Chapter 2

EEG Indices of Cortical Network Formation and Their Relevance for Studying Variance in Subjective Experience and Behavior

Thomas Koenig, Miralena I. Tomescu, Tonia A. Rihs, and Martha Koukkou

Abstract

The EEG is a highly sensitive marker for brain state, such as development, different states of consciousness, and neuropsychiatric disorders. The classical spectral quantification of EEG suffers from requiring analysis epochs of 1 s or more that may contain several, and potentially quite different brain-functional states. Based on the identification of subsecond time periods of stable scalp electric fields, EEG microstate analysis provides information about brain state on a time scale that is compatible with the speed of human information processing. The present chapter reviews the conceptual underpinnings of EEG microstate analysis, introduces the methodology, and presents an overview of the available empirical findings that link EEG microstates to subjective experience and behavior under normal and abnormal conditions.

Key words EEG, Microstates, Networks, Working memory, State-dependent information processing, Development

1 Introduction

The scope of the book with the title "In vivo Neuropharmacology and Neurophysiology" is to present methods developed for and applied to the study of the brain functions which create and form subjective experience and behavior.

Our work in neurophysiology uses the electrically manifested brain-functional states (the electroencephalogram; EEG) during different stages of development and of consciousness in order to investigate individual variance of subjective experiences and behavior. We have discussed the subject on the basis of an integrative brain model, a theoretical framework that in agreement with related attempts [1, 2] proposes that the human brain is a self-organizing system that creates individual variance of subjective experiences and behavior on the basis of its biography (e.g. [3–6]).

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Based on the proposal of this model of the brain functions that create autobiography (individual thoughts, emotions, plans, dreams, and behavior), we have discussed: (a) The psychosocially manifested developmental changes as the products of the brains learning and memory functions that create the contents of the autobiographical memory via experienced dependent cortical plasticity (cortical network formation) which goes parallel with the developmental changes (increase of complexity) of the EEG. (b) The role of the brain's EEG-state-dependent but memory-driven retrieval processes in forming the individual's momentary thoughts, emotions, and behaviors as well as their conscious perceptions.

2 Why Using the EEG?

More than 80 years of work in neurophysiology using the electroencephalogram have shown that there are well established correlations between psychosocially manifested behavioral development and

(a) systematic changes of cortical functioning as manifested in the systematic changes of the EEG amplitude, wave frequency, coherence between regions, between hemispheres and between anterior and posterior areas during wakefulness from birth to adulthood as well as of dimensional complexity

(b) systematic changes of cortical neuroanatomy as manifested in the increase of cortico-cortical connections, the experience-dependent cortico-cortical synaptic complexity, i.e. of the neuronal networks that represent ("materialize") individual experiences; the concepts of autobiographical memory (*see* [1, 7, 8]).

In sum, studies in cortical neuroanatomy during development have shown that the increase in cortico-cortical connectivity which is considered to be the product of experience-dependent cortical plasticity, goes hand in hand with the increase of EEG complexity and of the behavioral changes that characterize psychosocial development.

It is more or less generally accepted that the developmental EEG changes during wakefulness reflect the developmental increase in cortico-cortical synaptic connectivity and imply that with age the complexity of the mnemonic networks (i.e. the number of involved neuronal populations and their quantity) increases; in other words, the amount of autobiographical knowledge increases [1].

The functional significance of these well-established parallel developmental changes in EEG and of cortico-cortical connectivity during human psychosocial development is considered to reflect

(a) the increasing complexity of the synaptic connectivity among cortical networks, as well as between hemispheres and between anterior and posterior sites within a hemisphere and to imply

(b) that with age, the activity and/or the number of neuronal populations involved in information processing increases [1].

Thus developmental changes in the brain-functional state as manifested in the EEG during wakefulness reflect the level of attained complexity of the neuronal representations of the autobiographical memory contents.

2.1 The EEG State Dependency of the Memory Driven Brain Information Processing Operations: The Concept of Multifactorially Defined Brain-Functional States with EEG State-Dependent Accessibility of Knowledge for the Organization of Behavior

Studies of information processing operations have shown differing results depending on the momentary brain-functional state as measured with the EEG. In other words, the same information treated during different brain-functional states has different results in subjective experiences and behavior. The brain can be said to be in one particular global functional state at each moment in time, however complex that state might be [3].

Based on the proposals of the model of the brain functions, which create and form subjective experiences and behavior we have summarized:

(a) the brain-functional state as manifested in the scalp EEG represents the level of achieved complexity and the level of the momentary excitability of the neuronal network (of the representational network),

(b) at each given age and time moment, a multifactorially and dynamically determined representational network is active and thus, accessible as contents of working memory to the memory-driven information processing operations for the organization of behavior (EEG-state-dependent information processing) and

(c) dynamically readjust via the continuously functioning memory-driven information processing operations which underlie the initiation of a non-unitary, adaptive orienting response and its "habituation" and which are the pre-attentive operations underlying allocation of attention [9].

This continuous readjustment of the brain-functional state corresponds to the updating of working memory; it can be measured as EEG reactivity [4, 5, 10]; it reflects the dynamics of the associative memory described as semantic priming and semantic inhibition.

The functional state of the brain is reflected in numerous subjective and objective parameters, among them brain electromagnetic activity (EEG). EEG offers a high sensitivity to state changes as well as a high time resolution—down to split-second range—that is adequate for the assessment of the brain functions of perception, cognition, and emotion. The temporal–spatial EEG (e.g. wave frequency, coherence, global dimensionality) patterns closely co-vary with developmental age and vigilant levels, reflecting the complexity level of the momentarily activated neuronal networks [3–6]. The temporo-spatial EEG patterns also co-vary sensitively with normal and pathological mental conditions. The momentary functional state of the brain constrains the available range of the subsequent state, the processing options, and the read-out from and deposit into memory.

The functional state of the brain, as studied with the EEG, is constraint by developmental age (infancy, childhood, adulthood) and by normal and abnormal metabolic conditions. Within these constraints the brain-functional state varies over time in a non-steady way, displaying extended quasi-steady periods that are constrained by rapid, almost stepwise changes.

2.2 From Macro EEG States to Micro EEG States

The central concepts described were developed on the basis of research findings that have shown close relations between cognitive, emotional, and action styles with EEG macrostates during development and during wakefulness and sleep as well as more specifically with EEG macrostates during adult wakefulness. However, the traditional method of quantifying EEG macrostates, namely the spectral analysis of EEG, has the shortcoming that it is typically based on analysis epochs that extend over periods that may contain several, and potentially quite different brain-functional states. In order to overcome this problem, so-called EEG microstates can be extracted, which provide information about brain state on a time scale that is compatible with the speed of human information processing.

3 How Do We Observe, Quantify, and Interpret Microstates?

In the late 1970s, Dietrich Lehmann and his colleagues developed an innovative method to quantify the spatio-temporal dynamics of neuronal networks both for task evoked and spontaneous brain activity, the EEG spatio-temporal segmentation [11–13]. The EEG segmented map series are characterized by quasi-stable (±100 ms) potential field configurations across time [14], named EEG microstates.

Since the initial description of EEG microstates, the methods to computationally identify EEG microstates have undergone substantial changes. The current mostly employed methodology is based on a methodological contribution by RD Pascual-Marqui et al. [15]. In this approach, in the typical first step, the momentary EEG topographies of the EEG to be analyzed are submitted to a modified k-means clustering algorithm (Fig. 1). This algorithm groups these EEG topographies into a predefined number of classes of topographies. This grouping is based upon the spatial similarity among these topographies, and strives for maximizing

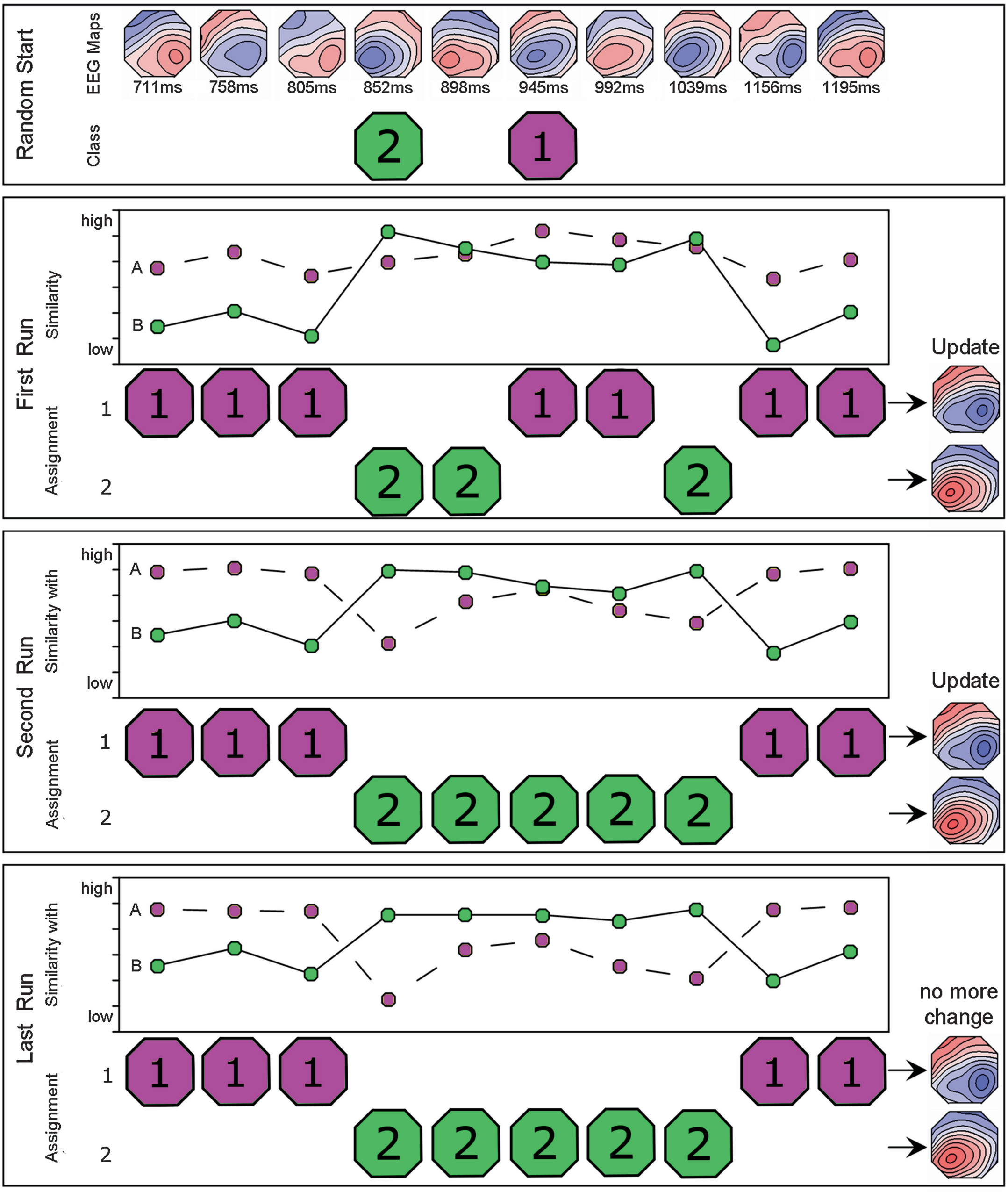

Fig. 1 Identification of two microstate prototype maps and assignment of microstate time periods using the obtained maps. The map in the *top row* shows a sequence of raw EEG data as scalp field maps, selected at momentary maxima of the GFP. Two of these maps are randomly selected and serve as initial microstate maps 1 and 2. First, the raw EEG maps are compared to the initial microstate maps using the squared correlation coefficient (similarity). Each raw map is labeled according to the best-fitting microstate map, as indicated by numbers 1 and 2, and by color. The microstate templates are then updated based on all raw EEG maps belonging to the class of each template. This procedure is repeated (second and last run) while changes in labeling occur, and stopped when the procedure has converged. Modified after [16]

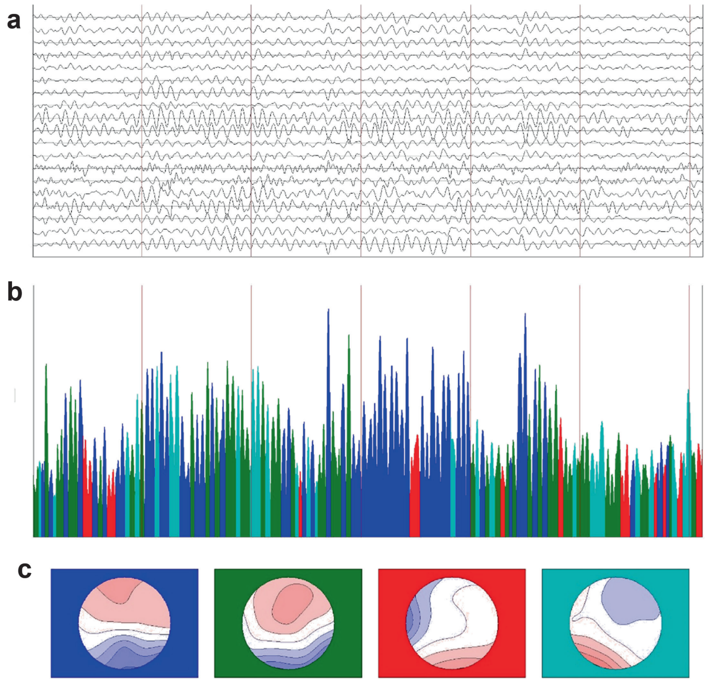

Fig. 2 Example of a microstate analysis of a 6 s epoch of spontaneous EEG. (**a**) The single traces of the EEG. (**b**) The Global Field Power (GFP) of the same data, color coded by the assignment to one of the four microstate prototype maps shown in (**c**). No obvious relation between the dominant EEG frequency and the microstate segment borders can be seen

this spatial similarity among all topographies assigned to the same class. Importantly, each topography is being assigned to exactly one class. Once this grouping algorithm has converged, the mean topography of each topographic class is computed, yielding the so-called microstate prototype map of each class [15]. This step of identifying microstate prototype maps may be further elaborated by again grouping EEG prototype maps obtained in individuals into group prototype maps [16]. Alternatively, if some normative EEG prototype maps are already available [17], the entire procedure may be skipped and the identification of the actual microstates in some continuous EEG data may be based on those a-priori defined prototype maps.

Once a set of EEG microstate prototype maps is available, the momentary maps of the continuous EEG are labeled according to the label of the best fitting prototype map. This labeling may alternatively be applied only to moments of a momentary maximum of the Global Field Power [16], or to the entire data. Additionally, the labeling may be smoothed over time [15]. Finally, EEG microstates are defined as continuous time periods where all momentary maps have received the same label (Fig. 2). An extensive discussion about the methodology for the identification of EEG microstates can for example be found in [18].

Methodologically, three main arguments support the importance and usefulness of this methodology. First of all, looking at scalp topographies keeps you safe from the reference problem, since potential maps are independent of the reference choice [19]. Secondly, the potential maps equally consider all electrodes and do not restrict the analysis to an a priori selection of electrodes. Last but not least, the maps are essential precursors of the source localization of the neuronal generators. By looking at the flattened amplitude distribution of the EEG sensors, the space-oriented configuration of the maps, the topography, is defined by the position of the positive and negative centroids of the maximal field strength. The EEG microstates represent the transient activity distributed in the time of synchronous neuronal generators in the brain. Practically, during resting state, i.e. during a state without external input, EEG microstates are scalp patterns with temporal stability or around 100 ms frames that represent different underlying resting cognitive states [20]. The spatial configuration (the topography) and the temporal parameters (mean duration, time coverage, occurrence) of the EEG microstates are very consistently replicated across many studies adding hundreds of participants from multiple recording sites [17, 21, 22]. Captured at the scalp level, changes in the topography of the microstates directly indicate changes in configuration of the neuronal generators [19]. The spatial recurrent topographical distribution of the ongoing potential has been shown to be explained by only four classes of topographies which are associated with certain resting state networks (RSNs): class A—left posterior and right anterior centroids associated with auditory and language processing; class B—left anterior and right posterior centroids—related to visual processes; C—midline frontal—anterior axis centroids—associated with the salience network involved in the detection of and orientation to both internal events and external stimuli of importance; D—centrally midline and low posterior midline centroids—related to cognitive processes responsible for decision making, control of attention and working memory [23].

3.1 EEG Microstates as "Atoms of Thought" Relate to Normal Psychological Conditions

One of the first studies on EEG microstates found that different classes of microstates are indexing different types of mental activity. In this study, participants were asked to rate their momentary thought content into either visual-concrete or abstract thoughts at a given sound prompt (each 2 s). The topography of the EEG microstate activity differentiates two categories of thought content. One microstate class was present during visual imagery and another class during abstract thought [20, 24]. Similarly, after participants were presented with either abstract or visual-concrete nouns, different classes of microstates followed the two conditions [25]. It was thus proposed that "the seemingly continuous stream of consciousness consists of separable building blocks which follow each other rapidly and which implement different, identifiable mental modes, actions or functions" ([20], p. 9). The EEG microstates were hypothesized to represent the "atoms of thought" and their temporal dynamics (duration, occurrence, time coverage, etc.) would be essential for optimal information processing ([20], p. 9). Indeed, the notion of EEG microstates is most compatible with the idea of rapidly changing spontaneous information processing units. The large-scale neuronal networks mediating mental activity are composed of widespread functional cortical areas that need to flexibly change depending on the momentary cognitive process [26]. Consequently, these networks need to reconfigure in the millisecond time range both while individuals are engaged in a task and during resting. In a revised conceptualization of the initial proposal, the EEG microstates have been proposed as "neural implementations of the elementary building blocks of consciousness content" in the neuronal workspace model [27]. This model argues that distributed cortical networks form a spatio-temporal pattern of activity that lasts for about 100 ms, only briefly separated by sharp transitions [28, 29]. The EEG microstates might be the electrophysiological correlate of the global integrations units of local processes leading to consciousness, assuming that conscious cognitive processing occurs through a stream of discrete units or epochs rather than as a continuous flow of neuronal activity [27]. Indeed, the fact that the temporal parameters of the EEG microstates with the critical stability in the millisecond time range are similar to the time range of cognitive processing, is a strong argument for the building blocks of information processing (atoms of thought) units model. More evidence sustaining this notion is advanced in a recent study showing that the time course of the EEG microstates follows a scale-free dynamic [30]. Demonstrating for the first time a fractal behavior in the context of brain functioning, the EEG microstates significantly maintained the self-similar particularity from 256 ms to 16 s. In other words, the EEG microstates show the same temporal dynamic across different temporal scales. However, the microstate parameter essential for the long-range dependency seems to be the mean duration of the EEG microstates. This behavior was completely lost when matching the duration of all EEG microstates, a result that strongly suggests the temporal dynamics of the EEG microstates does not reflect a random process [30]. Most probably, the temporal parameters of the microstates is the key element in the rapid reorganization and adaptation of network function in the context of the real, eternally changing environment. This is further supported by studies reporting significant changes of the temporal parameters across brain development [17], during sleep [31], hypnosis [32], during induced thinking modalities like after verbal or visual perception [33], and most recently, during neurofeedback [34]. Interestingly, there are also animal studies that have identified microstates [35].

3.2 Microstates During Development

More than 400 participants were investigated to see if the presence of certain classes of EEG microstates might vary as a function of age [17], see also Fig. 3. They found a complex dynamic of temporal parameters with age where the microstate temporal dynamics delimited four developmental stages ([17], p. 44). In childhood (6–12 years) similar temporal dynamics were observed between the four classes of microstates. With early adolescence (12–16 years), A, B, and D became shorter while class C became longer, and an overall increase in frequency of occurrence (microstates per second) was present. By late adolescence (16–21 years), there was an increase in duration and frequency of class C and a decrease of class D duration and occurrence. Across adulthood, microstate class C remained the more frequent and longest class while class A and class B were the shortest but more frequent than across adolescence. The authors are proposing that developmental trajectories of the EEG microstates could reflect an adaptive biological process that selects those brain-functional states optimal for age-specific learning and behavior ([17], p. 46). Taking into account the association between the EEG microstates and the RSNs [23], the results would be compatible with structural and functional changes of these networks with healthy brain development [36–38].

In a study further investigating the different types of mental activity indexed by each microstates class, the authors compared different eyes closed conditions: object-visualization, spatial-visualization, verbalization, and resting [33]. Before each condition, participants were presented with stimuli corresponding to the eyes closed condition and were asked to continue thinking at that particular stimulus during the following eyes closed recording. Most significant results show differences between the verbal and visual conditions. During these conditions there was increased temporal parameter of class A and class B, respectively. Only one microstate class D was significantly more present during no-task resting state eyes closed condition ([33], p. 653). These results are in line with previous studies showing that classes A and B are correlates of visual and auditory processes while C and D represent higher order cognitive processes like salience, executive control and attention [23]. The authors propose that for the continuous stream of thoughts, the interaction between the four classes of microstates would be essential ([33], p. 654) supporting the "atoms of thought" framework of Lehmann [39].

3.3 EEG Microstates During Sleep and Hypnosis

Investigating changes in microstates temporal parameters with different stages of sleep, differences were most significant in the third stage of sleep. The deep sleep compared to the wake condition revealed an overall increased duration, and a higher transition probability within the same microstate class [31]. The authors interpret this finding as reflecting a "slowing down" of the information processing steps needed for mentation, probably because

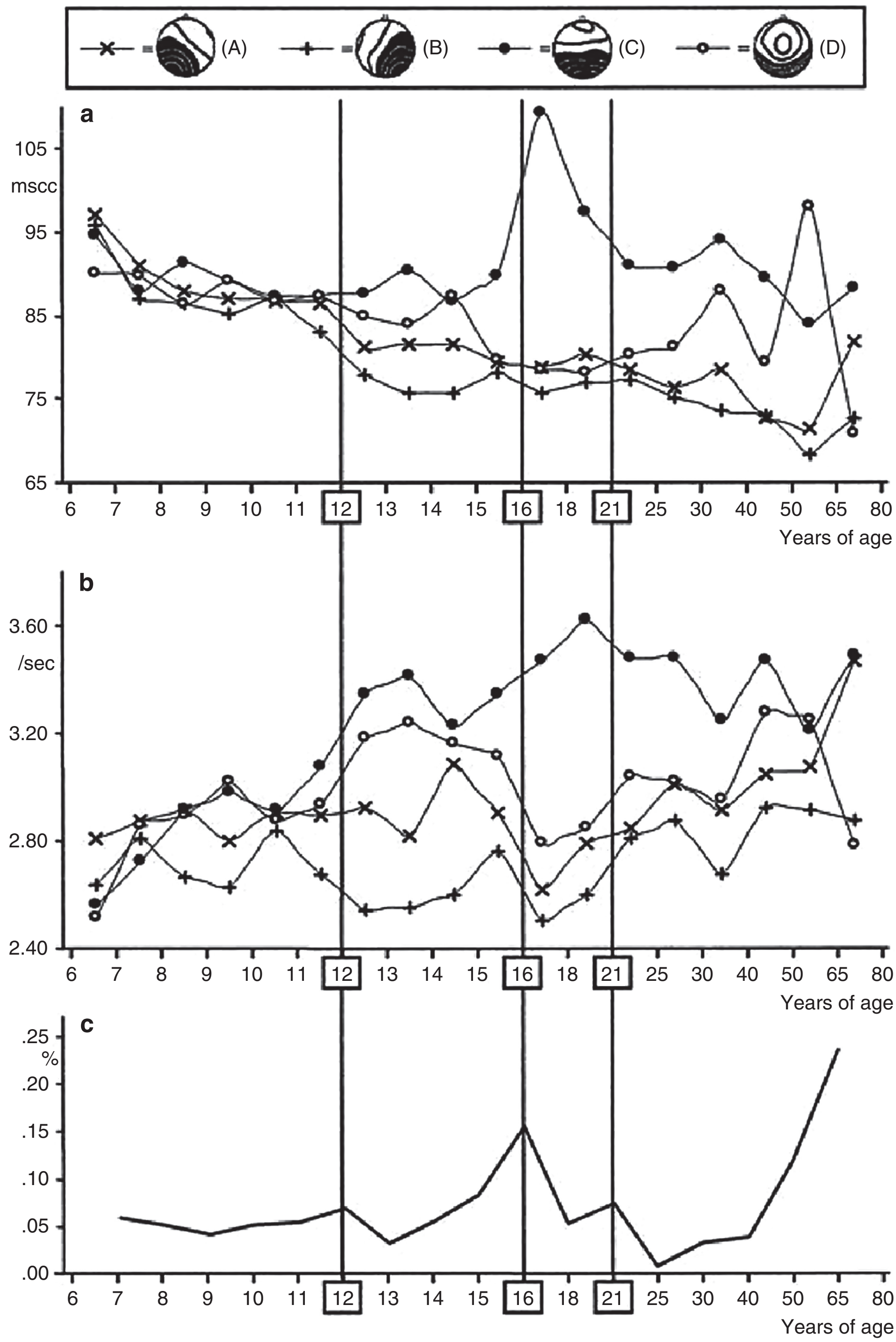

Fig. 3 Mean microstate duration in milliseconds (*upper graph* **a**) and number of microstates per second (*middle graph* **b**) against age (horizontal). The legend on *top* indicates the assignment of the used markers to the four microstate classes. The curves show complex trajectories that are incompatible with a continuous, unspecific maturation process. By comparing microstate profiles of adjacent age groups using a microstate change ratio (*lower graph* **c**), three peaks were identified which delimited four developmental stages. The *vertical lines* indicate their borders and latencies. Reprinted from [17] with permission of Elsevier

of a reduction in the amount of information compared to wakefulness and/or a higher looping within the same networks with reduced vigilance [31]. Healthy individuals going from wake to deep hypnosis also presented increased duration of class A and C microstates [32]. However, the authors also report similar findings with studies investigating individuals with schizophrenia: reduced class B and class D microstates [22].

3.4 EEG Microstate Abnormalities During Psychopathological Conditions

A growing body of the microstates literature focused on different neuropsychiatric disorders as we would expect deviant temporal dynamics of the EEG microstates with psychopathology. Panic disorder (PD) is a frequent psychiatric mood disorder characterized by anxiety and panic attacks. The authors show an increased duration and time coverage for class A and decreased occurrence for class C in unmedicated, PD patients with respect to controls [40, 41]. The authors speculate that PD symptoms could arise from the aberrant connectivity between the insula and the anterior cingulate to form a coherent representation of body sensation reflected by the decreased microstate class C duration ([41], p. 4).

Another devastating neuropsychiatric disease characterized by a broad range of cognitive dysfunctions including memory, central executive, and language impairments is dementia. Early studies on moderate and mild Alzheimer's disease (AD) patients found a decreased duration and an anteriorization of the gravity center [42, 43]. However, in a recent study, no difference in temporal dynamics was found for patients diagnosed with AD versus controls but reduced class C microstate duration was observed in frontotemporal dementia (FTD) patients compared to both AD and controls. As Class C microstates was attributed to the salience RSN [23], the authors speculated that the decreased class C presence would reflect disturbances of the insular-cingulate network also linked to severity of symptoms like disinhibition and apathy [44], symptoms shared with other brain disorders which might be explained by similar neuronal mechanisms [45].

More than half of the studies investigating EEG microstates in psychiatry reported abnormalities in schizophrenia patients compared to controls. In acute neuroleptic-naive schizophrenia individuals, the deviant temporal dynamics of EEG microstates were first reported to be shortening in microstate class D, which was also negatively correlated with the severity of the paranoid symptoms [16], see also Fig. 4. This relation was further validated in a study investigating schizophrenia patients while subjectively reporting auditory hallucinations compared to non-hallucinatory resting periods [46]. The authors speculated that sufficiently long durations of class D microstates might have a protective role which is then lost while experiencing positive symptoms if terminated prematurely ([46], p. 1181). Furthermore, in drug naïve schizophrenia patients which responded to treatment (risperidone—a second-generation neuroleptic) compared to non-responders there

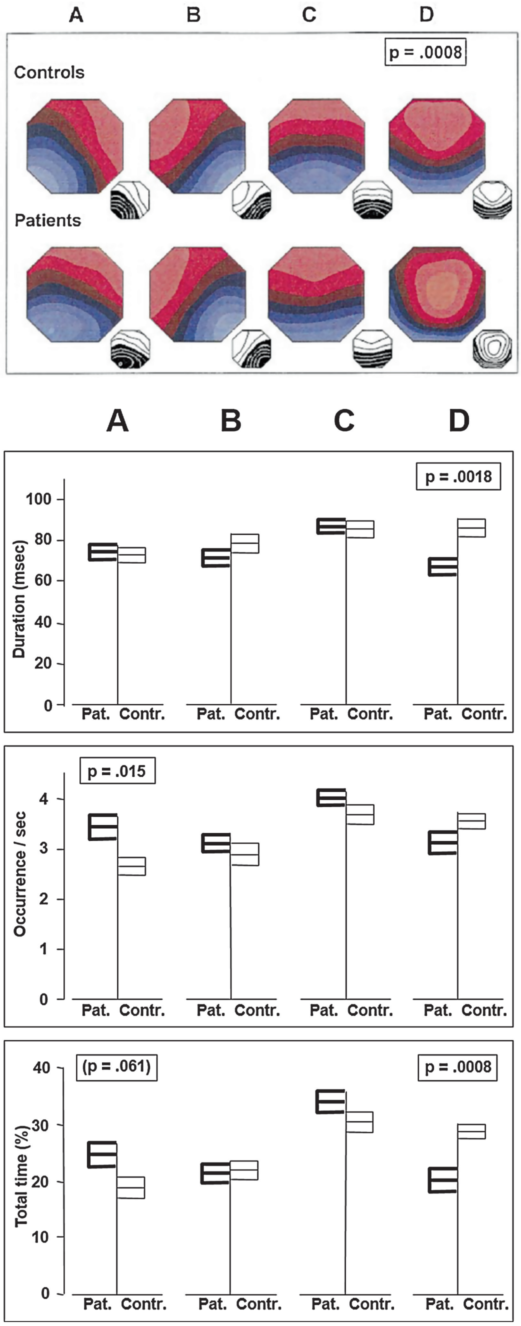

Fig. 4 First findings on EEG microstate clusters in schizophrenia. *Upper part*: Microstate classes of patients and controls. Mean normalized equipotential maps of the four microstate classes (*A*–*D*) of the patients and controls; the spatial configurations of the class *D* maps differed significantly (Bonferroni-corrected *p* value). Using a linear color scale, the map areas of opposite polarity are arbitrarily coded in *blue* and *red*; the small *inset* maps display the identical information in *black* and *white*. *Lower part*: Duration, occurrence/second, and percent total time covered, of the four microstate classes (*A*–*D*) of patients and controls. In the graphs, the three lines in the "flags" indicate mean ± standard errors of the patients (*heavy lines*) and controls (*thin lines*). Significant differences between controls and schizophrenics are indicated by their *p*-values. Reprinted from [16] with permission of Springer

was even more decreased class D and more frequent class C microstates ([47], p. 168). Interestingly, following risperidone therapy responders had significantly increased duration of class A and D microstate duration compared to non-responders ([47], p. 169). Different types of antipsychotic drugs have been reported to change the overall duration of the microstates [48–50], while only perospirone (a serotonin and dopamine receptors antagonist) increased only the duration of class D microstates [50]. On the other hand, a very recent study investigated another possible form of therapy for psychotic symptoms: EEG microstate neurofeedback [34]. Based on converging results of deviant EEG microstates in schizophrenia, the authors explored the feasibility to modulate the presence of microstates in healthy participants. Using microstate neurofeedback, controls were trained to upregulate the duration of microstates at values that eventually would be sufficient for an improvement of clinical positive symptoms [34]. Class D microstate was previously associated with the attention resting state network (RSN) and, as a confirmation, there was a negative relation with alpha power during neurofeedback. The promising results of this study encourage for further investigation of microstate neurofeedback use as a possible new form of therapy for psychotic symptoms.

Investigating temporal dynamics of EEG microstates in individuals at risk for developing schizophrenia differences were found between schizophrenia patients (SZ) and the high-risk individuals (HR) [51]. Class A microstate showed increased occurrence and coverage in HR individuals, while class B showed decreased duration and occurrence in HR with respect to SZ patients [51]. Class B deviant dynamics are related to previous findings in schizophrenia [22, 44, 52], whereas class A impaired dynamics are discussed with respect to another brain disorder showing similar differences, namely panic disorder [41]. However, another study showed comparable EEG microstate abnormalities in another high-risk population to develop schizophrenia [53]. The 22q11 deletion syndrome (22q11DS) adolescents have a 30-fold increased risk for psychosis and represents a good model condition to investigate vulnerability to develop schizophrenia. Such adolescents showed prolonged duration of class C (associated with preclinical positive symptoms) but also as most replicated finding in schizophrenia, decreased class D duration [53]. When the high-risk 22q11DS adolescents were compared with a group of full clinically diagnosed schizophrenia patients, the EEG microstates were similar (increased class C and decreased class D microstates). This further sustains the possibility of EEG microstate to constitute neurophysiological markers for schizophrenia [54]. Deviant EEG microstate temporal dynamics of classes C and D could thus be a promising endophenotype candidates for schizophrenia which could distinguish individuals at risk and allow for early therapeutic interventions; however, longitudinal studies are need to further prove this possibility. A recent meta-analysis over the available EEG microstate analysis literature in schizophrenia has however confirmed that both microstate class C and D abnormalities have clinically relevant effect sizes [55].

The class C microstates shown here to be significantly increased in the 22q11DS adolescents were previously proposed as the electrophysiological correlate of the salience RSN with one of the main nodes in the anterior cingulate cortex (ACC) [23, 56, 57]. The authors proposed that the deviant pattern of temporal dynamics reflects a defect of information processing strategy related to aberrant salience mapping, or a compensatory mechanisms for this shortcoming. Interestingly, in another study investigating the auditory p50 gating mechanism in the 22q11DS adolescents there was again an aberrant activation of the (ACC) followed by a downstream reduction of activity in auditory cortex [58]. Taken together, the results of these two studies lead to an interesting question: are the results of the auditory task a consequence of the deviant pre-state/resting deviant activity? In other words, is the perception of a stimulus a state-dependent process?

3.5 The Transition from the Pre-stimulus to the Post-stimulus State, and Its Relation to Subjective Experience

In the previous sections, we have presented a large body of evidence that EEG microstate features have specific associations with normal and abnormal cognitive states that in turn alter our perception, subjective experience, and behavior. In the following section, we will discuss studies that investigated if there is also evidence for a direct link between EEG microstate features and perception. This issue is important in two ways. Firstly, it is interesting to understand how the state of the brain shapes the fate of incoming information, both in a functional and a dysfunctional context [25, 59]. In a reversal of that view, adequate responses to external stimuli imply that functional networks have to be generated dynamically, flexibly, and in an adaptive way in order to respond to changing demands of either the environment or intrinsic brain activity.

Contrary to the standard methods to analyze event-related brain activity, this implies that spontaneous activity is not just noise but has functional significance, this can be investigated with studies that combine task-related responses with spontaneous activity in a task context.

3.6 Pre-stimulus EEG Microstate Influences on Stimulus Processing

The following paragraphs will briefly characterize the literature that investigated state-dependent information processing with EEG microstates.

This review will start with pre-state analysis for visual perception. Visual perception is particularly suited to investigate the influence of pre-states on subsequent perceptual processing since stimulus materials can be found where identical physical stimuli lead to different percepts such as in the case of bistable forms or binocular rivalry.

But even with basic visual stimuli, the relationship between the pre-stimulus state and the post-stimulus reply of the brain can be investigated as this was already shown early on [60, 61]. In a more recent study, bistable visual stimuli were investigated using the stroboscopic bouncing ball illusion to evoke illusory motion and by asking participants to press a key at each perceived change to have readout of the percept [62]. In this paper they showed that in the time preceding perceptual reversals, the probability of one state over the other changed. Initially, the microstate C was most likely to occur directly after the preceding stimulus, but before a perceptual reversal the probability of a different microstate increased. This microstate closely resembles the microstate B in other studies. As discussed previously, this microstate has been implicated as a visual state during resting state conditions [23].

The field of bistable perception was also investigated with higher density electrode configurations [63] and Necker cube stimuli. Here, the authors found a characteristic microstate that was more likely to appear before a perceptual reversal and conversely another state more likely to indicate a stable percept as the intermittent design allowed for participants to also indicate stable percepts. In this case, the difference between the two states was localized to the right inferior parietal cortex, a region that was also shown to be implied in perceptual reversals in FMRI [64].

Another way to study the influence of pre-states is to investigate subthreshold stimuli [65] in which a physically identical stimulus is perceived in only 50% of the times. In this study, the authors could show that the conscious perception of the stimulus was significantly correlated with the presence or absence of two types of microstates in the time period immediately preceding the stimulus.

4 Conclusions

We presented findings of studies that used the electrically manifested brain-functional states (the EEG) during development and adulthood as well as during different states of consciousness in order to investigate brain functions, which create and form the individual's variance in subjective experiences and behavior.

Initially, such studies used the spectral analysis of the EEG for quantifying the electrically manifested brain-functional states (the EEG macrostates) during adult wakefulness and development. However, this method is typically based on the analysis of epochs that extend over time periods (seconds) that may contain several and potentially different brain-functional states.

Dietrich Lehmann and his colleagues developed a method to quantify EEG brain-functional states on a time scale that is compatible with the speed of human information processing: the method of the EEG spatio-temporal segmentation (= the EEG microstates).

Focusing on the scope of this book to present methods developed for and applied to the study of the brain functions which create and form subjective experiences and behavior, we have presented the results of the research literature which studied the role of the brain EEG-state-dependent, but memory-driven retrieval processes in forming the individual's momentary thoughts, emotions and behaviors as well as their conscious perceptions.

The EEG analysis of microstates is applied to study

(a) categories of thought content
(b) differences after presentation of abstract or visual concrete nouns
(c) changes in microstates' temporal parameters during different stages of sleep
(d) going from awake to deep hypnosis
(e) classes of EEG microstates in childhood, adolescence, late adolescence, and adulthood
(f) different eyes closed conditions
(g) during abnormal (altered) perception, subjective experiences, and behavior
(h) in schizophrenia (drug-naïve and persons responding to treatment) and in other populations

Thus a large body of evidence indicates that EEG microstate measures have specific associations with normal and abnormal cognitive, emotional and behavioral states.

We have discussed the functional significance of such studies on the basis of the proposals of an integrative model of the brain functions that create the contents of the autobiographical memory via experience-dependent cortico-cortical plasticity, the neuronal networks which represent (materialize) the memory contents.

The increase of the neuronal networks goes parallel with the increase of the complexity of the EEG. The brain-functional states as manifested in the EEG during wakefulness reflect the level of attained complexity of the neuronal representations of the autobiographical contents and form subjective experience and behavior.

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