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Research Report

Tonic Activity Level in the Right Prefrontal Cortex Predicts Individuals' Risk Taking

Lorena R.R. Gianotti,¹ Daria Knoch,^{2,3,4} Pascal L. Faber,¹ Dietrich Lehmann,¹ Roberto D. Pascual-Marqui,¹ Christa Diezi,¹ Cornelia Schoch,¹ Christoph Eisenegger,² and Ernst Fehr^{2,4}

¹The KEY Institute for Brain-Mind Research, University Hospital of Psychiatry, University of Zurich; ²Institute for Empirical Research in Economics, University of Zurich; ³Department of Neurology, University Hospital Zurich; and ⁴Collegium Helveticum

ABSTRACT—Human risk taking is characterized by a large amount of individual heterogeneity. In this study, we applied resting-state electroencephalography, which captures stable individual differences in neural activity, before subjects performed a risk-taking task. Using a source-localization technique, we found that the baseline cortical activity in the right prefrontal cortex predicts individual risk-taking behavior. Individuals with higher baseline cortical activity in this brain area display more risk aversion than do other individuals. This finding demonstrates that neural characteristics that are stable over time can predict a highly complex behavior such as risk-taking behavior and furthermore suggests that hypoactivity in the right prefrontal cortex might serve as a dispositional indicator of lower regulatory abilities, which is expressed in greater risk-taking behavior.

Some individuals are more likely to take risks than others are (Weber, Shafir, & Blais, 2004), resulting in important social and health consequences such as crime and substance use. There has been much work focusing on psychological characteristics that underlie individual differences in risk taking (for a review, see Reyna & Farley, 2006). However, no study has yet investigated whether neural dispositional determinants might explain

this variability. Evidence from neuropsychology and neuroimaging suggests that the prefrontal cortex (PFC) is involved in risky-decision-making processes, raising the prospect that differences in the neural functioning of the PFC may explain individual differences in risk taking. Previous neuroimaging studies of risk taking, however, have focused on brain activity during the decision-making process, rather than examining individuals' pretask neurophysiological characteristics. Resting-state electroencephalography (EEG) is a method that measures the tonic cortical activity, that is, the cortical activity before task performance. Various studies investigated the intraindividual stability of human EEG, revealing a stability over a period of years (e.g., Kondacs & Szabo, 1999). Thus, this method is able to capture dispositional individual differences.

Patients with traumatic brain injuries or other pathologies affecting the PFC show a tendency for riskier, "out of character" decision making and an apparent disregard for negative consequences of their actions (Rahman, Sahakian, Cardinal, Rogers, & Robbins, 2001). This seems particularly true for patients with right-sided lesions (Clark, Manes, Antoun, Sahakian, & Robbins, 2003). In a previous study, we were able to manipulate risky decision making by modulating brain activity in the PFC by means of repetitive transcranial magnetic stimulation (rTMS), a technique that allows transient and noninvasive interference with cortical activity. Subjects displayed significantly riskier decision making after disruption of the right, but not the left, lateral PFC, choosing a larger potential reward even at a greater risk of penalty (Knoch et al., 2006). Resting EEG studies have shown that frontal hemispheric activation asymmetry in favor of the right PFC reflects a trait-like individual predisposition to respond in terms of withdrawal-related behavior (e.g., Davidson, 2004; Harmon-Jones, 2004).

Lorena R.R. Gianotti and Daria Knoch contributed equally to this work. Address correspondence to Lorena R.R. Gianotti, The KEY Institute for Brain-Mind Research, University Hospital of Psychiatry, Lenggstrasse 31, 8032 Zurich, Switzerland, e-mail: lgianott@key.uzh.ch, or to Daria Knoch, Institute for Empirical Research in Economics, University of Zurich, Blümlisalpstrasse 10, 8006 Zurich, Switzerland, e-mail: dknock@iew.uzh.ch.

These findings indicate that trait-like tendencies measured from resting asymmetry would be associated with an individual's risk proneness, and that tonically decreased activity in the right PFC may predispose an individual to behave in a risky manner.

METHOD

Subjects

Forty right-handed female students (mean age = 24.8 years, $SD = 5.8$ years) recruited at the University of Zurich participated in the study. We limited the sample to females to reduce possible sex-related variability in physiological responses, and right-handed subjects were selected to avoid physiological differences due to brain laterality (e.g., Davidson, Ekman, Saron, Senulis, & Friesen, 1990). All subjects were screened for health problems by using a detailed health questionnaire. They had no current or previous history of neurological or psychiatric disorder or alcohol or drug abuse. The local Ethics Committee approved the study. Subjects were remunerated with 30 Swiss francs for participating in addition to the money earned in the risk task.

Procedure

Subjects signed a written, informed consent during electrode attachment. Subjects were seated comfortably in a dimly illuminated, sound- and electrically shielded recording chamber with intercom connection to the experimenters. Subjects were instructed that EEG recording was to be done while they rested with their eyes alternately open or closed, and that they would later participate in a decision-making task; they were not informed that the task actually served to detect risk proneness.

The EEG protocol consisted of the participants resting for 20 s with their eyes open, followed by 40 s with their eyes closed; this was repeated four times. The data from the 160 s eyes-closed condition were analyzed following the standard procedure for baseline determination. Thirty minutes after the recording of the resting EEG, subjects received written instructions for the risk task. After the experiment, subjects filled out personality questionnaires that assessed their motor impulsivity (Patton, Stanford, & Barratt, 1995) and self-control (Tangney, Baumeister, & Boone, 2004). As women's risk-taking behavior might be influenced by their menstrual-cycle phase, we assessed this for each of the subjects (Chavanne & Gallup, 1998) and collected data on subjects' current use of hormonal contraceptives, if any.

Risk Task

We measured the brain activity using EEG at rest before the subjects performed a risk task (Slovic, 1966). In this task, the risk associated with acting increases dynamically with each additional action taken (Fig. 1).

In each of 50 trials, subjects were presented with an array of seven closed boxes on a computer screen. They were told that six



Fig. 1. Example of the computer display of the risk task. Four boxes are already open (i.e., 10 win points), and the subject has to decide whether to open another box. Opening the box might add 5 win points to the subject's total or might erase all win points for that trial. Instead of opening the box, the subject has the option of terminating the trial and collecting the 10 win points.

boxes contained monetary rewards ("win boxes"), and one box (the "loss box") contained a "devil" that would end that particular trial and would make them lose all the money they had collected in it. The devil was randomly assigned to one of the seven boxes in each trial. Subjects opened the boxes in sequence from left to right. If it was a win box, the first box contained 1 win point (corresponding to 0.35 Swiss francs), the second box contained 2 win points, the third box contained 3 win points, and so on. After the opening of each win box, a subject had to decide whether to open another box or to terminate the trial and to collect the accrued win points. If the loss box was opened, the subject earned nothing for that trial. Opening 4.5 boxes yielded the highest expected value. Because the likelihood of experiencing a loss within each trial increased with each opened box, opening more boxes was associated with greater outcome variability and therefore was a riskier strategy than opening fewer boxes was. Thus, the average number of opened boxes was used as an indicator of a subject's level of risk taking. It has been shown that this task, as well as a very similar task that was later based on this task (Lejuez et al., 2002), has predictive value for real-world risky behaviors, health-related risk-taking behaviors, or both (Hoffrage, Weber, Hertwig, & Chase, 2003; Lejuez, Aklin, Zvolensky, & Pedulla, 2003).

EEG Recording and Processing

EEG was recorded at a sampling rate of 256 Hz with a bandpass of 0.5 to 125 Hz from 58 electrodes of the 10-10 system montage (Nuwer et al., 1998). The electrode at the position Cz (vertex of the head) was the recording reference. Horizontal electro-oculographic (EOG) signals were recorded at left and right outer canthi, and vertical EOGs were recorded below the left eye. Impedances were kept below 10 k Ω . Independent component analysis was applied to remove eye-movement artifacts from the EEG. The data were recomputed against the average reference and inspected for remaining artifacts by using a moving, non-overlapping 2-s window. On average, 69.0 epochs ($SD = 9.3$) per subject were eventually available. Fast Fourier transformation (using a square window) was applied to each epoch and channel to compute the power spectra with 0.5-Hz resolution. The spectra for each channel were averaged over all epochs for each

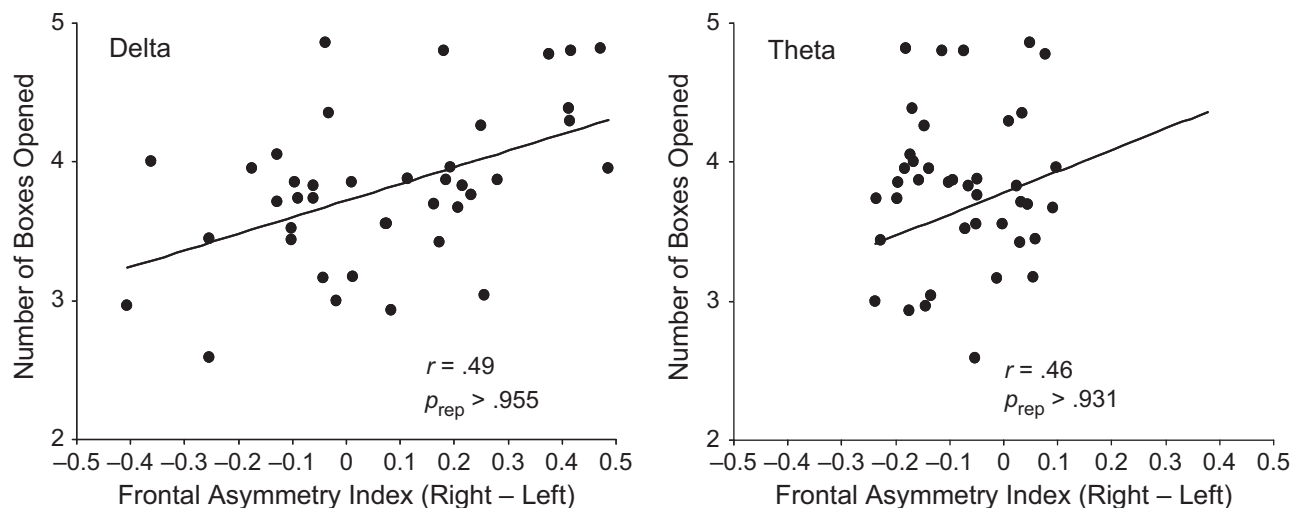


Fig. 2. Risk-taking behavior as a function of the intracerebral frontal asymmetry index in the delta (left) and theta (right) frequency bands. This index was computed by subtracting the activity in the left frontal hemisphere from the activity in the homologous areas in the right frontal hemisphere. Positive values on the x -axis reflect higher right than left electroencephalographic (EEG) activity in a specific frequency band. The regression lines and the correlation values are also shown. Higher delta and theta EEG activity reflects lower cortical activity.

subject. Absolute power spectra were integrated for the following seven independent frequency bands (Kubicki, Herrmann, Fichte, & Freund, 1979): delta (1.5–6 Hz), theta (6.5–8 Hz), alpha1 (8.5–10 Hz), alpha2 (10.5–12 Hz), beta1 (12.5–18 Hz), beta2 (18.5–21 Hz), and beta3 (21.5–30 Hz).

Source Localization

Standardized low-resolution brain electromagnetic tomography (sLORETA; Pascual-Marqui, 2002) was used to estimate the intracerebral electrical sources that generated the scalp-recorded activity in each of the seven frequency bands. sLORETA computes electric neuronal activity as current density (A/m^2) without assuming a predefined number of active sources. The sLORETA solution space consists of 6,239 voxels (voxel size: $5 \times 5 \times 5$ mm) and is restricted to cortical gray matter and hippocampi, as defined by the digitized Montreal Neurological Institute probability atlas. To reduce confounds that have no regional specificity, such as total power intersubject variability, a global normalization of the sLORETA images was carried out prior to statistical analyses.

Statistical Analyses

In a first step, current density was averaged across all voxels belonging to the PFC (Brodmann's areas 8, 9, 10, 11, 44, 45, 46, and 47), separately for the left and the right hemisphere. Next, the intracerebral frontal brain asymmetry index was computed by subtracting the log-transformed averaged current density in the left PFC from the log-transformed averaged current density in the right PFC, separately for each frequency band. The asymmetry indices for all seven frequency bands and the indices of risk-taking behavior were distributed normally (all Shapiro-Wilks W s $> .96$). Then, the asymmetry indices were correlated (Pearson correlation) with risk-taking behavior, that is, with the

average number of opened boxes in the risk task. All p values were Bonferroni corrected. In the frequency bands that yielded significant correlations, voxel-by-voxel correlations between sLORETA current density in PFC and the average number of opened boxes were computed.

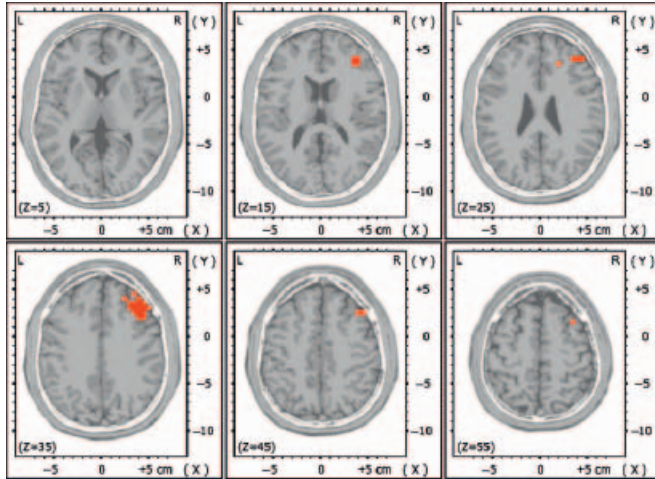
RESULTS

Subjects opened 3.81 boxes on average ($SD = 0.55$; range = 2.59–4.86). Risk-taking behavior¹ (i.e., the mean number of boxes opened) was positively correlated with relatively greater right than left pretask slow-wave oscillations in prefrontal areas, delta: $r(38) = .49$, $p_{\text{rep}} > .955$, Bonferroni corrected; theta: $r(38) = .46$, $p_{\text{rep}} > .931$, Bonferroni corrected (Fig. 2). In other words, the extent to which pretask cortical hypoactivity (as indicated by slow-wave oscillations; see Oakes et al., 2004; Pizzagalli et al., 2004) was greater in the right hemisphere than in the left hemisphere was positively associated with how many boxes were opened.

Subsequent source-localization analyses specified that this hypoactivity was generated in right lateral PFC areas (Fig. 3), and specifically that the significant voxels fell into Brodmann's areas 8, 9, 10, and 46 (see Table 1). Meng's tests (Meng, Rosenthal, & Rubin, 1992) for dependent correlations confirmed the laterality effect: The correlation between the number of opened boxes and current density in the right lateral PFC was significantly stronger than the correlation between the number of opened boxes and current density in the homologous area in the left lateral PFC, delta: $Z = 2.02$, $p_{\text{rep}} > .877$; theta:

¹Oral-contraceptive use and menstrual-cycle phase had no effects on risk-taking behavior, $F(1, 24) = 0.92$, $p_{\text{rep}} < .638$, and $F(3, 24) = 0.95$, $p_{\text{rep}} < .567$. Their interaction was also not significant, $F(3, 24) = 0.44$, $p_{\text{rep}} < .362$.

Delta



Theta

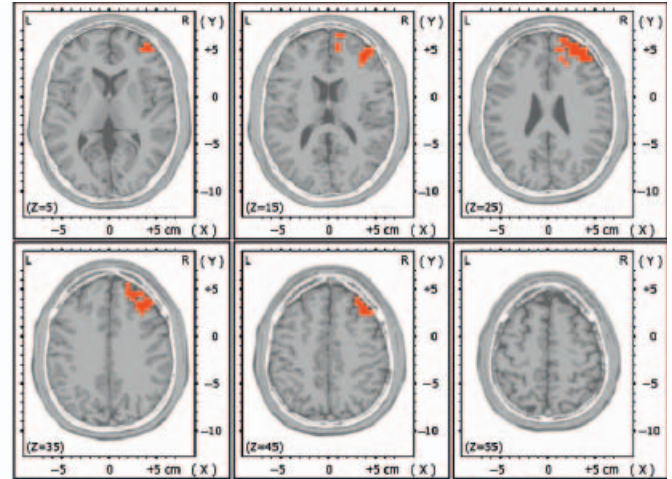


Fig. 3. Source localization of risk-taking behavior. Images of the correlations between the number of opened boxes and delta (left) and theta (right) activity in the prefrontal areas are shown. For each frequency band, six axial brain slices are shown in steps of 10 mm from the most inferior level ($z = 5$) to the most superior level ($z = 55$). Coordinates are given in millimeters (Montreal Neurological Institute atlas), and the origin is at the anterior commissure.

$Z = 1.97, p_{\text{rep}} > .877$. The two trait measures of impulsivity and self-control correlated with the intracerebral frontal brain asymmetry index in neither delta nor theta; indeed, the relation between the asymmetry index and the risk-taking behavior remained significant after partialing out the covariation for impulsivity scores, delta: $r(38) = .47, p_{\text{rep}} > .955$; theta: $r(38) = .45, p_{\text{rep}} > .955$, and for self-control scores, delta: $r(38) = .35, p_{\text{rep}} > .877$; theta: $r(38) = .34, p_{\text{rep}} > .877$.² Also, partialing out the covariation for age did not affect the results, delta: $r(38) = .48, p_{\text{rep}} > .955$; theta: $r(38) = .44, p_{\text{rep}} > .955$.

DISCUSSION

We measured brain activity using EEG at rest before subjects performed a risk task to investigate whether individual differences in tonic cortical activity level in the PFC reflect an individual's propensity to engage in risk-taking behavior. We found that individuals with high risk propensity showed a higher prevalence of slow-wave oscillations (i.e., cortical hypoactivity) in the right PFC than did those with low risk propensity. These results are in line with previous findings from patients with lesions in the right PFC and healthy subjects with "virtual lesions" in the right PFC (created using rTMS), who show a reduced cognitive control capacity. This finding confirms the hypothesis that the variability among individuals with regard to monetary risk-taking behavior corresponds to different levels of activity in the right lateral PFC.

Our findings are consistent with studies on individuals with attention deficit/hyperactivity disorder, who are generally

characterized by low self-regulation capacity and who show increased slow-wave baseline frontal EEG activity (Hermens et al., 2005). The hypoactivity in the right PFC may thus reflect a lack of regulatory abilities to suppress an option that appears more seductive because of the higher payoffs. Studies showing that a lack of inhibitory control and concomitant behavioral problems in a variety of developmental stages are associated with increased slow-wave oscillations further support this interpretation (Knyazev, 2007). Our results are also interesting in view of adolescents' increased risk-seeking behavior (for a review, see Reyna & Farley, 2006). In adolescents, the PFC has not yet attained its full functional maturity (e.g., Sowell et al., 2003). This could explain the reduced capacity for self-regulation in that age group, expressed in greater risk-taking behavior among adolescents. It is tempting to speculate that the tonic activity level in the right PFC might determine the individual variability observed in other domains constituting a self-regulatory challenge, such as prejudice control (Amodio, Devine, & Harmon-Jones, 2007). Our findings might also be interpreted in the light of studies suggesting that hypoactivity in the right PFC reflects a selective neglect for negative consequences (Bechara & Damasio, 2005) or reflects approach-related behavior (e.g., Davidson, 2004), or both. An alternative interpretation of our finding of higher risk taking among individuals with right PFC hypoactivity could be that such individuals may seek out risks as a means to drive a relatively underactivated system.

The finding that risk-taking behavior was not related to self-reported measures of impulsivity and self-control is consistent with previous studies that failed to observe relations between self-reports and behavioral measures (e.g., Crean, de Wit, & Richards, 2000). The lack of such a correlation might be due to the fact that self-report measures rely on subjects' self-perceptions, which may not accurately reflect their behavior, whereas

²The trait measures of impulsivity ($M = 20.9, SD = 3.3$) and self-control ($M = 41.1, SD = 7.6$) did not correlate with risk-taking behavior, $r(38) = .16, p_{\text{rep}} < .638$, and $r(38) = -.15, p_{\text{rep}} < .638$, respectively.

TABLE 1
Summary of Voxels Showing Significant Correlations Between the Average Number of Opened Boxes and Delta (1.5–6 Hz) and Theta (6.5–8 Hz) Current Density

BA	Side	Highest correlation	Coordinates of the voxel with the highest correlation			Number of voxels	Mean correlation
			x	y	z		
Delta frequency							
8	Right	.32*	45	25	45	4	.31
9	Right	.35*	30	35	30	34	.32*
10	Right	.34*	35	40	15	4	.33*
46	Right	.35*	35	35	15	6	.32*
Theta frequency							
8	Right	.36*	35	35	45	10	.33*
9	Right	.38*	40	40	35	43	.34*
10	Right	.36*	35	45	30	43	.33*
46	Right	.35*	45	40	30	8	.33*

Note. Coordinates are given in millimeters (Montreal Neurological Institute atlas), with the origin at the anterior commissure. For each Brodmann's area (BA), the number of voxels exceeding the statistical threshold is reported; the mean correlation is averaged across all voxels belonging to the BA. Significant correlations ($p < .05$) are marked with an asterisk.

performance on a behavioral task is both less sensitive to biased self-perceptions and less influenced by social desirability (see also Reynolds, Ortengren, Richards, & de Wit, 2006).

From a therapeutic viewpoint, our findings might serve to promote neurofeedback training to alter the frontal asymmetry and increase the tonic level of activity of the right PFC to enhance self-regulation abilities and, thus, adaptive decision making under risk. Neurofeedback is a technique that aims to shape an individual's brain electrical activity in a desired direction through continuous, real-time feedback of the EEG. This training has proven successful in altering frontal asymmetry in a variety of contexts (Allen, Harmon-Jones, & Cavender, 2001).

More broadly, this research provides a cognitive neuroscience approach to investigating individual differences in complex forms of decision making, such as risk-taking behavior. Extending this line of work, future studies should elucidate the putative components (e.g., gain-loss sensitivity, probability perception) that are individually responsible for the effects.

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