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Temporal Characteristics of EEG Microstates Mediate Trial-by-Trial Risk Taking

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Abstract People seem to have difficulties when perceiving events whose outcome has no influence on the outcome of future events. This illusion that patterns exist where there are none may lead to adverse consequences, such as escalating losses in financial trading or gambling debt. Despite the enormous social consequences of these cognitive biases, however, their neural underpinnings are poorly understood. Attempts to investigate them have so far relied on evoked neural activity, whereas spontaneous brain activity has been treated as noise to be averaged out. Here, we focus on the spontaneous electroencephalographic (EEG) activity during inter-trial-intervals (ITI) in a sequential risky decision-making task. Using multilevel mediation analyses, our results show that the percentage of time covered by two EEG microstates (i.e., functional brain-states of coherent activity) mediate the influence of outcomes of prior decisions on subsequent risk taking on a trial-by-trial basis. The devised multilevel mediation analysis of the temporal characteristics of EEG microstates during ITI provides a new window into the neurobiology of decision making by bringing the spontaneous brain activity to the forefront of the analysis.

Keywords Risk taking · EEG · Microstates · Temporal characteristics

Dietrich Lehmann: Deceased.

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Introduction

Our brain identifies patterns from past events to make predictions about upcoming ones (Huettel et al. 2002). Outcomes of prior decisions are perceived as patterns, and these patterns form the expectations that influence subsequent decisions. In effect, we tend to learn to make decisions that have had preferable outcomes in the past. However, sometimes we make decisions based on illusory patterns. For example, a person playing roulette often bets more after winning (Croson and Sundali 2005). In this case, the player has mistakenly inferred from prior outcomes that they are on a "hot streak" and they are more likely to win in subsequent rounds. When decisions are influenced by illusory patterns, people often face adverse consequences, such as escalating losses in financial trading (Odean 1998), gambling debt (Croson and Sundali 2005), and risky health-related behavior (Cvetkovich et al. 1975).

Given these socially significant consequences, many studies have investigated the underlying psychological processes of the influence of outcomes of prior decisions on subsequent decisions (see Oskarsson et al. 2009 for a review). In the recent years, researchers have begun to probe the neural underpinnings of risk processing in

general (for a review, see Knutson and Huettel 2015), how changing contextual factors influences risk taking (e.g. Kolling et al. 2014) and specifically how prior experience influences forthcoming decisions (Cohen and Ranganath 2005; Paulus et al. 2003; Xue et al. 2010, 2011). These studies have focused on evoked neural activity, whereas spontaneous activity has been treated as noise to be averaged out. However, accumulating evidence suggests that spontaneous brain activity embodies a fundamental aspect of brain function with behavioral relevance (Raichle 2015). Fluctuations in spontaneous brain activity give rise to hemodynamic signals that temporally covary in discrete sets of functionally related regions—so-called functional intrinsic connectivity networks (ICNs; Sadaghiani et al. 2010). It has been shown that such spontaneous activity is modulated by recent tasks (e.g., Waites et al. 2005; Tung et al. 2013) and impacts future behavior (e.g., Coste et al. 2011). Based on these studies, our question was whether spontaneous brain activity is also modulated by outcomes of decisions and whether such modulation influences future decisions.

A majority of studies that have demonstrated relations between spontaneous activity and mental processes have characterized brain activity by means of hemodynamic signals, representing a temporally distal correlate of brain activity. Lehmann and coworkers (1987) established a more proximal characterization of spontaneous brain activity by parsing ongoing electroencephalographic (EEG) signals into so-called *EEG microstates*. EEG microstates define subsecond time epochs with quasi-stable and unique EEG field topography. The analysis of EEG microstates yields a compact and comprehensive repertoire of brain topographic maps, so-called *EEG microstate classes*, which may be considered to reflect global functional states and have been suggested to correspond to the basic building blocks of human information processing (e.g., Khanna et al. 2015; Lehmann et al. 1998; Michel et al. 2009).

Recently, researchers have recognized EEG microstates as the electrophysiological signature of ICNs (Britz et al. 2010; Musso et al. 2010; Yuan et al. 2012). Importantly, it was suggested that the constitutive features for the functionality of EEG microstates are their temporal characteristics (Van De Ville et al. 2010). The temporal characteristics—mean duration, coverage, and frequency of occurrence—are straightforwardly traceable in standard EEG data and offer a large number of sampling points in a short time, therefore providing an efficient way to investigate trial-by-trial fluctuations of functional spontaneous activity. Based on this, we tested whether the temporal characteristics of EEG microstates after the outcomes of decisions mediate the influence of those outcomes on subsequent decisions on a trial-by-trial basis.

Methods

Participants

Thirty-nine right-handed female participants (mean age ± SD = 25 years, ±5.8 years, range 18–44 years) were recruited at the University of Zurich. The sample was limited to right-handed females to reduce sex- and handedness-related variability in physiological responses (Davidson et al. 1990). Participants were screened for health problems with a health questionnaire. They had no history of neurological or psychiatric disorder or substance abuse. The local ethics review committee approved the study. All participants were paid 30 Swiss francs for participating, in addition to the money earned in the experimental task. Participants signed a written informed consent before the start of the experiment.

Procedure

Participants were seated in a comfortable chair in a sound, light, and electrically shielded EEG recording room. The experimenter in the adjacent recording room was in contact with the participant via an intercom. During recording, the participant's head was placed in a forehead–chin rest so that the distance between eyes and PC screen was constant (100 cm) and head movements were minimized.

While continuously recording EEG, participants carried out a risk task (Slovic 1966). In each of 150 trials, participants were presented an array of seven closed boxes. They were told that six boxes contained a monetary reward ("win boxes") and one box (the "loss box") contained a "devil" that would end the particular trial and cause them to lose the money they had collected in it. In each trial, the devil was randomly assigned to one of the seven boxes. Participants sequentially opened the boxes from the left to the right. If the first box was a win box, participants gained one point (=0.35 CHF). The second box contained two win points, the third box contained three win points and so on. After opening each win box, participants had to decide whether to open another box or to terminate the trial and to collect the accrued win points ("win trial"). If the loss box was opened, the participants earned nothing for that trial ("loss trial"). Because the probability and magnitude of experiencing a loss increased with the number of opened boxes, stopping behavior in this task can be considered an index of risk taking (Slovic 1966). It has been demonstrated that this task and similar tasks have predictive value for real-world risky behaviors, health-related risk-taking behaviors, or both (e.g., Aklin et al. 2005; Hoffrage et al. 2003; Lejuez et al. 2002, 2003).

The 150 trials were played in six blocks. Within a trial, participants could choose to open a box or terminate the

trial at a self-paced speed. The inter-trial-interval (ITI) consisted of a fixed amount of time of 3 s (the outcome of the last trial was presented for 2 s, followed by a blank screen for 1 s) plus a variable amount of time until the next trial started (mean total ITI ± SD = 4.83 ± 0.76 s).

EEG Data Acquisition and Preprocessing

Scalp EEG was recorded at a sampling rate of 256 samples/s with a bandpass of 0.5–125 Hz from 58 electrodes placed in a 10–10-system montage (Nuwer et al. 1998). The recording reference was Cz (at the vertex of the head). Horizontal electrooculographic (EOG) signals were recorded at left and right outer canthi, and vertical EOGs were recorded below the left eye. Impedances were kept below 10 kΩ.

Eye movement artifacts were removed in the data using independent component analysis. Data were visually inspected for remaining artifacts. The data were then bandpassed between 2 and 20 Hz, using Butterworth zero phase filters, recomputed against the average reference and downsampled to 128 samples/s.

The goal of this study was to identify key neural mechanisms through which a risk experience affects subsequent risk taking. Accordingly, only time epochs between trials (i.e., ITIs) were further analyzed. EEG time epochs during ITIs (average total time per participant ± SD = 11.52 ± 1.09 min) were extracted. On average, ±SD of 149.1 ± 1.0 ITI epochs were available per participant. The average duration of the artifact-free ITI epochs was 4.6 ± 0.44 s.

Analysis Strategy

In a first step, we determined which aspects of decision outcomes influence subsequent risk taking (see "Behavioral Data Analysis" section). We then parsed the series of momentary potential EEG maps during ITI into functional microstates and calculated their temporal characteristics (see "EEG Microstate Analysis" section). In the last step, multilevel mediation analyses were conducted to test whether the association between a decision outcome in a specific trial and the subsequent risk-taking decision can be explained by the functional indirect pathway via the potential mediator, i.e., a parameter of the temporal characteristics of the microstates during ITI (see Multilevel Mediation Analysis" section).

Behavioral Data Analysis

Risk taking was operationalized as the number of opened win boxes, which reflects the standard measure in sequential risk-taking tasks (i.e., Lejuez et al. 2003; Pleskac 2008). The rationale behind this is that in loss trials the appearance of the devil curtails the participant from revealing his/her true preference. As a consequence, only ITI periods before win trials were analyzed.

Using a set of four regression analyses, we tested how different aspects of a risk experience in trial t influence risk taking in the subsequent trial $t+1$. Specifically, the first regression assessed whether the binary outcome of winning or losing in trial t (win trial vs. loss trial) influences risk taking in trial $t+1$. Win and loss trials were modeled as a binary regressor (*"outcome"*) with values of 1 for win trials and 0 for loss trials:

$$risk_{t+1} = d_1 + \beta_1 outcome_t \quad (1)$$

The second regression tested whether the number of opened boxes (*"boxes"*) in trial t, irrespective of the outcome, influences risk taking in trial $t+1$:

$$risk_{t+1} = d_2 + \beta_2 boxes_t \quad (2)$$

The last two regressions tested whether the number of opened boxes in trial t influences risk taking in trial $t+1$, depending on the outcomes (*"winboxes", "lossboxes"*):

$$risk_{t+1} = d_3 + \beta_3 winboxes_t \quad (3)$$

$$risk_{t+1} = d_4 + \beta_4 lossboxes_t \quad (4)$$

Using ordinary least squares, the coefficients of the four regressors (β_1, β_2, β_3 and β_4) and intercepts (d_{1-4}) were estimated for each participant, and were then tested against a mean of zero with one sample t tests (Lorch and Myers 1990), indicating whether they significantly characterize the association between a risk experience and subsequent risk taking.

EEG Microstate Analysis

Brain electric field data recorded simultaneously from many electrodes on the scalp can be viewed as a series of momentary spatial distributions of electric potentials (i.e., momentary maps) (Lehmann 1971). In continuously recorded EEG, series of momentary maps show short epochs of quasi-stable map configurations called functional microstates (Lehmann et al. 1987) that are concatenated by rapid transitions to new configurations. Different map configurations directly indicate different generator configurations in the brain. Given this physical fact, it is reasonable to assume that different map configurations reflect different brain functions, i.e., different functional states of the brain (Michel and Murray 2012).

To restrict the analysis to data with optimal signal-to-noise ratio, the momentary maps at peak times of the Global Field Power (GFP, Lehmann and Skrandies 1980) were selected (mean number ± SD of GFP peaks = 15,762 ± 3308

per participant, and 106 ± 22 per ITI). Separately for each participant, these GFP peak maps entered a set of modified k-means clustering analyses seeking for 3–10 classes of maps (prototype maps, Pascual-Marqui et al. 1995) of different configurations. The clustering criterion was the Global Map Dissimilarity (GMD, Lehmann and Skrandies 1980). According to the modified Krzanovski-Lai criterion (Murray et al. 2008), we fixed the number of prototype maps to four for all participants. To make direct statistics over participants and provide comparability between participants, the four prototype maps of each participant were averaged across participants using a permutation algorithm that maximizes the common variance over participants (Koenig et al. 1999), yielding four mean prototype maps. All momentary maps of each participant during ITI were assigned to one of the four mean prototype maps, based on the smallest GMD value between the mean prototype maps and the tested momentary maps. Successive momentary maps assigned to the same mean prototype map were recognized as belonging to one "microstate" (labeled as EEG microstate class "1", "2", "3", and "4"). The temporal characteristics of the microstate classes are described by three parameters: the mean duration ("duration"), reflecting the average time in milliseconds covered by a given microstate class, mean number of distinct microstates of a given class occurring within a 1 s window ("occurrence"), and the percentage of time covered by a given microstate class ("coverage"). For each participant and each ITI, the three parameters were computed separately for the four microstate classes.

Multilevel Mediation Analysis

The goal of this last analysis step was to identify neural markers (characterized as microstate class parameters) through which risk experience affects risk taking in the subsequent trial. To reach this goal, multilevel mediation analyses were applied. For each participant, a relational triangle can be formalized using a path model (see Fig. 1), where the independent variable (X) is the risk experience in trial t, the dependent variable (Y) is the extent of risk taken in trial $t+1$, and putative mediator variables (M) are the three parameters, *Duration, Occurrence* and *Coverage* of the four EEG microstate classes. Three paths constitute the model: indirect path a represents the influence of the risk experience in trial t on a specific EEG microstate parameter during subsequent ITI ($X \rightarrow M$). Indirect path b represents the influence of a specific EEG microstate parameter on subsequent risk taking, while controlling for prior risk experience ($M \rightarrow Y$). Finally, path c' represents the direct effect of the risk experience to subsequent risk taking, while controlling for a specific EEG microstate parameter ($X \rightarrow M$). The mediation test indicates whether a specific

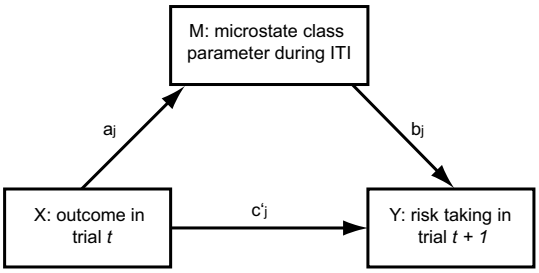

Fig. 1 Path model. The independent variable (X) corresponds to the risk experience in trial t. The dependent variable (Y) corresponds to the amount of risk taken in trial $t+1$, and the putative mediator variable (M) is one of the microstate parameters, duration (ms), occurrence (per s) and coverage (%) of a given microstate class. Path a represents the influence of the risk experience in trial t on microstate parameters during ITI. Path b represents the influence of a particular microstate parameter on subsequent risk taking, while controlling for the prior risk experience. Path c' represents the direct effect of the risk experience to subsequent risk taking, while controlling for the putative mediator. The index j indicates that the path relations vary across participants

EEG microstate parameter during ITI is in a causal chain between the risk experience and the subsequent risk taking. Significant mediation was defined as significance in three tests (MacKinnon et al. 2007): (a) significant indirect path a, relating the independent variable to the mediator ($X \rightarrow M$). (b) Significant indirect path b, relating the mediator to the dependent variable ($M \rightarrow Y$). (c) Significant functional mediation pathway by showing that the $a*b$ cross product is significantly different from 0. Given that in our data putative mediations take place on a trial-by-trial basis (at first-level), our goal was to statistically test for reliable mediation effects across participants (at second-level). Accordingly, we applied a multilevel mediation analysis, as implemented in the Multilevel Mediation Moderation (M3) toolbox (http://wagerlab.colorado.edu/files/tools/mediation.html) (Wager et al. 2009). The population regression coefficients of a, b and $a*b$ were estimated using a weighted least squares-based mixed-effects model that takes into account within- and between-participants variation (see supplementary Materials in Wager et al. 2009). Statistical inference on the population coefficients a, b and $a*b$ was rendered using permutation tests with 10,000 permutations (Nichols and Holmes 2002). The strength of the total mediation effect $a*b$ in a multilevel mediation analysis is influenced not only by the product of the means of a and b but also by the covariance between a and b (see Kenny et al. 2003, Eq. 9). In other words, an $a*b$ effect can be driven by a first-level mediation, which is replicable in the group (i.e., the product of the means of a and b) or can stem from individual differences in coherent pathway strength (i.e., the covariance of a and b). As we were interested in reporting first-level mediation effects that generalize to the population, we

will only report effects that show significant results on *a, b* and *a*b* combined with a non significant covariance of *a* and *b* (tested with Pearson correlations).

Source Localization

We used standardized low-resolution brain electromagnetic tomography (sLORETA; Pascual-Marqui 2002) to compute the cortical three-dimensional (3D) distribution of current density of the EEG microstate classes that were shown to significantly mediate the relation between experienced outcomes and successive risk-taking decisions. The sLORETA method is a properly standardized discrete, 3D distributed, linear, minimum norm inverse solution. The particular form of standardization used in sLORETA endows the tomography with the property of exact localization to test point sources, yielding images of standardized current density with exact localization, albeit with low spatial resolution (i.e., neighboring neural sources will be highly correlated). sLORETA has recently been validated in several simultaneous EEG/fMRI studies (Mobascher et al. 2009a, b) and in an EEG localization study for epilepsy (Rullmann et al. 2009).

In the current implementation of sLORETA, computations were made in a realistic head model using the MNI152 template (Mazziotta et al. 2001), with the 3D solution space restricted to cortical gray matter, as determined by the probabilistic Talairach atlas (Lancaster et al. 2000). The intracerebral volume is partitioned in 6239 voxels at 5 mm spatial resolution. Thus, sLORETA images represent the standardized electric activity at each voxel in neuroanatomic Montreal Neurological Institute (MNI) space as the exact magnitude of the estimated current density.

Using the momentary EEG maps at GFP peaks during ITI epochs, the first spatial principal components were calculated separately for each participant and microstate class, resulting in a polarity independent mean map per microstate class and participant. The inverse solutions for these mean maps were then calculated using the sLORETA algorithm.

Results

Behavioral Data Analysis

Our results indicate that participants were generally risk aversive, because they opened an average ± SD of 3.43 ± 0.28 boxes, compared to the optimal number of opening 4.5 boxes, yielding the highest expected value. These decisions led to appearances of the "devil" and hence losses in 51 ± 0.08%. The trials preceding these losses were excluded from further analyses as the appearance of the devil "truncated" risk taking in these trials, leaving an average of 74 trials per participant for the remaining analysis.

The analysis on the character of linkage between decision outcomes and subsequent risky decisions revealed that participants were more risk taking after experiencing wins compared to losses [Eq. (1), $\beta_1 = 0.30$: $t(38) = 4.881$, $p < 0.001$] (see Fig. 2). Since this was the only significant type of linkage, we simplified the information about outcomes for the further analyses to binary outcomes, dissociating losses and wins. In contrast to this, the number of previously opened boxes did not influence participants' subsequent risk taking. This was neither the case if this relation was analyzed separately for win outcomes [Eq. (3), $\beta_3 = -0.02$: $t(37) = -0.523$; $p > 0.604$] and loss outcomes [Eq. (4) $\beta_4 = 0.04$: $t(38) = 1.253$: $p > 0.218$], nor was it the case if it was analyzed together for win and loss outcomes [Eq. (2), $\beta_2 = 0.05$: $t(38), = 1.728$; $p > 0.092$].

EEG Microstate Analysis

Figure 3 illustrates the mean prototype maps of the four microstate classes and reports the mean values and standard deviations for the temporal dynamic parameters, *duration, occurrence*, and *coverage*. The mean prototype maps of the four microstate classes explained 51.28 ± 0.04% of the total variance.

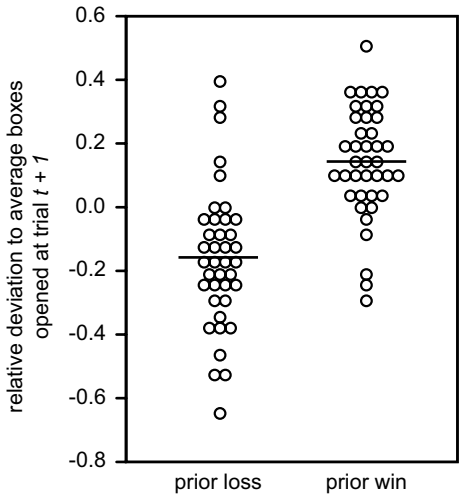

Fig. 2 Influence of prior outcomes on subsequent risk taking. Depicted is the participant-wise demeaned number of averagely opened win boxes at $t+1$ after win trials and after loss trials at *t*. *Solid lines* indicate the mean across participants

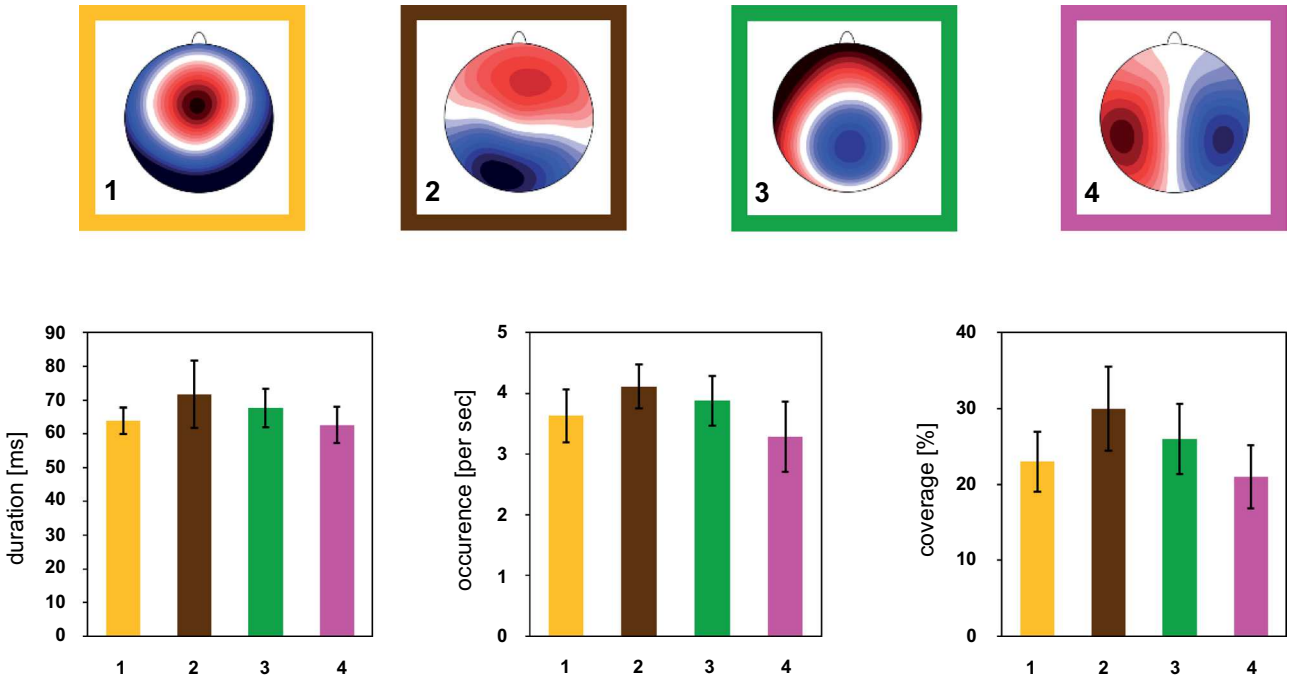

Fig. 3 EEG microstate classes (*upper panel*) and their temporal characteristics (*lower panel*) during ITI. *Error bars* indicate standard deviation of the mean

Multilevel Mediation Analysis

Our results, summarized in Table 1, suggest an opposite role of two brain networks reflected by microstate classes 1 and 2, with the first one acting as a "brake pedal", dampening future risky behavior, which is "pushed" for a relatively greater duration after experiencing losses and the latter one acting as an "accelerator pedal", augmenting future risky behavior, which is "pushed" for a relatively greater duration after experiencing wins. Specifically, the multilevel mediation analysis shows that a negative outcome (i.e., a loss trial) leads to greater time coverage of microstates belonging to class 1 ($Z=-3.89$, $p<0.0001$) during ITI, which in turn leads to less risky decisions in the subsequent trial ($Z=-2.43$, $p<0.0153$). The contrary was observed for the coverage of microstates belonging to class 2: a positive outcome (i.e., a win trial) leads to greater time coverage during ITI ($Z=3.896$, $p<0.0001$), which in turns leads to marginally significantly more risky decisions in the subsequent trial ($Z=1.85$, $p<0.0644$). The remaining microstate classes 3 and 4 did not play a mediation role in the association between decisions outcomes and subsequent risk taking.

Source Localization

A direct comparison of the sLORETA images between EEG microstate class 1 vs. EEG microstate class 2 results in two source localization images showing those neural sources that uniquely characterize microstate classes $1>2$ and $2>1$. The whole-brain voxel-by-voxel paired t-comparisons (corrected for multiple testing, Nichols and Holmes 2002) indicate that the EEG microstate class 1, compared to EEG microstate class 2, is reflected by higher neural activity in the prefrontal cortex, bilaterally ($t(38)>9.50$, $p<0.005$, Fig. 4, upper panel). The peak voxel was located at X = −35, Y = 40, Z = 40 (MNI coordinates), Brodmann area 9. Conversely, the EEG microstate class 2, compared to EEG microstate class 1, was reflected by higher neural activity in the left temporo-parieto-occipital cortex ($t(38)>-9.32$, $p<0.005$, Fig. 4, lower panel). The peak voxel was located at X = −35, Y = −90, Z = 15 (MNI coordinates), Brodmann area 19.

Discussion

We used EEG in conjunction with a sequential risk-taking task to study how risky decision making varies as a function of prior outcomes. Specifically, we parsed epochs of spontaneous EEG between trials into four EEG microstate classes and tested whether the temporal characteristics of these microstates causally chained experienced outcomes with forthcoming risk taking.

Our results demonstrated that our group of young healthy participants were more risk seeking after winning

Table 1 Multilevel mediation results

Microstate classes	A					B				
Path	a	b	a*b		Corr (a, b)	a	b	a*b		Corr (a, b)
Duration (ms)										
Slope	−0.2246	−0.0041	−0.0009	*R*	−0.1100	0.0400	0.0000	0.0011	*R*	0.0023
STE	0.0591	0.0117	0.0012			0.0556	0.0065	0.0007		
Z	−4.0556	−0.3510	−0.7473			0.6933	0.6461	1.5893		
p	0.0001	0.7256	0.4568		0.4549	0.4881	0.5182	0.1120		0.9888
Occurrence/s										
Slope	−0.0569	−0.0446	0.0011	*R*	0.2497	0.1249	0.0282	0.0018	*R*	0.2779
STE	0.0326	0.0179	0.0011			0.0363	0.0169	0.0009		
Z	−1.7358	−2.4977	1.0163			3.4808	1.6611	1.9574		
p	0.0826	0.0125	0.3095		0.1253	0.0005	0.0967	0.0503		0.0867
Time coverage (%)										
Slope	−0.0100	−0.5523	0.0025	*R*	0.2092	0.0105	0.3475	0.0028	*R*	0.1560
STE	0.0029	0.2336	0.0012			0.0028	0.1898	0.0011		
Z	−3.8906	−2.4252	2.0803			3.8906	1.8494	2.6000		
p	0.0001	0.0153	0.0375		0.2012	0.0001	0.0644	0.0092		0.3430
Microstate classes	C					D				
Path	a	b	a*b		Corr (a, b)	a	b	a*b		Corr (a, b)
Duration (ms)										
Slope	−0.1063	0.0009	−0.0016	*R*	−0.2935	−0.1347	0.0139	0.0000	*R*	0.0350
STE	0.0604	0.0064	0.0006			0.0607	0.0068	0.0004		
Z	−1.7583	0.1435	−2.6159			−2.2130	2.1003	−0.0362		
p	0.0787	0.8859	0.0089		0.0698	0.0269	0.0357	0.9711		0.8327
Occurrence/s										
Slope	−0.0342	−0.0083	0.0003	*R*	−0.0812	0.1674	0.0044	0.0006	*R*	−0.1706
STE	0.0313	0.0168	0.0007			0.0372	0.0171	0.0011		
Z	−1.0826	−0.4819	0.4044			4.0556	0.2715	0.5065		
p	0.2790	0.6299	0.6859		0.6232	0.0001	0.7860	0.6125		0.2992
Time coverage (%)										
Slope	−0.0064	−0.1596	−0.0017	*R*	−0.3195	0.0068	0.3082	−0.0006	*R*	−0.2938
STE	0.0030	0.2064	0.0013			0.0025	0.1907	0.0009		
Z	−2.1987	−0.7524	−1.3018			2.8943	1.6160	−0.6084		
p	0.0279	0.4518	0.1930		0.0474	0.0038	0.1061	0.5429		0.0694

Path *a* represents the link between decision outcomes and microstate parameters of classes A–D. Path *b* represents the link between microstate parameters and subsequent risk taking. Path *a*b* indicates a mediation effect. The correlation of *a* and *b* [*corr* (*a, b*)] informs to what extent a mediation effect may be driven by individual differences in coherent pathway strength

than after losing, exhibiting so-called positive recency. Thus, in a first step, we could confirm that outcomes of previous decisions influence subsequent risk taking. The finding of positive recency is in line with previous experimental studies (Chau and Phillips 1995; Cummins et al. 2009; Leopard 1978; Thaler and Johnson 1990) and field data (Croson and Sundali 2005) showing that individuals are more willing to take risks after successes (but see Staw 1976 for the opposite effect).

Going further by examining the spontaneous brain activity during inter-trial-intervals using EEG microstates, our study revealed that four classes of EEG microstates explained 51% of the data variance. Crucially, applying multilevel mediation analysis we found that the percentage of time covered during inter-trial-intervals by two of these four EEG microstates classes causally mediates the effect of prior outcomes on subsequent decisions.

Functionally, the two mediators act akin to a "brake pedal" and an "accelerator pedal", respectively. After losses, the brake pedal (EEG microstate class 1) was longer active, leading to fewer risk-seeking decisions in

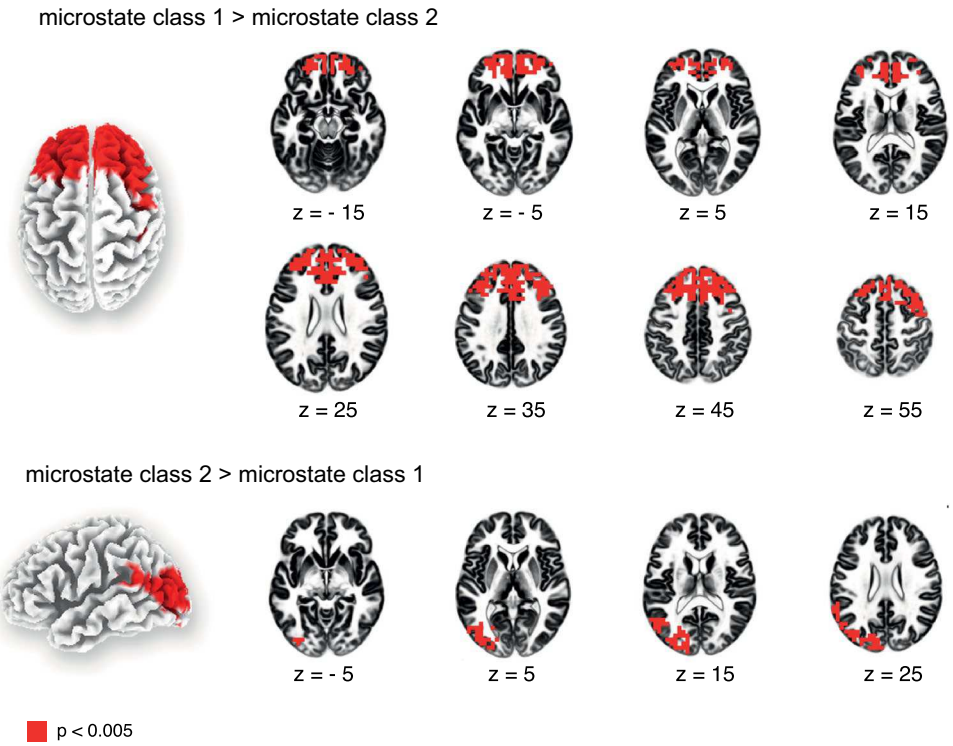

Fig. 4 Localization of the neural sources that characterize microstate classes 1 (*upper panel*) and 2 (*lower panel*). The inverse solutions of the first principal component of the momentary EEG maps at GFP peaks within ITIs of each participant of microstate class 1 and microstate class 2 were contrasted using paired *t* tests ($p < 0.005$)

the subsequent trials. After wins, the accelerator pedal (EEG microstate class 2) was active for longer, leading to more risk-seeking decisions in the subsequent trials (for a schematic overview see Fig. 5). Thus, the two microstate classes revealed opposing behavioral effects. Keeping this in mind, we characterized the intracortical sources of the two EEG microstate classes by contrasting them against each other.

EEG microstate class 1 was characterized by activation of a bilateral prefrontal network, whereas EEG microstate class 2 was characterized by activation of a distributed posterior network, encompassing inferior temporo-parietal and occipital regions. In line with our interpretation of EEG microstate class 1 as a "brake pedal", converging evidence showed that lateral prefrontal regions are critically involved in self-regulatory processes (e.g., Aron 2008; Diamond 2013; Heatherton and Wagner 2011). Interestingly, an individual's degree of inhibitory control across a wide range of regulatory processes is related to baseline activation level in the lateral prefrontal cortex measured by resting EEG (e.g., Knoch et al. 2010; Gianotti et al. 2012). In particular, two studies that used the same risk task as we used have shown that individuals with higher levels of baseline activation in the lateral prefrontal cortex are less swayed by looming financial wins and take smaller risks to attain them (Gianotti et al. 2009; Studer et al. 2013). Here we show that from trial to trial, the *percentage of time* a prefrontal network is activated during inter-stimulus-intervals predicts risk taking.

EEG microstate class 2, which we interpret as an "accelerator pedal", is characterized by a distributed posterior network—including the inferior parietal cortex. Previous studies have highlighted the role of the inferior parietal cortex in decision making under risk: Neural responses in this area reflected the probability of winning during gambling (Huettel et al. 2005; Smith et al. 2009; Studer et al. 2012; van Leijenhorst et al. 2006). Our results add to this research, showing that from trial to trial, the *percentage of time* for which a distributed posterior network is activated during inter-stimulus-intervals is positively associated with the optimistic expectation of winning in the subsequent trial, which increases risk taking.

Previous neuroimaging research on the impact of prior risk experiences on subsequent risky decision making has focused on how gambling decisions were modulated by the activation strength of their underlying neural correlates (Buchel et al. 2011; Xue et al. 2010, 2011). The present study sheds light on another aspect—the temporal one. Yet, how can temporal dynamics of brain activity affect behavior? Our results suggest that EEG microstates need to be repeatedly and/or enduringly activated (the combination of both factors reflecting the time coverage) to become behaviorally effective. The coverage of an EEG microstate class can be considered a measure of the "opportunities" for processing the functions that are specific to the underlying network. Furthermore, it has been suggested that recurrent network activity may lead to persistent activity, which is argued to be a general mechanism by which internal

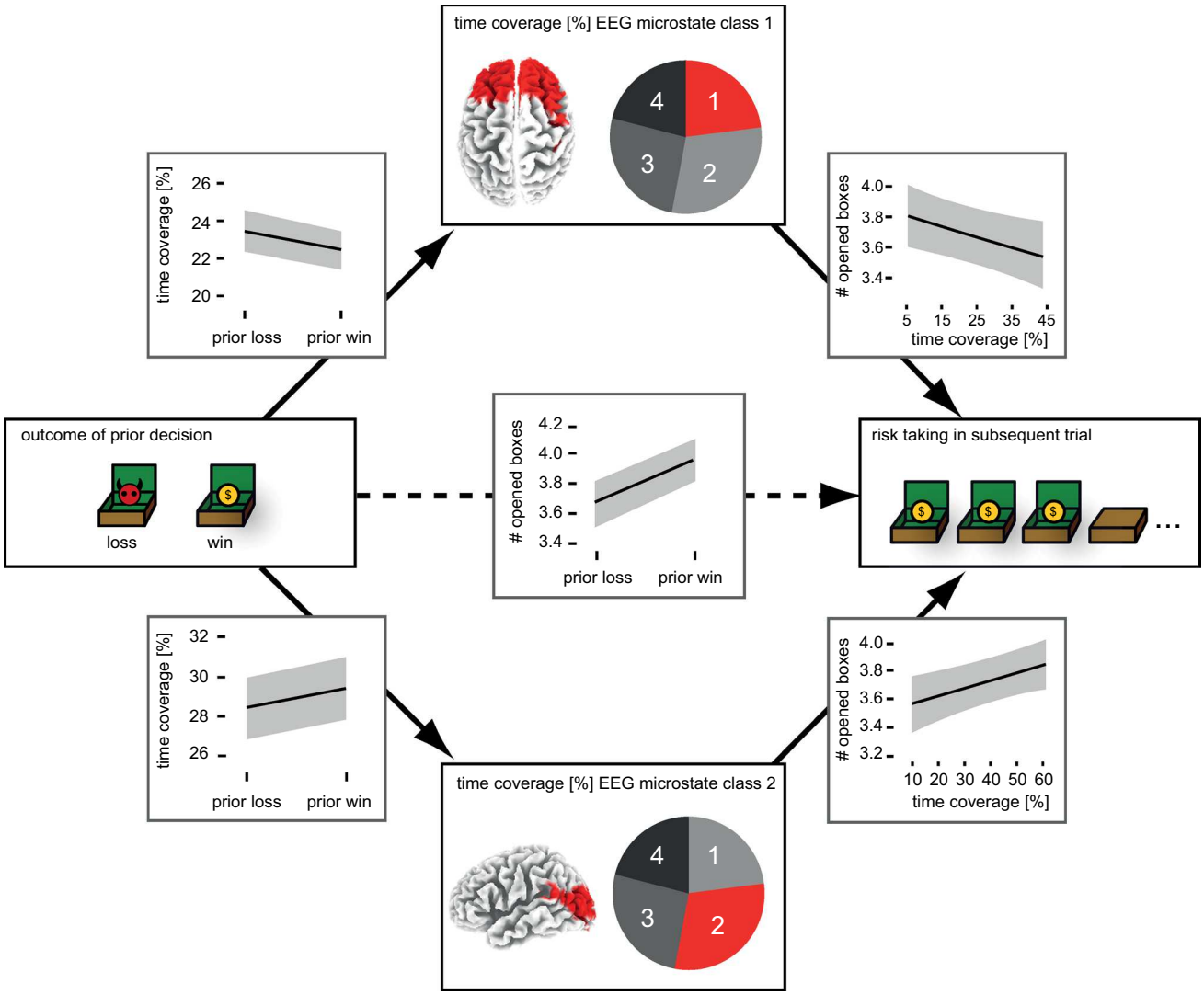

Fig. 5 Temporal dynamics of EEG microstates mediate the influence of prior outcomes on subsequent risk taking. The time coverage of microstate class 1 is negatively related to the success in the preceding trial and to the riskiness of the subsequent decision. Microstate class 1 therefore reduces risky behavior. On the other hand, the time coverage of microstate class 2 is positively related to the success in the preceding trial and is positively related to the riskiness of the subsequent decision. Microstate class 2 therefore increases risky behavior. The *black line* shows the group average, and the *shaded gray* area shows the 95% confidence interval for the regression slopes

representations, such as behavioral tendencies or reward expectancies, are maintained in an active state (Curtis and Lee 2010). Still, it remains unclear how the percentage of time covered by microstates during inter-stimulus-intervals influences the execution of decisions taken multiple seconds later. A worthwhile idea, which could be substantiated in future studies, would be that increased time coverage in a certain EEG microstate class facilitates future activation of the associated network, or parts of the network. Thus, increased time covered by a certain EEG microstate during inter-stimulus-intervals may "prime" the activation of the underlying neural network and increase the likelihood of being in that EEG microstate during the evaluation and execution of the subsequent decision. As previous studies have shown that neural processing is highly state dependent (e.g., Destexhe and Contreras 2006; Britz and Michel 2011; Britz et al. 2014; Müller et al. 2005), the subsequent decision may be biased towards more or less risk taking, depending on the prevailing state. This in turn is in line with the idea that induced neural activation influences future network activity (Guidotti et al. 2015) and network activity influences future behavior (Sadaghiani et al. 2015; Albert et al. 2009; Lewis et al. 2009).

In sum, our results emphasize the importance of focusing on spontaneous brain activity, besides evoked brain activity. In addition, we demonstrate that the "effect size" of a functional network is defined not only by the intensity of its activation, but also by its temporal characteristics.

Furthermore, the fact that we were able to pin down markers of brain activity in the time window of the ITI influencing future decisions that are executed multiple seconds later implies that decisions are not exclusively made immediately preceding the execution of the decision. This also suggests that the temporal characteristics of EEG microstates may represent a way to transfer information about behavioral tendencies over time, biasing future behavior, based on previous experience.

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Compliance with Ethical Standards

Conflict of interest The authors declared that they had no conflict of interest with respect to their authorship or the publication of this article.

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