processing seems to be provided. In addition, magnitude of activation in structures included in emotional processing appear to explain variance in the subsequent decision.

Knoch, Pascual-Leone, Meyer, Treyer, & Fehr, (2006) demonstrated that low-frequency TMS of the right dlPFC led to an increased acceptance rate of unfair offers in the Ultimatum Game compared to a placebo stimulation. According to Knoch et al. these findings suggest that the right dlPFC may not be critical in controlling the impulse of rejecting unfair offers, but rather represents offers as fair or unfair. As a consequence subjects with impaired dlPFC accept all offers.

Finally Polezzi, Daum, Spitzer, & Kiefer, (2008) conducted an EEG-study to further investigate the Ultimatum Game. Unfair offers (90/10 split) as well as midfair offers (70/30 split) elicited a particular component called the feedback negativity, which is sensitive to negative feedback, indicating erroneous responses or the loss of money (Gehring and Willoughby, 2002; Holroyd and Coles, 2002).

3. Feedback-Negativity

Learning from feedback how to behave and how to guide future behavior is a fundamental cognitive skill. The ability to differentiate between positive feedback and negative feedback forms the basic principle for such learning (Nieuwenhuis, Ridderinkhof, Talsma, Cols, Holroyd, Kok, & Van der Molen, 2004). Measures of event-related brain potentials (ERPs), derived from EEG recordings display differential neural response to negative and positive feedback. Certain ERP components seem to be selectively sensitive to the perception of positive or negative feedback.

Various studies have reported that feedback related to performance elicits a negative going brain potential, peaking about 250 ms following feedback presentation, and being maximal over medial frontal scalp locations. The amplitude of this component, called the feedback-negativity (FN) is more pronounced for feedback stimuli indicating negative outcomes, such as the loss of money or incorrect response, than for feedback stimuli associated with positive outcomes (Miltner, Braun, & Coles 1997; Gehring & Willoughby, 2002; Holroyd & Coles, 2002; Nieuwenhuis et al.,2004).

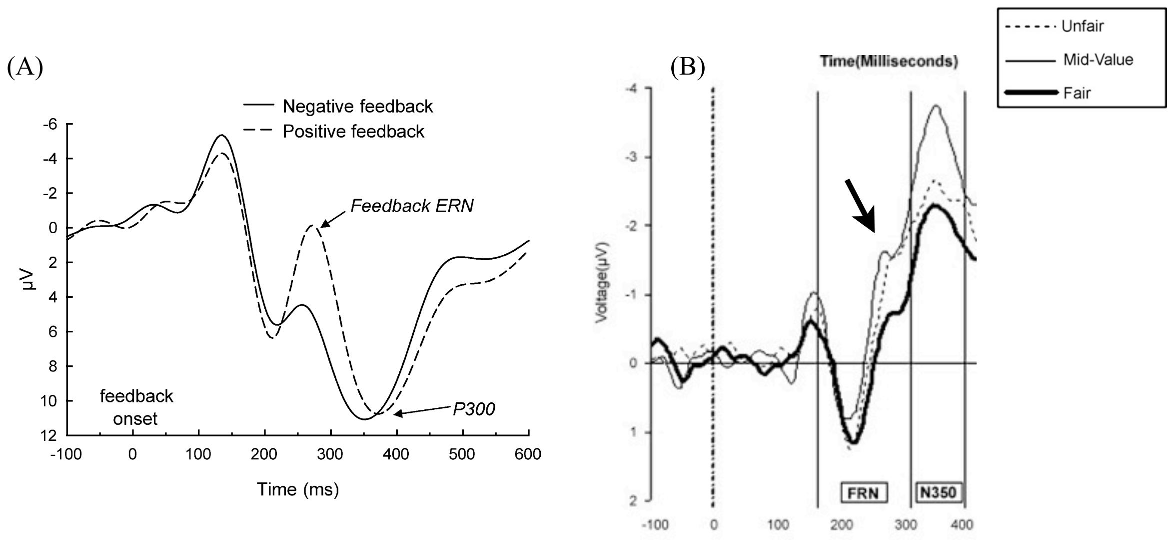


Fig.3:(A)Typical example of event-related brain potentials associated with negative and positive feedback (adapted from Nieuwenhuis et al., 2002). Negative is plotted up by convention. Waveforms were recorded from electrode Cz. (B) FN reported by Polezzi et al. (2008) in the Ultimatum Game (adopted from Polezzi et al. 2008)

The characteristics of the FN resemble in various ways those of another negative ERP-component: the error-related negativity, ERN, (Gehring, Goss, Coles, Meyer, & Donchin 1993) or error negativity, NE, (Falkenstein, Hohnsbein, Hoorman, & Blanke, 1990), following erroneous responses in simple choice tasks, peaking within 100 ms and appearing over medial frontal scalp locations (for reviews, see Falkenstein, Hoorman, Christ, & Hohnsbein, 2000; Holroyd & Coles, 2002). Its amplitude is correlated with subjective judgments of response accuracy (Scheffers & Coles, 2000) and is increased when response accuracy is emphasized over speed (Falkenstein et al., 1990; Gehring et al., 1993). Furthermore the amplitude of the ERN is reduced following incorrect responses to stimuli that are presented relatively infrequently (Holroyd & Coles, 2002). Source localization analyses have detected the medial frontal cortex, in or near the anterior cingulate cortex (ACC) as the most likely generator for both components, feedback-negativity and error-related negativity (Miltner et al., 1997, Gehring and Willoughby, 2002; Ruchsow, Grothe, Spitzer, & Kiefer, 2002).

3.1 Anterior Cingulate Cortex and Feedback-Negativity

The anterior cingulate cortex, a structure located on the medial surface of the frontal lobes, has diverse functions. The anterior cingulate cortex is subdivided into „cognitive“ and „affect“ regions (Bush, Whalen, Rosen, Jenike, McInerney, & Rauch, 1998; Vogt, Finch, & Olson, 1992).

Dorsal regions of the ACC, including cortex on the dorsal and ventral banks of the cingulate sulcus (BA 24b´-c´ and 32c´), represent the cognitive subdivision being crucial for error processing (Carter, Braver, Barch, Borvinick, Noll, & Cohen, 1998) and for mediating processes such as response inhibition (Bush et al., 1998). This cognitive subdivision is part of a distributed attentional network (Bush et al., 2000), maintaining reciprocal interconnections with lateral prefrontal cortex (BA 46/9), parietal cortex (BA 7), and premotor and supplementary motor areas (Devinsky, Morrell, & Vogt, 1995). These connections suggest that these ACC regions play a critical role in high level motor-control and action selection. Caudal-dorsal regions share further connections with other neural systems involved in reward processing and decision making, such as the mesencephalic dopamine system (Crino, Morrison, & Hof, 1993) and orbitofrontal cortex (van Hoesen, Morecraft, & Vogt, 1993). The ERN (Dehaene, Posner, & Tucker, 1994; Holroyd, Dien, & Coles, 1998) and the FN (Gehring and Willoughby, 2002; Holroyd et al., 2004; Miltner et al., 1997) seem to be generated in dorsal regions of the ACC, although the source of the FN is controversial (Nieuwenhuis, Slagter, von Geusau, Heslenfeld, & Holroyd, 2005).

The rostral-ventral ACC (rostral areas 24a-c and 32, and ventral areas 25 and 33) corresponds to the affective subdivision, and is connected to the amygdala, periaqueductal gray, nucleus accumbens, hypothalamus, hippocampus, anterior insula and orbitofrontal cortex (Devinsky et al., 1995). This affective subdivision is concerned with processing and integration of emotional information (Bush, Luu, & Posner, 2000; Simpson, Drevets, Snyder, Gusnard, & Raichle, 2001).

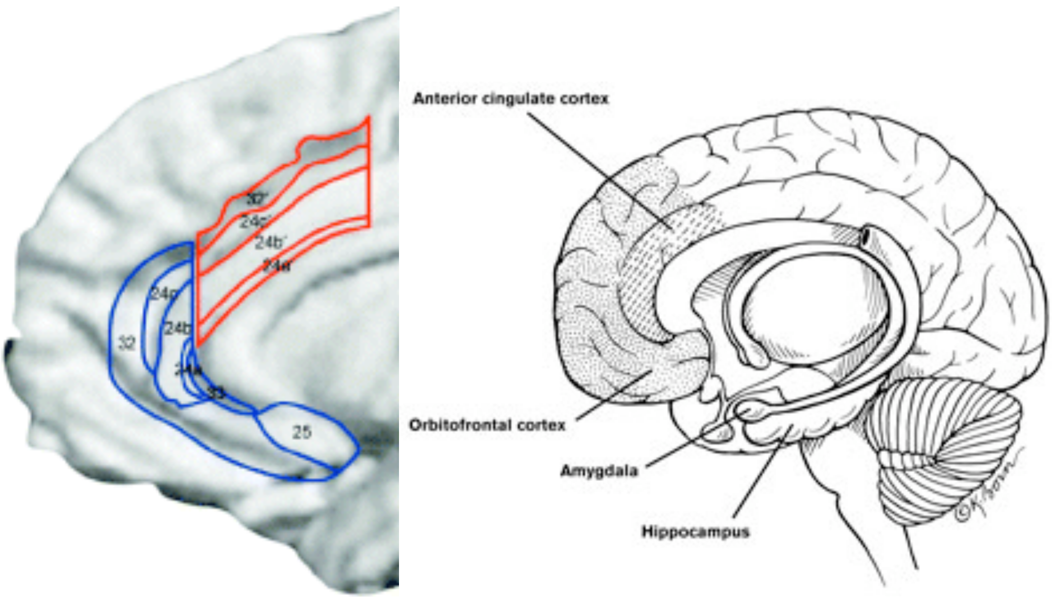


Fig.4: Cytoarchitectural subregions of anterior cingulate cortex (ACC) per Brodmann system (dACC subregions in red and rACC subregions in blue). (adapted from Bush et al. 2000)

Additional to source localization analyses, which identified the ACC as probable generator of the feedback negativity, neurophysiological evidence is consistent with this position. fMRI studies found enhanced activation related to error feedback (Ullsperger & Von

Cramon, 2003) and to unexpected decreases in rewards (Bush, Vogt, Holmes, Dale, Greve, Jenike et al., 2002; Holroyd, Nieuwenhuis, Yeung, Nystrom, Mars, Coles et al., 2004) in a dorsal region of the ACC. Single-cell recording studies in primates reported increased activity of neurons in the ACC following negative outcomes, such as the absence of expected rewards (Niki & Watanabe, 1979; Ito, Stuphorn, Brown, & Schall, 2003). In addition, a study by Holroyd et al. (2004) described a single area in caudal and dorsal ACC as being activated by both error responses and by error feedback. Finally the orientation of pyramidal cells in the anterior cingulate sulcus, in contrast to the cortical layers in the nearby cingulate gyrus and supplementary motor area (SMA), could generate a negative frontocentral negativity such as the feedback negativity (Holroyd & Coles, 2002).

Consistent with these findings that the caudal-dorsal ACC is involved in feedback and reward processing, as well as in high-level motor control and action selection, ACC has been implicated in various critical cognitive functions, such as response conflict monitoring (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Yeung, Botvinick, & Cohen, 2004), error detection (Miltner et al., 1997), evaluation of reward value (Gehring & Willoughby, 2002), and response selection or selection for action (Picard & Strick, 2001; Holroyd and Coles, 2002).

According to Miltner et al. (1997) the FN reflects the operation of an error-processing system. They further proposed that FN and error-related negativity are functionally similar. Miltner et al. (1997) suggested that these two components may reflect activation of a generic error detection system. FN and ERN are thought to reflect the outcome of a comparator process that detects errors as mismatches between the actual response and knowledge about the correct or intended response(Coles, Scheffers, & Holroyd, 2001; Falkenstein et al., 1991, 2000; Gehring et al., 1993; Scheffers, Coles, Bernstein, Gehring, & Donchin, 1996; Scheffers & Coles, 2000).

Conflict monitoring theory, another theory of anterior cingulate function, acts on the assumption that ACC regions detect response conflict. Response conflict is defined as the coactivation of mutually incompatible responses (Yeung, Ralph, & Nieuwenhuis, 2007), detected by the ACC to signal the requirement for increased cognitive control to the lateral prefrontal cortex, when conflict is high (Botvinick et al., 1999; Carter et al.,1998). In connection with errors conflict develops when continued stimulus processing after an error leads to activation of the correct response (Yeung et al.,2007). Activation of the correct response results in conflict with the incorrect response just produced. From this point of view the ACC carries out a monitoring function and instigates intervention in other systems, to regulate behavior.

The conflict monitoring theory suggests that the error-related negativity is elicited by these particular conflicts, proposing that the higher the conflict, the larger the ERN (Botvinick et al., 2001). According to Holroyd and Coles, the weakness of the conflict monitoring theory is due to the insufficient possibility to account for the FN, because the FN follows the response and cannot be explained as an outcome of conflict emerging in the response generation.

Two related theories (Holroyd & Coles,2002; Gehring & Willoughby, 2002) have emphasized the reward signaling function of feedback and associate the FN with processing of the reward value and motivational significance of ongoing events, rather than relating the FN specifically to error monitoring.

3.2 Reinforcement learning theory

Holroyd and Coles (2002) extend Miltners hypothesis that negativities subsequent to response errors (ERN) and negative feedback (FN) were related to the same neural and cognitive error detecting process (1997), by suggesting that the ERN as well as the FN are produced by a dopamine system for reinforcement learning. This assumption is based on preceding research, which connected the basal ganglia and midbrain dopamine system with reinforcement learning and reward prediction.

According to this previous research (Barto, 1995; Montague, Dayan, & Sejnowski, 1996) the basal ganglia, a group of interconnected subcortical nuclei, compute the value and the change in value of ongoing events. In other words, the basal ganglia predict whether ongoing events will end in success or failure (Nieuwenhuis et al., 2004). Whenever the basal ganglia determine that ongoing events are worse than expected, they induce phasic increase in the activity of midbrain dopaminergic neurons. Conversely, if the basal ganglia adjust their predictions for the better (ongoing events are better than expected), they induce phasic increases in dopaminergic activity. The basal ganglia use these phasic increases and decreases in dopamine activity to update their predictions. Holroyd and Coles propose that these reward predictions can be based on internal information (erroneous responses) or external information (negative feedback). The dopamine signals are carried to several cortical brain regions, including a fraction of the ACC, serving as reinforcement learning signal to modify adaptive behavior.

According to Holroyd and Coles (2002) the ACC is the recipient of these reinforcement learning signals. They suggest that the arrival of information about changes in reward prediction elicits the feedback negativity in the ACC. Holroyd and Coles further propose that phasic decreases in dopamine activity (ongoing events are worse than expected) are connected with larger FNs and phasic increases in dopamine (ongoing events are better than expected) are connected with small FNs. Positive dopamine signals inhibit the apical dendrites of motor neurons in ACC, while negative dopamine signals disinhibit these apical dendrites, which is displayed at the scalp in the form of the FN. Thus, the FN is elicited whenever the monitoring system detects that the consequences of an action are worse than expected. The size of the prediction error is proportional to the amplitude of the FN. Consequentially the reinforcement learning theory suggests that the FN is sensitive to deviance from the expected value of the reward (Nieuwenhuis et al., 2004). According to this position, the ACC uses information, conveyed by the midbrain dopamine system, to learn about consequences of recent actions and to consequently improve future response selection. Thus, the dopamine signals are used to guide action selection mediated by cingulate motor areas via negative reinforcement of inappropriate behavior.

Gehring and Willoughby (2002) proposed a related theory that differs in the assessed role of the ACC. While Holroyd and Coles assume that ACC is the recipient of evaluative information, Gehring and Willoughby suggest that FN directly reflects the role of ACC in evaluating the motivational significance of ongoing events. From this point of view ACC is seen as the source of evaluative information, while the FN reflects this evaluation of whether ongoing events are bad or good. Thus, the FN is suggested to reflect a rapid assessment of the motivational impact of an event. This assessment contributes to the evaluation of outcomes, which in turn is particularly sensitive to losses (Gehring & Willoughby, 2002). Contrary to the reinforcement learning theory these evaluated events are not bound to executed actions.

If the FN reflects an evaluation of ongoing events, regardless of whether those events are connected to recently executed actions, the feedback negativity should be related to feedback stimuli in general, whereas if it reflects the usage of this reward information to reinforce or punish recently executed responses, FN should only follow feedback to a specific performed action (Yeung, Holroyd, & Cohen, 2005)
However several studies (Yeung et al., 2005; Donkers, Nieuwenhuis, & van Boxel, 2005) demonstrated that the FN can be elicited by outcomes that are not contingent upon recent actions. For instance Yeung et al. (2005) demonstrated that the FN occurs as well for passive tasks, with negative outcomes. These findings suggest that the FN reflects the reward signal alone and therefore, the evaluation of the motivational impact of outcomes.
According to Yeung et al. (2005) another possible explanation for these findings in accordance with the assumption that the ACC plays a crucial role in action selection (Picard & Strick, 2001; Holroyd & Coles, 2002) would be that the ACC does not only use reward signals to reinforce representations of actions in terms of instrumental conditioning. In fact the ACC could use these representations of actions to learn about contingencies in the external environment (classical conditioning). Thus, Yeung and colleagues suggest that expectations about environmental contingencies could be regarded as covert responses, which in turn may be reinforced or punished. Therefore the reinforcement learning theory will need to be extended in future research to match these findings.

4. Emotional faces

Humans use a wide range of information available to form expectations about other people‘s behavior. According to Scharlemann, Eckel, Kacelnik, & Wilson (2001) people predict the choices of others based on a vector of characteristics, which can be either inherent or intentional. Inherent characteristics include gender, ethnicity, or age. These characteristics signal a type. Additionally, individuals display social signals through language, body language and facial expressions.

Particularly the human face appears to be an outstanding source of information and seems to play an important role in signaling social intentions. An extensive body of research is addressed to the investigation of human faces and what their expressions mean to observers. Darwin (1872/1998) suggested that humans, as well as animals, have evolved patterns of signaling behavior, such as facial expressions. Ekman (1972;1983), who follows Darwin‘s account, acts on the assumption that if facial expressions are evolved, humans must share a common universal set. Since many facial expressions are involuntary, the question arises what faces reveal about the underlying emotional state of the expressor. Ekman (1972) argued that facial expressions signal corresponding emotional feelings. From this point of view facial expressions signal a specific emotional state of the expressor. This emotional content should be apparent to others, since the expressions are evolved and all humans share the same universal repertoire of expressions. Support for these assumptions comes from findings that demonstrated that humans, regardless of the culture, identify several expressions of emotions in the same way (Ekman, 1983). According to Ekman (1983) six distinct emotions exist, including surprise, sadness, fear, disgust, anger and happiness.

Fridlund (1994) challenges this „emotions view“ with the proposal of a „behavioral ecology“ view of faces. According to Fridlund facial expressions are social tools, evolved to convey intentions to a certain audience. Humans have an evolved awareness and ability to understand the social implications of faces. The impact of facial expressions varies in dependence of the social context and the facial displays occur due to social motivation. A smile for example, could convey solidarity, sympathy, approval or appeasement.

The social functional analysis of emotions (Frijda, 1994; Keltner & Haidt, 1999) takes up a related position. According to Keltner and Haidt (1999) especially in dyadic settings the communication of emotions conveys essential information to receivers about the sender’s beliefs and intentions.

In the end these theories share the assumption that people derive information from the observation of faces of others, no matter whether facial expressions signal a specific emotional state or serve as a social tool.

4.1 Display of emotions in negotiations

As mentioned above people infer information and expectations about other peoples‘ behavior from displayed social signals, such as the facial expression. Based on this assumption research on negotiation behavior includes the investigation about how emotions and emotional display affect interdependent decision making. In this context emotional states and the display of emotions are regarded as predictors of negotiated outcomes (Kopelman et al. 2006). Displayed emotions, whether positive or negative, may influence social interactions in various ways, since they could convey information which in turn may have behavioral consequences. Furthermore, displayed emotions have influence on strategic information processing (Forgas & George, 2001) and may serve as means of persuasion (Forgas, 2001).

Generally induced positive emotions seem to increase cooperative behavior (Forgas, 1998), while negative affect may have an opposed impact, as demonstrated by Pillutla and Murnighan (1996) in the Ultimatum Game. People in negotiations seem to reciprocate their opponent's emotions (Keltner & Haidt, 1999). They get angry when confronted with an angry opponent and happy when confronted with a happy opponent (Friedman, Anderson, Brett, Olekalns, Goates, & Lisco, 2004).

In respect of displayed emotions, more precisely the display of emotional faces, Kopelman , Rosette, & Thompson (2006) found that those players who displayed negative emotions in the Ultimatum Game prior to making an offer were more likely to elicit rejections than those displaying either neutral or positive emotions.

Thus, facial signals conveying social intentions seem to have considerable influence on peoples‘ emotions and how they evaluate and behave towards other people.

5. Recapitulation and Preview

As stated in the theoretical part, the FN is a component of the event-related brain potential that is elicited by feedback stimuli indicating unfavorable outcomes. The reinforcement learning theory considers the FN to reflect a negative reward prediction error signal that is elicited when the monitoring system detects that the consequences of recently executed actions are worse than expected. Furthermore this error signal is used to negatively reinforce inappropriate behavior. Thus, the FN is regarded to reflect a process of performance monitoring and/or learning about recently executed actions. However Yeung et al. (2005) demonstrated that the FN also occurs for passively experienced negative outcomes. Since the FN was elicited by outcomes that were not contingent with recent actions, Yeung et al. suggested that expectations of rewards associated with particular stimulus characteristics, thus, expectations about environmental contingencies, could be regarded as covert responses, which in turn may be reinforced or punished.

To test this suggestion the present study evaluated the FN while diverse facial expressions (happy, angry) of the proposers in the Ultimatum Game served as stimuli, which were meant to affect expectations of succeeding offers. The presumption that the diverse facial expressions lead to diverse expectations towards succeeding offers, is based on the postulation that communicated emotions convey essential information to receivers about the sender's beliefs, intentions and emotions (Keltner and Haidt, 1999). According to Fridlund (1994) the intention communicated via an angry face would be „readiness to attack", while a happy a face would convey solidarity, sympathy, approval or appeasement. It is assumed that these intentions will be perceived by the participants, who took over the role of responders in the Ultimatum Game, and will result in diverse expectations towards offers provided by proposers displaying either a happy facial expression or an angry facial expression. Prior to the particular offers pictures of the proposers, either displaying a smile or an angry face, were shown to the participants. In accordance with the finding of Polezzi et al. (2008) the FN should be elicited, whenever the responders are confronted with low offers, since people tend to expect fair offers (Chang & Sanfey, 2009). If the FN reflects a monitoring system that is not exclusively sensitive to performance but also to deviations from expected environmental contingencies, the amplitude of the FN should be more pronounced at low offers provided by smiling proposers, than at low offers provided by proposers with an angry face. Low offers made by proposers showing a smile prior to the offer should violate the proposers expectations to a larger extent than low offers provided by angry proposers, which in turn should affect the amplitude of the FN.

Furthermore it is assumed, that the FN is generated in or near the anterior cingulate cortex.

Empirical Part

1. Materials and Methods

1.1 Participants

Thirty right-handed subjects, fifteen women and fifteen men, between the ages of 18 and 33 years, participated in the current experiment. The data of two male participants had to be excluded from further analysis due to inadequate behavior. The mean age of the remaining 28 subjects was 25,75 years (standard deviation [SD] = 3,11). Handedness was assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). All Participants had normal or adequately corrected vision, were free of neurological diseases and had no psychiatric history. The study was conducted in accordance with the Declaration of Helsinki and local guidelines and regulations of the University of Vienna. Prior to participation, written informed consent was obtained from each participant.

Participants were told that they would be paid based on their choices in the game, but in fact, performance was unrelated to subjects‘ remuneration. All subjects received € 10 for participating, subsequently to the experiment.

1.2 Task and Procedure

The participants were comfortably seated at a viewing distance of roughly 70 cm in front of a 19-in. CRT computer monitor in a sound-attenuated room. Stimulus presentation and synchronization with the EEG data collection was controlled by E-Prime 2.0 (Psychology Software Tools, Inc.; http://www.pstnet.com). The participants assumed the role of the responder in the Ultimatum Game. Participants were told that they would play with several proposers and that on each trial a proposer would make an offer of how to split € 10 between them. Furthermore the participants were instructed to decide if they would accept or reject the offer.

Each trial started with a black fixation cross on a grey background, having a duration of 2000 ms. Subsequently the participants were presented with a grayscale frontal photographic image of the face of the current proposer (8,7 cm × 9,5 cm; adopted from the

Averaged Karolinska Directed Emotional Faces; Lundqvist, Flykt, & Öhman,1998) for 2000 ms. The selected photographs included 60 posers (30 male and 30 female) each depicting two facial expressions (angry, happy). In the following 1500 ms the participants were presented with the offer made by the proposer, indicated through two numbers, displayed one above the other, where the bottom number represented the amount of money the participant would receive. There were three different offer conditions: a fair condition (participant received € 5, proposer kept € 5), a midfair condition (participant received € 3, proposer kept € 7) and an unfair condition (participant received € 1, proposer kept € 9). After the presentation of the particular offer, participants had to accept or reject the offer by keypress. Two boxes, one left of the center, the other one right of the center were displayed beneath the offer. One of the two boxes included the word „accept“, the other one the word „reject“. The participants used the right index finger on the „1“ key of the numeric keypad to choose the box on the left side of the screen and the middle finger on the „2“ key of the numeric keypad to choose the box on the right side. The assignment of the two response options („accept“ and „reject“) towards the two boxes varied randomly throughout the task, in order to keep attention high. The stimuli remained on until the participants‘ decision and keypress.

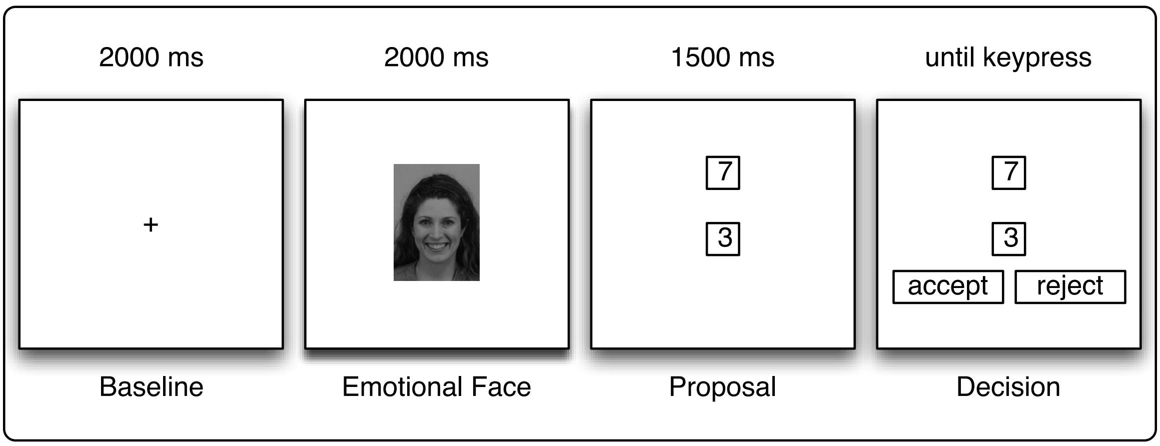


Fig 5: Example trial: trial sequence for a midfair offer provided by a happy proposer.

The task consisted of 360 trials, resulting from the combination of each of the 120 emotional face stimuli (60 happy, 60 angry) with each offer condition (fair, midfair, unfair).

Hence there were six experimental conditions that guided the data analysis:

1. happy proposer - fair offer
2. happy proposer - midfair offer
3. happy proposer - unfair offer
4. angry proposer - fair offer
5. angry proposer - midfair offer
6. angry proposer - unfair offer

All of the 360 trials were presented fully randomized within six blocks of 60 trials each. At the end of each block during self-controlled rest breaks, participants received visual feedback indicating the cumulative amount of money earned. Each block was initiated by the participants at their own pace. The entire task lasted approximately 55 minutes.

2. Electroencephalographic recording

EEG recordings were taken from 61 Ag/AgCl electrodes equidistantly embedded in an elastic electrode cap (EASYCAP GmbH; http://www.easycap.de, model M10). A noncephalic sternovertebral reference (Stephenson and Gibbs, 1951), consisting of two electrodes, one placed at the 7th cervical vertebra and the other at the right sternoclavicular junction, was used for all EEG channels. The electro-oculogram (EOG) was recorded from electrodes placed above and below the left eye, and from electrodes placed on the outer canthi of each eye with a bipolar setting to allow off-line eye movement correction. The ground electrode was placed on the forehead. To ascertain stable and homogenous electrode impedances below 2 kΩ the skin was scratched using a sterile single-use needle to slightly remove dead skin cells (Picton & Hillyard, 1972) at each electrode site prior to

EEG recording. Degassed electrode gel (Electro-Gel, Electrode-Cap International, Inc., Eaton/OH, USA) was filled into each electrode. Impedances were measured for each electrode by a manual impedance meter and kept below 2 kΩ. Individual 3D coordinates of 17 pre-defined electrode locations, referenced to nasion, inion, and the two preauricular electrodes, were measured for all subjects with a photogrammetric head digitizer (3D-PHD; Bauer, Lamm, Holzreiter, Holländer, Leodolter, & Leodolter, 2000). A standard head model was fit into these 17 pre-defined electrode positions and the missing electrodes were interpolated based on the eqidistant electrode montage.
All signals were recorded within a frequency range of 0.1 to 125 Hz and sampled at 250 Hz for digital storage.

3. Data analysis

3.1 Behavioral Data

Friedmans *ANOVA* was performed with type of *OFFER* (fair, midfair, unfair) and *FACIAL EXPRESSION* (happy, angry) as independent variables and acceptance rates as dependent variable. Furthermore pairwise comparisons were accomplished using Wilcoxon signed-rank tests. For each comparison Bonferroni corrections were used.
A 3 x 2 repeated measures *ANOVA* was carried out with type of *OFFER* (fair, midfair, unfair) and *FACIAL EXPRESSION* (happy, angry) as independent variables and reaction times (RTs, the time period between offer onset and keypress) as dependent variable.

3.2 EEG Data

Artefacts due to eye movements were removed by successive subtraction of the weighted horizontal and vertical EOGs from each EEG channel trial by trial. Weights were calculated as the ratio of the covariance between each EEG channel and the EOG, and the variance within the EOG channels. These parameters were derived from two pre-experimental calibration trials where subjects performed guided vertical and horizontal eye movements (Bauer & Lauber, 1979). Blink coefficients were calculated using a template matching procedure and subtracted from each EEG channel trial by trial (see Lamm, Fischmeister, & Bauer, 2005, for a detailed description).

Off-line analysis was performed using EEGLAB 6.03b (Delorme & Makeig, 2004), implemented in Matlab 7.5.0 (The MathWorks). EEG data were low-pass filtered with a cut-off frequency of 30 Hz (roll-off 6 dB per octave) and epoched for each trial, starting 200 ms before feedback onset and lasting for 1200 ms. The 200 ms interval preceding stimulus onset served as baseline. A semi-automatic artefact removal procedure was applied to the data of all subjects. Artefact-affected trials meeting the following criteria were labelled and finally rejected after visual inspection: voltage values exceeding +/-75µV in any channel or a voltage drift of more than 75 µV. Furthermore trials containing muscular or movement artefacts were rejected based on visual inspection. Seven subjects of the original sample were excluded from further analysis due to enormous artefacts (21 subjects, 12 women and 9 men, remained, with a mean age of 25,71 years (standard deviation [SD] = 2,95).)

3.3 ERP Data Analysis

Signal averaging was carried out separately per subject and per condition and grand averages of the six conditions were calculated. Data were grouped into 6 conditions including the factors facial expression and proposal: (i) happy proposer - fair offer *(happy-fair)*, (ii) happy proposer - midfair offer *(happy-midfair)*, (iii) happy proposer - unfair offer *(happy-unfair)*, (iv) angry proposer - fair offer *(angry-fair)*, (v) angry proposer - midfair offer *(angry-midfair)*, (vi) angry proposer - unfair offer *(angry-unfair)*. To quantify the FN peak to peak voltage differences between the first negative peak 200-300 milliseconds after the onset of the Ultimatum Game offer and the average voltage value of the immediately preceding and following positive peak were assessed at electrode Fz (electrode Fz was chosen based on visual inspection of the grand mean and consistent to relevant literature on the FN; see for example Gehring and Willoughby, 2002). This method was employed according to Polezzi et al. 2008. The resultant FN data were analyzed using a 2 x 3 repeated measures analyses of variance (*ANOVA*) with *FACIAL EXPRESSION* (happy, angry) and *OFFER* (fair, midfair, unfair) as repeated-measures factors. The significance threshold was set at $P \leq 0.05$, two-tailed. P-values were corrected by the Greenhouse-Geisser adjustment where appropriate. Furthermore, planned contrasts were accomplished. Additionally, mean amplitude measures were calculated within a window of 200-300 ms following the presentation of the proposal and subjected to a repeated measures *ANOVA* with the factors *LOCATION* (electrode sites Fz, FCz, Cz and Pz), *FACIAL EXPRESSION* (happy, angry) and *OFFER* (fair, midfair, unfair).

3.4 Source analysis

Source localization and analysis was carried out using standardized low-resolution brain electromagnetic tomography (sLORETA; Pascual-Marqui, 2002). sLORETA is an inverse solution technique that estimates the distribution of the electrical neuronal activity in three-dimensional space by assuming that neighboring neurons are simultaneously and synchronously activated, followed by an appropriate standardization of the current density, producing images of electric neuronal activity without localization bias (Greenblatt, Ossadtchi, & Pflieger, 2005; Pascual-Marqui, 2002). sLORETA does not require any assumptions about the number, localization, configuration, or extent of neuronal sources. Mean amplitudes between 60 ms and 460 ms subsequent to the feedback onset using a step size of 20 ms were transformed. Individual electrode coordinates acquired via PHD were cross-registered to the standard Talairach atlas (Talairach & Tournoux, 1988) resulting in three-dimensional distributions of cortical activation for each subject and each condition. The sLORETA solution space is restricted to cortical gray matter and hippocampus, defined via the MNI (Montreal Neurological Institute) reference brain and subdivided into 6239 voxel, with a spatial resolution of 5 x 5 x 5 mm^3. Subsequently MNI space is transformed to Talairach space. sLORETA computes the electric activity at each voxel as the squared standardized magnitude of the estimated current density. A regularization parameter of zero was used for the transformation to achieve the smoothest of all possible solutions. Overall signal-to-noise-ratio was set at a ratio of 100 within the transformation process. The voxel-based sLORETA-images were compared between the conditions using the sLORETA-built-in voxelwise randomization tests (5000 permutations) based on statistical non-parametric mapping (SnPM) (for details see: Holmes, Blair, Watson & Ford, 1996).

4. Results

4.1 Behavioral Results

4.2 Acceptance rates

Acceptance rates differed significantly (see Fig. 6) among conditions ($\chi 2(5)$=68, 64, *Asymp. P* = 0,000). Wilcoxon tests were used to follow up this finding. A Bonferroni correction was applied and so all effects are reported at a 0,003 level of significance. Subjects accepted fair offers from happy proposers significantly more often (96.6%) than midfair offers (59.2%), (T = 1.5, Z = - 3.765, *Exact. P* = 0.000) and unfair offers (19.2%), (T = 1, Z = - 3.987, *Exact. P* = 0.000) from happy proposers. Furthermore midfair offers yielded higher acceptance rates than unfair offers (T = 5.5, Z = - 3.603, *Exact. P* = 0.000) in the happy proposer condition.

Similarly, subjects accepted fair offers (90.7%) significantly more often than midfair offers (37.3%), (T = 3, Z = - 3.911, *Exact. P* = 0.000) and unfair offers (14.3%), (T = 1, Z = - 3.992, *Exavt. P* = 0.000) from angry proposers. Midfair compared to unfair offers approached significance (T = 18, Z = - 2.773, *Exact. P* = 0.004).

Finally the facial expression of the proposer significantly affected the acceptance rates of midfair offers (see Fig. 7). Midfair offers provided by happy proposers were significantly less often rejected than midfair offers provided by angry proposers (T = 16, Z = - 3.181, *Asymp. P* = 0.001). In contrast, unfair and fair offers were rejected similarly often for happy and angry proposers.

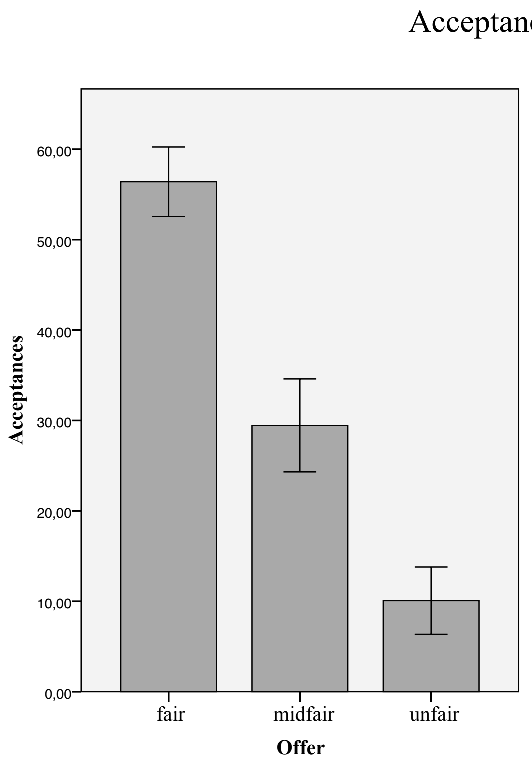
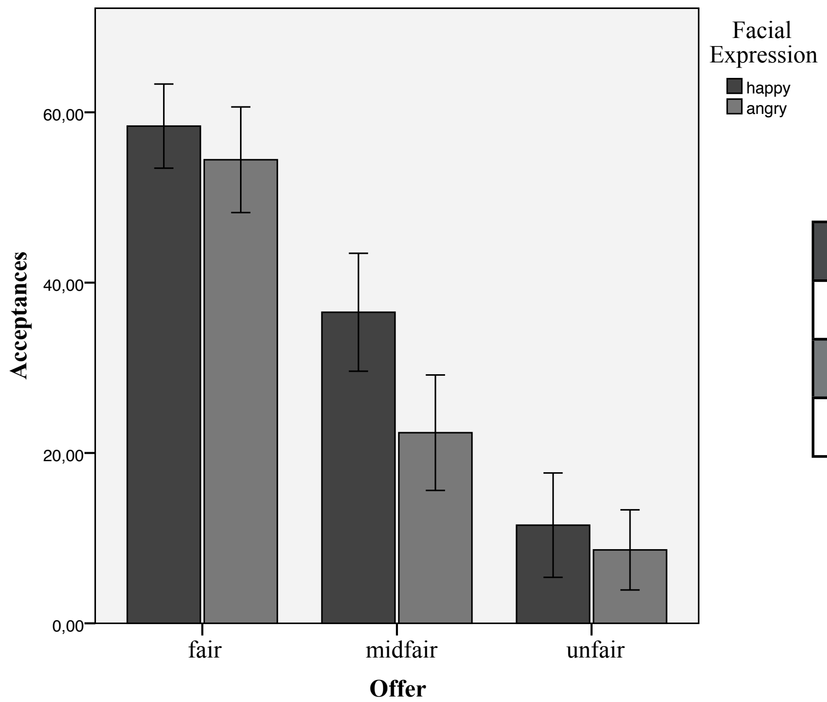


Fig.6: Acceptance rates for the three types of offers displayed in absolute values (maximum = 60, as each of the six conditions contained 60 trials) and error bars (CI = 95%).



Acceptance Frequency

fair	midfair	unfair
96,66%	59,206%	19,206%
fair	midfair	unfair
90,71%	37,30%	14,36%

Fig.7: Acceptance rates for the different types of offers and facial expressions displayed in absolute values and error bars (CI = 95%).

4.3 Reaction times

Following the procedure suggested Knutson, Rick, Wimmer, Prelec, & Loewenstein (2007) RTs were transformed using a logarithmic function. As illustrated in Fig. 8, RTs differed significantly between types of offers ($F_{(2, 40)} = 6.1$, $P = 0.004$). Planned contrasts revealed that decisions in the *HAPPY* condition about midfair offers (1118 ms) took significantly longer compared to fair offers (931 ms) (Fig.9), (midfair vs. fair: $F_{(1, 20)} = 12.48$ $P = 0.002$). No other contrast reached significance. The repeated measures *ANOVA* of the RTs showed no main effect for *FACIAL EXPRESSION* ($F_{(1, 20)} = 0.61$, $P = 0.44$), indicating that the facial expression of the proposer had no impact on the RTs (see Fig. 7).

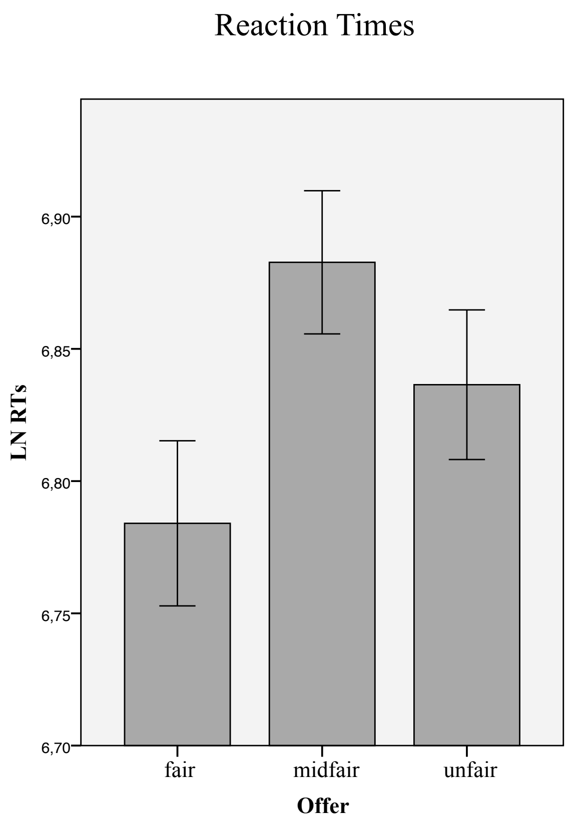


Fig.8: LN RTs for the three different types of offers and error bars (CI = 95%).

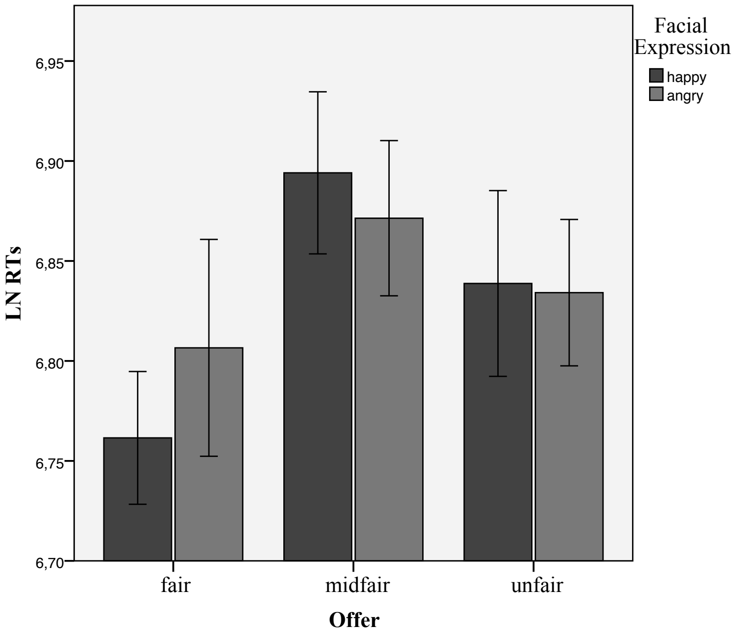


Fig.9: LN RTs for the different types of offers and facial expressions and error bars (CI = 95%).

Mean LN RTs / RTs in ms

fair	midfair	unfair
6,76 931 ms	6,88 1118 ms	6,84 1048 ms
fair	midfair	unfair
6,80 1010 ms	6,86 1106 ms	6,83 1039 ms

Total Mean	SD
1042,3 ms	674,45

4.4 ERP DATA

4.4.1 Mean Amplitude Measures

Mean amplitude measures were calculated within a time window of 200-300 ms following the presentation (see Nieuwenhuis, Yeung, Holroyd, Schurger, & Cohen, 2004) of the offer and submitted to a 4 x 2 x 3 repeated measures *ANOVA* with the factors *LOCATION* (electrode sites Fz, FCz, Cz and Pz), *FACIAL EXPRESSION* (happy, angry) and *OFFER* (fair, midfair, unfair). There were no significant main effects. The interaction effect between the two factors *LOCATION* and *OFFER* reached the statistical threshold ($F(2.39, 47.85) = 3.28$, $P = 0.038$). Planned contrasts revealed significant differences when comparing electrodes FCz and Pz for fair offers compared with unfair offers ($F(1, 20) = 7.985$, $P = 0.01$). Furthermore significant differences were revealed when comparing electrodes Cz and Pz for fair offers compared with unfair offers ($F(1, 20) = 7.987$, $P = 0.01$), indicating larger differences in the FN amplitude between fair and unfair offers at electrode positions FCz and Cz, than at electrode Pz. No other interactions were significant.

Due to differences in FN latencies at electrode FCz (significant main effect for FACIAL EXPRESSION ($F(1,20)$ = 4.92, P = 0.038)), and at electrode Fz (significant main effect for *OFFER* ($F(2,42)$ = 3.39, P = 0.043)) and the risk of other components contaminating the FN (overlap with the P300, while differences in absolute reward magnitude affect the amplitude of the P300; see Sutton, Tueting, Hammer, & Hakerem, 1978) the results of the mean amplitude measures calculation are reported but will not enter the discussion.

4.4.2 FN – Amplitude / Peak-to-Peak

Grand-average waveforms for all conditions, for the *HAPPY* condition, for the *ANGRY* condition and for unfair offers in both facial expression conditions at electrode site Fz are displayed in Figures 12 and 13.

Scalp topographies of the voltage differences for the FN peak latency (235 ms) between unfair and fair offers in the *HAPPY* condition, in the *ANGRY* condition and differences in the unfair offer condition between *FACIAL EXPRESSION* conditions are displayed in Figure 14.

FN data were analyzed using a repeated-measures *ANOVA* with *FACIAL EXPRESSION* (happy, angry) and *OFFER* (fair, midfair, unfair) as repeated-measures factors.

As illustrated in Fig. 10, FN amplitudes differed significantly between the different types of offers ($F(2, 19)$ = 6.60, P = 0.007). Planned contrasts revealed that the FN was significantly smaller for fair compared to midfair offers (midfair vs. fair: $F(1, 20)$ = 7.36, P = 0.013). The difference between fair and unfair offers reached significance (fair vs. unfair: $F(1, 20)$ = 12.11, P = 0.002), indicating a more pronounced FN-amplitude for unfair offers. Contrasts for unfair and midfair offers did not show significant amplitude differences (midfair vs. unfair: $F(1, 20)$ = 0.633, P = 0.43). Moreover, FN amplitudes differed significantly between the two types of facial expressions, ($F(1, 20)$ = 7.79, P = 0.011), indicating more pronounced FN amplitudes in the happy proposer condition. Furthermore there was a significant interaction between the two factors *OFFER* and *FACIAL EXPRESSION* ($F(2, 19)$ = 4.255, P = 0.03). This indicates that the facial expression of the proposer had different effects on the amplitude oft the FN, depending on which type of offer was made. Contrasts revealed that facial expressions differentially influenced the FN amplitude only for fair vs. unfair offers ($F(1, 20)$ = 8.89, P = 0.007). This effect shows that happy facial expression (compared to angry facial expression) elicited a more pronounced

FN amplitude for unfair offers than it did for fair offers (see Fig. 11). The remaining contrasts revealed no significant interactions.

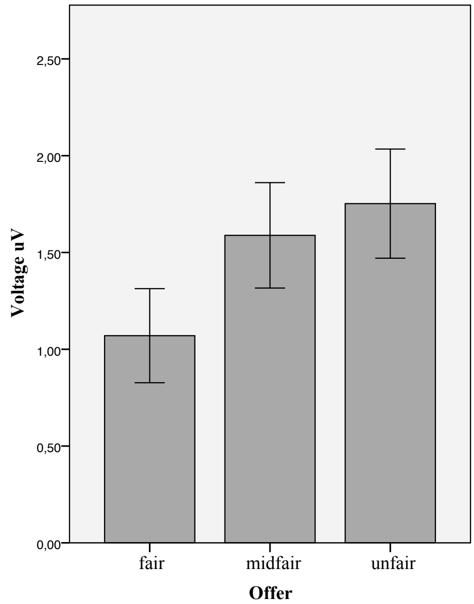


Fig. 10: mean peak-to-peak amplitudes of the FN for the three offer conditions.

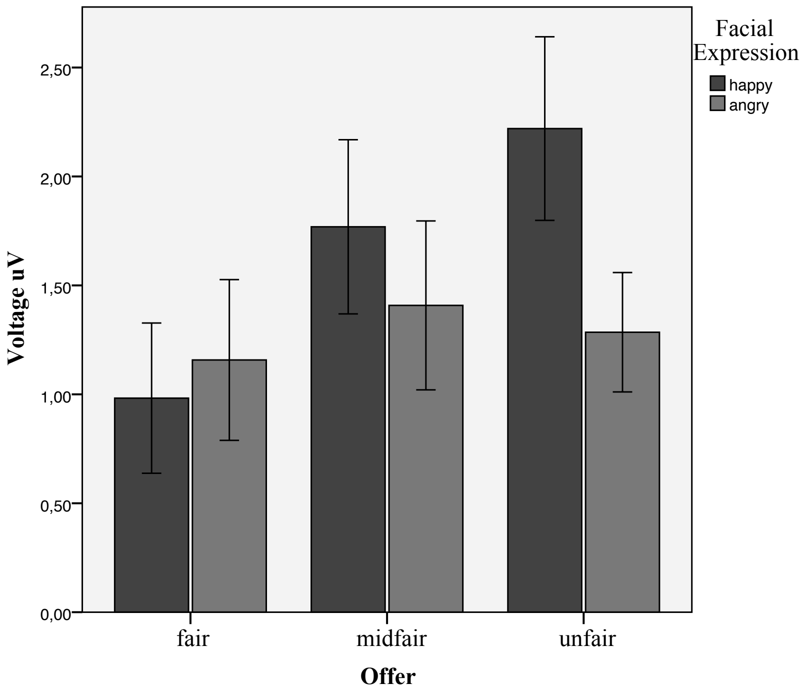


Fig. 11: mean peak-to-peak amplitudes of the FN for all six conditions.

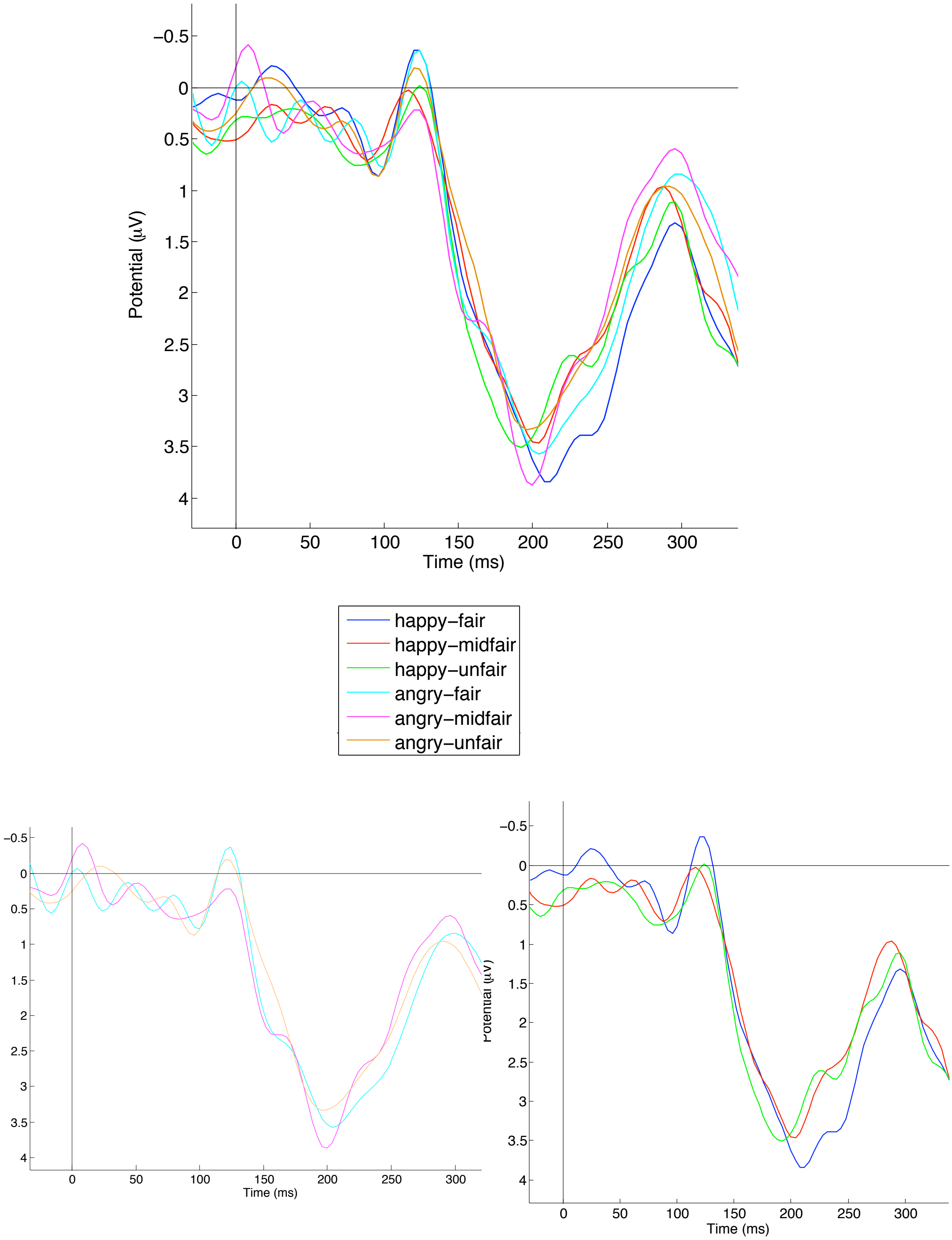


Fig. 12: Grand-average waveforms at electrode site Fz for the six different conditions (upper middle panel), and separately for the angry proposer conditions (lower left panel), for the happy proposer conditions (lower right panel).

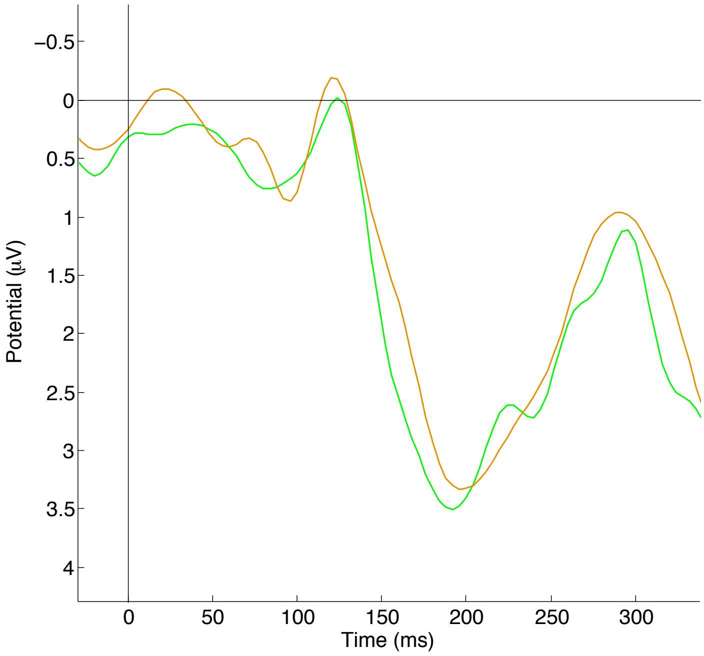


Fig. 13: Grand-average waveforms at electrode site Fz for unfair offers in both facial expression conditions.

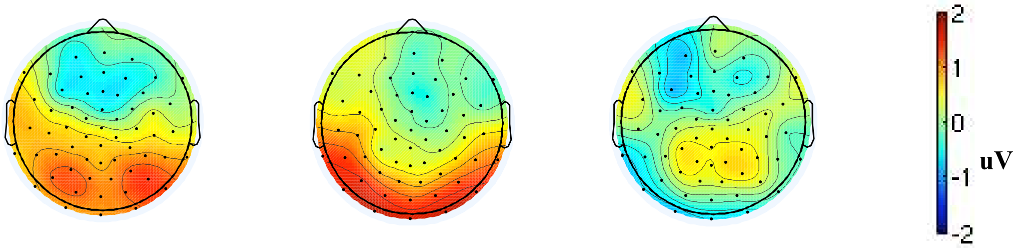


Fig. 14: Scalp topographies of the voltage differences for the FN peak latency (235 ms) between unfair and fair offers in the HAPPY condition (left panel), in the ANGRY condition (middle panel) and differences in the unfair offer condition between FACIAL EXPRESSION conditions (right panel).

4.5 Source analysis

4.5.1 Descriptive statistics of sLORETA brain activity patterns

The grand averages of the conditions *HAPPY-FAIR, HAPPY-MIDFAIR, HAPPY-UNFAIR, ANGRY-FAIR, ANGRY-MIDFAIR* and *ANGRY-UNFAIR* showed similar activity patterns at the FN latency (220-240 ms) in the parietal lobe, including the superior parietal lobule (BA7) and precuneus (BA7) (see Table 1). Figure 15 illustrates activity patterns at FN latency in the *HAPPY-UNFAIR* condition.

Condition	Latency-Range	Anatomical region (BA)	MNI Coordinates
HAPPY-FAIR	220-240 ms	Superior Parietal Lobule (7)	(X)25, (Y)-70, (Z)50
		Precuneus (7)	(X)20, (Y)-70, (Z)50
HAPPY-MIDFAIR	220-240 ms	Superior Parietal Lobule (7)	(X)25, (Y)-70, (Z)55
		Precuneus (7)	(X)30, (Y)-65, (Z)50
HAPPY-UNFAIR	220-240 ms	Superior Parietal Lobule (7)	(X)25, (Y)-70, (Z)50
		Precuneus (7)	(X)20, (Y)-75, (Z)50
ANGRY-FAIR	220-240 ms	Superior Parietal Lobule (7)	(X)30, (Y)-70, (Z)50
		Precuneus (7)	(X)25, (Y)-75, (Z)50
ANGRY-MIDFAIR	220-240 ms	Superior Parietal Lobule (7)	(X)25, (Y)-70, (Z)55
		Precuneus (7)	(X)25, (Y)-75, (Z)50
ANGRY-UNFAIR	220-240 ms	Superior Parietal Lobule (7)	(X)25, (Y)-70, (Z)50
		Precuneus (7)	(X)20, (Y)-75, (Z)50

Table 1: Localization of FN estimated activation maxima with sLORETA grand averages .

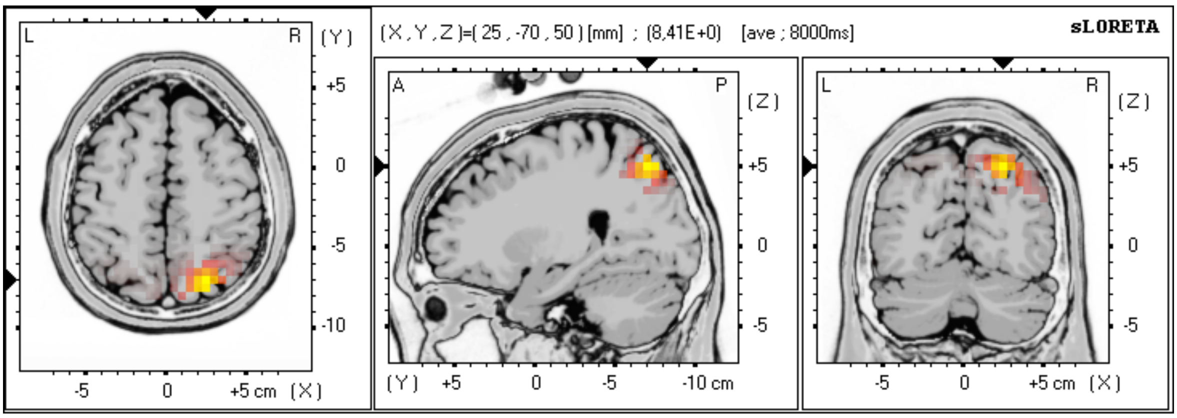


Fig.15: sLORETA images of grand averages at FN latency showing standardized estimated maxima for happy-unfair. Coordinates, anatomical structures are presented. Estimated cortical activation is shown from three perspectives (axial, sagittal, and coronal view), displayed with a scale exponent of 5.75. Activation maxima are coded in yellow and red.

4.5.1 sLORETA within-subject comparisons

SnPM was performed to address activation differences between each of the offer conditions and to compare similar offer conditions between the two facial expression conditions (comparisons of fair and midfair offers, fair and unfair offers, and midfair and unfair offers. Furthermore, *happy-fair* was compared with *angry-fair*, *happy-midfair* with *angry-midfair* and finally *happy-unfair* with *angry-unfair*). Cortical activation did not differ at the FN latency (220-240 ms) in any of the comparisons.

5. Discussion

Yeung et al. (2005) demonstrated that the FN, an ERP component related to the processing of unfavorable outcomes, can also be elicited by outcomes that are not contingent upon recent actions, such as by negative outcomes in passive tasks. This finding has been taken to suggest that the FN might not exclusively reflect the evaluation of recently executed actions as suggested by the reinforcement learning theory (Holroyd and Coles, 2002), but might reflect as well the evaluation of expectations about environmental contingencies. From this point of view environmental contingencies are considered to be covert responses which in turn may be punished or reinforced to improve the predictive validity of these expectations. The present study attempted to test this suggestion by evaluating the feedback negativity while expectations about contingencies in the Ultimatum Game were manipulated. Participants were confronted with proposers, displaying a smile or an angry face. These facial expressions were meant to affect expectations about succeeding offers.

It was predicted that low offers in general would elicit larger FN amplitudes than fair offers. In addition, the we expected that the amplitude of the FN should be more pronounced for low offers provided by smiling proposers, than for low offers provided by proposers with an angry face.

The principal findings of the present research may be summarized as follows. First, on a behavioral level, the results were very similar to those found in other Ultimatum Game experiments (Polezzi et al., 2008; Sanfey et al., 2003). Almost all fair offers (proposed split of 5/5) were accepted. Acceptance rates decreased as the offers became less fair. About half of the 7/3 offers (59.2 % in condition *HAPPY* and 37.3 % in condition *ANGRY*) and still less 9/1 offers (19.2 % in condition *HAPPY* and 14.3 % in condition *ANGRY*) were accepted. The acceptance of midfair offers was significantly influenced by the facial expression of the proposers. Midfair offers provided by angry proposers were less often accepted than midfair offers provided by happy proposers. This result stays in line with the finding of Kopelman et al. (2001) that proposers who displayed negative emotion in the Ultimatum Game were more likely to elicit rejections than those displaying either neutral or positive emotions and furthermore leads to the conclusion that the manipulation of the facial expression had relevant effects on a behavioral level. Reaction times highly resembled those reported by Polezzi and colleagues (2008), even though the button functions changed in the present study, whereas in the study conducted by Polezzi et al. (2008) participants had to press the same keys to accept or reject an offer throughout the whole experiment. Decisions about midfair offers took longer compared to fair offers.

On the electrophysiological level, larger FN amplitudes were elicited following unfavorable outcomes, more precisely after unfair and midfair offers, compared to FN amplitudes following fair offers. Differences between the FN amplitudes following fair and unfair offers were larger for the happy facial expression condition. Thus, happy proposers offering an amount of money perceived as unfair elicited a more pronounced FN amplitude compared to angry proposers offering the same amount of money.

The former result replicates the finding of Polezzi et al. (2008) that unfair and midfair offers in the Ultimatum Game elicit a larger FN than fair offers. As in this study no differences were detected between unfair and midfair offers. Furthermore the morphology of the FN found in the present study resembles the one described by Polezzi et al. (see Fig. 3, Fig.9).

This result is consistent with previous findings of large FNs being associated with unfavorable outcomes, e. g. losses in gambling tasks (Gehring and Willoughby, 2002; Hajcak et al., 2006) or negative performance feedback in a time estimation task (Miltner et al., 1997). Furthermore the finding that larger FN amplitudes were elicited following unfair and midfair offers than following fair offers matches the assumption of the reinforcement learning theory that the FN reflects an evaluation of ongoing events along an abstract good-bad dimension (Nieuwenhuis et al. 2004). Thus, the detected FN amplitudes in the present study seem to represent a rapid distinction between offers perceived as fair and the other offer conditions (midfair offers, unfair offers). Assuming that responders in the Ultimatum Game expect a fair offer (Chang & Sanfey, 2009) and that deviations from the 50-50 split equal a violation of these expectations, another basic assumption of the reinforcement learning theory, namely that the FN amplitude depends on the relation between actual versus expected outcome (Nieuwenhuis et al. 2004), applies to the recent finding.

More immediate relevance regarding the latter assumption implies the result that happy proposers offering an amount of money perceived as unfair elicited a more pronounced FN amplitude compared to angry proposers offering the same amount. Following Fridlunds „behavioral ecology“ view of faces (1994), the social signals conveyed by a happy face should lead people to expect fair rather than unfair offers, since a happy face communicates intentions as solidarity, sympathy, approval or appeasement. In contrast people should not be astonished getting unfair offers from angry looking proposers, as they signal `readiness to attack´. Whenever the actual offer deviated (in a negative direction) from expected offers, a more pronounced FN was elicited. Thus, the different FN amplitudes in the facial expression conditions can be attributed to diverse expectations.

Due to the fact that the reinforcement learning theory relates the FN to the evaluation of recently executed actions, the present results contrast at this point with the original speculation of Holroyd and Coles (2002), since prospected outcomes were not contingent upon recent actions. The finding that the FN can also be elicited by outcomes that are not contingent on recent actions is not new, since several studies (Yeung et al., 2005; Donkers et al. 2005) reported FNs in tasks where no action or response was required from the participants. The present study attempted to test the suggestion by Yeung et al. (2005), who speculated that the FN might additionally reflect the evaluation of expectations about environmental contingencies (precisely, expectations of rewards associated with particular stimulus characteristics). The present findings support this suggestion, since the combination of a happy proposer with an unfair offer presumably led to violations in expectancies, and therefore, to a larger FN. Additionally presumed violations of general expectations and fairness considerations were reflected in the FN‘s amplitude, with larger FN amplitudes following unfair and midfair offers in general.

Furthermore source analyses of the current data did not yield any significant activations. The absence of significant results could be related to the differences in FN latencies and the possibility of other components contaminating the FN amplitude. Thus, results should be interpreted with caution. Nonetheless it should be noted that it is generally assumed that the ACC is the most likely generator of the FN (e.g. Gehring and Willoughby, 2002; Holroyd and Coles, 2002), with larger FN amplitudes being associated with stronger ACC activity. Sanfey and colleagues (2003) reported heightened ACC activity for unfair offers in the Ultimatum Game which would be in accordance with the findings of the present study that unfair offers led to pronounced FN amplitudes. Furthermore, scalp topographies of the voltage differences for the FN peak latency showed a frontocentral distribution (see Figure 10)

Activation maxima with sLORETA grand averages for the six conditions were found in parietal regions (Brodmann area 7, precisely superior parietal lobe and precuneus). The superior parietal lobe was recently demonstrated to be affected by the presence of response conflict (Wendelken, Ditterich, Bunge, & Carte, 2009). Response conflict in the Ultimatum Game may be associated with the rejection of unfair offers, namely the rejection of an economically advantageous situation because of a subjective perception of unfairness. Higher activation in the precuneus in the Ultimatum Game, was reported by Rilling, Sanfey, Aronson, Nystrom, & Cohen (2004), when subjects were interacting with presumed human partners compared to computer partners. Rilling and colleagues suggested the precuneus to be one of the areas, which are recruited when participants are inferring the intentions of social partners. Thus, reported activation maxima seem to be consistent with relevant literature, but have to be interpreted with caution due to the absence of significant differences between the conditions.

To the authors‘ knowledge, the current study is the first to explicitly address the relation of the FN and environmental contingencies. The studies conducted by Yeung et al. (2005) and

Donkers et. al. (2005) concentrated on the relation of the FN and the impact of outcomes that were not contingent upon recent actions without manipulating or controlling expectations about environmental contingencies. Therefore the present study can be seen as a first step to shed light on the FN recognized as learning signal in a context including environmental expectancies.

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Appendix

I. Instruction in German

Die Spielregeln

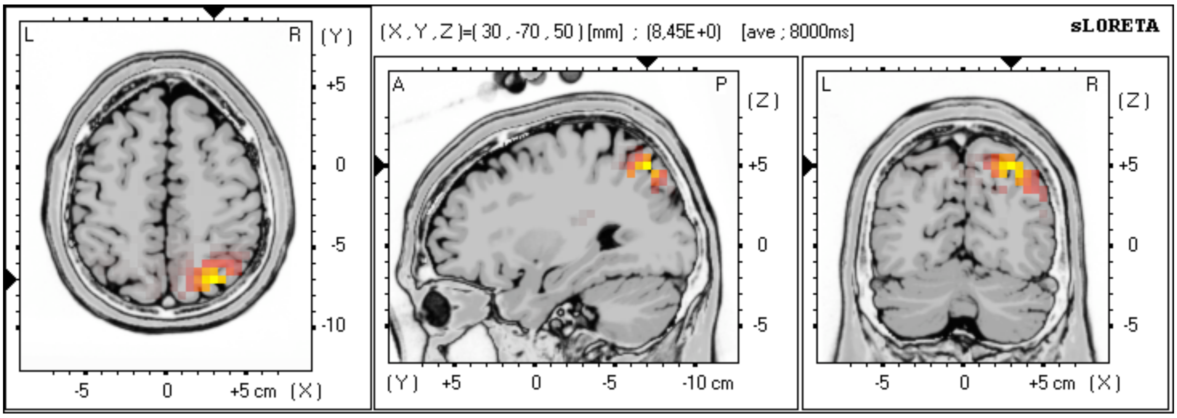
In diesem Spiel gibt es zwei Spieler (Anbieter, Spieler 1) und einen Geldbetrag von 10 €. Der Anbieter entscheidet wie er diesen Geldbetrag aufteilen möchte. Du als Spieler 1 kannst entscheiden ob du dieses Angebot annehmen oder ablehnen willst. Nimmst du das Angebot an erhalten sowohl du, als auch der Anbieter den Teil des Geldbetrags, wie er vom Anbieter aufgeteilt wurde.
Lehnst du das Angebot ab gehen sowohl du, als auch der Anbieter leer aus.

Du wirst das Foto des jeweiligen Anbieters sehen, danach folgen deren Angebote. Nach jedem Angebot erscheinen am unteren Teil des Bildschirmes zwei Kästchen mit den Antwortmöglichkeiten „annehmen" oder „ablehnen". In welchem der beiden Kästchen die jeweilige Antwortmöglichkeit steht, variiert während dem Experiment. Solltest du jene Antwortmöglichkeit wählen die rechts am Bildschirm steht, drücke bitte die Taste 2 (am Ziffernblock). Solltest du jene Antwortmöglichkeit wählen die links am Bildschirm steht, drücke bitte die Taste 1 (am Ziffernblock). Nach dem Tastendruck siehst du das Foto des nächsten Anbieters und später sein Angebot usw.

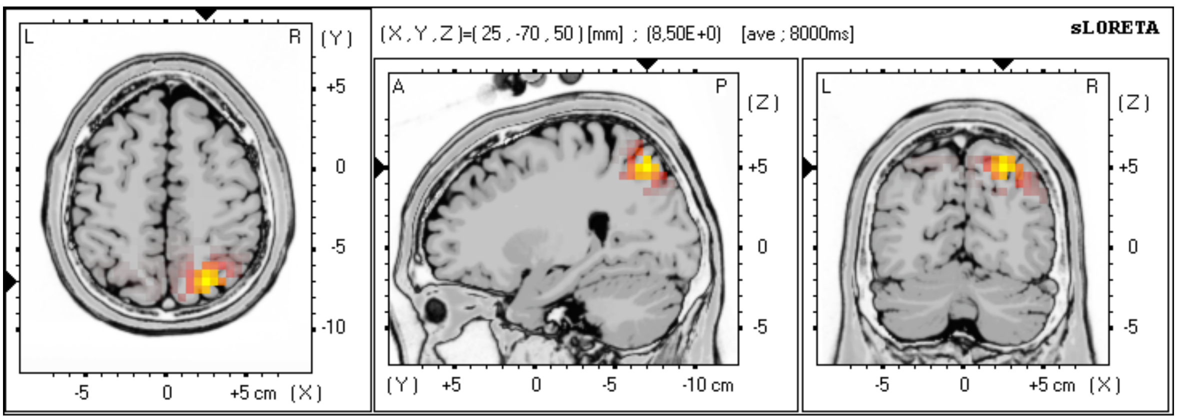
Bezahlung: Die Summe des Gewinnes wird nach einem bestimmten Punkteschlüssel berechnet, der davon abhängig ist, wie du dich im Spiel entscheidest.

II. sLORETA images of grand averages

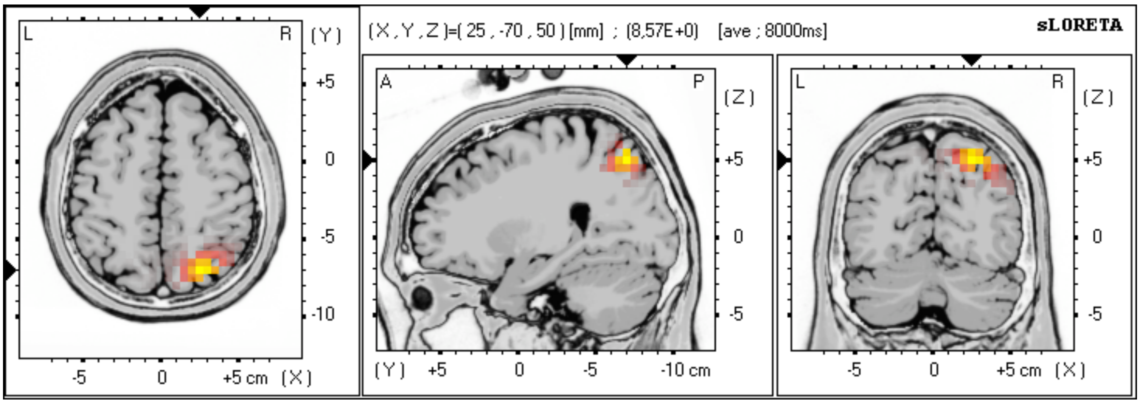
sLORETA images of grand averages at FN latency showing standardized current density maxima for the six conditions. Coordinates, anatomical structures, and Brodmann areas are presented. Estimated cortical activation is shown from three perspectives (axial, sagittal, and coronal view), displayed with a scale exponent of 5.75. Activation maxima are coded in yellow and red.



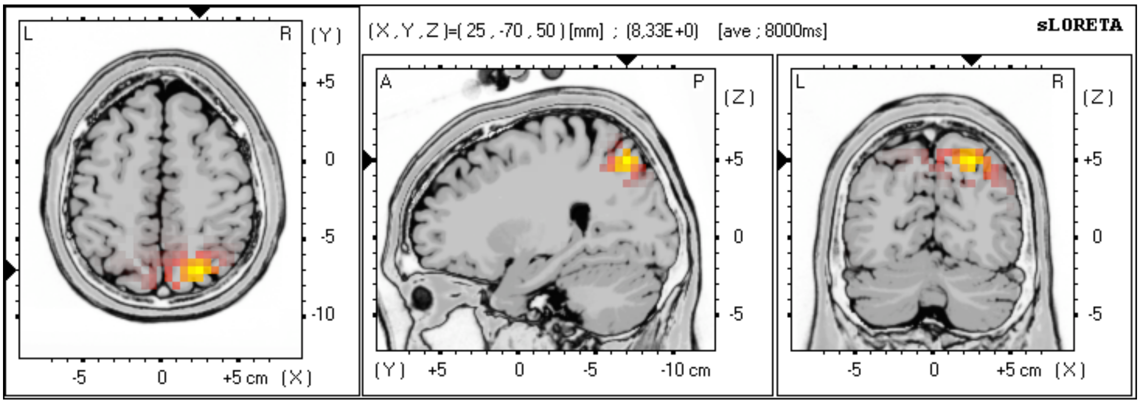
condition *ANGRY-FAIR*



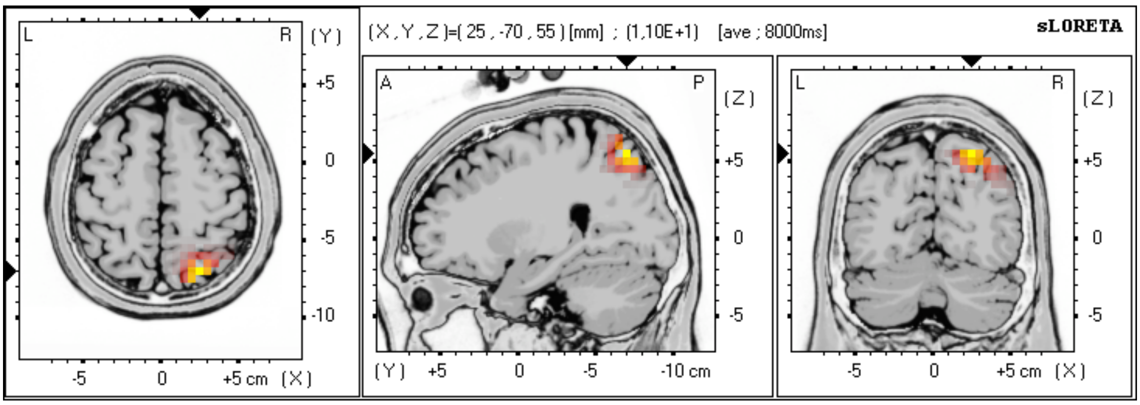
condition *ANGRY-MIDFAIR*



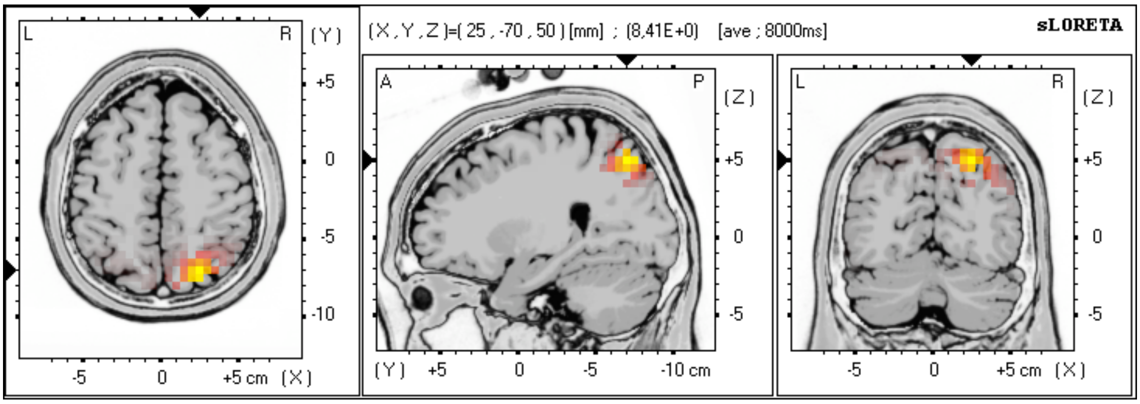
condition *ANGRY-UNFAIR*



condition *HAPPY-FAIR*



condition *HAPPY-MIDFAIR*



condition *HAPPY-UNFAIR*

Abstract in german

Bei der feedback negativity handelt es sich um eine negative Komponente des ereigniskorrelierten Potentials, die sensibel auf Feedback in Zusammenhang mit negativen Ereignissen oder monetären Verlusten reagiert. Da die feedback negativity zumeist mit Hilfe von experimentellen Paradigmen untersucht wurde, in denen die Folgen einer Handlung mit dem Verhalten der Versuchspersonen übereinstimmten, wurde davon ausgegangen, dass die feedback negativity einen Prozess der Verhaltensüberwachung bzw. des Lernens über kürzlich ausgeführte Handlungen widerspiegle.

In verschiedenen Studien konnte jedoch mittlerweile nachgewiesen werden, dass die feedback negativity auch dann hervorgerufen werden kann, wenn Resultate nicht mit vorherigem Verhalten oder vorherigen Entscheidungen übereinstimmen. Diese Ergebnisse führten zu der Vermutung, dass die feedback negativity auch die Evaluation von Erwartungen bezüglich Umweltkontingenzen (zum Beispiel erwartete Zusammenhänge zwischen Belohnungen und Eigenschaften der Stimuli in den entsprechenden Studien) reflektieren könnte.

Das Ziel der vorliegende Studie lag nun in der Überprüfung dieser Vermutung, indem versucht wurde die Erwartungen der Versuchspersonen, die die Rolle von Annehmern im Ultimatum Spiel übernahmen, bezüglich Zusammenhängen von Angeboten im Ultimatum Spiel und dem Gesichtsausdruck der jeweiligen Anbietern aufzubauen und die feedback negativity zu evaluieren. Die Anbieter mit denen die Versuchspersonen konfrontiert wurden, zeigten, bevor sie den Versuchspersonen unterschiedlich faire Angebote unterbreiteten, entweder einen freundlichen oder einen verärgerten Gesichtsausdruck. Diese unterschiedlichen Mimiken sollten die Erwartungen der Versuchspersonen in Bezug auf die nachfolgenden Angebote beeinflussen.

Nach unfairen Angeboten wurden im Vergleich zu den restlichen Angeboten größerer feedback negativity Amplituden ausgelöst. Des Weiteren lösten freundliche Anbieter, die einen als unfair wahrgenommenen Geldbetrag offerierten, eine größere feedback negativity Amplitude aus, als verärgert aussehende Anbieter, die denselben Betrag anboten. Demzufolge scheinen Erwartungsverletzungen in Bezug auf Kontingenzen im Ultimatum

Spiel (freundliche Anbieter unterbreiten unfaire Angebote) zu vergrößerten feedback negativity Amplituden zu führen.

Curriculum vitae

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