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# Distinct cognitive mechanisms in a gambling task share neural mechanisms

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**Abstract**

Distinct psychological processes have been proposed to unfold in decision making. The time course of neural mechanisms supporting these processes has not been fully identified. The present MEG study examined spatio temporal activity related to components of decision making proposed to support reward valuation, reward prediction, and outcome evaluation. Each trial presented information on reward value (10 or 50 cents) and reward probability (10%, 50%, or 90%). Brain activity related to those inputs and to outcome feedback was evaluated via electromagnetic responses in source space. Distributed dipole activity reflected reward value and reward probability 150 350 ms after information arrival. Neural responses to reward value information peaked earlier than those to reward probability information. Results suggest that valuation, prediction, and outcome evaluation share neural structures and mechanisms even on a relatively fine time scale.

**Descriptors:** Decision making, Magnetoencephalography, MEG, Reward prediction, Gambling

The decision making literature has proposed several distinct cognitive components, including appraisal of the target of choice (reward valuation), estimation of the chance of receiving a reward (reward probability), and feedback based evaluation of outcome relative to expectation (for overviews, see Bechara, Damasio, Tranel, & Damasio, 2005; Cohen, Elger, & Ranganath, 2007; Ernst & Paulus, 2005; Knutson, Fong, Bennett, Adams, & Hommer, 2003; Knutson, Rick, Wimmer, Prelec, & Loewenstein, 2007; Smith et al., 2009). Although models of decision making suggest that these components interact (e.g., Ernst & Paulus, 2005; Fishbein & Ajzen, 1975), the mechanisms and time courses of these interactions remain a matter of investigation, and their neural implementation remains to be fully described (Rangel, Camerer, & Montague, 2008). Hemodynamic neuroimaging studies have identified cortical and subcortical brain areas as active in decision making tasks, including orbitofrontal cortex, anterior cingulated cortex, insula, striatum, and nucleus accumbens (Bechara et al., 2005; Knutson et al., 2007; Rushworth & Behrens, 2008; Sanfey, Hastie, Colvin, & Grafman, 2003; Sanfey, Loewenstein, McClure, & Cohen, 2006). Across these studies, some specific relationships between brain structures and neural and cognitive processes during decision making have been delineated. In concert, they point to interactions or interdependencies in the sense of a structural and functional decision making network. A more precise description of the spatiotemporal course of brain activity preceding and following the overt decision would add to the understanding of these relationships.

Particularly understudied are precise temporal relationships among processes related to reward valuation and reward prediction. Exploiting the high temporal resolution of magnetoencephalography (MEG), the present study sought information about the time course of brain events related to the time course and sequence of cognitive decision making steps thereby focusing on event related fields, the magnetic counterpart of event related EEG potentials, i.e., the averaged electrophysiological response to an internal or external stimulus. For an introduction to MEG methodology, see, e.g., Hansen, Kringelbach, and Samelin (2010) or Hauk (2004).

Most relevant studies have examined brain responses to feedback as a function of prediction alone, as a function of value appraisal alone, or as a function of both when the two types of information are presented simultaneously. The present study provided the two types of information in succession within a trial, varying the sequence orthogonally, to examine the respective time courses of activity of potentially different circuits involved in processing these two types of information.

Hemodynamic neuroimaging studies typically trade temporal resolution for spatial resolution, hence the need for studies emphasizing temporal resolution. This approach faces the same

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Address correspondence to: Astrid Steffen, Department of Psychology, University of Konstanz, P.O. Box D23, D 78457 Konstanz, Germany. E mail: Astrid.Steffen@uni konstanz.de trade off, however. Spatial resolution with MEG approximates that of routine fMRI (Miller, Elbert, Sutton, & Heller, 2007), even for deep structures under some circumstances (e.g., Hanlon et al., 2005; Miller, 2010; Weisend et al., under review), but those circumstances are often infeasible. The present investigation did not attempt to assess activity in the full range of structures that the human hemodynamic or animal literatures have proposed as playing a role in decision making. For example, hemodynamic neuroimaging studies suggest that brain mechanisms supporting decision making involve activity in a mesolimbic frontocortical system (e.g., DeQuervain et al., 2004; Ernst & Paulus, 2005; Knutson et al., 2007; Kringelbach, 2005; Peters & Büchel, 2009; Rangel et al., 2008; Rushworth & Behrens, 2008; Schultz, 2004; Smith et al., 2009), deeper portions of which can be challenging for MEG to assess. The aim of this study was not to replicate these or other specific locations. Rather, the present focus was on the time course of readily recorded cortical activity that covaried rapidly with manipulations of reward value, reward probability, and feedback. In turn, MEG source analysis estimated activity from the recorded magnetic fields.

EEG studies provide some guidance about rapid phenomena during decision making tasks, with activation related to reward valuation at 150 200 ms after stimulus onset. A negative deflection of the event related brain potential (ERP) in Go/NoGo paradigms around 200 ms (N200) has been related to information based decisions (Sasaki & Gemba, 1986; Schmitt, Schlitz, Zaake, Kutas, & Münte, 2001; Steffen, Rockstroh, & Jansma, 2009). Thus, a first prediction in the present study was a modulation of activity apparent by 200 ms following value and/or probability information delivery.

Besides reward value and reward probability, aspects of decision making can be framed in terms of risk. Kahneman and Tversky (1979) proposed that risky decisions involve more deliberative effort and are more difficult to make. Brandstätter, Gigerenzer and Hertwig (2006) emphasized that decisions at the certainty equivalent, that is, decisions for which a person has no preference, or there is no difference between the gamble and the certain amount, are most difficult to make. Modulation of frontal activity by uncertainty in the estimation of reward expectation and risk aversion has been reported (e.g., Fecteau et al., 2007; Krain, Wilson, Arbuckle, Castellanos, & Milham, 2006; Rushworth & Behrens, 2008; Smith et al., 2009). Thus, a second prediction was that the riskiness/difficulty of a decision to gamble would modify the spatio temporal activity pattern.

Studies of feedback related negativity (FRN, 250 350 ms) suggest that feedback evoked activity varies with the certainty and confirmation (or violation) of prediction (Hajcak, Moser, Holroyd, & Simons, 2006; Moser & Simons, 2009; Yu & Zhou, 2009). Activity at 300 ms (P300) has also been reported in response to feedback stimuli (Carlson, Zayas, & Guthormsen, 2009; Leng & Zhou, 2010). Thus, a third prediction was that modulation of activity between 200 and 350 ms as a function of feedback would parallel that following value and probability information.

The hemodynamic literature has not determined the extent to which reward valuation, reward probability, and feedback evaluation are supported by distinct neural systems (Rangel et al., 2008). Thus, beyond these specific predictions, a primary goal was the spatiotemporal differentiation of brain mechanisms related to reward valuation, reward probability, and feedback evaluation.

## Methods

### Participants

Twenty right handed healthy volunteers (9 female; mean ± standard deviation age 25 ± 2.2 years, range 21 30 years), students at the University of Konstanz, were included if they did not meet criteria for a psychiatric disorder (screened with the MINI interview; Ackenheil, Stotz Ingenlath, Dietz Bauer, & Vossen, 1998), if they were not taking psychotropic medication, and if they denied a history of serious neurological conditions or head trauma including loss of consciousness. Participants had normal or corrected to normal vision and were right handed based on an adapted version of the Edinburgh Handedness Inventory (Oldfield, 1971). Upon completion of the experiment, participants received 10 € plus payment depending on individual success in the gambling task. The total payment varied between 19 and 23 €.

### Design and Procedure

The study was approved by the Ethics Committee of the University of Konstanz. Each participant was informed in detail about the MEG measurement procedure and the experimental task and provided written consent according to the World Medical Association Declaration of Helsinki guidelines (http://www.wma.net/e/policy/b3.htm).

A variant of a common gambling design was used (see Figure 1 for illustration of a typical trial). On each trial, visual information indicating the potential monetary gain and its probability was presented sequentially. The sequence of value and probability information was a between subject factor: for 10 participants, value information was presented first in each trial, followed by probability information. For the other 10, probability information preceded value information. For each participant, the second stimulus served as the decision prompt, upon which the participant chose by button press whether to gamble. The value information (10 or 50 Eurocents per trial) and the probability information (10/90%, 50/50% or 90/10% likelihood of gain/loss) were combined in random order in a 2 (value) × 3 (probability) repeated measures design. Following a 2000 ms decision interval, a feedback stimulus informed the participant about gain or loss. When participants chose to gamble, feedback informed them about gaining or losing the respective amount of money. When participants chose not to gamble, feedback notified them that their balance remained unchanged (neither gain nor loss). If the participant did not press either button within 2 s, the feedback indicated that the trial was discarded (neither gain nor loss).

Reward value was conveyed by a picture of a 10 or 50 c Eurocent coin (108 × 109 pixels; see Figure 1). Reward probability was conveyed by a picture of a slot machine (130 × 182 pixels) displaying 10%, 50%, or 90% probability of gain ( = 90%, 50%, or 10% probability of loss). Within 2000 ms of onset of the second stimulus, participants indicated their decision by pressing one of two adjacent buttons on a response pad, defined as 'yes' and 'no' buttons, with the index or middle finger of their dominant hand. Subjects were instructed to respond as quickly as possible. A 1500 ms feedback display indicating gain, loss, no gamble, or no response appeared after the decision interval.

Each participant began with a balance of 10 €, which could be increased or diminished by gambling. Participants were not in

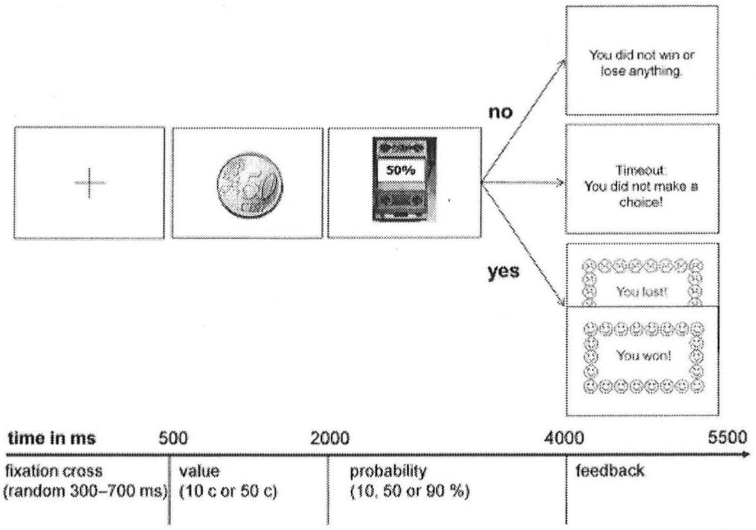

**Figure 1.** Illustration of the experimental design with an example of the sequence and timing of stimuli in a typical trial. Words were presented in German, translated for illustration here. For 10 of the 20 participants, the presentation order of the value and probability information in each trial was reversed from that illustrated here.

formed at this stage that an additional 10 € would be added to their winnings to ensure a positive outcome. Subjects did not receive feedback about their net gain on each trial but rather at the end of the experimental period. The portion of the payment based on gambling outcome was calculated from the net gain/loss across 20 trials randomly chosen during the experimental period.

Each of the 240 trials began on average every 5580 ms: 300 700 ms fixation cross, 1500 ms value or probability stimulus, 2000 ms probability or value stimulus (providing 2000 ms for decision and button press following onset of second stimulus), 1500 ms feedback stimulus, and 80 ms blank screen between trials. Given the 2 value × 3 probability design, there were 40 trials for each of the 6 cells. The session lasted about 1.5 h including preparation for MEG recording.

Timing and sequence of stimulus presentation were controlled using Presentation software (Neurobehavioral Systems, http://www.neurobs.com/). Stimuli were projected onto a 46 cm (diagonal) screen 60 cm from the participant's eyes using a computer projector with 60 Hz refresh rate. The visual angle was 5.7° in height and width for the value stimuli, 8.6° in height and 5.7° in width for the probability stimuli, and 6.7° in height and 16.1° in width for the feedback stimuli.

### Data Acquisition and Analysis

Button press reaction times were measured to the nearest ms. MEG was recorded continuously, while participants were in a prone position, using a 148 channel magnetometer (MAGNES 2500 WH, 4D Neuroimaging, San Diego, CA). MEG was digitized at 678.17 Hz per channel after a bandpass filter of 0.1 to 200 Hz. For artifact control, the vertical and horizontal electrooculogram from four electrodes placed near the left and right temporal canthus and above and below the right eye and the electrocardiogram from two electrodes attached to the left forearm and the right clavicle were recorded using three bipolar channels of a SynAmps I amplifier (NeuroScan, Compumedics Europe, Singen, Germany). The location of the participant's nasion, left and right ear canal, and head shape were digitized with a Polhemus 3Space Fasttrack (Colchester, VT) prior to each session. Following noise reduction, MEG data were corrected for heartbeat related artifacts: in epochs with R wave artifact, an average magnetocardiogram was subtracted, calculated as a moving average over 20 heartbeats (4D Neuroimaging "cardiac comber" software). Trials with eye blinks were excluded from further data analyses. Due to a trigger code error, MEG following feedback could be analyzed only for the 10 participants who received probability information before value information.

For each subject and channel, the continuously recorded MEG data were epoched around three events per trial: value information onset, probability information onset, and feedback stimulus information onset. Within each trial, the second stimulus served as the decision prompt, whether representing value or probability information. The analysis of responses to the decision prompts was of interest primarily because it permitted an analysis of the value × probability interaction. Therefore, trials were epoched again, including value and probability information. Results for the decision prompt are reported separately from those for the value and the probability events. All trials included in analyses, epochs including 100 ms before and 500 ms after onset of each such stimulus, were averaged and filtered with a 0.5 Hz (12dB/octave, zero phase shift) high pass and a 40 Hz (12dB/octave, zero phase shift) low pass filter. BESA software (Megis Software GmbH, Munich, Germany) was used for preprocessing. The window of 500 ms following stimulus onset was chosen based on knowledge that (a) major event related responses reflecting stimulus related processing occur during the first 300 400 ms, (b) using a multiple of 100 controls for alpha artifact in averaging, and (c) longer intervals may include activity related to the upcoming response, hence, augmenting the chance of movement related artifacts.

In order to illustrate the analysis procedure, Figure 2a provides the root mean square of the grand average sensor space waveforms showing the time course of magnetic field strength

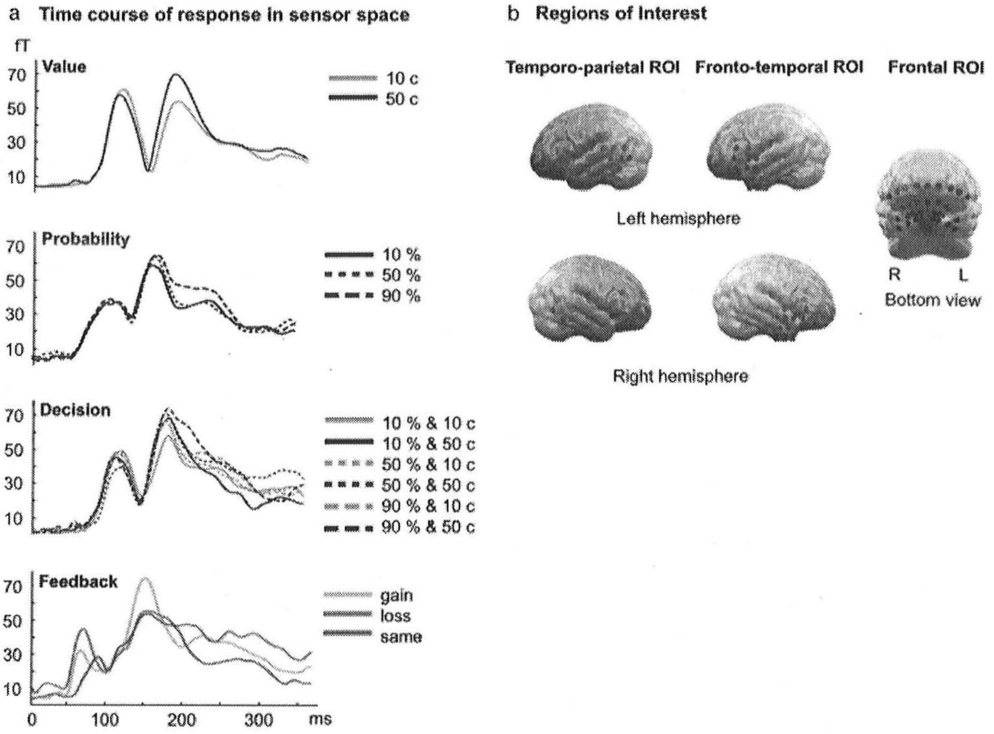

**Figure 2.** (a) Time course of response in MEG sensor space averaged across all sensors and subjects, separately for effects of the two reward value levels (10 c, 50 c), the three reward probability levels (10%, 50%, 90%), the decision prompt (the second stimulus, whether value or probability), and the three types of feedback (gain, loss, no change in balance due to choice not to gamble). (b) The dipole projections forming the regions of interest (ROIs) are marked by (inflated) black dots on left, right, and bottom rendering of spherical configurations.

combined across all sensors (root of the global field power), in response to value, probability, decision, and feedback stimuli.

Source space analyses explored cortical activity during time intervals identified as follows. The L2 Minimum Norm Pseudoinverse (L2MNP) was used for inverse modeling, providing minimum norm estimates (MNE) of cortical activity without any assumption regarding the location and/or number of current sources[1] (Baillet, Mosher, & Leahy, 2001; Haemaelaeinen & Ilmoniemi, 1984; Hauk, 2004; Hauk, Keil, Elbert, & Müller, 2002). Relying on EMEGS software (Junghöfer & Peyk, 2004) written in Matlab (MathWorks Inc., Natick, MA), a spherical shell with 2 (azimuth, polar direction) × 350 dipoles evenly distributed throughout cortex served as the source model. These 350 dipoles effectively tessellated a source shell with radius at 87% of the individually fitted head radius, approximating the depth of cortical gray matter. A Tikhonov regularization parameter of ($\lambda = 0.2$) was applied.

To define temporal windows and regions of interest (ROIs) for source analysis, repeated measures analyses of variance (ANOVAs) were calculated for each dipole and time point across the $-100$ to 500 ms epoch, with stimulus (value, probability, decision, or feedback) the independent variable. This produced statistical parametric maps (SPMs) of $F$ ratios indicating significant ($p < .05$) stimulus effects. ROIs were determined as groups of at least 12 contiguous, significant dipoles in a time window. The problem of false discovery rate in multiple testing, especially considering dependent dipole activity, was addressed by considering significant effects only when they included a minimum of 27 contiguous data points (40 ms, as determined by Peyk, Schupp, Elbert, & Junghoefer, 2008). Moreover, ROIs were determined for 10 participants chosen at random and applied to the other 10 participants. Replication of identified ROIs and consistency with peaks in scalp waveforms (Figure 2a) were considered evidence for non arbitrary results.

The SPMs from the source analysis identified three bilateral regions of differential brain activity (ROIs, see Figure 2b). The average activity in each ROI was scored for several time windows (see Figure 3a). First, bilateral temporo parietal ROIs were

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[1] Various methods to localize activity measured with MEG are available, including discrete source models and minimum norm estimates. Source models can be under or over determined. Discrete source models (as used in BESA, Megis Software GmbH, Munich, Germany) use hypotheses from previously identified research results to determine sources. Under determined models may be used in cases where several possible current distributions could explain the measurement results and, e.g., so many different distributed areas are activated that it is difficult to derive all involved sources from specific literature based hypotheses (such as in decision making). Out of several possible solutions only the most likely was chosen here. An example for under determined models is the L2 minimum norm pseudoinverse model that provides minimum norm estimates (MNEs) for the source current distribution with minimal *a priori* assumptions, calculating the shortest vector in the source current space that can explain the measurements (Haemaelaeinen & Ilmoniemi, 1984; Hauk, 2004; Hauk, Keil, Elbert, & Muller, 2002). The resulting source current space is modeled as a spherical configuration of evenly distributed dipoles, the MNEs. As no results from comparable sequential MEG or EEG studies of decision making were available when analyzing the data of this study, the under determined MNP was the method of choice.

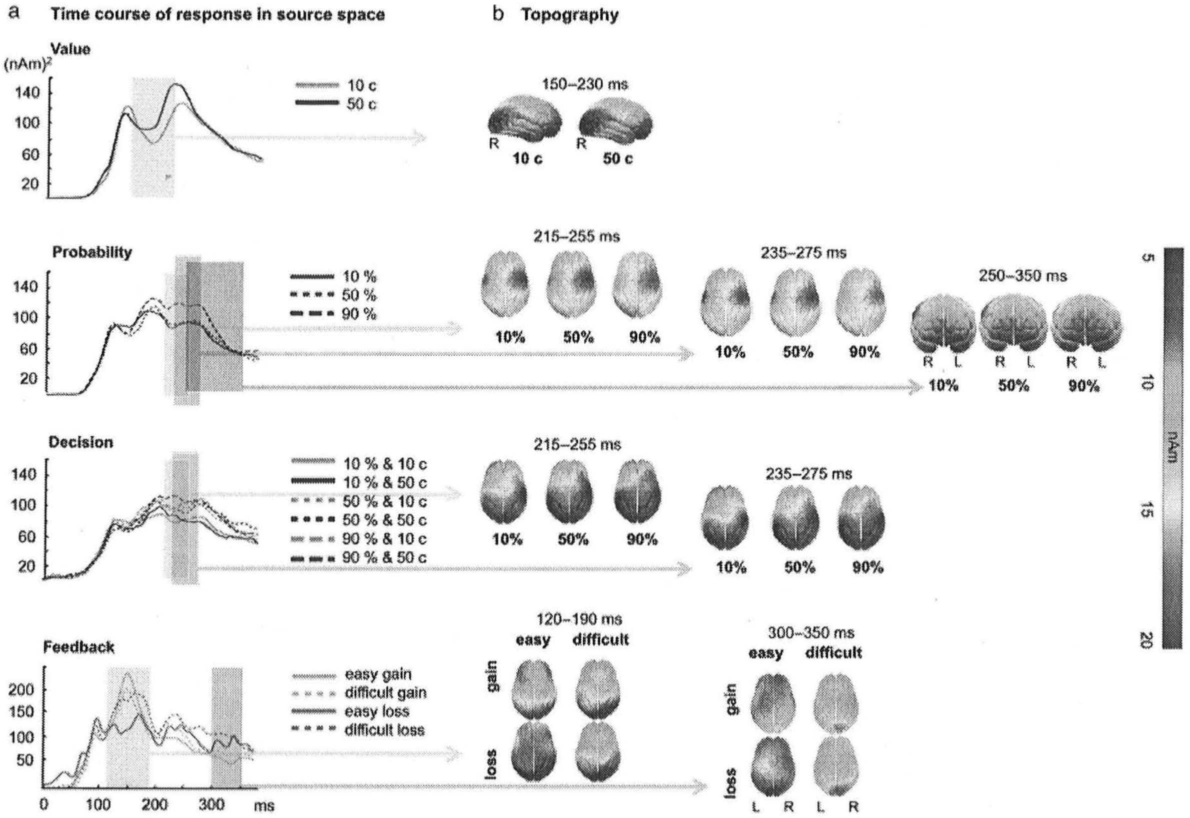

**Figure 3.** (a) Time course of response in dipole source space averaged across dipoles with an ROI and subjects, separately for effects of reward value, reward probability, decision prompt, and feedback. Time intervals considered for topographical analyses are marked by gray shaded bars, with arrows pointing to the topographical maps illustrated in (b) related to these time intervals. (b) Dipolar activity projected on standard cortical sheet with yellow and red colors indicating more power or higher MNE values. Activity is averaged across participants, trials, and time points during the respective time intervals. Top row: 150 230 ms after onset of reward value information. Second row: 215 255 ms, 235 275 ms and 250 350 ms after onset of probability information. Third row: 215 255 ms and 235 275 ms after onset of decision prompts. Bottom row: 120 190 ms and 300 350 ms after onset of feedback, separately for gain (upper graphs) and loss (lower graphs) on easy (left) and difficult (right) trials.

scored as the average activity of 12 clustered dipoles in the left and 12 clustered dipoles in the right hemisphere. This pair of ROIs was scored during two overlapping windows. The impact of the value stimulus was scored 150 230 ms after onset. A 215 255 ms window was used to score both the response to the probability stimulus and the response to the second stimulus, i.e., the decision prompt, irrespective of whether the second stimulus was the value or the probability stimulus. Second, bilateral frontotemporal ROIs were scored as the average activity of 17 clustered dipoles per hemisphere 235 275 ms following the probability stimulus and the decision prompt. Third, bilateral frontal ROIs were scored as the average activity of 16 clustered dipoles per hemisphere 250 350 ms following onset of the probability stimulus and the decision prompt and 120 190 ms and 300 350 ms after onset of the feedback stimulus.

Effects of the distinct types of information on brain activity in the respective time windows and ROIs were evaluated in a series of repeated measures ANOVAs. The effect of value information was evaluated in an ANOVA with the within subject factors value (10 c, 50 c) and hemisphere (left ROI, right ROI), irrespective of whether value information appeared first or second. The effect of probability information was evaluated with the within subjects factors probability (10%, 50%, 90%) and hemisphere, irrespective of whether probability information appeared first or second. The effect of decision prompt was evaluated with a value × probability × hemisphere ANOVA (including an average 236 ± 10 trials per subject), irrespective of whether the decision prompt was the value or the probability information.

Individuals in a gambling task typically want to maximize their decision outcome (cf. Brandstätter et al., 2006; Kahneman & Tversky, 1979; March, 1978; Savage, 1954; Tversky & Kahneman, 1981; von Neumann & Morgenstern, 1947). Therefore, the decisions in 10% or 90% probability trials in the present experimental design were easy and fairly predictable: with a rapid, automatic evaluation, subjects could choose not to gamble given a 10% probability of winning and to gamble given a 90% probability of winning, thereby (in the long run) maximizing their gains. For the Difficulty factor, we defined ‘no’ responses on 10% trials and ‘yes’ responses on 90% trials as “easy” choices (on average 154 ± 16 trials). Decision making given 50% probabilities is more difficult: the outcome if choosing to gamble is uncertain. Brandstätter et al. (2006) called this a risky decision. In the long run, these two choices at a 50/50% probability provide the same expected gain (neither gain nor loss). Objectively, it makes no difference whether participants consistently choose yes or no answers. This makes the decision more difficult, as more (calculation) effort is needed to determine which could be the "right" decision in the 50/50 than in the 10/90 case.

Thus, for the Difficulty factor, we defined no and yes choices given 50% probabilities as "difficult" choices (on average 79 ± 20 trials). Taken together, this provided an average of 226 ± 18 trials per subject to explore whether probability information prompted a more complex process of reward prediction, which includes the difficulty (and riskiness) of a decision to gamble in the light of the probability of gain. Responses to feedback were evaluated in two ANOVAs, one with the within subject factors feedback (gain vs. loss) and hemisphere using just those 121 ± 18 trials on which participants chose to gamble and one with the within subject factors difficulty of decision (easy vs. difficult decisions), decision choice (yes vs. no responses), and hemisphere using all 235 ± 4 trials on which subjects made a choice (on 'no' responses feedback indicated that there was neither gain nor loss).

Except for feedback related measures, on an exploratory basis the between subject factor presentation order was added to the ANOVAs outlined above, comparing the 10 participants who received value information first with those 10 who received probability information first. These ANOVAs found no effects involving presentation order. Thus, analyses reported here did not include that factor.

The alpha level was set at .05 for each comparison. Reported $p$ values use the Huynh Feldt epsilon correction where appropriate. Significant effects were explored with $t$ tests. *Post hoc* findings that met the .05 threshold are designated in the figures.

## Results

A primary goal of this study was the spatiotemporal differentiation of brain mechanisms related to reward valuation, reward probability, and feedback evaluation, particularly when value and probability information are presented sequentially. The pattern of brain activity as a function of the distinct types of information inputs demonstrates the unfolding of a pattern of activity in the course of decision making.

### Reaction Times

As illustrated in Figure 4, reaction times were faster when the probability of gain was 90% (625 ± 134 ms) than 10% (734 ± 174 ms) and 50% (793 ± 162 ms; $F(2,18) = 12.6$, $p < .001$), which differed marginally ($t(1,19) = 2.0$, $p < .06$). Decision time did not vary as a function of value. Responses were faster on easy (684 ± 150 ms) than on difficult (819 ± 200 ms) trials ($F(1,17) = 15.8$, $p = .001$). Independent of decision difficulty, decisions not to gamble (787 ± 203 ms) were slower than decisions to gamble (716 ± 145 ms; $F(1,17) = 4.6$, $p < .05$). The decision difficulty × decision choice interaction was not significant.

### Dipole Activity

Figure 3b illustrates neural source topographies, and Figure 5 provides significant statistical effects in the respective ROIs. Across stimuli and ROIs, activity tended to be larger in the right than in the left hemisphere (value stimuli, temporo parietal: 150 230 ms, $F(1,19) = 6.8$, $p < .05$; 215 255 ms, $F(1,19) = 5.0$, $p < .05$; probability stimuli: temporo parietal, 215 255 ms, $F(1,19) = 5.5$, $p < .05$; decision prompt: temporo parietal, 215 255 ms, $F(1,19) = 5.3$, $p < .05$, and frontal, 250 350 ms: $F(1,16) = 6.3$, $p < .05$). Hemisphere did not interact with other factors and will not be considered further.

Reward value information evoked temporo parietal activity 150 230 ms after stimulus onset, which varied with value: The 50 c reward prompted more activity than did the 10 c reward ($F(1,19) = 8.2$, $p = .01$).

Reward probability information prompted activity in the same temporo parietal ROIs (though somewhat later, 215 255 ms after onset). Probability of 90% evoked more activity than did 10% or 50% probability, which did not differ ($F(2,38) = 7.6$, $p < .01$). Higher probability prompted more activity in later intervals in the other ROIs as well, fronto temporal at 235 275 ms ($F(2,38) = 3.5$, $p < .05$) and frontal at 250 350 ms ($F(2,38) = 7.44$, $p < .01$).

The analysis of responses to the decision prompts (the second stimulus, whether value or probability information) was of interest primarily because it permitted an analysis of the value × probability interaction. (The main effects are substantially re

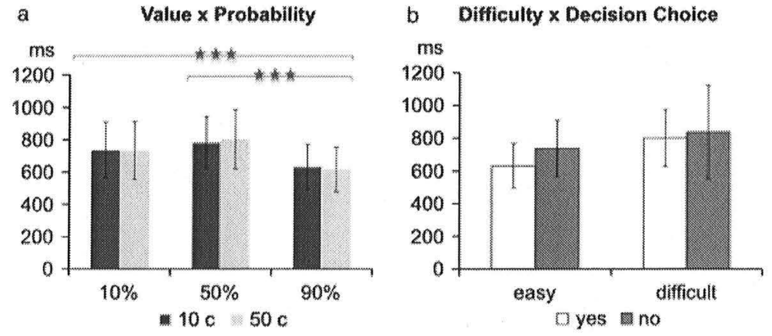

**Figure 4.** Mean reaction times (ms ± 1 *SD*) indicating decision speed as a function of reward value and reward prediction: (a) Reaction times averaged across 'yes' and 'no' responses as a function of value and probability. (b) Mean reaction times as a function of decision difficulty and decision choice, separately for decisions to gamble (black bars: 'yes' responses) and decisions not to gamble (dark gray bars: 'no' responses. Easy decisions (left bars) include 'yes' responses to 90% probability stimuli and 'no' responses to 10% probability stimuli. Difficult decisions (right bars) include 'yes' and 'no' responses to 50% probability stimuli. Stars indicate significant pairwise differences: ***$p < .001$.

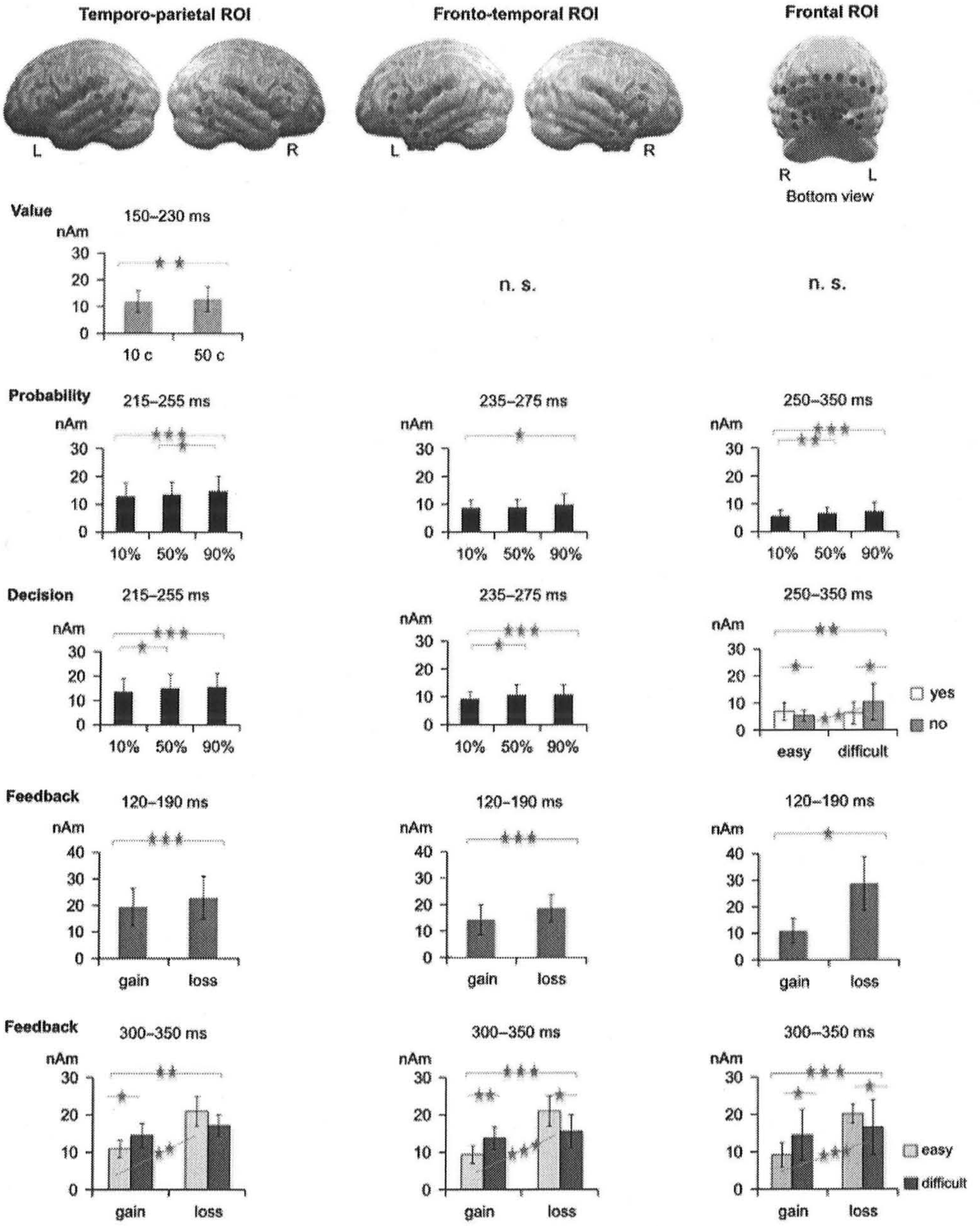

**Figure 5.** Top row: Schematic illustrations of regions of interest (ROIs) as described in Figure 2. Remainder: Bar charts showing significant effects in the respective time windows. The error bars are 1 *SD*. *Post hoc* confirmation of significant pairwise differences indicated by *$p < .05$, **$p < .01$, ***$p < .001$.

dundant with the value and probability analyses reported above.) The value × probability interaction did not approach significance for any of the ROIs.

Comparisons of difficult and easy decisions identified an impact in the temporo-parietal ROI 215–255 ms and the frontal ROI 250–350 ms after decision prompt onset. The temporo-parietal activity at 215–255 ms was higher on easy trials (15 ± 4 nAm) than difficult trials (13 ± 4 nAm; $F(1,16) = 26.2$, $p < .001$). This later reversed, with frontal activity at 250–350 ms being higher on difficult trials than on easy trials ($F(1,16) = 8.8$, $p < .01$).

The frontal effect was confined to trials on which subjects chose not to gamble: higher activity preceded both a choice to gamble on easy trials and a choice not to gamble on difficult trials (decision difficulty × decision choice interaction ($F(1,16) = 7.5$, $p < .05$; see Figure 6). *Post hoc* tests confirmed more activity for the difficult/gamble-no choice than for each of the other combinations.

Feedback evoked activity with latencies at 120–190 ms and 300–350 ms in the same temporo-parietal, fronto-temporal, and frontal ROIs as pre-decisional stimuli. Feedback signaling monetary loss evoked larger dipole activity than feedback signaling gain.

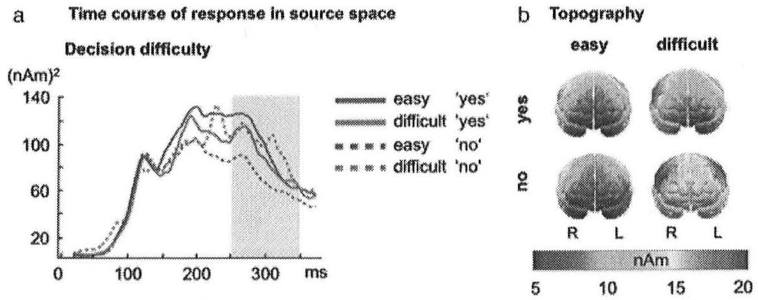

**Figure 6.** (a) Time course of response in dipole source space to the onset of probability information (averaged across levels) separately for decisions to gamble ('yes' responses) and decisions not to gamble ('no' responses) for perceived easy and difficult decisions. The 250 350 ms interval defined for ROI analysis is marked by a gray shaded bar. (b) Topographical map (front view) of dipolar activity projected onto a standard cortical sheet, averaged across participants for the 250 350 ms after onset of probability information separately for easy and difficult decisions and separately for trials in which the participant decided to gamble ('yes' responses, top) and trials in which the participant decided not to gamble ('no' responses, bottom).

This was confirmed at 120 190 ms for temporo parietal ($F(1,9) = 29.9$, $p < .001$), fronto temporal ($F(1,9) = 55.4$, $p < .001$), and frontal ROIs ($F(1,9) = 7.0$, $p < .05$) and at 300 350 ms for temporo parietal ($F(1,9) = 35.8$, $p < .001$), fronto temporal ($F(1,9) = 63.6$, $p < .001$), and frontal ROIs ($F(1,9) = 14.0$, $p < .01$).

Moreover, feedback evoked activity at 300 350 ms varied as a consequence of the difficulty of the preceding decision: when loss feedback followed an easy decision (that is, when a confident outcome expectation was violated), brain activity was more pronounced than following gain feedback (feedback × decision difficulty, temporo parietal ROI, $F(1,9) = 15.5$, $p < .01$, fronto temporal ROI ($F(1,9) = 21.2$, $p < .001$), and frontal ROI, $F(1,9) = 9.7$, $p < .01$). Activity was also more pronounced in response to gain feedback following a 'yes' decision on difficult (50% chance of gain) trials (that is, when expectation was low but the decision to gamble was rewarded) than on easy trials. In contrast, feedback about a loss evoked similar activity regardless of difficulty ($p > .05$). Thus, activity was more pronounced when the outcome was less than expected (loss after easy decisions) or more than expected (gain on difficult decisions). Spatio temporal patterns of activity related to outcome evaluation were similar to those evoked by outcome prediction.

## Discussion

Value appraisal and reward prediction have been proposed as interacting in their impact on decision making. The present study provided value and probability information sequentially and orthogonally. Results supported the assumption of an extended, successively activated cortical network that is active while proposed psychological components of decision making unfold. Moreover, activity in this network was shown to vary as a function of decision difficulty and feedback.

In line with the first hypothesis, value information differentially affected detectable cortical responses within 150 ms, whereas activity did not vary as a function of probability information until 215 ms. Importantly, this more rapid initial registration of differential value than of differential probability did not depend on whether value information preceded or followed probability information. Neither reaction time nor the likelihood of participants choosing to gamble on a given trial depended on the sequence of value vs. probability information. Value and probability manipulations also differed in the extent of their anatomical and temporal impact: whereas activity sensitive to value was confined to the bilateral temporo parietal ROI and ended quickly (230 ms), activity sensitive to probability was more sustained and involved a cascade of all three ROIs, spreading from temporo parietal to fronto temporal to frontal ROIs over a period of about 100 ms. Finally, no value × probability interactions occurred: evaluation of differential probability information did not wait for value information, nor was it delayed or diminished by the absence of that information. In combination, these findings indicate that value and probability play distinct roles within the first few hundred milliseconds of processing, that they involve somewhat different brain regions at different times, and that they contribute additively rather than interactively to decision making, at least of the sort assessed in the present task.

With respect to the second hypothesis, activity following the decision prompt was modulated by decision difficulty and decision choice, in particular with more frontal activity on difficult trials than easy trials on which subjects chose not to gamble. Difficult trials, with 50/50 probability, presumably required more computational effort to estimate outcome. A gambling context can encourage risk taking (e.g., framing effects reported by Tversky & Kahneman, 1981). Such a disposition was evident in present behavioral data: subjects chose to gamble on 78% of 50/50 trials. Responses were faster on easy than on difficult trials. Together, these results indicate that decisions not to gamble on difficult trials required additional effort to inhibit acting out a response disposition. Enhanced frontal activity has been found in the context of uncertainty/risk and of inhibition of response tendencies (e.g., Chikazoe et al., 2009; Neubert & Klein, 2010). Present results are also in line with studies examining modulation of frontal activity by aspects of decision risk such as trade offs between options including potential gain and loss, uncertainty in the estimate of the reward expectation, and risk aversion (e.g., Fecteau et al., 2007; Hsu, Bhatt, Adolphs, Tranel, & Camerer, 2005; Krain et al., 2006; Rushworth & Behrens, 2008; Smith et al., 2009). Thus, it can be argued that, in the present task, inhibition of response was accompanied by up regulating frontal cortex within about 300 ms when deciding not to gamble (see also Chikazoe et al., 2009; Falkenstein, Hoormann, & Hohnsbein, 1999; Funahashi, 2001; Sasaki & Gemba, 1986).

Whereas frontal activity in response to feedback was to be expected from the literature, feedback also evoked activity in those temporo parietal and fronto temporal regions that were active in response to the decision prompt. Rather than showing the posterior to anterior cascade seen during the decision making process, all three ROIs were more active as early as 120 ms after loss feedback than after gain feedback. The three areas also showed a later, orthogonal effect, more active when expectations were violated, around the latency of the FRN at 300 350 ms (e.g., Hajcak et al., 2006). This later activity confirmed hypothesis 3. Specifically, this decision difficulty effect was most pronounced when high expectation of gain (on easy trials) was violated. Activity was also enhanced when a difficult decision (on 50% probability trials) was rewarded. In combination, these results suggest that this late activity reflects the evaluation of unexpected rather than negative events.

This finding can be understood in light of Koechlin and Summerfield's (2007) model of hierarchically ordered executive control functions implemented in prefrontal cortex. The model parses cognitive control into branching, episodic, and contextual control processes proposed to unfold in a regionally organized temporal cascade. The present enhancement of feedback evoked frontal activity when outcome predictions were not met would be interpreted as reflecting an adjustment of episodic executive control (essentially, an adjustment of gambling strategy) upon receipt of unexpected contextual information. The present frontal ROI, more active following unexpected feedback events, subsumes their proposed frontal subregion supporting this function.

Limitations of the present study can be noted. The present design sought to address psychological components proposed to represent core elements of decision making (Ernst & Paulus, 2005) but did not include experimental manipulations that allow the analysis of potential contributions of other elements such as memory updating, emotional and behavioral strategies, or reinforcement learning (Dehaene & Changeux, 2000). Additional processes may be involved in decision making and outcome evaluation, processes suggested by cognitive (Gigerenzer, 1996; Kahneman & Tversky, 1979), economic (e.g., Klein, 1993), and neurobiological (e.g., Sanfey & Chang, 2008) models. Moreover, present analyses did not examine how outcome affects processing on immediately subsequent trials (Dehaene & Changeux, 2000; Holroyd & Coles, 2002). Whereas analyses should consider the variation of effects across trials, this would be difficult with present data in light of averaging across many trials in EEG and MEG studies.

The present characterization of a spatio temporal pattern of cortical activity adds to the understanding of brain mechanisms in pre and post decision processes. In particular, evidence of early, rapid, posterior processing of reward value information and subsequent processing of reward probability information involving additional brain regions suggests a progression of parietal to frontal mechanisms. In contrast, the absence of this anterior cascade during feedback processing indicates that the latter is not simply a replay of pre decisional computations. Finally, the modulation of frontal activity in response to the decision prompt by decision difficulty/risk evaluation suggests a specific inhibitory process involving frontal regions in order to overcome a pro gambling disposition on ambiguous (50/50) trials.

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