Reward expectation and prediction error in human medial frontal cortex: An EEG study

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ABSTRACT

The mammalian medial frontal cortex (MFC) is involved in reward-based decision making. In particular, in nonhuman primates this area constructs expectations about upcoming rewards, given an environmental state or a choice planned by the animal. At the same time, in both humans and nonhuman primates, the MFC computes the difference between such predictions and actual environmental outcomes (reward prediction errors). However, there is a paucity of evidence about the time course of MFC-related activity during reward prediction and prediction error in humans. Here we experimentally investigated this by recording the EEG during a reinforcement learning task. Our results support the hypothesis that human MFC codes for reward prediction during the cue period and for prediction error during the outcome period. Further, reward expectation (cue period) was positively correlated with prediction error (outcome period) in error trials but negatively in correct trials, consistent with updating of reward expectation by prediction error. This demonstrates in humans, like in nonhuman primates, a role of the MFC in the rapid updating of reward expectations through prediction errors.

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Introduction

Decision making under uncertainty is progressively attracting the attention of cognitive neuroscience. The role of reinforcement learning (RL) in decision making has been widely demonstrated, and recent work points to a pivotal role of the medial frontal cortex (MFC), and in particular of the anterior cingulate cortex (ACC), in RL (Jessup et al., 2010; Nee et al., 2011; Silvetti et al., 2013a). In non-human primates, the MFC contains neural populations responding to stimuli or actions as a function of reward expectations linked to them (reward expectation) (Amiez et al., 2006). Moreover, the MFC multiplexes choice values across several decision parameters, such as expected effort or delay in order to weigh possible gains against costs (Kennerley et al., 2011). Single unit recordings in nonhuman primates documented that MFC codes for the difference between expected reward and actual outcome (prediction error) (Kennerley et al., 2011; Matsumoto et al., 2007). Prediction error coding was documented also in humans by fMRI studies (Jessup et al., 2010). Earlier EEG study (Oliveira et al., 2007) indicated that feedback related negativity (FRN), EEG component originating from the MFC (Walsh and Anderson, 2012) has higher amplitude when there is a discrepancy between expected and actual outcome. A more recent EEG study (Talmi et al., 2013) confirmed prediction error coding in the MFC in both reward and aversive conditioning. Moreover, recent neuro-computational work modeled the formulation of reward expectations based on prediction error signals in MFC, and showed that these basic RL operations can provide a unified explanation for the several different findings ascribed to separate MFC functions in the past (e.g. conflict monitoring or error processing) (Alexander and Brown, 2011; Silvetti et al., 2011, 2013a). Recently, the latter theoretical framework revealed to be promising also in neuropsychiatric domain (Silvetti et al., 2013b). These models predict a stronger cue-related signal for trials with higher reward probability (reward expectation), and a stronger outcome-related signal for trials with lower reward probability when reward is delivered (positive prediction error). They also predict a stronger outcome-related signal for trials with higher reward probability when reward is not delivered (negative prediction error). To test these predictions, here we exploited the high temporal resolution of EEG, during a reinforcement learning task. We used a target detection task in which different trial types were labeled with colors (cues). Each color was linked to a different probability of success and hence of obtaining a monetary reward. This is similar to the probabilistic monetary incentive delay task, where a cue indicates the probability of successfully completing a trial and hence the probability of reward (Knutson et al., 2005). In this way, we could separately investigate signals during reward expectation (cue period) and expectation–outcome comparison (outcome period). In order to analyze the activity specifically originating from the MFC (region of interest analysis), we used independent component analysis (ICA) to localize the region of interest. This methodology, already reported in Roger et al. (2010) and in
Gentsch et al. (2009), starts with finding the IC corresponding to the cortical generator of the error-related negativity (ERN). The ERN is a large negative EEG wave observed in error trials which develops at the time of the response (Falkenstein et al., 1991; Gehring et al., 1993). Importantly, it is known to be generated by the MFC (Debener et al., 2005; Dehaene et al., 1994). Once the IC is found, it can be used to reconstruct the MFC activity corresponding to any time segment during the experiment (e.g. cue period). Expected results are described in Fig. 1, where we summarize the expected MFC activation in different trial epochs in our task. Additionally, at the individual difference level, we predicted a negative relation between cue- and outcome-related activity in correct trials (higher expectation implies lower positive prediction error), but a positive relation between cue- and outcome related activity in error trials (higher expectation implies higher negative prediction error) (cf. also Kennerley et al., 2011). We investigated this by means of a mixed linear model analysis on cue- and outcome-related activity.

Materials and methods

Subjects and behavioral task

Fifteen right-handed healthy volunteers (mean age 22, range 19–23, 10 female) gave written informed consent to participate in the study. Subjects performed a perceptual task with monetary reward (0.05 cents) for each correct response (variant of probabilistic monetary incentive delay task, Knutson et al. (2005)). The same task was used before with fMRI to study MFC activity related to different levels of incentive delay task, Knutson et al. (2005)). The same task was used before with fMRI to study MFC activity related to different levels of environmental volatility and uncertainty. Each trial was characterized by a cue assuming one of two possible colors that indicated the reward probability: 80% for Easy trials and 40% for Hard trials (Knutson et al., 2005; Silvetti et al., 2013a), Fig. 2 shows the sequence of events within each trial. At 900 ms after trial onset, the central fixation point changed color (cue). After 1500 ms, three disks appeared, surrounding the cue point, and having the same color as the cue. One of the three disks was slightly brighter than the other two. Subjects were asked to press a button indicating which disk was the brightest. The brightness of the target disk was dynamically adjusted to obtain the desired reward rates for each cue color (Silvetti et al., 2013a). In Hard trials, due to the near-chance level reward rate (40%), the luminance difference between the target disk and the other two was on average extremely small. At 500 ms after the response, an accuracy feedback sign was displayed. Reward delivery was deterministic and exclusively determined by response correctness, in other words, the accuracy feedback always reported the true outcome of the trial. Subjects were not informed about the predictive value of the colors, and we instructed them simply to perform the perceptual task. In our earlier fMRI study (Silvetti et al., 2013), at the end of the task subject were asked whether they perceived one color more rewarding than the other (unpublished results). The majority of subjects (78%) were able to indicate the color that was actually linked to the highest reward probability. 17% were not able to answer and 5% indicated the wrong color. This demonstrates that this task actually allows subjects to formulate conscious reward expectations linked to cue type. Each subject performed six experimental blocks, separated by resting pauses. Each block consisted of 246 trials (50% of each color), for a total of 984 trials for the whole experiment. In each block we used different pairs of cue colors.

Electrophysiological recordings

EEG data were recorded using the BioSemi ActiveTwo system (Biosemi, Amsterdam, The Netherlands). 64 channels of EEG data (10–20 system positions) were recorded with active scalp electrodes at a rate of 1024 Hz per channel (filters: DC to 268 Hz, 3 dB/octave). The reference was the mastoid derivation. Four external electrodes were also included in order to record vertical/horizontal eye movements. Vertical EOG was recorded from infraorbital and supraorbital electrodes placed in line with the pupil of the left eye. The horizontal EOG was measured with two electrodes placed on the left and right canthus.

EEG pre-processing

All ERP analyses were performed using the Brain Vision Analyzer software (Brain Products). The continuous EEG was filtered off-line with high-pass filter of 0.16 Hz, and 100 Hz low-pass filter. The statistical method of Gratton et al. (1983) was used to correct eye movement artifacts. All other artifacts were rejected after visual inspection of individual traces. After artifact removal the EEG data was downsampled to 256 Hz.

Independent component analysis (extraction of MFC time course)

We used ICA to extract specifically the signal from the MFC (analogous to region of interest (ROI) analysis in fMRI studies). This method allowed us to find the channels’ linear combination that best represented the signal originating from the MFC. In this way we reduced the dimensionality of our single subject data sets to just one single time course for subject, representing MFC activity throughout the whole task execution. The extraction of this time course could be summarized in two different steps. In step one, the ICA algorithm decomposes the data into independent components (ICs) that have a fixed topography and a variable time course. Among the different ICs, we identified the IC reflecting the ERN activity which has a temporal dynamic and a typical topography that is easy to identify (Dehaene et al., 1994; Falkenstein et al., 1991; Gehring et al., 1993). The selected IC contains the topography of the cortical structure generating the ERN (i.e. the MFC). In step two, we compute activity of the
MFC based on the identified component and on the complete EEG time series. Via this method, we investigate the MFC activity during cue, response and feedback (i.e., outcome) periods of different conditions (e.g., Easy-error or Hard-correct). The same procedure was applied in other EEG studies, to which the reader can refer for further methodological details (Gentsch et al., 2009; Hoffmann and Falkenstein, 2010; Roger et al., 2010; Wessel and Ullsperger, 2011). We now describe the two successive steps in more detail.

Step one — identification of the IC representing MFC activity

This step is aimed to identify, in each subject, the IC that represents the MFC activity. Since the ERN occurs during error trials at the time of the response, we ran the ICA decomposition on the segmented epochs from −200 to 200 ms locked to the response onset only in error trials (both Easy and Hard conditions). ICA was applied at single-subject level to the above described datasets by using the *runica* function implemented in the EEGLAB software (Delorme and Makeig, 2004). We limited the outcome of the ICA to 32 components per subject.

ICA provided 32 ICs for each subject. Each IC consisted of a topography vector (64 weights, corresponding to the number of channels) and a time course vector. We searched for the IC (out of 32) that could best account for the ERN. ICs representing the ERN were selected on the basis of both scalp topography and the averaged time course. Specifically, we searched for a radial fronto-central topographic scalp distribution, which had a phasic activity whose projection on the scalp was of negative polarity. In terms of the time course we checked that the averaged source waveform showed a maximal activity in the time range 0 to 150 ms relative to the error response onset for each participant. At the end of this procedure, we obtained one ERN-related IC for each subject.

In order to test the goodness of the selected ICs, we both plotted the grand average (across subjects) of the ERN-related IC and localized an active polarity. In terms of the time course we checked that the averaged source waveform showed a maximal activity in the time range 0 to 150 ms relative to the error response onset for each participant. At the end of this procedure, we obtained one ERN-related IC for each subject. In order to test the goodness of the selected ICs, we both plotted the grand average (across subjects) of the ERN-related IC and localized an atomically its corresponding signal source. The second operation was executed by the plug-in LORETA in the EEGLAB software. This plug-in allowed exporting the IC vector of each subject to a format compatible (voltage map) with the EEG source localization software sLORETA (Pascual-Marqui et al., 1994). We averaged the exported ICs across subjects and used sLORETA to localize their common source.

Step two — reconstructing the time course of MFC activity

For each subject, we multiplied the IC weight matrix (Delorme and Makeig, 2004) by the data matrix of dimension time points × 64 channels corresponding to the segments of cue periods (Easy, Hard) (from −200 to 1500 ms cue onset locked), response periods (correct, error) (from −200 to 200 ms response-locked) and feedback periods (correct, error) (from −200 to 250 ms feedback onset locked). This operation resulted in six matrices of dimensions 32 × time points (two matrices for cue period, two for response period, and two for feedback period). In each matrix, each row represents the time course of one IC for the corresponding time segment. In each subject, the vector representing the MFC time course was the row corresponding to the previously identified IC (Step one).

Time course analysis

All the analyses were executed on baseline-corrected MFC time courses derived from the ICA analysis. The baseline was computed as the mean signal between 200 ms before and the onset of the event of interest. We used 2-tailed paired t-tests.

Cue-locked activity

We compared the MFC activity related to cue periods (reward prediction) of Easy and Hard trials. A slow wave potential developed after 200 ms following cue onset. We measured the amplitude of this wave by computing the mean signal between 200 ms and 650 ms after the cue onset (Zaepfel and Brochier, 2012). Given that the cue-locked activity developed similarly to a lateralized readiness potential (LRP) (i.e. not as a peak but as a slow wave) we decided to measure it also by computing the slope of the line regressing the data, which is a method commonly used to quantify the amplitude of these components (Masaki et al., 1998, 2004; Plat et al., 2000). The regression line was estimated between 400 ms and 600 ms after the cue onset, the time window in which the Easy and Hard signals diverged. We then ran a repeated-measures two-tailed t-test comparing Easy and Hard conditions with both their average values and their slopes.

Response-locked activity

The response-locked activity was measured in both correct and error trials. In this response-locked analysis, we considered only Easy trials. Indeed, in Hard trials subjects should rely on feedback to evaluate the accuracy of their responses given that the luminance difference between the target and the other disks was extremely small (Heldmann et al., 2008). In order to motivate our choice of analyzing the outcome-related MFC activity during the response-locked period for Easy trials and during the feedback-locked period for Hard trials, we compared the general MFC activity during those periods, regardless of accuracy (see Supplementary Material). Similar results were found by Eppinger et al. (2008). The selective effect of self-monitored and feedback-based error detection on, respectively, the response-locked and feedback-locked EEG signal is well documented in Gentsch et al. (2009). For each subject we measured both the amplitudes of the negative peak (ERN/CRN in error and correct trials respectively) and the positive peak following the ERN (positive error wave, typically called Pe) (Dhar and Pourotos, 2011; Nieuwenhuis et al., 2001; Ridderinkhof et al., 2009) and the positive peak following the CRN (positive correct wave, Pc). The amplitude of the ERN/CRN was measured as the difference of the negative peak in a time window 0 to 50 ms after button press onset and the preceding positive peak time in the window −100 to 0 ms. The amplitude of the response-related positive waves (Pe and Pc) was measured as the difference...
between the positive peak in a time window 50–150 ms after button press onset and the preceding negative peak time in the window 0 to 50 ms. Group analysis was conducted by two-tailed t-tests, in which we compared the amplitudes relative to correct and error trials for the negative (ERN/CRN) and positive (Pe, Pc) waves separately.

**Feedback-locked activity**

The feedback-locked activity was quantified as the feedback-locked MFC time course of each subject. Here we considered only Hard trials. Indeed, as mentioned above, in Hard trials subjects had to wait for the feedback in order to monitor their performance, while in Easy trials an internal performance monitoring was possible due to the large luminance difference between disks (Heldmann et al., 2008). Analogously to what we did for the response-locked period, for each subject we measured both the amplitudes of the first negative wave and the following positive wave after feedback onset. The negative wave (negative feedback-locked wave, NFW) was measured as the difference between the maximum positive value at around 90 ms and the maximum negative value at around 150 ms after feedback onset. The positive wave (positive feedback-locked wave, PFW) was measured as the difference between the maximum negative value between at around 150 ms following feedback onset and the first most positive point between this maximum and 250 ms. We then ran the group analysis by a repeated measures two-tailed t-test comparing the values of error and correct trials. NFW and PFW occurred in an earlier time bin than the one in which the feedback related negativity (FRN) is typically observed (Gehring and Willoughby, 2002). However, for completeness we also computed the statistical significance (repeated measures two-tailed t-test) of the FRN (difference wave error-correct) in Hard trials.

**Cue-outcome regression analysis**

As a further investigation we computed a regression analysis between the cue-locked activity (reward prediction) and the outcome-locked activities (prediction error) at between subjects level. We estimated a linear mixed model where we used single-subject average cue-locked activity (reward prediction) as dependent variable, four covariates consisting of the single-subject average outcome-locked activity (prediction error) described in the previous sections, and subject as a random factor. Eq. (1) represents the mixed linear model we estimated to find the regression coefficients linking the cue-related activity and the outcome-related activity:

\[
\text{Cue}_i = \beta_0 + \beta_1 \cdot En_i + \beta_2 \cdot Cn_i + \beta_3 \cdot Ep_i + \beta_4 \cdot Cp_i + \gamma \cdot Sbj_i + \epsilon_i. 
\]

\(\text{Cue}\) (cue-related activity), \(En\) (negative wave in error trials), \(Cn\) (negative wave in correct trials), \(Ep\) (positive wave in error trials) and \(Cp\) (positive wave in correct trials). The Cue vector and each fixed effect vector (\(En, Cn, Ep,\) and \(Cp\)) were composed of 30 elements, the first 15 represented single subject averages for easy trials and the second 15 for hard trials. The vector \(Sbj\) represents the subject random factor. Negative waves single subject averages (ERN/CRN and NFW) were multiplied by \(-1\) in order to make the regression coefficients comparable across predictors. The variable \(\epsilon\) represents random noise, \(\beta_0\) is the intercept.

**Results**

**Behavioral**

Reaction times (RTs) were slower for Hard trials (mean = 616 ms, SD = 195 ms) than for Easy trials (mean = 552 ms, SD = 159 ms): \(t(14) = 23.50, p < 0.001\). The average reward rates (average accuracies) were very close to the desired ones: Easy: 76%, Hard: 43%.

**EEG signal from MFC**

After preprocessing, we excluded on average 26% (SD = 5.1%) of trials in each of the analyzed epochs. Fig. 3 shows the scalp topography, the anatomical localization and the ERN time course of the average (across subjects) of the ICs we used to extract the MFC activity. The average IC has a medial prefrontal scalp topography (Fig. 3a), and the response-related time course of the IC in error trials (Fig. 3b) showed waveform and timing closely matching with the classical ERN recorded from the FCz electrode (Fig. 3c) (Falkenstein et al., 1991; Gehring et al., 1993). Finally, the cortical localization of the selected IC (Fig. 3a) clearly suggests the MFC (Fig. 3d). All these findings confirm that the ICs we selected represent the MFC source.

Fig. 4a shows the cue-locked MFC activity related to reward expectation and prediction error. The MFC showed a more negative time course for Easy trials than for Hard trials. This result was found by comparing the slopes of the respective regression lines (\(t(14) = 2.32, p = 0.036\)), and also by comparing the mean signals (\(t(14) = 2.24, p = 0.041\)). Concerning outcome periods, consistent with the hypothesis, the MFC showed, for Easy trials, higher amplitude for Easy-error than for Easy-correct, for both the negative (ERN/CRN) \((t(14) = 2.43, p = 0.029)\) and the positive \((t(14) = 4.33, p < 0.001)\) response-related peaks (Pe, Pc; Fig. 4b: negative prediction error signal). In contrast, for Hard trials, the amplitude of the PFW was higher for Hard correct than for Hard error (Fig. 4c, \(t(14) = 3.58, p = 0.003\); positive prediction error signal). We found no differences between correct and error trials in the NFW \((t(14) = 0.6, p = 0.55)\). To summarize this, mean amplitudes are shown in Figs. 3b-c. Again, in error trials, the outcome-locked MFC activity has the same pattern as cue-locked (Easy < Difficult), but it reverses in correct trials (Difficult > Easy). Finally, in the feedback period of Hard trials, we obtained a wide negative wave for error trials (FRN), rising at 190 ms and peaking at 254 ms (difference wave error-correct: \(t(14) = 6.54, p < 0.0001\)).

**Cue-outcome regression analysis**

Fig. 5d shows the regression coefficients between the (dependent variable) cue-locked activity and the positive waves during the outcome periods (i.e. Pe/Pc and PFW, explanatory variables in the linear model). In error trials the amplitude of the outcome-related response is positively correlated with the activity during the cue period \((\beta_3\) parameter of Eq. (1)), indicating negative prediction error \((t(13) = 2.39, p = 0.032)\). This means that the higher the reward expectation the higher the error-related activity during the outcome, as a missed reward after high reward expectation evokes a strong negative prediction error signal. By contrast, in correct trials, the outcome-related activity is negatively correlated with the cue-locked activity \((\beta_3\) parameter of Eq. (1)), indicating positive prediction error \((t(13.7) = 2.41, p = 0.031)\). In this case, the lower the reward expectation, the higher the correct-related activity during outcome, indicating the response to unexpected rewards (positive prediction error). Beta values for negative waves (ERN/CRN and NFW, respectively parameters \(\beta_1\) and \(\beta_2\) of Eq. (1)) resulted non significant (ERN/CRN: \(t(12.9) = 0.8, p = 0.43\); NFW: \(t(16.7) = 0.58, p = 0.57\)).

**Discussion**

In this study we compared the time course of the human MFC during cue and outcome periods in a reinforcement learning task. During the cue period, the MFC activity coded for reward expectation, with a slow wave rising after cue onset, whose steepness encoded the expectation level. This is compatible with the well-known contingent negative variation (CNV) (Nagai et al., 2004; Tecce, 1972; Walter et al., 1964). The CNV was classically associated with anticipatory and expectancy operations, motor preparation and attentional engagement. CNV typically has higher amplitude in easy (high probability of success) than in difficult (low probability of success) trials (McEvoy et al.,...
Hence, we propose that CNV amplitude, at least for the part due to the contribution of MFC, codes for reward expectation. In the outcome (response and feedback) periods, the MFC coded for prediction error, with a dominance of negative prediction error in Easy trials (Figs. 4b, 5b) and for positive prediction error in Hard trials (Figs. 4c, 5c), signaling the difference between reward expectation and actual outcomes. Note that the Easy-trial data replicates classical ERN/CRN results (e.g., Falkenstein et al., 1991; Gehring et al., 1993) and Pe/Pc results (e.g. Falkenstein et al., 2000; Ridderinkhof et al., 2009) because trials in experimental tasks typically have high accuracy (i.e., are easy). This effect was (as predicted) reversed in Hard trials. Note that because of this reversal, MFC signal cannot be confounded with task difficulty (which is the same in cue and outcome period) nor by pure error detection.

The reversal in Hard trials replicates a similar finding in fMRI by Jessup et al. (2010) who observed more MFC activation for both negative and positive prediction errors than for expected outcomes. Similarly, using EEG, Oliveira et al. (2007) found a modulation of the feedback-related activity from the Fz channel by the prediction formulated during the epoch preceding the feedback. A similar modulation was reported by Nunez Castellar et al. (2010), who showed a larger P3 wave in Fcz for easy-error than easy-correct trials, but a larger P3 wave in Fcz for hard-correct than hard-error trials. Converging experimental evidence (Doricchi et al., 2010; Glascher et al., 2010; Summerfield and Egner, 2009; Summerfield and Koechlin, 2008) has recently been revealing that calculating prediction error can be a general adaptive process in neural circuits (Friston, 2009). Reward prediction error could be just the dopamine-based variety of this general learning mechanism.

Further, these findings reveal a substantial overlap between the MFC functions in human and nonhuman primates (Amiez et al., 2006; Kennerley et al., 2011; Matsumoto et al., 2007). Indeed, our results are consistent with those obtained by Kennerley et al. (2011), who showed that monkey MFC cells having a positive correlation with stimulus value (reward expectation) flipped their correlation sign to negative for outcome periods of rewarded trials (positive prediction error). Similarly, a strong feedback- or response-locked signal on reward trials predicted a weaker cue-locked signal (Fig. 5d). Remarkably, in our study, though both ERN/CRN and the following Pe/Pc were modulated by prediction

Fig. 3. Analysis of the IC vector representing the MFC activity. a) Scalp map of the average MFC IC. b) Time course of the MFC IC activity during the response periods in error trials. c) Time course of the ERN (grand average) from Fcz channel. The ERN wave was used as a localizer to find the IC that best represented the MCF ROI. d) Anatomical localization of the MFC IC. Local maximum located at [5,5,45] MNI reference system.

Fig. 4. Time course of MFC activity (to be compared with plots in Fig. 1). a) Cue-locked activity for Easy and Hard trials. Gray area: time bin of signal averaging for data analysis. b) Response locked activity in Easy trials for error (unrewarded) and correct (rewarded) responses. Gray area: time bin in which we performed the peak-to-peak analysis for the negative wave (ERN/CRN). Dark gray area: time bin in which we performed the peak-to-peak analysis for the positive wave (Pe/Pc). c) Feedback-locked activity in Hard trials for error (unrewarded) and correct (rewarded) responses. Gray area: time bin in which we performed the peak-to-peak analysis for the negative wave (NFW). Dark gray area: time bin in which we performed the peak-to-peak analysis for the positive wave (PFW). Outcome effects were analyzed in two different periods (response and feedback, respectively for Easy and Hard trials) in order to take into account the performance self-monitoring that subjects could execute in Easy trials (see Materials and methods).
error, only Pe/Pc predicted cue activity at the individual difference level. Whereas ERN/CRN has typically been associated with (reward) prediction error, the Pe/Pc has been more commonly related to the subsequent (conscious) detection of and dealing with errors (Nieuwenhuis et al., 2001; Ridderinkhof et al., 2009). These findings from the regression analysis could be due to the fact that only conscious error detection led to sufficiently strong prediction error during the response-locked period, when the external feedback was not yet provided. In conclusion, we provided here experimental evidence that human MFC shares RL processing features with the MFC of nonhuman primates, computing reward expectations and comparing them with environmental outcomes. These findings corroborate the new theoretical perspective according to which the many different functions attributed to the MFC could be explained in terms of RL processing.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.neuroimage.2013.08.058.

References


