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Brain maturation during adolescence and young adulthood

–

an EEG study

vorgelegt von:
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Abstract

Objective: Adolescence is a period of major maturational changes in the brain. It is particularly the maturation of the frontal cortex and its interactions with other brain regions that dominates this late stage of development and has important implications for the cognitive abilities during the entire adult life.

Methods: In this thesis, developmental changes in the δ (0 - 4 Hz), θ (4 - 7 Hz) and γ (28 - 48 Hz) frequency bands were investigated in adolescents (13 - 15 years) and adults (20 - 27 years) during resting and cognitive states. Four tasks were conducted: the spontaneous EEG (eyes-open), the ambiguous task, the unambiguous task and the visual oddball task. During the ambiguous task, participants were exposed to the Stroboscopic Ambiguous Motion (SAM) paradigm. SAM is a multistable stimulus that, when viewed continuously, induces internally-generated changes in the perceived direction of motion. For the unambiguous task, a modified version of the SAM was used. In this case, the perceived direction of motion was controlled externally. In the visual oddball task, randomly interspersed targets had to be identified in a train of frequent non-targets. Single-trial amplitudes of δ, θ and γ activity obtained during the spontaneous EEG were compared between the groups to assess general maturational changes in the developing brain. The task-related enhancement of the oscillatory activity was compared between the groups in order to assess developmental changes in task performance.

Results: The previous findings of δ and θ amplitudes decreasing with age during the spontaneous EEG were replicated. Similarly to previous studies, our results also indicate that for spontaneous EEG γ amplitudes do not profoundly differ between adolescents and adults. Moreover, the present study supports previous findings from adult research which have established a functional relationship between δ, θ and γ activities and higher cognitive processes. It has further been found that the developmental changes correlated with task difficulty. Only for the - most challenging - ambiguous task the γ oscillations were found to reflect a change in task-related cortical processing during adolescence, whereas no age-related differences of γ responses were detected for less demanding tasks (the unambiguous and visual oddball tasks). The event-related θ responses were found to increase with age for the ambiguous and visual oddball tasks and did not depend on age for the unambiguous task. Furthermore, the event-related δ responses increased with age for all tasks.

Conclusions: The main finding of this study is that functional networks of δ, θ and γ activity undergo maturational changes during adolescence. The found differences in the task-related activations may indicate a protracted development of higher-order cognitive processes during adolescence. The developmental changes of task-related activations seem to vary with task difficulty and frequency band.

Significance: Systematic studies on developmental changes of brain oscillations in cognitive tasks are still infrequent and specifically the time period of adolescence has been rarely investigated. The typical age of onset for mental disorders, such as schizophrenia, is the late stages or shortly after the onset of adolescence, rendering the outcome of brain maturation during this period of immense importance for life-long mental health. Thus, it is critical to extend our understanding of the mechanism behind the appearance of cognitive functions during adolescence.

Kurzfassung

Grundlagen: Während der Adoleszenz kommt es zu einer erheblichen Umstrukturierung des Gehirns. Verläuft diese erfolgreich, ermöglicht sie die Entwicklung höherer kognitiver Prozesse, wie z. B. das nachträgliche Überdenken von Handlungen.

Methoden: In der vorliegenden Studie wurden elektrophysiologische Daten von Jugendlichen (13 - 17 Jahre) und jungen Erwachsenen (20 - 27 Jahre) erhoben. Diese wurden mittels Ruhe-EEG und kognitiver Aufgaben auf eine Veränderung von elektrophysiologischen Antworten (δ, θ und γ - Aktivität) während des Reifungsprozesses des Gehirns untersucht. Diese Aufgaben umfassten ein Oddball-Paradigma und die endogene und exogene stroboskopische Alternativbewegung (SAB). Bei der endogenen SAB wurden die Probanden einer optischen Täuschung ausgesetzt: Die Bewegungsrichtung von zwei diagonal entgegengesetzten Punkten wird entweder als vertikal oder als horizontal wahrgenommen, obwohl sich die physikalischen Reizbedingungen nicht ändern. Bei der exogenen SAB ändert sich ebenfalls die wahrgenommene Bewegungsrichtung von zwei Punkten, dies wird aber extern durch Veränderung des Reizmusters erreicht. Bei dem visuellen Oddball-Pardigma mussten die Probanden zwischen (den selteneren) Zielreizen und den häufigeren Nicht-Zielreizen unterscheiden. Die δ, θ and γ - Aktivität beim spontanen Ruhe-EEG mit geöffneten Augen wurde in Hinblick auf generelle Reifungsprozesse des Gehirns untersucht, da eine Analyse der eregniskorrelierten Antworten möglicherweise Hinweise auf altersabhängige Veränderungen der kognitiven Funktionen liefern kann.

Ergebnisse: Frühere Studien, nach denen die δ und θ Aktivität beim spontanen Ruhe-EEG mit dem Alter abnimmt, konnten repliziert werden. Auch die γ - Aktivität von Jugendlichen und Erwachsenen scheint keine signifikanten Unterschiede aufzuweisen. Zudem unterstützt die vorliegende Arbeit Ergebnisse früherer Studien an Erwachsenen, bei denen ein funktionaler Zusammenhang zwischen der δ, θ und γ - Aktivität und höheren kognitiven Prozessen nachgewiesen wurde. Ferner konnte hier eine Korrelation zwischen Reifungsprozessen und dem Aufgabenschwierigkeitsgrad aufgezeigt werden: So spiegelte nur die (anspruchvollste) endogene SAB eine Änderung der aufgabenbezogenen kortikalen Verarbeitungsprozesse bei Heranwachsenden im γ - Band wider, während keine altersspezifischen Unterschiede für die weniger anspruchsvollen Aufgaben festgestellt wurden. Die ereigniskorrelierten θ - Antworten änderten sich nur für manche Aufgaben mit dem Alter, während die δ - Antworten für alle Aufgaben mit dem Alter anstiegen.

Schlußfolgerung: Das Hauptergebnis der vorliegenden Studie ist, dass funktionale δ, θ und γ - Netzwerke bei Heranwachsenden einem Reifungsprozess unterliegen. Die bei den ereigniskorrelierten Antworten aufgezeigten Unterschiede deuten auf eine andauernde Entwicklung höherer kognitiver Funktionen hin. Altersspezifische Unterschiede scheinen hierbei mit dem Schwierigkeitsgrad der Aufgaben und den Frequenzbändern zu variieren.

Signifikanz: Systematische Studien altersspezifischer Hirnoszillationen bei kognitiven Aufgaben sind, insbesondere mit Schwerpunkt auf Heranwachsende, selten. Jedoch ist es genau dieses Alter, in dem typischerweise psychische Krankheiten, wie z. B. Schizophrenie, entstehen. Damit kommt gerade in diesem Alter einer erfolgreichen Ausreifung der Hirnstrukturen eine immense Bedeutung zu. Es ist daher zwingend erforderlich, unser Verständnis der Entwicklungsmechanismen kognitiver Funktionen bei Heranwachsenden weiter zu konsolidieren.

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Glossary

AM	Apparent motion
EEG	Electroencephalography
EP	Evoked potential
ERD	Event-related desynchronization
ERO	Event-related oscillations
ERP	Event-related potential
ERS	Event-related synchronization
fMRI	Functional magnetic resonance imaging
hMT+	the primary motion processing area of the brain
ITC	Inter-trial coherence
MEG	Magnetoencephalography
ROI	Region of interest
SAM	Stroboscopic alternative motion
MT/V5	the visual area (V5) of the cortex, also called MT

Overview of the thesis

Adolescence is a period of major maturational changes in the brain [Konrad and Uhlhaas, 2011, Spear, 2000]. Recent research has shown the maturation of the frontal cortex to occur later when compared to other parts of the brain. If this maturation process is completed successfully, it results in a better cognitive performance with regard to decision making, logical thinking and the assessing of potential risks [Amso *et al.*, 2014, Anderson *et al.*, 2001, Blakemore and Choudhury, 2006]. If this process fails, it may result in the development of psychopathology, particularly schizophrenia, since adolescence is thought to be a critical period of enhanced vulnerability for the onset of pathological changes of the brain [Pantelis *et al.*, 2003, Uhlhaas and Singer, 2011]. Given the importance of understanding the maturational changes throughout adolescence, it is surprising that, until recently, little research was conducted with healthy or at-risk adolescents in order to gather empirical insights about this issue. Such evidence may be very informative in order to understand at which stage of brain development maturational processes become impaired and what could be done to prevent the onset of such diseases as e. g. schizophrenia [Uhlhaas and Singer, 2011].

Visual illusions, such as ambiguous patterns, provide a tool to investigate developmental changes of the brain, particularly the maturation of the frontal cortex. Ambiguous patterns make up a well-known class of visual phenomena in which one invariant stimulus pattern elicits a perceptual reversal between two different, mutually exclusive alternatives [Long and Toppino, 2004]. Experiencing a perceptual reversal is thought to involve sensory as well as higher-order cognitive processes (e. g. focused attention) in the brain [Long and Toppino, 2004]. These processes are known to require temporal integration and interregional connectivity of brain networks. Thus, the electroencephalography (EEG) and in particular brain oscillations seem to be a mostly suitable method to study the role of the processes involved in experiencing perceptual reversals [Basar-Eroglu *et al.*, 1993, Basar-Eroglu *et al.*, 1996].

Recent research on adults and children performed in our group has shown that the frontal cortex is involved in the ability to experience a perceptual reversal [Basar-Eroglu *et al.*, 1996, Ehlers *et al.*, in press, Mathes *et al.*, 2014, Strüber *et al.*, 2000]. The prominent activation of the frontal cortex, reflected in brain oscillations in the θ (4-7 Hz) and γ (28-48 Hz) frequency bands, was observed in adults, whereas 11 year old children did not show such a prominent activation. Furthermore, interregional connectivity between the frontal and parietal cortices reflected in long-range brain oscillations of the δ (0.5-4 Hz) frequency band, which may be essential to experience a perceptual reversal [Mathes *et al.*, 2006], was found to be less mature compared to adults [Ehlers *et al.*, in press].

In the study presented in this thesis, the impact of maturational changes of the brain throughout adolescence on temporal dynamics, with a focus on the maturation of the frontal cortex, as well as the interregional connectivity of brain networks involved in experiencing a perceptual reversal were explored.

The thesis in hand is divided into a theoretical and an experimental part. In the theoretical part, a brief description of structural and functional changes in the brain throughout the development during adolescence is given (Section 1). Subsequently, an introduction to ambiguous patterns and their role as a research tool that empirically supports theories on visual perception is provided. Furthermore, the role of ambiguous patterns as a tool for investigating neural correlates of visual perception is discussed (Section 2). In Section 3, the theoretical background of electroencephalography is provided. Particular attention is given to the measurement of brain oscillations and its role in investigating sensory and cognitive functions. Readers already familiar with the theoretical background are suggested to directly jump to Section 4, the onset of the experimental part of this thesis. Here, after a brief summary of the theory, the aim of the study, the methodology, and the results of the thesis are provided, followed by a discussion of the results in respect to the existing literature. In the end, a summary of the work and an outlook on further research are formulated.

SECTION 1

Brain development during adolescence

Adolescence, i.e. the time span between childhood and adulthood, is one of the most important periods in our life. Indeed, in no other period of life does so much change in cognitive and emotional development occur as during adolescence [Spear, 2000]. While infants and children of course also develop rapidly, they acquire new competences rather continuously [Johnson, 2010]. A physical and mental metamorphosis begins with the onset of puberty at an age of 12 - 13 years and ends around an age of 25 years [Spear, 2000]. This marks a time when the stages of cognitive and emotional development are completed, allowing a person to be responsible for the actions and decisions taken [Steinberg, 2005].

Until recently, it was assumed that the critical phases for structural and functional changes in the brain are limited to pre- and postnatal periods [Blakemore, 2012]. More recent evidence has, however, shown that adolescence is a period of major maturational changes in the brain which continue until adulthood [Shaw *et al.*, 2008].

1.1. Structural changes during adolescence

The maturation of brain regions is thought to depend on structural changes in grey and white matter which underlie regressive and progressive processes over childhood and adolescence.

One of the highly replicated findings related to the structural changes is a significant decline in the amount of cortical grey matter during adolescence. Many studies have shown that the amount of grey matter increases only until the onset of adolescence, followed by a decline during adolescence [Giedd *et al.*, 1996, Gogtay *et al.*, 2004]. This decline of cortical grey matter is thought to be related to the so-called *synaptic pruning* - the regressive process by which excess neurons and their synaptic connections are eliminated [Huttenlocher, 1979, Petanjek *et al.*, 2011]. This process is accompanied by a strengthening of the remaining synapses, which results in more efficient and fine-tuned synaptic connections [Casey *et al.*, 2008]. Furthermore, it was shown that the decline of cortical grey matter is different for different brain regions. The primary sensorimotoric areas seem to be the first ones affected by the loss of grey matter, whereas the decline of grey matter in the dorsolateral prefrontal cortex seems to occur latest [Gogtay *et al.*, 2004, Shaw *et al.*, 2008]. The regionally-specific decline of cortical grey matter may reflect temporal development of cognitive functions throughout adolescence. The maturation of the brain regions associated with sensory and motor skills occurs first, followed by a maturation of such brain regions as the prefrontal cortex, which is associated with processes involved in decision making, planning and action control [Uhlhaas and Singer, 2011].

One more finding related to the structural changes in the developing brain is an increase of cortical white matter over childhood and adolescence until reaching the adulthood. A number of different studies showed that the increase of white matter during adolescence occurs mostly in the frontal and parietal cortices [Barnea-Goraly *et al.*, 2005, Blakemore, 2012, Paus *et al.*, 1999, Sowell *et al.*, 1999, Yakovlev and Lecours, 1967]. *Myelination* - the progressive process of forming a myelin sheath around axons of neurons - is thought to be responsible for the increase in white matter during childhood and adolescence [Paus *et al.*, 2008]. Myelination of axons enables the connecting pathways between and within different brain regions to conduct neural information rapidly. A number of studies showed that the increase of white matter with age is more or less linear [Barnea-Goraly *et al.*, 2005, Giedd *et al.*, 1999, Paus *et al.*, 1999]. However, the longitudinal study performed by Lebel and Bealieu in 2011 reported on non-linear changes in white matter maturation [Lebel and Beaulieu, 2011].

Summarizing, significant structural changes of the cortex, particularly in the frontal and parietal regions, take place during adolescence. These changes have a dynamical nature with respect to maturational changes of grey and white matter: a non-linear reduction in grey matter, especially in the frontal cortex, and a simultaneous increase in white matter [Blakemore, 2012].

1.2. Cognitive changes during adolescence: evidence from neuroimaging studies

As discussed above, two brain regions (the frontal and parietal cortices) change considerably during adolescence due to structural development of the brain. Given the structural changes in these brain regions, it might be assumed that cognitive abilities that rely on the functioning of these regions and their complex interconnectivity with other brain regions might be affected by developmental changes during adolescence [Johnson, 2010].

There is a growing amount of neuroimaging studies which tried to link cognitive abilities regulated by the frontal cortex, such as "cognitive control", with maturational changes in this brain region during childhood and adolescence. Cognitive control refers to the brain processes which allow information processing and behavior to vary adaptively from moment to moment in accordance with internally generated goals and plans [Niendam *et al.*, 2012, Miller, 2000]. For example, selective attention, decision-making or inhibiting of irrelevant information play a role in cognitive control. Since these processes are thought to be mediated by the frontal cortex, it has been suggested that performance in tasks which require involvement of cognitive control might improve during adolescence [Blakemore and Choudhury, 2006].

Indeed, it has been found that the performance of adolescents in tasks involving inhibitory control [Leon-Carrion *et al.*, 2004, Luna *et al.*, 2010], working memory [Anderson *et al.*, 2001, Amso *et al.*, 2014, Luna *et al.*, 2004, Luna *et al.*, 2010] and decision making [Luciana *et al.*, 2005] continues to improve during adolescence and even in early adulthood. The improvement of performance in these studies could be linked to the maturational processes in the frontal cortex, such as synaptic pruning and myelination. There is also evidence that the parietal cortex is involved in cognitive control processes, although its specific contribution is yet unclear [Brass *et al.*, 2005]. Recently, it was shown that the working memory capacity improves during adolescence and may correlate with the myelination process taking place in the parietal cortex of the developing brain [Klingberg *et al.*, 2002].

Basing on the imaging studies discussed above, it can be assumed that the development of higher-order cognitive functions continues over adolescence and could be linked to the structural changes taking place in the brain. However, it would be wrong to assume that developmental changes in cognitive ability can only be linked to maturation of functionally segregated brain regions. Evidence from the brain research published in the last years supposes that widely-distributed brain regions have to communicate in a coordinated manner in order to mediate goal-directed behavior within different cognitive contexts [Stevens, 2009]. The correlated activity of different brain regions related to a cognitive or perceptual task is known as a brain functional network [Müller *et al.*, 2011]. As mentioned above, cognitive control processes, for example, rely on a set of brain regions within frontal and parietal cortices which together build so-called fronto-parietal control network. According to recent findings, the brain networks related to a variety higher-order cognitive functions become less diffused (meaning that fewer brain regions become activated in response to a task) and more focal (meaning that smaller areas of activation produce stronger response to a task) throughout adolescence, resulting in more reliable performance in cognitive tasks [Durston *et al.*, 2006, Durston and Casey, 2006]. Taking together all evidence, it can be assumed that immature brain networks of adolescents recruit many of the same key brain regions related to a task as seen in adults, but the strength of interconnectivity among these regions will improve throughout development, whereas recruitment of brain regions which are task-unspecific will be weakened [Johnson, 2010].

1.3. Brain oscillations in developmental research

While imaging techniques like the functional magnetic resonance imaging (fMRI) have an advantage to enable the localization of brain regions belonging to a functional network, the fMRI hemodynamic response is too slow to capture *ongoing* temporal dynamics underlying cognitive and perceptual processes.

Electroencephalography (EEG) - the tool that was employed to gather the data discussed throughout this thesis - not only has sufficiently high-temporal resolution in order to investigate cognitive dynamics in the time frame in which cognition occurs, but also can help to gain relevant knowledge about dynamic formation of brain networks underlying cognitive processes [Basar, 2011]. EEG measures brain oscillatory activity [Basar, 1998]. The amount of evidence that brain oscillations play a fundamental role in cognitive functions increases every year. Because of the specific characteristics of brain oscillations, functionally and topographically specialized cortical activity can be identified [Basar, 2011]. Due to the vast changes in brain development throughout the human life, age is one of the most important factors that determines changes in electrical brain activity reflected in different frequency bands (δ: 0.5 - 4 Hz, θ: 4 - 7 Hz, α: 8 -12 Hz; β: 12 - 30 Hz; γ: 30 - 80 Hz) [Basar, 2011].

Hans Berger, considered as the father of the EEG, was the first who reported about significant developmental changes of the brain oscillations in different frequency bands [Uhlhaas *et al.*, 2010]. Lots of subsequent studies have shown that both the *spontaneous* and *event-related* oscillations - brain responses to external or internal events - in different frequency bands undergo developmental changes during childhood and adolescence [Segalowitz *et al.*, 2010].

Considering the changes in the *spontaneous* brain oscillations during adolescence, it was shown that the absolute power (power integrated over a particular frequency band) of the oscillations declines with age over a wide frequency range. Here, low frequencies (δ and θ) seem to be mostly affected [Lüchinger *et al.*, 2012]. The power decrease at low frequencies was found to occur mostly in the frontal and parietal areas of the cortex and might reflect the decline of grey matter due to synaptic pruning throughout adolescence [Whitford *et al.*, 2007].

It is essential to note that not only the power but also the synchrony of the oscillations shows maturational changes. The synchrony reflects the stability of phase relationships of neural oscillations within a local population of neurons or between two distant populations [Uhlhaas *et al.*, 2010]. Thus, local and long-range connections within the brain can be investigated [Uhlhaas and Singer, 2011]. The development of the two types of connections is thought to be related to maturation of white matter which results in more coherent brain oscillations. In the study performed by Thatcher *et al.* with participants being between 2 months and 16 years old, the coherence of brain oscillations at short (6 cm between electrodes at the scalp) and long (>24 cm between electrodes at the scalp) distances was assessed. It was found that in the β band the degree of coherence between electrodes at short distances becomes larger as a function of age, whereas the coherence between electrodes at long distances seems to be unaffected by age. According to the authors, the same results were also observed for the δ, θ and α frequency bands [Thatcher *et al.*, 2008].

Recent findings from some studies with adolescents also indicate that *event-related* oscillations undergo maturational changes over adolescence. Changes in the *event-related* oscillations in the γ band observed during auditory attention tasks were demonstrated by Yordanova *et al.*. Children and adolescents at an age of 9 to 16 years participated in the study and had to respond to a so-called target stimulus (stimulus that occurs less frequently) which was presented embedded into a sequence of non-target stimuli. It was found that distinct spatially localized gamma networks are involved in specific aspects of task-stimulus processing. Furthermore, developmental differences in task processing strategies are reflected in specific patterns of γ networks [Yordanova *et al.*, 2002].

Uhlhaas *et al.* investigated the development of *event-related* oscillations and their synchronization during Gestalt perception from childhood and adolescence until adulthood [Uhlhaas *et al.*, 2009]. The brain oscillations were analyzed in a frequency range from 4 Hz to 75 Hz. It was found that perceptual processing undergoes developmental changes up to the adult age and that these changes can be captured by event-related oscillations in different frequency bands. Particularly, the power in the γ band was found to increase significantly during the transition from childhood to adulthood. The power change was accompanied by an enhanced long-range phase-synchronization between frontal and parietal regions of the brain in the θ and β bands [Uhlhaas *et al.*, 2009].

Developmental changes in event-related θ oscillations were found recently during reward processing over late childhood and adolescence [Crowley *et al.*, 2014]. It was found that both, the event-related power as well as the phase synchronization in the θ band over frontal regions of the brain, undergo maturational changes during reward processing and might be associated with aspects of greater reward sensitivity in adolescents.

Summarizing, brain oscillations represent an appropriate tool to investigate developmental changes over adolescence in different mental states, both at rest as well as during the performance of cognitive or perceptual tasks. Due to a variety of techniques that can be used to pick up changes in the brain oscillation as a function of time, frequency, power and phase (the power and phase are distinct measures since they provide largely independent information [Cohen, 2014]), the adolescent brain can be investigated in all its complexity in respect to the speed of information processing, a change of task-dependent strategy as well as the development of higher-order cognitive abilities.

SECTION 2

Multistable perception

Certain visual patterns, as for instance those shown in Fig. 2.1, induce a so-called *multistable phenomenon*. When viewed continuously, the pattern can be perceived in at least two different, mutually exclusive ways. For instance, the Necker cube shown in Fig. 2.1(b) appears to reverse its orientation, either pointing to the lower left side or to the upper right side [Leopold and Logothetis, 1999].

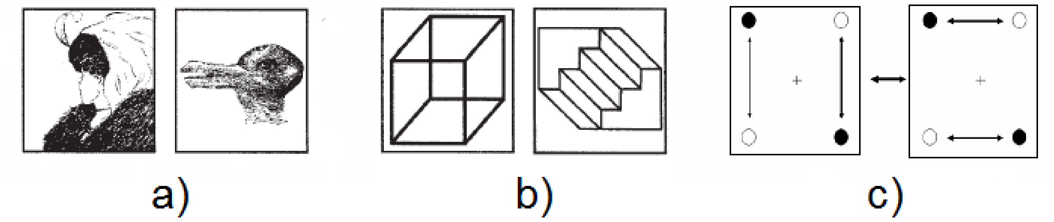


Figure 2.1.: Illustration of figures with (a) an ambiguous semantic content, (b) an ambiguous geometry, and (c) of the stroboscopic alternative motion. Adapted in modified form from Long and Toppino, 2004.

2.1. Multistable phenomenon as a research tool on visual perception

After the discovery of the Necker cube by the Swiss naturalist in 1832, many scientists from different fields were fascinated by ambiguous figures and especially by the fact that a simple drawing gives a definite interpretation only during a short time and then the same drawing can be interpreted in a different way again only for an instant. Thus during observation of the drawing the perception continuously alternates. Ambiguous figures were recognized to be useful in order to investigate processes that are required to extract a shape from a vague visual stimulus. Since these processes seem to be the same as those involved in normal visual perception, ambiguous figures can be used as a tool to provide insights into the sensory and cognitive processes underlying visual perception [Long and Toppino, 2004].

Ambiguous figures were used as a research tool by adherents of the Gestalt psychology. According to Köhler, the subjective percept of spatial objects is correlated with electrical fields in the brain that copy the form of the perceived objects. These electric fields oscillate and try to reach an equilibrium state which results in a stable perception. Ambiguous figures help to make the underlying dynamic nature of the brain processes apparent. For instance, when looking at the old/young woman in Fig. 2.1 (a), the initial perception e. g. results at first in the stable perception of the old woman, until brain areas related to this interpretation become satiated. The dynamic processes caused by the satiation displaces the equilibrium associated with the percept of the old woman to the equilibrium related to the young woman's percept, until this interpretation also becomes fatigued and so on, see also the discussion below. Although the theory of electrical fields could not be verified by modern neurophysiological methods, the study of the dynamical processes similar to those that were investigated by Köhler (1940) and are known nowadays as "neural adaptation" is the subject of extensive research in our days [Long and Toppino, 2004].

In search for explanations of the neurophysical process being responsible for the spontaneous perceptual reversals, two broad directions were followed by the scientific community since about the mid of the twentieth century [Long and Moran, 2007]. The first one is a passive, the so-called *bottom-up* approach already briefly introduced above, assuming an increasing fatigue of the neural channels involved in one particular perception of a multistable image and a simultaneous recovery of the corresponding cortical structures responsible for the perception of the "alternative" image [Köhler, 1940]. The other category of explanations relies on an active and thus a so-called *top-down* approach in which the perceptual reversals are dominated by the involvement of higher-order cognitive processes, e. g. the observer's expectations and attention. In the following, a detailed discussion of the two approach categories is presented.

2.1.1. Bottom-up approach

As discussed above, an interpretation of multistable phenomena basing on a passive bottom-up approach has a long history. Köhler's electric field theory [Köhler, 1940] assumes electric fields in the brain to create a copy of the perceived shape, thus leading to a direct correlation between the subjective perception of a spatial shape/object and the corresponding electrical response that undergoes an evolution to a state of equilibrium, hence resulting in a stable perception [Long and Toppino, 2004]. Ambiguous or multistable processes are a valuable tool for demonstration and study of the dynamic nature of brain processes. A variety of examples can be given here, such as the already discussed young/old woman, the Maltese Cross favored by Köhler or the duck/rabbit figure shown in Fig. 2.1 (a). In all of them, initially one figure, e. g. a grey rabbit in the latter case, is perceived. The perception that reached an equilibrium gradually builds up a "fatigue" or satiation of the brain areas involved. The process is thus purely passive, basing only on a satiation of the neurons exposed to the stimulus. This satiation finally results in a dynamical process, in which the "rabbit" equilibrium can no longer be hold up and shifts to a new "duck" equilibrium, involving fresh brain areas. Again, a satiation gradually sets in, while the areas involved in the rabbit percept recover simultaneously, until they finally can again dominate the perception, leading to a new switch and restoring the first percept. Thus, over time an observer experiences a continuous alternation of percepts.

Attempts for verification of the electric field theory undertaken in the 1950s failed to find conclusive evidence for the flow of electric fields as suggested by Köhler, leading to an abandoning of the theory in modern research. Nonetheless, several basic conclusions derived from this approach have found empirical support. One evidence repeatedly referred to by supporters of a passive process is the fact that with observation time the number of reversals increases, which, in other words, means that the time span for which a single equilibrium state exists continuously decreases the longer an ambiguous figure is observed. As shown in Fig. 2.2, the resulting *learning curve* approaches a maximum. This observation was taken for evidence of an incomplete recovery of the brain areas involved in the formerly dominant percept, that grows the stronger the longer the fatigue-recovery cycle is ongoing, leading to a gradual fatigue build-up. Thus, the reversal threshold is reached faster, resulting in an accelerated reversal rate. Further findings that support this conclusion are that this response pattern can be disrupted introducing either a period of rest [Spitz and Lipman, 1962] or moving the percept to a different retinal location [Köhler, 1940], while an increase of the illumination level causes an increase of the reversal rate [Lynn, 1961].

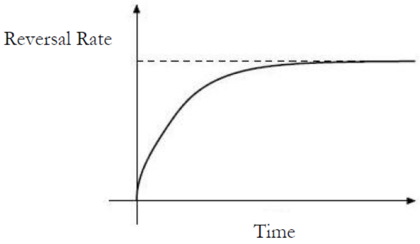


Figure 2.2.: This so-called *learning curve* visualizes the interdependence between the observation time and the reversal rate for an ambiguous stimulus. Adapted from Kruse and Stadler, 1995.

Another point in favor of the bottom-up approach was brought up by Long and Toppino in 2004 and Long and Moran in 2007: A "satiation" can be reached when exposing a test person to a modified, formerly ambiguous figure for which only one interpretation remained after the modification. When after a rather long observation time the observer is confronted with the original, non-modified and thus multistable image, the percept of the opposite interpretation is clearly favored. Also, in the case multiple multistable images are simultaneously presented to an observer, the occuring reversals will be independent from each other.

An interesting theory was brought up by Kruse and Stadler in 1995: The authors postulate that the "Gestalt" aspects of perception increase in dominance with the complexity of the visual stimuli. This leads to the fact that the simpler and more common interpretations are favored, while the non-salient ones are effectively suppressed [Hoff, 2014, Westheimer, 1999]. Hence Kruse and Stadler assume that essentially any visual stimulus has a multistable nature. However, accumulated experience acts as an internal "filter" for the interpretation, assigning probabilities of how well a specific interpretation fits the concrete situation. The perception aspects that appear to be more probable are addressed as *attractors* by the authors. The figural organization of the most probable attractors is believed to be created through attention, thus involving top-down processes in the full picture, while less probable interpretations can be actively trained through dedicated learning [Kruse and Stadler, 1995].

2.1.2. Top-down approach

Taking into consideration the findings summarized above, an involvement of bottom-up processes for multistable perception can obviously not be neglected. But then again, studies dating back as early as to the 19th century (published in the "‘Handbuch der physiologischen Optik"’, Leipzig, by von Helmholtz in 1867) suggested the possibility of a significant voluntarily control of the perceptional reversals (and thus the involvement of higher-level cognitive functions). For a detailed review of the research history, see [Long and Moran, 2007] and the references therein. Most recent results have clearly shown that the reversal rate can be significantly influenced performing a conscious voluntary control [Strüber and Stadler, 1999, Mathes *et al.*, 2006]. In particular, the reversal rate could be influenced "on demand" by the test persons, leading to an intended increase or decrease of the rate. It is worth noting that this control was more effective in the case a multistable image with a semantic content (like the rabbit/duck or young girl/old lady examples) was employed, in contrast to geometric images like the Maltese cross or the Necker cube [Strüber and Stadler, 1999]. An interesting effect in this respect is the involvement of secondary, purely cognitive-process-related tasks in the main viewing task. Examples may be that while a test person is exposed to a multistable image, (s)he is asked to memorize a string of integers or to count numbers backwards [Reisberg, 1983, Reisberg and O'Shaughnessy, 1984]. In a control experiment, test persons were exposed to the same multistable stimuli, but without any secondary tasks. The expectation of the researchers was that if no cognitive processes were involved in the perception and processing of multistable images, the results of the two experiments should be identical. However, Reisberg and O'Shaughnessy found that both the initial reversal time and the reversal rate were affected, where the former was delayed and the latter correspondingly reduced. From these results, they concluded that reversal processes obviously involve higher cognitive functions such as working memory [Reisberg and O'Shaughnessy, 1984].

Boundary conditions such as knowledge, intention and context were found to be further parameters directly influencing the perception of a reversal. In their experiment no. 1, Rock *et al.* e. g. have shown that in order to experience a reversal the test persons should not only know the fact that they are observing a multistable image, but even more concretely be familiar with or at least aware of the possible percepts [Rock *et al.*, 1994b]. In a different experiment (no. 2), Rock *et al.* have furthermore shown that distractors play a significant role and - when used - lead to a decrease of the reversal rate. However, basing on previous studies of top-down processes, an influence of automatic processes on multistable perception can not be excluded for sure. It was e. g. shown that even test persons not informed that they were observing a multistable image nevertheless experienced reversals [Rock *et al.*, 1994b].

2.1.3. The hybrid model

As happens so often in science, the real situation seems to be situated between the two extremes. A prominent analogy, although not related to the present discussion, can be found in the wave-particle dualism in quantum physics, where neither an exclusive wave nor a classical particle approach to describe e. g. a photon can result in a full description of the system that can explain *all* observations from different experiments. In 2004, Long and Toppino proposed a hybrid model that takes into account both active top-down as well as passive bottom-up approaches for the processing of multistable patterns. In this model, the initial processing of the elementary features of a multistable pattern is either automatic or sensory-driven (if once again an analogy to quantum physics is permitted by the benevolent reader, resembling very much the spontaneous and stimulated decay of excited energy levels, e. g. fundamental for the working principle of a laser). Then, in a second step the information obtained in the elementary processing is forwarded to intermediate cortical levels. There, a construction of representations of all possible patterns takes place, while simultaneously information on possible previous experience, expectations and context is provided by extrasensory higher-cognitive areas. Thus, both, sensory and higher cognitive areas exhibit an influence on the intermediate-level representations and hence both play a role for the reversal of multistable patterns [Long and Toppino, 2004].

2.2. Physiology of the multistable phenomenon

In this section, the most important physiological aspects of multistable perception are discussed. First, the role of eye movements for multistable perception is addressed, followed by the discussion of neurophysiological correlates underlying the occurrence of perceptual reversals.

2.2.1. Eye movements and blinks and the multistable phenomenon

The role of eye blinks and movements in multistable perception has been under discussion for a long time. Already Necker reported that it is possible to influence a perceptual reversal of the Necker cube by adjusting the eye focus to certain aspects of the figure [Necker, 1832]. Several recent studies provided evidence that one or the other percept can be favored by concentrating on different aspects of the figure (see references in [Long and Toppino, 2004]).

Modern eye tracking technology has made it possible to clarify the effect of eye position on the perception of multistable stimuli. In the study performed by Einhäuser *et al.*, the effect was investigated using the Necker cube under the so-called *free-viewing* condition - participants were instructed not to fixate their gaze on a certain aspect of the cube as usually done. A close relationship between the perception of the Necker cube and the eye position was found: The eye position is shifted to observe a newly established percept after the occurrence of a perceptual reversal [Einhaeuser *et al.*, 2004]. One further study examined the relationship between perceptual reversals and potentially preceding (micro)saccades / blinks, but found no positive correlation [Van Ee *et al.*, 2005].

Taking in account the facts discussed above, it can therefore be said that the occurrence of a perceptual reversal can not be a consequence of (micro)saccades / blinks.

2.2.2. Lesion studies and the multistable phenomenon

Lesion studies performed on patients with specific brain damage exposed to multistable stimuli provided important insights with respect to which brain regions are involved in perceptual reversals.

Already in the 1960s it was found that frontal lobe damages could have a significant influence on the number of perceptual reversals when patients were exposed to the Necker cube [Cohen, 1959]. Namely, patients with unilateral lesions in the right frontal hemisphere were able to experience less perceptual reversals compared to the patients with bilateral frontal lesions. Furthermore, it was shown that an injury of posterior brain regions had almost no impact on the number of perceptual reversals.

Ricci and Blundo in 1990 examined patients with unilateral left or right frontal and posterior brain damages and matched controls on their ability to recognize two possible interpretations of such visual stimuli as the young/old woman, duck/rabbit, and so on. It was shown that the number of prompts required to recognize both possible interpretations was larger for the frontal patients compared to the matched controls. Also, a shift between two possible interpretations was easier for patients with posterior brain damages and controls compared to patients with both, left and right frontal-lobe lesions [Ricci and Blundo, 1990]. In order to investigate lateralization effects, another study using the same stimuli was performed by Meenan and Miller in 1994. The study showed that only patients with right frontal lesions had difficulties in recognizing the second possible interpretation of the stimuli [Meenan and Miller, 1994]. The authors concluded that the right frontal region of the brain plays an important role in the ability to shift visual perspective.

The role of the prefrontal cortex in attentional control during exposure to multistable stimuli was investigated in patients with lesions originating from brain tumors in the study performed by Windmann *et al.*. According to the authors, the role of the prefrontal cortex is especially important, steering the visual attention according to the concrete situation at the moment of perception and thus initiating perceptual reversals [Windmann *et al.*, 2006].

Summarizing, the results from the lesion studies could indicate that the frontal brain regions (especially its right part) play an important role in the ability to initiate a perceptual reversal and in the shift of perception to an emerging percept [Meenan and Miller, 1994].

Modern neuroimaging techniques such as fMRI and EEG offer an unique possibility to study the brain regions and neural dynamics underlying multistable perception. The insights gained by means of these methods are discussed below.

2.2.3. fMRI and the multistable phenomenon

The brain activity associated with multistable perception has been extensively investigated using fMRI. Muckli *et al.* in 2002 and 2005 found correlations in hMT+ cortex areas, suggesting these areas to be involved in the interpretation of single spatially separated spots to an apparent motion (AM). Comparing endogenously and exogenously induced perceptual reversals, the authors in both cases found increased activity patterns in the primary motor and somatosensory areas, the insula, the right frontal cortex, the supplementary motor area and the central anterior cingulum. Merely the (quite low) activation in the hMT+ areas showed a slight difference. From this identity of the activation patterns, the authors deduced that the main part of the activation was due to manual response, visualizing the importance of motor activity for such a subtle perceptual change as apparent motion. Varying the illumination frequency of the (AM), the authors found evidence that the perceptual change from single flashing points to an apparent motion is a direct consequence of the hMT+ activity. Taking into account the studies on apparent motion and motion imagery by Goebel *et al.* in 1998, the authors concluded that motion imagery requires a bottom-up activation of the hMT+ area, while a top-down activation of this area is necessary for the perception of a "real" apparent motion. They further concluded that perceptual reversals can be attributed to adaptive and competitive processes in the hMT+ which can not be initiated by top-down processes [Hoff, 2014, Muckli *et al.*, 2002, Muckli *et al.*, 2005].

Furthermore, for the stimulus knows as *Rubin's vase*, Kleinsmidt *et al.* found a temporary activation at the ventral occipital and the intraparietal areas that are responsible for the higher visual processing, as well as a deactivation in the primary visual cortex and the pulvinar. The authors concluded that perceptual switches involve a brief activation of widely distributed cortical areas as well as an intermittent activity decrease in areas thought to be responsible for the upkeep of percepts [Kleinschmidt *et al.*, 1998]. Going one step further, Andrews *et al.* found that a conscious percept of Rubin's vase can be predicted from an activation of the fusiform gyrus [Andrews *et al.*, 2002].

Later studies using the apparent motion paradigm in order to investigate neurophysiological correlates of multistable perception found that an activation of the right inferior frontal cortex precedes that of V5/MT for endogenously- compared to exogenously-induced perceptual reversals [Sterzer and Kleinschmidt, 2007]. Shen *et al.* in 2009 obtained similar results using the Necker lattice (an array of Necker cubes). Taking into account these findings, one may conclude that the activity in frontal and parietal cortices is essential for perceptual transitions during multistability [Sterzer *et al.*, 2009]. Recent studies provided evidence that the fronto-parietal network is not only responsible for perceptual transitions, but also for percept stabilization [Pearson and Brascamp, 2008, Shen *et al.*, 2009]. It was suggested that such neural mechanisms as working memory and attentional selection may play an important

role in percent stabilization during multistable perception [Sterzer *et al.*, 2009].
Taking into account the findings discussed above, it can be stated that both low- and high-level brain regions, such as those composing the fronto-parietal network, are involved in the processing of multistable stimuli. The exact role of such high-level brain regions and their interaction is yet unclear [Knapen *et al.*, 2011].

2.2.4. EEG and the multistable phenomenon

EEG has been successfully applied in order to investigate the interplay of top-down and bottom-up processes involved in experiencing perceptual reversals. Compared to fMRI, EEG measures ongoing, rhythmic neural oscillations which reflect temporal integration and interregional connectivity of brain networks underlying sensory or cognitive processes. This is a very useful feature in order to investigate a temporal process like a perceptual reversal [Basar-Eroglu *et al.*, 1993].
Top-down processes involved in the experiencing of a perceptual reversal are presumably reflected in a slow positive wave that was for the first time detected by Basar-Eroglu *et al.* in 1993 during the perception of the stroboscopic alternative motion (see Fig. 2.1 (c)). The SAM was generated by repeated alternation of two pairs of dots located at opposite corners of an imaginary rectangle. The repeated alternation of one pair of dots to the other one evoked the perception of a vertical or a horizontal apparent motion. The positive wave was detected about 500 ms preceding the button press that was used by the participants to indicate a reversal between two possible interpretations of the SAM, and was found to be most prominent in the δ band. Taking into account the component's posterior distribution, it was assumed that this positive wave occurs immediately after a perceptual reversal and belongs to the family of well-known stimulus-locked P300 waves. Because of the similarity between these two components, the slow positive wave is thought to reflect the conscious recognition of a perceptual reversal and the closure of the reversal process [Strüber and Herrmann, 2002].
Furthermore, an increase in the γ band during a perceptual reversal found by Basar-Eroglu *et al.* in 1996 may reflect the involvement of top-down processes in multistable

perception. This enhancement was most significant over the frontal regions and reached up to 50 % in comparison to spontaneous EEG recordings with no ambiguous patterns presented. The enhancement in this frequency band was thought to be related to the destabilization of the perceptual system. However, other top-down processes like focused attention, decision making or involvement of learning and memory processes could also be influential [Basar-Eroglu *et al.*, 1996].

Later, Strüber *at al.* investigated the perceptual reversal phenomenon between participants with high versus low reversal rates using the SAM. The authors found that the participants with a high reversal rate showed significantly higher γ activity over the frontal regions compared to the participants with a low reversal rate. The authors concluded that the enhanced gamma activity in the group of participants with a high reversal rate may reflect a stronger involvement of attentional top-down resources compared to the other group [Strüber *et al.*, 2000].

A participant's intent to hold the currently perceived interpretation was found to be correlated with more enhanced γ activity over frontal regions as well as a greater deflection of the slow δ component compared to the intent to switch the currently perceived interpretation [Mathes *et al.*, 2006]. The authors interpreted their findings as an indication for the significance of focused attention for experiencing a perceptual reversal. Furthermore, the modulation of the δ and γ band activity during the voluntary control of a perceptual reversal was interpreted to provide an evidence for the involvement of the fronto-parietal network in top-down regulated attentional processes during multistable perception [Mathes *et al.*, 2006].

Also, the activity in the θ band was found to be correlated with top-down processes underlying multistable perception. In 2005, Nakatani *et al.* investigated the perceptual reversal phenomenon between participants with high versus low switching rates using an ambiguous stimulus (Necker cube) as well as unambiguous stimuli (two biased Necker cubes that were presented alternately). They found that only the participants with a high switching rate showed a significant θ band activity at the frontal midline region. Since the θ activity was seen not only during the perceptual switching but also while viewing the unambiguous stimuli, the authors concluded that it could be related to concentration on the task [Nakatani and van Leeuwen, 2005].

Recently, the involvement of θ activity in top-down processing of a perceptual reversal was clarified using the SAM paradigm. It was shown that the activity in the θ band is more pronounced at anterior than at posterior brain regions by viewing an ambiguous version of the SAM compared to θ activity elicited by viewing the disambiguous version of the pattern. This may be indicative for the enhanced involvement of top-down processes which support coherent subjective experience of the world [Mathes *et al.*, 2014].

In 2000, Isoglu-Alkac *et al.* found a significantly decreased α power preceding the report of a reversal of Necker's cube that was connected to an increase in the slow δ activity during the processing of a peceptual reversal. The α decrease was confirmed in 2002 by Strüber and Herrmann using magnetoelectroencephalography (MEG). The authors reported the α activity generated by exposure to ambiguous and disambiguous versions of the SAM to differ not only in amplitude and topography, but also to have different time courses. The time course of the α activity caused by the disambiguous SAM was characterized by a more or less constant oscillation during the interval that preceded a reversal and by a sudden activity suppression at about 300 ms before the button press. The α activity was most prominent at the occipital locations. The time course caused by the ambiguous SAM was, on the other hand, characterized by a constant decrease of the α activity that started before an estimated reversal and lasted until the button press. The decrease of the endogenously induced α activity could reflect a satiation of the neural network. The perceptual reversal could occur when the α activity reaches a certain level of satiation [Strüber and Herrmann, 2002].

In a follow-up study performed by Isoglu-Alkac and Strüber in 2006, the alpha band was divided into three sub-bands (lower-1: 6-8 Hz, lower-2: 8-10 Hz, upper: 10-12 Hz) in order to define more specifically the functional roles of each sub-band. It was found that the desynchronization of the lower-1 band may reflect bottom-up processes such as an automatic arousal induced by a reversal of the Necker cube, whereas the desynchronization of the lower-2 band may be related to attentional processes like the expectancy to perform another task as e. g. a button press following a reversal.

Summarizing, the reversal-related changes observed in different frequency bands during the perception of ambiguous patterns imply that superimposed and selectively-distributed networks of various frequency ranges are involved in the integration of sensory and cognitive processes. The reversal-related responses found in the δ, θ and γ bands seem to be correlated with top-down processes. The findings in the α band seem to be related to both, top-down and bottom-up processes.

One aspect common to most of the experiments discussed above which was criticized by Kornmeier and Bach in 2004 is the fact that these base on response-locked experimental designs. Here, the perceptual reversal is "detected" through a manual (button-press) response of the test person and the observed brain activity interpreted as *induced rhythms.* Therefore, individual variations in reaction time of up to 200 ms directly find their way into the measurement data in an uncontrolled way. Kornmeier and Bach attempted to avoid this problem by correlating a perceptual reversal with a stimulus onset. For this purpose, a presentation of flashed ambiguous "Necker lattices" with interstimulus intervals was used. The participants were instructed to compare a given stimulus to the preceding one and to indicate a perceptual reversal or the perceptual stability via a button press. Thereby, it was possible to average either perceptually stable or unstable epochs time-locked to the corresponding stimulus onset. This approach helped to reveal two new ERP components presumably related to processing of the perceptual reversals [Kornmeier and Bach, 2004]. However, this approach is not suitable for an investigation of the intrinsic dynamics of the multistable perception. In order to investigate the dynamics, a perceptual reversal has to occur spontaneously during the continuous observation of ambiguous patterns.

2.3. Multistable perception in developmental research

Almost for 200 years, ambiguous figures have been used as a research tool for investigating complex interaction of perceptual bottom-up and cognitive top-down processes underlying visual perception in general and a perceptual reversal in particular [Long and Toppino, 2004]. Nevertheless, the specific processes that allow the brain to generate a coherent experience of the world around us even when sensory information is inconclusive remain mysterious [Sterzer *et al.*, 2009].

Considering the extensive use of ambiguous figures in a variety of psychological studies with adult participants, it is surprising that until recently only a few studies were performed aiming at the investigation of developmental aspects of bottom-up and top-down processes underlying multistable perception.

For the first time, young children were shown ambiguous figures by Rock *et al.* in 1994, in order to clarify the role of bottom-up vs. top-down processes underlying multistable perception. The authors claimed that three prerequisites have to be fulfilled in order to be able to experience a perceptual reversal:

1. be aware of the ambiguous nature of the stimulus,
2. know the specific interpretations, and
3. intend to perceive a reversal.

In order to test the hypothesis that if participants are naive, the percentage of spontaneous reversals would be nearly zero, it was necessary that the participants have no prior knowledge of ambiguous figures [Rock *et al.*, 1994a]. Since these figures are quite popular, Rock *et al.* decided to test preschool children. The study supported the above hypothesis. It was found that children were not able to reverse if they were not aware of the ambiguous nature of the figures used. The authors deduced that the experience of a perceptual reversal is more than a low-level perceptual process [Mitroff *et al.*, 2006]. Furthermore, it was found that 3 year old children and approximately half of the 4 year olds were not able to reverse even being aware of the two possible interpretations of an ambiguous figure. This findings were replicated by Gopnik *et al.* in 2001 and Doherty and Wimmer in 2005. According to these studies, it seems probable to assume that the understanding of the fact that one object can have multiple meanings develops during the early childhood and probably requires the development of such abilities as metarepresentation, mental imagery and inhibition. Wimmer and Doherty investigated around sixty children in the age between 3 and 5 years in order to clarify the role of these abilities in experiencing a perceptual reversal [Wimmer and Doherty, 2011]. The main outcomes of the study were

1. the *concept* of ambiguity seems to develop between the ages of three and four. During this period, conceptual understanding (top-down knowledge) about pictorial ambiguity is developed.
2. between the ages of four and five, additional processes required for *perception* of the two interpretations of ambiguous figures develop: inhibition and image generation.

The conceptual representation seems to develop until adolescence. In the study performed by Taylor *et al.* in 1999, children were exposed to ambiguous figures with semantic content, among which was a triangle that can be interpreted both as a witch hat and as a ship's sail. Thereafter they were presented the same stimuli in a disambiguous context, e. g. a witch wearing the hat or a ship with it's sail hoisted. Four years olds were convinced that an external observer would instantly interpret the ambiguous figure as exactly the disambiguous alternative that was shown to them in the second experimental step. Six year old children, on the other hand, already seemed to have developed a basic understanding of the dynamics of ambiguous figures and mostly gave the correct answer to the question concerning the beliefs of the external observer [Taylor *et al.*, 1999].

Mitroff *et al.* investigated the ability to reverse some ambiguous figures spontaneously in 5- to 9 year old children. 35 % of the naive participants were able to reverse the ambiguous figures when uninformed. The authors claimed that specific cognitive abilities, such as conceptual representation with different degree of difficulty, have to be available in order to reverse an ambiguous figure spontaneously, rather than the availability of prior knowledge [Mitroff *et al.*, 2006].

Summarizing, the results of the studies discussed above suggest that the interplay between bottom-up and top-down processes involved in processing of multistable stimuli begins at the age between four and five years, as conceptual understanding of the fact that a single image can have multistable percepts is developed. Furthermore, the studies provide evidence that top-down processes underlying multistable perception continue to develop throughout childhood and adolescence.

SECTION 3

Electroencephalogram - theoretical background

Electroencephalography (EEG) is a relatively young field of science. It was only discovered about one century ago, namely in 1895, that electrical activity takes place in the brain. Richard Caton was the first researcher who investigated electrical activity in the brains of monkeys, dogs and rabbits. The techniques available at that time did, however, not allow him to record his observations for future generations [Libenson, 2012]. It was Hans Berger who was the first person to record an EEG from humans in the 1920s [Sanei and Chambers, 2008]. He was also the first one who suggested that changes in EEG signals can be linked to mental processes taking place in the brain [Libenson, 2012]. Since these initial studies, many years passed before the EEG became an acknowledged tool to investigate mental processes in normal and pathological brains [da Silva, 2010]. The somewhat obvious reason for this lies in the complexity of the underlying systems of neural generators responsible for mental processes, the topographical and electrical properties of the brain tissue as well as in the cerebral fluid and the thickness of the scalp [da Silva, 2010].

3.1. Biophysical basis of EEG

EEG measures the summation of excitatory and inhibitory post-synaptic potentials at the dendrites of ensembles of pyramidal neurons in the cerebral cortex which lie right under the scalp [Bear *et al.*, 2006]. The post-synaptic potential represents a decreased or an increased polarization of the cell membrane which occurs when ions flow into or out of a neuron as neurotransmitters activate ion channels on the cell membrane. When thousands of neurons aligned in the same orientation produce post-synaptic potentials synchronously, the field potentials sum up and the resulting electrical field can be measured by the electrode at the scalp [da Silva, 2010]. According to estimations, the number of neurons which contribute to a measured EEG signal ranges from 10.000 up to 50.000; these are mostly neurons from superficial cortical layers [Murakami and Okada, 2006]. The brain stem and the thalamus are supposed to be the main sub-cortical generators that force neurons to fire synchronously [da Silva, 2010].

The electrical activity recorded by EEGs can be divided in two types, namely into spontaneous and evoked activity. Is is generally assumed that the spontaneous activity is reflected by the *endogenous* neural activity patterns [Salek-Haddadi *et al.*, 2003]. Brain responses related to direct or peripheral stimulation (optical, acoustical, electrical and so on), to cognitive (e. g. attention or working memory) or to motor behavior (e. g. a button press) also manifest in the EEG. Such induced changes of the electrical activity can be extracted from the recorded currents by means of various signal processing techniques. The obtained neural responses are called *event-related potentials* and *event-related oscillations* [Basar, 1998]. Their main characteristics are discussed in the following.

3.2. Event-related potentials

The raw EEG currents recorded at the scalp are a relatively course measure of the underlying brain activity. Nevertheless, brain responses to a cognitive event can be measured by the EEG. In order to isolate such responses, an event has to be presented repeatedly. This results in a number of similar segments in the EEG data. A simple averaging technique, when applied to such segments, attenuates the non-specific EEG activity and reveals a brain response to the event. Such brain responses are called event-related potentials (ERPs) [Luck, 2014]. An ERP consists of a sequence of positive and negative voltage deflections, the so-called ERP components. The ERP components are thought to reflect sensory, cognitive or motor processes. The ERPs components can have positive or negative polarity. The positive components are labeled as 'P', the negative as 'N'. According to their occurrence after an event, the components are also labeled with numbers. For example, the P1 component means a positive deflection after 100 ms upon an event occurrence [Luck, 2014].

The components which occur within 100 ms after an event are thought to reflect sensory processing. They are called *exogenous* potentials. *Endogenous* potentials are evoked later and are thought to reflect such psychological factors as expectancy, attention or other mental activities [Sanei and Chambers, 2008]. The amplitude provides an index for the extent of the neural activity in response to a stimulus. The ERP amplitudes are relatively small and reach values up to 30 μV. The higher the amplitude of a component, the stronger is the neuronal response to the corresponding stimulus [Birbaumer and Schmidt, 2006].

P300 is one of the most investigated endogenous components. P300 occurs in the time window from 300 ms up to 600 ms and is associated with a various number of cognitive functions. P300 is elicited in the *oddball* task. During this task, test persons have to pay attention to targets that appear relatively rarely in contrast to non-targets. [Luck, 2014]. It is thought that the P300 wave is related with cognitive functions, as e. g. contextual updating, attention, response modulation and resolution [Dien *et al.*, 2003]. P300 can be further subdivided into the two subcomponents

- P3a, which is responsible for automatic shifts of attention to novel or already experienced (salient) stimuli. This shifts do not depend on task relevance [Polich, 2007]. The generation of P3a involves prefrontal, frontal and anterior temporal brain regions.

- P3b, a peak of centroparietal origin which is characterized by a longer latency and by a less rapid habituation than P3a [Luck, 2014]. Infrequent task-relevant stimuli elicit this component. The stimulus complexity, along with the selection efficiency and the sustained attention mainly determine the latency of the P3b wave [Luck and Kappenman, 2011]. This makes the P3b wave highly sensitive to target probability: a decreasing probability leads to an increase in P3b amplitude [Duncan-Johnson and Donchin, 1977].

Several theoretical models try to explain how P300 is generated. The so-called *contex-updating* model assumes that after an initial sensory input, a memory comparison process is engaged in order to verify whether the current input is identical to the previous one or not. In the case of identity of incoming and preceding inputs, "the current mental model or *scheme* of the stimulus context is maintained and only sensory potentials are evoked (N1, P2, N2)" (Luck and Kappenman, 2011, p. 161). If the incoming input differs from the preceding, the attentional resources will be allocated to the target and the updating of the neural input representation occurs in the working memory, such that sensory potentials are elicited followed by P3b [Polich, 2007]. Depending on task demands, attention can be paid to non-target-events, followed by updating and modification of the current neural representation [Luck and Kappenman, 2011].

Recently, one more theoretical account for generation of the P300 component was suggested. The so-called *neuroinhibition* model assumes that during an oddball task, P3a is generated in the frontal lobe by attention-demanding stimuli (targets) when the contents of working memory are updated (the attention to non-target stimuli becomes inhibited). This may cause neural activity towards temporal and parietal regions of the brain, regions which are associated with the generation of P3b and memory storage. Thus, activation of frontal and parieto-temporal cortices might modulate the activity of P3a and P3b at the scalp [Luck and Kappenman, 2011].

3.3. Brain oscillations measured by EEG

A rhythmic alternation of states is called an oscillation. Oscillations are usually described by three parameters: frequency, power and phase. *Frequency* measures the speed of oscillations in Hz. *Power*, the squared amplitude of an oscillation, refers to the amount of energy in a frequency band and is measured in μV^2. *Phase* determines the position along the sine wave at any given time and is measured in degrees [Cohen, 2014].

In the brain, the term *oscillation* refers to rhythmic and/or repetitive fluctuations in electric activity of populations of neurons [Basar, 2013]. According to Basar, the brain oscillations measured by the EEG reflect the activity of populations of neurons that produce rhythmic oscillations in several frequency ranges [Basar, 1998]. These oscillations occur spontaneously and usually fluctuate in an uncorrelated manner. In response to external or internal events, the activity of populations of neurons begins to act coherently. The synchronization of local populations of neurons gives rise to evoked or induced brain responses in defined frequency ranges. These oscillatory responses associated with external or internal events are called event-related oscillations [Basar, 2013, Yordanova and Kolev, 2009].

Depending on different frequency ranges, the brain oscillation can be divided into five frequency bands [Basar, 1999]. These bands are named after letters of the Greek alphabet: δ (0-4 Hz), θ (4-7 Hz), α (8-12 Hz), β (12-30 Hz) and γ (30-80 Hz). A growing number of studies has shown that the brain oscillations in different frequency bands could reflect a neurobiological organization of frequency-specific networks when spontaneous oscillations are investigated, whereas the reorganization of these networks with respect to demands of sensory-cognitive processing is reflected by event-related oscillations [Basar, 2011, Engel *et al.*, 2001, Herrmann *et al.*, 2010, Yordanova and Kolev, 2009]. The functional correlates of event-related oscillations associated with the corresponding frequency bands are summarized in Tab. 3.1.

Name	**Frequency band**	**Function**
δ	0 - 4 Hz	sensory functions, signal detection, decision-making
θ	4 - 8 Hz	selective attention, association, short-term memory, executive control
α	8 - 12 Hz	sensory function, movement, working memory
β	12 - 30 Hz	sensory function, movement
γ	30 - 80 Hz	attention, signal detection, perceptual binding, perceptual switching

Table 3.1.: EEG frequency bands. An extensive overview of the single functions is provided in [Basar, 1999].

Any complex function can be created from a superposition of oscillations at different frequencies, as shown in Tab. 3.1. These oscillatory responses can be recorded at different scalp locations. This means that a selectively-distributed oscillatory network exists which generates the superimposed responses [Basar, 1998]. Examples of such responses are the evoked potentials (EPs) and in particular the ERPs. To support this assumption, it can be said that an interference of θ and the δ oscillations produces not only the structure but also the amplitude of the P300 ERP component that is measured in oddball paradigms [Karakas *et al.*, 2000]. It furthermore seems that acticity in the γ band is coupled to the P300 component in these paradigms [Basar *et al.*, 1993, Gurtubay *et al.*, 2001, Kranczioch *et al.*, 2006]

In his publication in 1999, Basar made a point that while the oscillatory responses behave like “single letters of the alphabet", brain functions represent “words" that consist of such letters (alpha, beta, gamma, . . .). This means that the potentials evoked by cognitive or sensory events are transmitted to various brain regions over networks and, in this picture, result in “words" (different brain functions).

Several other parameters play a role for the manifestation of these functions besides the frequency. Temporal relationships of superimposed oscillatory responses are characterized by the amplitude, the duration and by the delay of such responses as well as by their synchronization that depends on the degree of phase- and time-locking [Basar, 2011].

The spatial relationships of selectively-distributed and selectively-coherent oscillatory activities in neural populations are assessed by their degree of coherence [Basar, 2011].

3.4. Time-frequency analysis

The decomposition of the EEG signals into amplitude and phase components at specific frequencies performed by means of the wavelet transform allows a separate inspection of the event-related changes over a period of time [Roach and Mathalon, 2008].
The components are estimated by convolution of a scaled and translated version of a mother wavelet with the original time series of a single EEG epoch as represented by

$$W_x^{\psi}(b,a) = A_{\psi} \int \Psi^* \left(\frac{t-b}{a}\right) \cdot x(t) \cdot \mathrm{dt} \qquad . \tag{3.1}$$

Here, $x(t)$ is a single-trial EEG recording, Ψ^* denotes the complex conjugate of the scaled and translated wavelets with a and b being the scale and the translation parameter, respectively, and A denotes a normalization parameter. The translation parameter is related to the location of the window, as the window is convolved with the original time series of a single EEG epoch. The scale parameter is an inverse of the frequency. This means that high scales (low frequencies) represent global information contained in an EEG signal. Low scales (high frequencies) are useful for representing a short pattern of an EEG signal that appears from time to time as short bursts or spikes [Herrmann *et al.*, 2014].
The mother wavelet function used in the present study was the *Morlet* wavelet

$$\Psi(t) = \mathrm{e}^{j\omega_0 t} \cdot \mathrm{e}^{-t^2/2} \qquad . \tag{3.2}$$

Here, the multiplication of the first term (a complex sinusoid) with the envelope function (a Gaussian) results in the mother wavelet function as depicted in Fig. 3.1. The angular frequency ω_0 determines the width of the wavelet function in time. The Morlet wavelet function meets the requirements in order to be used to analyze an EEG signal because it

1. is finite in both, time and frequency space;

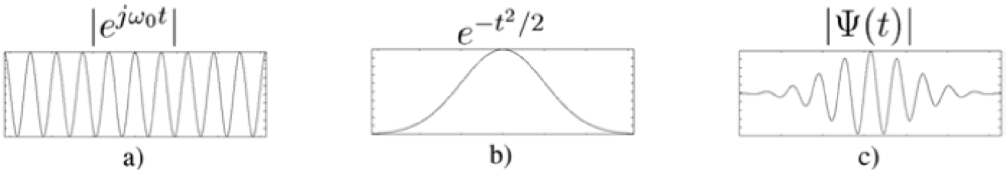


Figure 3.1.: The multiplication of the sinusoidal function (a) with the envelope function (b) results in the mother wavelet (c). Adapted from Herrmann *et al.*, 2005.

2. has zero mean amplitude;
3. reflects the features of a biological signal present in an EEG signal [Herrmann *et al.*, 2005].

The time and frequency resolution of a wavelet function depend on the choice of the Gaussian. The time resolution of a wavelet is determined by the standard deviation of the Gaussian in the time domain as given by

$$\sigma_t = \frac{m}{2\pi \cdot f_0} \quad . \tag{3.3}$$

Here, f_0 is an inverse of the scale parameter and m refers to the number of wavelet cycles. The time resolution of the central frequency (frequency at which the mother wavelet function is defined) can be estimated as the time after which the Gaussian has dropped to $\exp(-2) = 14\,\%$ [Torrence and Compo, 1998]. The frequency resolution of a wavelet is inversely related to the standard deviation of the Gaussian in the time domain as given by

$$\sigma_f = \frac{1}{2\pi \cdot \sigma_t} \quad . \tag{3.4}$$

The frequency resolution is usually given in units of the *full width half maximum* (FWHM) of the Gaussian. The relationship between FWHM and the standard deviation of the Gaussian is given by

$$\text{FWHM} = 2\sqrt{2\ln 2} \cdot \sigma \approx 2.355\sigma \quad . \tag{3.5}$$

A variable resolution in time and frequency domains is one of the advantages of the wavelet transform when compared to the standard short-time Fourier Transform. The choice of the wavelet parameters influences a trade-off between temporal and spectral resolution. Using appropriate parameters makes it possible to obtain a better time resolution for higher frequencies and a better frequency resolution for lower frequencies [Herrmann *et al.*, 2014].

SECTION 4

Aim of the study

For the readers who have - as suggested in Section - Overview of the thesis - skipped the Sections 1-3, a brief summary is provided below. Thereupon, the hypotheses underlying the study in hand are derived.

Adolescence is a period of major maturational changes in the brain [Spear, 2000, Uhlhaas *et al.*, 2010]. Specifically the maturation of the prefrontal cortex dominates this late stage of development. A successful maturation of this cortex has important implications for such cognitive abilities as self-control, decision making, attention and goal-directed behavior [Amso *et al.*, 2014, Anderson *et al.*, 2001, Blakemore and Choudhury, 2006]. Obviously, the prefrontal cortex does not operate in vacuum. Interactions between the prefrontal cortex and other brain regions, particularly with the parietal cortex, undergo maturational changes throughout adolescence [Blakemore, 2012, Darki and Klingberg, 2015, Ehlers *et al.*, in press].

According to recent findings, the fronto-parietal brain networks related to a variety of higher-order cognitive functions become less diffused (meaning that fewer brain regions become activated in response to a task) and more focal (meaning that smaller areas of activation produce stronger response to a task) throughout adolescence, resulting in more reliable performance in cognitive tasks [Durston *et al.*, 2006, Durston and Casey, 2006, Ehlers *et al.*, in press]. Taking into account this evidence, it can be supposed that immature brain networks of adolescents recruit many of the the same key brain regions related to a task as seen in adults. The strength of interconnectivity among these regions will, however, improve throughout development, whereas the recruitment of brain regions which are task-unspecific will be weakened [Johnson, 2010].

Visual illusions, such as ambiguous patterns discussed in Sec. 2, provide a tool to investigate how maturational changes of the prefrontal cortex and its connections to other brain regions throughout adolescence affect low-level perceptual (bottom-up) and higher-order cognitive (top-down) processes involved in multistable perception.

Considering the extensive use of ambiguous patterns in a variety of psychological studies with adult participants, it is surprising that until recently only a few studies have used ambiguous patterns as a tool to investigate developmental aspects of bottom-up and top-down processes underlying multistable perception. Behavioral studies with children suggested that the interplay between bottom-up and top-down processes begins at an age between three and four years, as conceptual understanding of the fact that a single image can have two interpretations is developed. Perceptual reversals between two possible interpretations also clearly require mental action from the viewer [Doherty and Wimmer, 2005]. According to Wimmer and Doherty, this mental action might be reflected in such top-down processes as executive inhibition, updating and monitoring representations in working memory and attentional selection which could play an important role in the ability to experience a perceptual reversal. These higher-order cognitive functions seem to develop between the ages of four and five, allowing children to reverse between two possible interpretations [Wimmer and Doherty, 2011].

The bulk of evidence from recent studies shows that higher-order cognitive functions like working memory, focused attention and decision-making ability, associated with prefrontal brain structures, continue to develop until young adulthood [Amso *et al.*, 2014, Anderson *et al.*, 2001, Blakemore and Choudhury, 2006]. The aim of this study was to investigate how maturational changes of the prefrontal cortex and its connections with other brain regions like the parietal cortex established throughout adolescence impact the top-down processes involved in the perception of ambiguous patterns. Since perceptual reversals occur in the range of milliseconds, the EEG is a mostly suitable method to study the role of top-down processes in reversals.

EEG measures brain oscillatory activity [Basar, 1998]. The amount of evidence that brain oscillations play a fundamental role in cognitive functions increases every year. Due to specific characteristics of brain oscillations, functionally and topographically specialized cortical activity can be identified [Basar, 2011]. Recently, the role of brain oscillations and the underlying maturational brain changes for investigation of cognitive development has also been recognized [Yordanova and Kolev, 2009].

The EEG-studies performed in our group with adults have shown that top-down processes related to a perceptual reversal require an activation of the prefrontal cortex and may correlate with event-related brain oscillations in the θ, γ and δ frequency bands [Basar-Eroglu *et al.*, 1993, Basar-Eroglu *et al.*, 1996, Mathes *et al.*, 2006, Mathes *et al.*, 2014, Strüber *et al.*, 2000].

Aim of the study

In the present study, the possible electrophysiological correlates of top-down processes (θ, γ and δ oscillations and their developmental aspects) were investigated in adolescents and young adults by exposure to ambiguous and an unambiguous control patterns. This design allowed us to differentiate processes involved in *endogenous* (internally-induced) and *exogenous* (externally-induced) perceptual reversals [Basar-Eroglu *et al.*, 1993, Mathes *et al.*, 2014]. Since the study of less complex processes can provide important insights for understanding of higher-order processes, the visual oddball task was conducted in order to obtain additional information on the role of δ, θ and γ bands in visual perception. Furthermore, the spontaneous EEG was evaluated in order to assess global maturational changes in the developing brain.

Specifically, we hypothesized that in accordance with previous studies (see Sec. 1), the EEG activity at rest in the δ and θ frequency bands will decrease with age, whereas no such tendency will be observed for the γ activity. In contrast to the decrease of EEG activity at rest, the task-related enhancement will increase with age in all frequency bands of interest. Additionally, the cortical localization of the task-related activity will be less localized in adolescent participants compared to adults. Given that the activity in these bands was found to correlate with top-down processes involved in visual processing in general, and especially in the multistable perception, the decreased level of task-related activity and its diffused cortical localization would indicate that maturational changes of the prefrontal cortex and its connections to other brain regions like the parietal cortex have an influence on the development of top-down processes.

SECTION 5

Methods

The aim of this chapter is to provide a comprehensive insight of the methods employed throughout the present study. The recruitment procedure and the demographic/ behavioral data acquisition will be outlined, along with the experiments performed by the participants in the EEG session. Furthermore, the set-up and recording of the EEG will be described along with the methods used to analyze the EEG data. Please note that the set-up as well as the analysis methods used in the present study were similar to some previous studies done in our group, especially to studies described in the following publication [Mathes *et al.*, 2014].

5.1. Participants

The original sample from which the participants were drawn consisted of 35 *adolescents* and 40 young *adults* aged from 10 to 30 years. The *adolescents* were recruited through visits to schools (secondary or comprehensive school) and/or through leaflets with the project's description. The recruitment process in schools included an information session and the distribution of parental consent forms. The *adults* were primarily students from the University of Bremen. All participants had German as their dominant language and did not report any history of psychiatric, neurological or other deceases. All participants gave their assent to participate in the study and parental consent was obtained for the *adolescents*. The *adolescents* were paid an allowance for their participation. The *adults* were either paid or got credit points for their participation.

Since the main aim of the present study was to investigate an impact of maturation changes of the brain on higher-order cognitive processes during adolescence, and taking into account the fact that maturation changes of the brain are most prominent at the peak of puberty (from 13 up to 15 years [Spear, 2000]), 22 participants in this age range were chosen among the total sample. The data of 7 *adolescents* had to be excluded from the further analysis due to extensive eye blinks and muscle artefacts. The remaining *adolescents* were included in the present study. Among the included participants (*adolescents*: n = 15), 6 were male. Since the most prominent maturation alternations in the brain are supposed to be completed until the early twenties and the first signs of aging processes in the brain can already be detected in the late twenties [Konrad and Uhlhaas, 2011], 15 participants (6 males) in the age range from 20 up to 27 years were chosen from the total sample to build the control group (*adults*). Table 5.1 summarizes age and sex distribution of the participants included in the present study. Also, all participants were right-handed and had normal or corrected-to-normal vision.

	Adolescents	**Adults**
Age	13 - 14 years	20 - 27 years
Mean age	14.11 (SD: .44)	23.59 (SD: 2.60)
Males / Females	6 / 9	6 / 9

Table 5.1.: Sample characteristics.

5.2. Stimuli

5.2.1. Ambiguous version of the stroboscopic alternative motion

The Stroboscopic Alternative Motion (SAM) used in the study had a 5:8 vertical-to-horizontal distance ratio (see Fig. 5.1 (a)). The SAM is generated by repeated alternation of two stimuli: Amb1 and Amb2, each showing a pair of dots located at opposite corners of an imaginary rectangle. The repeated alternation of one pair of dots to the other one evokes the perception of a vertical or a horizontal apparent motion. The dots were highlighted in white on a black screen. A white dot in the center of the imaginary rectangle served as a fixation point and was presented constantly. The flashing frequency of the SAM was 2 Hz. Each pair of dots was flashing for approx. 165 ms, followed by an inter-stimulus interval of approx. 85 ms. This timing works best to prevent the visual system from adapting to the stimulus, which would result in a decay of the apparent motion over time [Ramachandran and Anstis, 1983].

5.2.2. Unambiguous version of the stroboscopic alternative motion

The unambiguous SAM is a modified version of the ambiguous stimulus, as shown in Fig. 5.1 (b). A subsequent presentation of Vert1 - Vert2 causes the perception of a vertical direction of motion, while a subsequent presentation of Horz1 - Horz2 causes the perception of a horizontal direction of motion. The presentation of the unambiguous SAM was changed in random time intervals determined in earlier studies with healthy participants to resemble the reversal behavior during an exposure to the ambiguous SAM. It led to an externally-induced reversal of the perceived direction of motion. The dimensions and the flashing frequency of the unambiguous SAM were identical to the settings used in the ambiguous version.

5.2.3. Visual oddball paradigm

A visual oddball paradigm with checkerboard images was applied in the study (see Fig. 5.2). Target stimuli were displayed on the checkerboard images with a green fixation

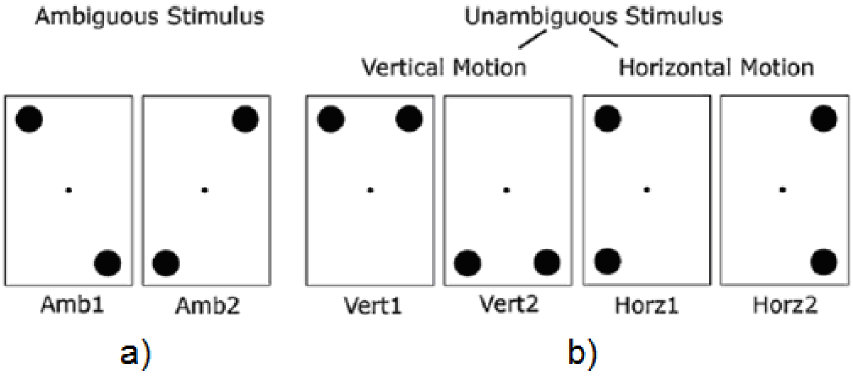


Figure 5.1.: a) An exposure to the ambiguous stimulus leads to the perception of either horizontal or vertical motion, respectively. b) A subsequent presentation of Vert1 - Vert2 causes the perception of a vertical direction of motion, while a subsequent presentation of Horz1 - Horz2 causes the perception of a horizontal direction of motion (from Mathes *et al.*, 2010).

spot positioned directly in the center of the images on a white check. The spot diameter was 1.1 cm, resulting in a visual angle of 0.4° at a distance of 150 cm from the participant to the screen. The checks' length and width were 2.7 cm, resulting in 1°, respectively. Non-target stimuli were displayed on the checkerboard images with the green fixation spot positioned directly on the crossing of four fields. During the experimental session, a participant was presented in total 150 stimuli, 112 stimuli were assigned as non-target and 38 stimuli as target stimuli, resulting in a ratio of 75 % non-targets to 25 % targets. Target and non-target stimuli appeared randomly between 1.6 s and 3.9 s in order to avoid any rhythmic adaptation of the subject to the temporal characteristics of the trial sequences.

5.3. Procedure

Prior to conducting the experiment, a brief description of the study's background, method (EEG) and the duration of the experiment were given. Also, the participants (in the case the participant was under 18 years old: both the parent and the teenager) were informed about the option to cancel the experiment at any time without explaining any reason.

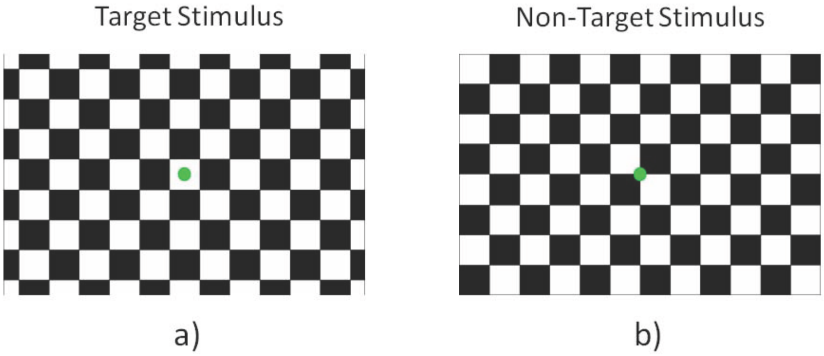


Figure 5.2.: Stimulus types in the visual oddball paradigm. a) Target stimuli appeared with a probability of 25 %. b) Non-target stimuli appeared with a probability of 75 %.

After that the participants (and their parents) had ample time to ask any questions. If there were no objections, the participants were asked to sign a consent form (see App. A). The parent of a teenager signed a parental consent (also shown in App. A).

After the description phase, an introductory interview that took approximately 10 minutes was conducted (see App. B). Data were gathered on personal and health details, school performance, as well as on pre-existing condition of neurological and psychiatric diseases of a participant and his/her relatives. Also, a participant was asked to make a self-assessment of physical and mental well-being on a scale from 1 to 10 (where 1 referred to a very bad and 10 to an excellent state) and of their current stress level (in this case, 1 referred to a low and 10 to a high stress level). Furthermore, in order to exclude confounding variables, the participants were asked about their sleeping habits and food and caffeine containing drinks intake. Oldfield's test was performed in order to identify the handedness of the participants [Oldfield, 1971].

Following this, the participants were introduced to two ambiguous stimuli: the ambiguous version of the SAM and the Necker cube. At this point in time, they were uninformed about the ambiguous nature of these stimuli in order to assess the spontaneous reversal ability of a participant. The stimuli were presented consecutively, each for two minutes. The presentation of the stimuli was randomized between the participants. A participant was instructed to describe each stimulus. If the ambiguous nature of a stimulus was figured out by a participant, it was noted that the participant can spontaneously reverse between two alternatives of the stimulus and the procedure was repeated with the next stimulus. If a participant failed to reverse spontaneously while exposed to the first stimulus, the procedure was repeated using the second stimulus without any explanation of the ambiguous nature of the stimulus.

Following the consecutive presentation of two ambiguous stimuli, a participant was introduced to the unambiguous alternatives of each stimulus. In the case when a participant was able to reverse spontaneously, this was done to ensure that the two alternatives were figured out correctly. In the case when a participant failed to reverse spontaneously, the ambiguous nature of the stimuli was explained to her or him. The procedure was repeated using the ambiguous stimuli in order to ensure that the participant was able to distinguish between the two ambiguous alternatives.

After that, a participant was asked whether (s)he had any experience with ambiguous figures in general and particularly with the two presented stimuli. According to the information obtained, a participant could be defined as naive and non-naive generally and regarding the stimuli used in the experiment. This state and the ability to reverse spontaneously was summarized for each participant as shown in Tab. 5.2. Thereafter, the EEG session described below took place. The total time taken to set up and record an EEG was approximately 90 min.

Ambiguous stimuli	**Self-report**	**Spontaneous reversal ability**
SAM	naive / non-naive	yes / no
NECKER	naive / non-naive	yes / no

Table 5.2.: Participant classification. For each stimulus, one entry for the state and the spontaneous reversal ability was chosen.

5.3.1. EEG session

The EEG session took place in a dimly lit, electrically shielded room. All stimuli used in the experiment were presented using *Presentation*® (v. 16.3) on a screen with a refreshing rate of 85 Hz and a resolution of up to 1024 × 768 pixels.

In one EGG session, each participant completed four tasks:

- *spontaneous EEG* : the participants were instructed to fixate their gaze on a cross in the center of the screen and to close their eyes as soon as the cross disappeared. Thereby, the spontaneous EEG with open and closed eyes was recorded for 1 min each. During this task, the participants were asked to relax and to minimize all movements and eye blinks;
- *ambiguous* task: the participants were exposed to the ambiguous SAM paradigm described in Sec. 5.2.1. They were asked to press a button whenever they perceived a change of the endogenously-induced direction of motion;
- *unambiguous* task: the participants were exposed to the unambiguous SAM paradigm described in Sec. 5.2.2. They were asked to press a button whenever they perceived a change of the exogenously-induced direction of motion;
- *visual oddball* task: the participants were exposed to the visual oddball paradigm described in Sec. 5.2.3. They were strictly instructed to respond as quickly as possible with a button press to each presentation of a target stimulus.

During an EEG session, the *spontaneous EEG* was always recorded first, whereas the task order of *ambiguous*/*unambiguous* and *visual oddball* tasks was counterbalanced. Prior to each experiment, participants were given exact instructions and completed a practice session to ensure full understanding of the task requirements.

5.3.2. EEG settings

The EEG activity was recorded during the performance of all tasks. Thirty Ag-AgCl electrodes were positioned according to the international 10 - 20 system [Jasper, 1958] at the locations shown in Fig. 5.3 in an electrode cap (Easycap, Falk Minow Services). Linked earlobe electrodes served as a reference. Two additional electrodes were positioned above and to the right of the right eye to record eye blinks. Electrolyte gel (Abrolyt HiCl) was inserted into each channel on the cap. The skin was slightly abraded to obtain an impedance level below 10 kΩ. The EEG signal was amplified by a 32 channel BrainAmp System (Brain Products®) and digitized at a sampling rate of 500 Hz, resulting in a band-pass of 0.1 - 250 Hz.

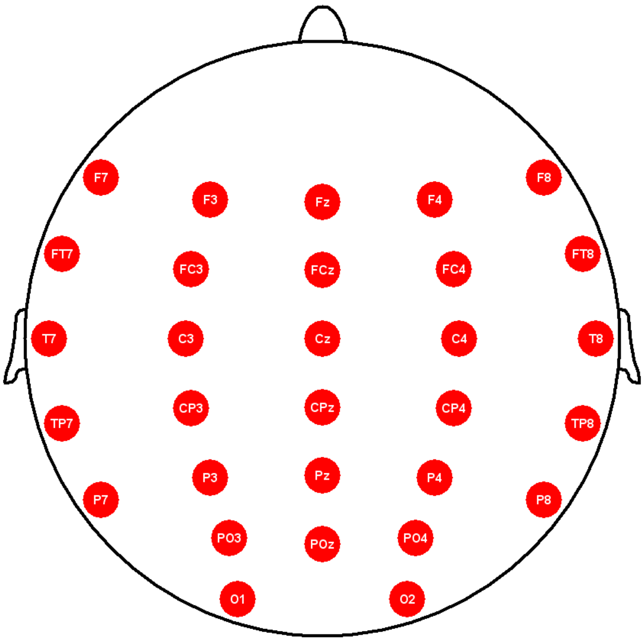


Figure 5.3.: Electrode placements according to the international 10 - 20 system as used in the study.

5.4. EEG data analysis

The preprocessing, segmentation and further data analysis of the EEG data was performed in Matlab® v.7.10. using custom-written scripts. The EEG data of three adult participants were corrupted during the spontaneous EEG. For this reason, the EEG data of three *adolescents* were excluded from further analysis. Therefore, only the EEG data of 12 participants from each group were further analyzed. For the *visual oddball* task, the EEG data of one adolescent participant were corrupted. This is why only the EEG data of 14 participants from each group were further analyzed.

5.4.1. EEG data preprocessing

The data sets that consist of the continuous EEG recordings of the tasks were segmented into EEG epochs using Matlab. The length of the epochs was chosen such that possible distortions of a signal (due to the time-frequency analysis discussed below) at the beginning and end of an epoch were avoided. The segmentation procedure of the EEG data for each task is discussed in detail below.

5.4.1.1. Definition of epochs for the spontaneous EEG task

In the case of spontaneous EEG, only the data recorded in the eyes-open condition were considered for further analysis. This data were segmented into 3998 ms epochs.

5.4.1.2. Definition of epochs for the ambiguous task

Fig. 5.4 schematically depicts the data segmentation procedure for the *ambiguous* task. The participant's manual response was used as time reference for the extraction of the so-called *switching* epochs – these are the epochs which contained an endogenously induced perceptual switching – from the continuous EEG-data. The epochs lasted 3998 ms (2000 ms before the manual response of a participant and 1998 ms after it). It was ensured that the time periods of two subsequent manual responses used to extract a *switching* epoch were separated by at least 1000 ms to avoid any overlapping of a switching-related activity with motor activity elicited by the subsequent manual response. The EEG data that did not overlap with the *switching* epochs and were free from any motor-related oscillations were used to construct so-called *non-switching* epochs. The *non-switching* epochs had – with 3998 ms – the same length as the *switching* ones. The zero of the *non-switching* epochs was set artificially after 2000 ms within the epoch.

5.4.1.3. Definition of epochs for the unambiguous task

For the *unambiguous* task, the data segmentation procedure into *switching* and *non-switching* epochs was the same as for the *ambiguous* task. Furthermore, for the *unambiguous* task only *switching* epochs in which the participants responded within 1500 ms after an externally-induced switching of the perceived direction of motion were characterized as correct and included in the further analysis. The epochs with withholding manual responses (omission errors) were rejected.

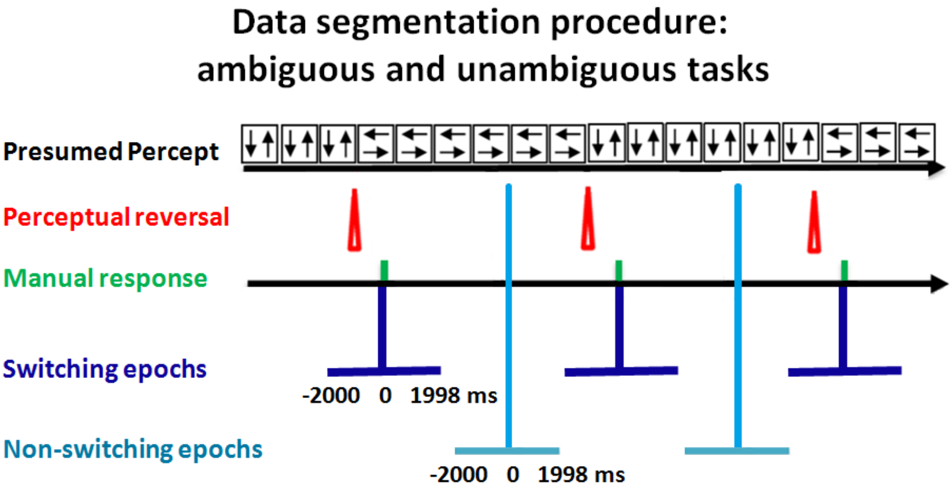


Figure 5.4.: A schematic illustration of the data segmentation procedure for the *ambiguous* and *unambiguous* tasks. On the top, each box indicate a presumed percept at an instant in time. Each short green bar represents the onset of a motor response given to indicate a perceptual reversal (depicted in red). This motor response was utilized to time-lock epochs containing perceptual switching (depicted in dark blue). Non-switching periods (depicted in light blue) were of the same duration, but did not contain a button press and did not overlap with the switching epochs.

5.4.1.4. Definition of epochs for the visual oddball task

Continuous data of the *visual oddball* task for both *target* and *non-target* conditions were segmented into 3998 ms epochs containing a 2000 ms pre-stimulus interval and a 1998 ms post-stimulus interval. Fig. 5.5 illustrates the segmentation procedure. It was also ensured that only epochs in which the participants responded within 1500 ms after a target onset were considered as correct and included in any further analysis. The epochs that contained withholding responses (so-called omission errors) to a target stimulus were excluded from any further analysis. For the *non-target* condition, the epochs were characterized as correct by the lack of a participant's motor response within 1500 ms after a non-target onset. The epochs which contain responses that occurred within 1500 ms from the onset of a non-target stimulus (so-called commission errors) were rejected from any further analysis.

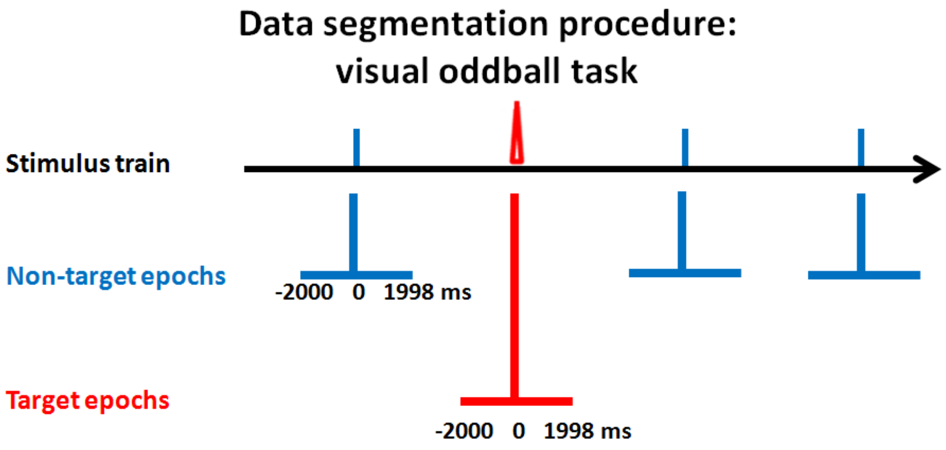


Figure 5.5.: A schematic illustration of data segmentation procedure for the *visual oddball* task. On the top, a train of used stimuli: a blue bar represents a *non-target*, a red bar represents a *target*. Each bar was utilized to time-lock epochs containing a target (depicted in red) or non-target (depicted in blue). Target and non-target epochs were of the same duration and did not overlap with each other.

5.4.2. Artefact rejection

The epochs obtained for all four tasks were searched for eye, muscle or technical artefacts in the time interval of 1000 ms after the start up to 1000 ms before the end of an epoch. The epochs with amplitudes above 100 µV for adult and 150,µV for adolescent participants were generally excluded from any further analysis.

5.4.3. Adjustment of epochs

Since the number of artefact-free epochs varied considerably among the participants for different conditions within each task, the number of epochs had to be adjusted between participants and conditions. The number of epochs accepted for each task and its conditions is presented in Tab. 5.3.

Task	**Condition**	**Groups**		**t-tests**
		Adolescents	**Adults**	
spontaneous EEG	eyes open	21.04 (SD: 6.02)	22.00 (SD: 6.70)	n.s.
ambiguous	switching	40.47 (SD: 18.45)	36.93 (SD: 18.56)	
	non-switching	41.07 (SD: 6.16)	39.60 (SD: 6.65)	n.s.
unambiguous	switching	33.53 (SD: 10.04)	37.13 (SD: 7.60)	
	non-switching	37.13 (SD: 7.60)	35.06 (SD: 10.44)	n.s.
visual oddball	target	25.26 (SD: 4.07)	27.67 (SD: 3.39)	
	non-target	26.00 (SD: 0.00)	25.97 (SD: 0.16)	n.s.

Table 5.3.: Mean numbers of epochs included from each experimental condition for further analysis.

5.4.4. Time-frequency analysis

One of the main spectral characteristics – the single trial activity – reflects the induced EEG response which occurs after a sensory stimulation but is not necessarily time-locked to a stimulus onset [Basar, 1998].

To derive the time-varying single-trial activity, a Morlet-wavelet-based time-frequency decomposition described in detail in Sec. 3 was applied to a single artefact-free epoch. Therefore, the obtained amplitude values were averaged over the epochs.

In the present study, single-trial activity at central frequencies of the *delta*, *theta* and *gamma* bands was derived. Parameters used for the analysis of each band of interest are summarized in Table 5.4 The wavelets were normalized to have unity energy. In order to enhance comparability with a signal amplitude if calculated by a Fourier transform, the transformed data was multiplied by the square-root of the sampling interval [Mathes *et al.*, 2014, Torrence and Compo, 1998].

Frequency band	Central frequency	Number of cycles	Time resolution	Frequency resolution
δ band	2.5 Hz	3	570 ms	1.5 - 3.5 Hz
θ band	5.5 Hz	6	500 ms	4.4 - 6.6 Hz
γ band	38 Hz	6	37 ms	30.6 - 45.4 Hz

Table 5.4.: Parameters used for time-frequency analysis.

Assessment of developmental changes reflected in single-trial EEG activity

In order to demonstrate developmental changes of EEG activity in the frequency bands of interest, single-trial activity at rest in eyes-open condition as well as during time periods preceding an event-processing in the *ambiguous*, *unambiguous* and *visual oddball* tasks was assessed. The time periods were defined as follows:

- the *non-switching* epochs of the *ambiguous/unambiguous* tasks;
- the time periods from - 300 up to - 100 ms preceding a target/non-target occurrence in the *visual oddball* task.

Assessment of developmental changes reflected in the enhancement of single-trial EEG activity during task-related processing

In order to demonstrate developmental changes in task-related processing for *ambiguous/unambiguous* and *visual oddball* tasks, a procedure described in detail by Delorme and Makeig (2004) was adopted and applied as follows:

- *ambiguous/unambiguous* tasks: the mean single-trial amplitudes for δ, θ and γ frequency bands were calculated over the time periods of 600 ms (in δ band), 750 ms (in θ band), and 800 ms (in γ band) for each artefact-free, *non-switching* epoch and averaged over all *non-switching* epochs separately for each task (*ambiguous/unambiguous*) as well as for each participant. The time periods were chosen in accordance to the time periods defined for a statistical analysis of switching-related activity in the frequency bands of interest (see Sec. 5.5.2). The resulting value was used as baseline and the mean baseline log spectrum was subtracted from each spectral estimate of the *switching* periods. Thus, the obtained values reflect the logarithm-transformed ratio of a single trial activity in the frequency bands of interest during *switching* periods relative to the *non-switching* periods. For the sake of simplicity, the logarithm-transformed ratio is in the following referred to as the *switching- or reversal-related enhancement.*

- the *visuall oddball* task: the mean single-trial amplitudes for δ, θ and γ bands were calculated over the time periods preceding a stimulus onset (δ, θ, γ band: -300 - -100 ms) for each artefact-free epoch and averaged over all epochs separately for each condition (target and non-target) and participant. The obtained values were supposed to represent the baseline activity. The logarithm-transformed ratio of a single trial activity during the stimulus processing periods in the frequency bands of interest was calculated relative to the baseline activity. For the sake of simplicity, the logarithm-transformed ratio is in the following referred to as the *target-related/non-target-related enhancement.*

5.5. Statistical analysis

In order to compare behavioral and EEG data between two age groups of interest, the Statistical Package for Social Science (SPSS v. 22) was used. The detailed procedure of the statistical analysis of the data is given below.

5.5.1. Statistical analysis of the behavioral results

The t-test procedure was applied to compare behavioral measures between two age groups of interest. Previous experience with ambiguous figures in general as well as the ability to experience perceptual switching being naive with respect to the ambiguous nature of the SAM and the Necker cube was compared between the groups. Furthermore, for the *ambiguous task* the reversal rate defined as the number of perceptual reversals per minute was compared between the groups.

For the *unambiguous* tasks, a t-test procedure compared the groups in respect to mean reaction time, standard deviation of individual reaction times as well as accuracy of performance.

Also, the groups were compared on the basis of the percentage of error responses after an externally-induced perceptual reversal during the *unambiguous* task. Due to the generally high performance, the error rate was assessed as the summed error score over all error types:

- *omission* errors - withholding manual responses after an externally-induced reversal occurrence within a time interval from 0 ms up to 1500 ms;
- *"too early"* errors - a manual response was given in a time interval from 0 ms up to 200 ms after an externally-induced reversal occurrence;
- *"too slow"* errors - a manual response was given later than 1500 ms after an externally-induced reversal.

For the *visual oddball* task, the same comparisons in respect to mean reaction time, standard deviation of individual reaction times as well as accuracy of performance were performed. Also, the groups were compared on the basis of the percentage of error responses after a target onset during the *visual oddball* task, as this was already described for the *unambiguous* task.

5.5.2. Statistical analysis of EEG data

Based on a visual inspection of the individual activity in the frequency bands of interest and to make the results obtained in the present study comparable to the other studies of our group, data from 11 electrodes (F3, Fz, F4, C3, Cz, C4, P3, Pz, P4, O1, O2) was included in the statistical analysis. Furthermore, the electrodes were grouped to the **Regions of Interest** (ROI) as follows: **frontal** (F3, Fz, F4); **central** (C3, Cz, C4); **parietal** (P3, Pz, P4); **occipital** (O1, O2). The grouping of electrodes to the ROIs allowed us to avoid a loss of statistical power [Mecklinger and Pfeifer, 1996].

Time windows for the statistical analysis were determined by visual inspection of an individual activity in the frequency bands of interest for each task and its conditions. As discussed above, the individual activity was assessed by two measures: the single-trial activity (measured in µV) and the event-related enhancement in the tasks (measured in dB).

5.5.2.1. Statistical analysis of single-trial activity in the frequency bands of interest

The statistical analysis of the δ, θ and γ single-trial responses was conducted separately for each task. The individual means of the single-trial activity were calculated over all data points within the defined time windows for the frequency bands of interest (see Tab. 5.5) and subjected to a repeated measure analysis of variance (ANOVA). For each task, a 2 x 4 ANOVA with GROUP (*adolescents* and *adults*) as the *between-subjects factors* and electrodes grouped to the respective ROIs (frontal, central, parietal and occipital) as the *within-subjects factors* was used to compare the groups.

5.5.2.2. Statistical analysis of task-related enhancement of single-trial activity in the frequency bands of interest

The statistical analysis of the task-related enhancement in the δ, θ and γ bands was conducted separately for the *ambiguous*, *unambiguous* and *visual oddball* tasks as described below.

For the *ambiguous* task, the individual means of switching-related enhancement were calculated over all data points within the defined time windows for the frequency bands of interest (see Tab. 5.6) and subjected to a repeated measure analysis of variance (ANOVA).

Task	**Conditions**	**Statistical time windows (ms)**		
		δ band	*θ band*	*γ band*
spontaneous EEG	eyes-open	-500 - 0	-750 - 0	-800 - 0
ambiguous	non-switching	-500 - 0	-750 - 0	-800 - 0
unambiguous	non-switching	-500 - 0	-600 - 0	-800 - 0
visual oddball	target non-target	-300 - -100	-300 - -100	-300 - -100

Table 5.5.: Statistical time windows of each task and its conditions for calculation of single-trial activity in the δ, θ and γ bands.

A 2 x 4 ANOVA with GROUP (*adolescents* and *adults*) as the between subjects factors and electrodes grouped to the ROI (frontal, central, parietal and occipital) the *within-subjects factors* was used to compare the groups in each frequency band of interest. The same procedure was applied to reveal group differences during the *unambiguous* task.

Task	**Conditions**	**Statistical time windows (ms)**		
		δ *band*	θ *band*	γ *band*
ambiguous	switching vs. non-switching	-500 - 0	-750 - 0	-800 - 0
unambiguous	switching vs. non-switching	-500 - 0	-600 - 0	-800 - 0

Table 5.6.: Statistical time windows for calculation of the switching-related enhancement in the *ambiguous* and *unambiguous* tasks.

For the *visuall oddball* task, a visual inspection of an individual activity revealed two distinct event-related responses. The first response was short and occurred in the time window from 0 up to 150 ms, whereas the second response was broader and occurred in the time window from 300 up to 700 ms. The individual means of event-related enhancement were calculated over the data points within the early and late time windows in each frequency band of interest (except for the δ band in the early time window). In order to make the interpretation of the results easier, the statistical analysis was performed separately for the early and late time windows. Hence, two ANOVAs (2 x 2 x 4) compared the GROUPs (*adolescents* and *adults*) across two CONDITIONs (*target* and *non-target*) at four ROIs (frontal, central, parietal and occipital) in each frequency band of interest. For *both* measures (single-trial activity and event-related enhancement) and *all* tasks, Levene‘s test was used in order to check whether the variances were homogeneous for all levels of the repeated measures variables. Greenhouse corrections were employed if a violation of the assumption of sphericity was detected by Mauchly’s test. Uncorrected degrees of freedom were reported. Following significant main or interaction effects in a repeated measures ANOVA, post-hoc comparisons using t-tests were employed. All post-hoc comparisons were corrected using the Sidak procedure. Corrected p-values are reported. In order to estimate effect sizes, partial η^2 values were calculated.

SECTION 6

Results

In this chapter, the results of the electrophysiological and behavioral measurements are described, beginning with a presentation of the behavioral results. Thereupon, the developmental changes reflected in the ongoing as well as in the task-related EEG activity of the δ, θ and γ bands is shown. Finally, a detailed statistical analysis of both types of EEG activity is provided.

6.1. Behavioral results

6.1.1. Spontaneous reversal ability

As shown in Fig. 6.1 (a), only participants from the *adults* group had previous experience with ambiguous figures ($t(28) = 7.48$, $p = .000$). Furthermore, all participants included in the study were naive with respect to the ambiguous nature of the SAM or the Necker cube. Fig. 6.1 ($b - c$) show the percentage of participants for both stimuli who were able to experience perceptual reversals spontaneously. The groups of interest did not differ in their ability to experience perceptual reversals spontaneously, exposed to either the ambiguous SAM ($t(28) = .36$, $p = .724$) or to the Necker cube ($t(28) = -1.47$, $p = .153$).

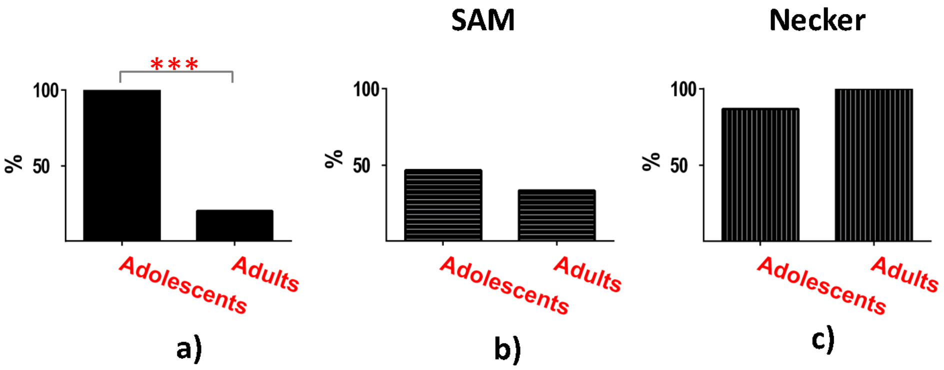


Figure 6.1.: (a) Percentage of participants without any previous experience with ambiguous figures in the groups of interest. (b) Percentage of participants with spontaneous reversal ability in the groups of interest who were exposed to the ambiguous SAM. (c) Same as (b), but exposed to the Necker cube. Asterisks indicate significance niveau: * $p \leq .05$, ** $p \leq .01$, *** $p \leq .001$.

6.1.2. Reversal rate for the ambiguous task

The mean reversal rate during the *ambiguous* task was 8.19 (SD: 4.73) in the group of *adolescents* and 6.77 (SD: 4.12) in the group of *adults*. The statistical comparison showed that the mean reversal rate during the *ambiguous* task was comparable between the groups ($t(28) = .88$, $p = .389$) and was slightly lower in both groups compared to the *unambiguous* task, where the reversal rate was set to 8.88 reversals per min. The mean reversal rate did not differ between the *ambiguous* and *unambiguous* tasks in both groups (*adolescents*: $t(14) = -.57$, $p = .579$; *adults*: $t(14) = -1.98$, $p = .067$).

6.1.3. Reaction times and accuracy measures for the unambiguous task

The behavioral accuracy measures and the mean reaction times for the *unambiguous* task are summarized in Table 6.1. The mean accuracy of correctly indicated perceptual reversals during the *unambiguous* task was above 95% and with no significant differences between the groups ($t(28) = -1.21$, $p = .235$). The mean reaction times of the correct responses upon exogenously-induced reversals did not differ between the groups ($t(28) = 1.40$, $p = .174$). The standard deviation of the individual reaction times was lower in *adults* compared to *adolescents* ($t(28) = 4.16$, $p = .000$).

	Adolescents	**Adults**	**Group comparisons**
Accuracy (%)	94.67 (SD: 4.56)	96.67 (SD: 4.48)	n. s
Reaction time (ms)	808.68 (SD: 149.74)	747.66 (SD: 167.74)	n. s
SD of individual RT	304.23 (SD: 88.98)	190.78 (SD: 56.94)	p = .000

Table 6.1.: Reaction times and behavioral accuracy measures between groups for the *unambiguous* task. SD: standard deviation, n.s.: not significant.

6.1.4. Reaction times and accuracy measures for the visual oddball task

Table 6.2 shows the mean reaction times and behavioral accuracy measures for each group. The groups almost always responded correctly during the task, with no significant differences between groups on correct responses in the *target* condition ($t(28) = -.54$, $p = .596$). There were no significant differences between groups concerning the mean reaction times ($t(28) = 1.09$, $p = .285$) or the standard deviation of the individual reaction times ($t(28) = 1.04$, $p = .307$).

	Adolescents	**Adults**	**Group comparisons**
Accuracy (%)	96.25 (SD: 5.22)	97,27 (SD: 2.31)	n.s
Reaction time (ms)	510.44 (SD: 62.06)	498.09 (SD: 72.18)	n.s
SD of individual RT	102.05 (SD: 24.89)	89.44 (SD: 35.54)	n.s

Table 6.2.: Reaction times and behavioral accuracy measures between groups for the *visual oddball* task. SD: standard deviation, n.s.: not significant.

6.2. EEG data

At the beginning of this section, the developmental aspects reflected in the single-trial activity of the δ, θ and γ bands are addressed. Thereupon, the grand averages of EEG activity filtered in the range of $0.5 - 48$ Hz of both groups for the *ambiguous* task are shown. After that, topographical distributions of *switching-related* enhancement of EEG activity in the δ, θ and γ bands are addressed, followed by a detailed statistical analysis in the distinct time windows determined by visual inspection of the individual EEG data sets. The results obtained for the *unambiguous* and *visual oddball* tasks are presented in the same order.

6.2.1. Developmental changes of single-trial EEG activity in δ, θ and γ frequency bands

Fig. 6.2 (a)depicts the topographical distribution of the single trial activity of the spontaneous EEG activity during the *eyes-open* condition for the frequency bands of interest.

6.2.1.1. δ band

The single-trial delta activity was found to decline with increasing age (see Fig. 6.2 (b), right), as shown by a significant main effect of the factor GROUP ($F(1, 24) = 26.93$, $p = .000$, $\eta^2 = .53$). Furthermore, the overall delta activity was found to have a fronto-centro-parietal maximum as indicated by a significant main effect of the factor ROI ($F(3, 72) = 11.54$, $p = .000$, $\eta^2 = .33$). The post-hoc comparisons showed that the delta activity at occipital regions was significantly decreased compared to all other regions ($p < .05$ for all comparisons).

6.2.1.2. θ band

The single-trial theta activity decreased with age (see Fig. 6.2 (b), center), as reflected by a significant main effect of GROUP ($F(1, 24) = 10.27$, $p = .002$, $\eta^2 = .34$). The overall theta activity had, in general, an anterior maximum ($F(3, 72) = 12.44$, $p = .004$, $\eta^2 = .30$). The post-hoc tests showed that fronto-central theta activity was larger compared to theta activity at parietal and occipital regions ($p < .001$).

6.2.1.3. γ band

The single-trial gamma activity was found to be more pronounced over the posterior regions (see Fig. 6.2 (b), left), as indicated by a significant main effect of ROI ($F(3, 72) = 5.06$, $p = .013$, $\eta^2 = .17$). The post-hoc comparisons showed that the gamma activity at occipital regions was significantly enhanced compared to parietal regions ($p < .05$).

The single-trial activity during the *non-switching* condition of the *ambiguous/unambiguous* tasks as well as the *pre-stimulus* activity in the *visual oddball* task was found to decrease with age and to have a topographical distribution in the δ and θ bands comparable to the *spontaneous EEG* in the *eyes-open* condition. Similar results were also obtained in the γ band (for more details, see Tab. 6.3).

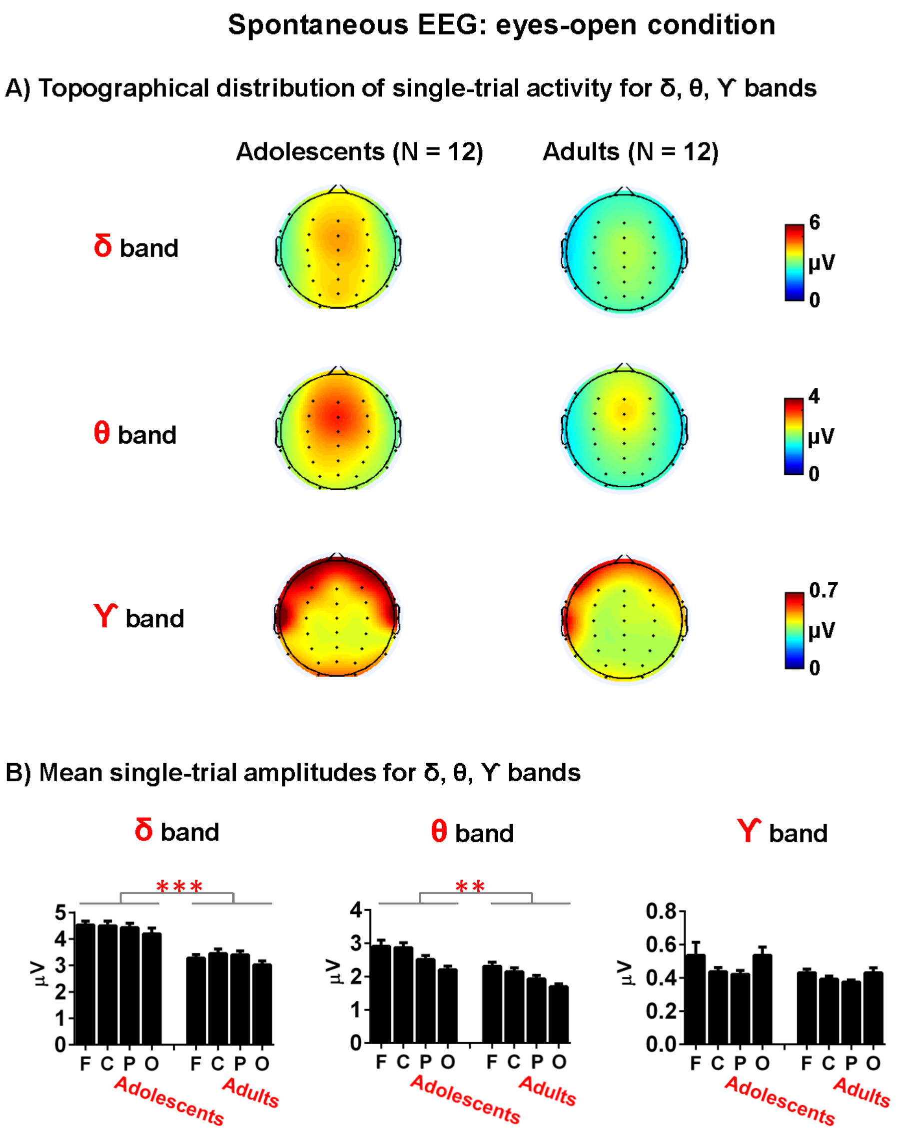


Figure 6.2.: a) Topographic head maps of single-trial activity for the *eyes-open* condition of the spontaneous EEG in the δ, θ and γ frequency bands for the groups of *adolescents* (N = 12) and *adults* (N = 12). b) Mean amplitudes of the single-trial activity for the *eyes-open* condition of the spontaneous EEG in both groups. Abscissa: mean amplitude in μV. Ordinate: regions of interest (**F** = frontal, **C** = central, **P** = parietal, **O** = occipital). The error bar indicates the standard error. Asterisks indicate the significance niveau: * $p \leq .05$, ** $p \leq .01$, *** $p \leq .001$. For the sake of simplicity, only groups and main interaction effects are shown.

Task	δ		θ		γ	
	GROUP	ROI	GROUP	ROI	GROUP	ROI
Spontaneous EEG	$p = .000$	$p = .000$	$p = .002$	$p = .000$	n.s.	$p = .013$
Ambiguous	$p = .000$	$p = .000$	$p = .000$	$p = .000$	n.s.	$p = .008$
Unambiguous	$p = .000$	$p = .025$	$p = .016$	$p = .000$	n.s.	$p = .003$
Visual oddball	$p = .000$	$p = .045$	$p = .001$	$p = .004$	n.s.	$p = .004$

Table 6.3.: Summary of significant results of the two factor variance analysis (2 GROUP × 4 ROI) found for the prestimulus single-trial activity in the δ, θ and γ bands for each task. n.s.: not significant.

6.2.2. Developmental changes reflected in a task-related enhancement of single-trial EEG activity in δ, θ and γ frequency bands

6.2.2.1. Ambiguous task

The grand averages of the EEG activity of the *switching* condition filtered in the range of $0.5 - 48$ Hz as well as single participant averages for both groups during the *ambiguous* task are shown in Fig. 6.3 and Fig. 6.4, respectively. The switching-related activity can be detected in the two groups in both, the grand averages as well as in the single participant averages, particularly over parietal and occipital regions. At these regions, the response begins about 500 ms before the button press in the group of *adults*, reaches its maximum at the time instant of the button press and disappears about 500 ms after it. The onset of the switching-related response seems to appear earlier in the group of *adolescents*. Furthermore, the switching-related activity seems to be slightly larger in the group of *adults* compared to the group of *adolescents*. For both groups, the switching-related activity is less pronounced at the frontal regions.

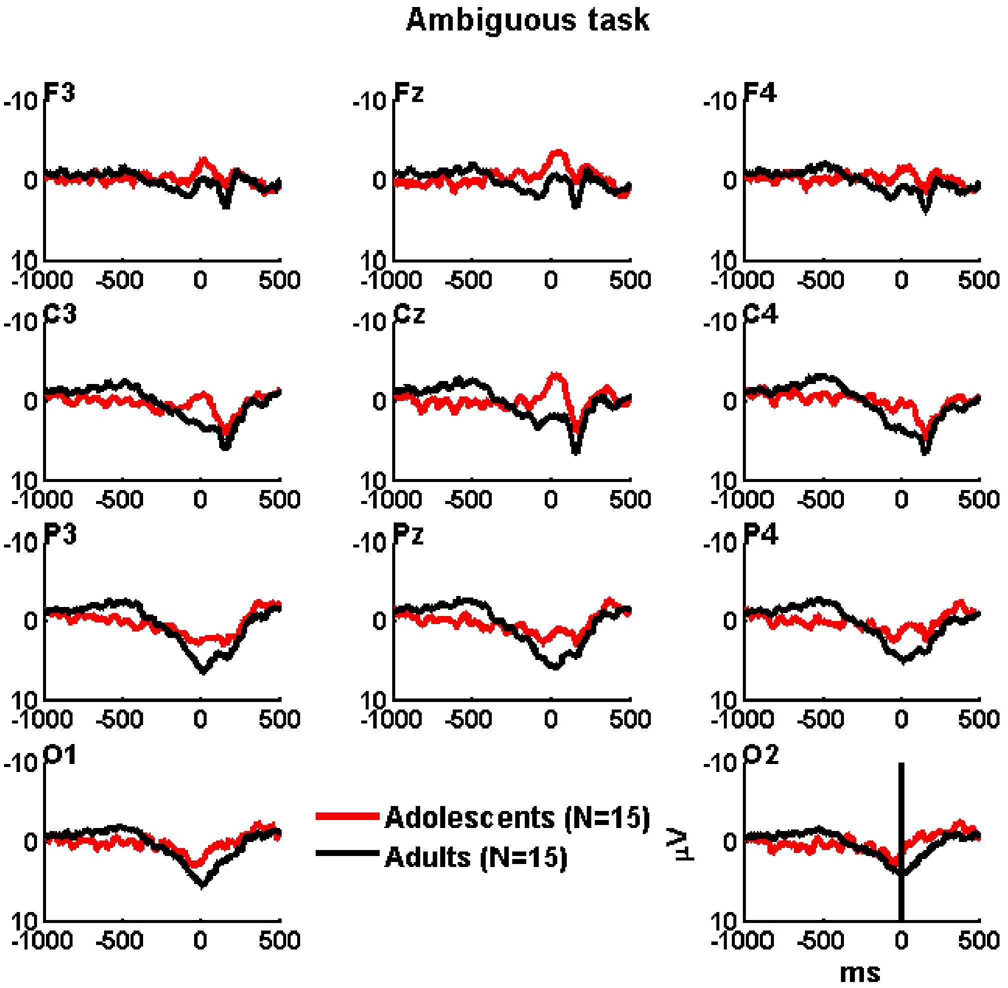


Figure 6.3.: Grand averages of the EEG activity of the *switching* condition in the *ambiguous* task filtered in the range of 0.5 – 48 Hz. Red: *adolescents* (N = 15); Black: *adults* (N = 15). Abscissa: time in ms. Ordinate: amplitude in µV. The vertical arrow marks the button press (t = 0).

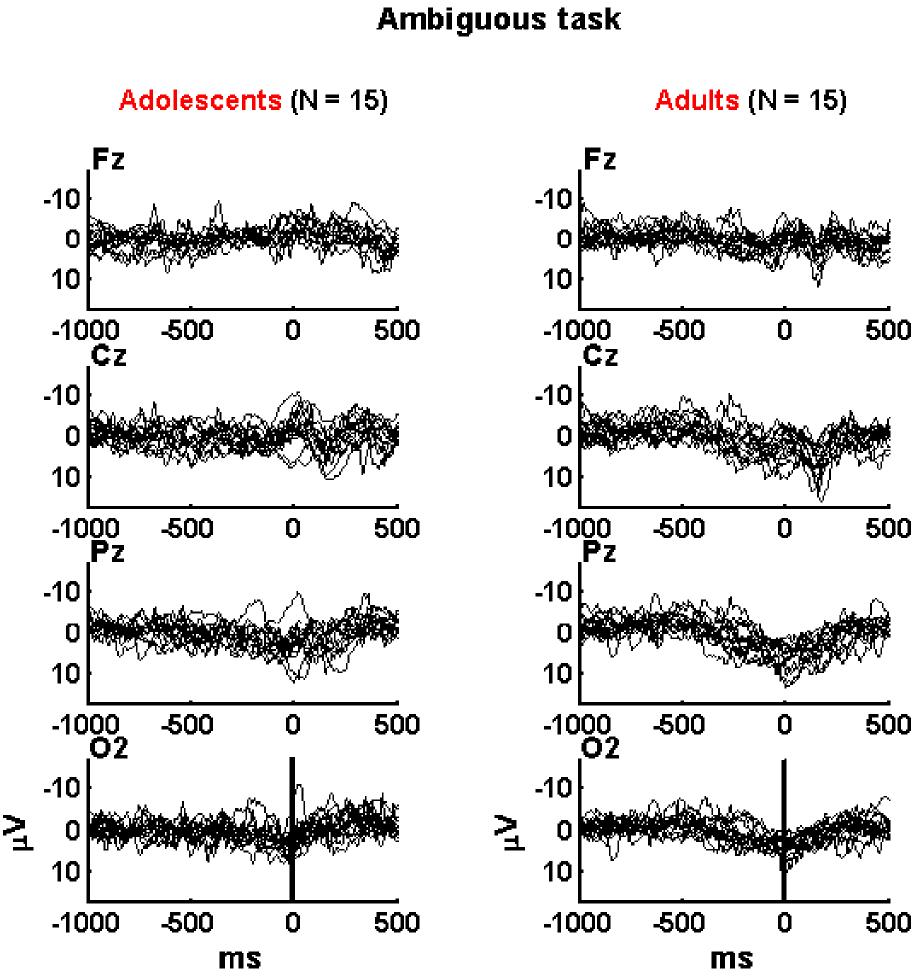


Figure 6.4.: The single participant averages of the EEG activity of the *switching* condition in the *ambiguous* task filtered in the range of 0.5 – 48 Hz for the groups of *adolescents* (N = 15) and *adults* (N = 15). Abscissa: time in ms. Ordinate: amplitude in μV. The vertical arrow marks the button press (t = 0).

Ambiguous task: the switching-related enhancement of single trial activity in the δ, θ and γ frequency bands

The distribution of the *switching-related* enhancement of single trial activity in the δ, θ and γ bands at the midline electrodes for both groups is shown in Fig. 6.5 (a) and Fig. 6.6 (a). The head maps in Fig. 6.5 (b) and Fig. 6.6 (b) depict the topographical distribution of the *switching-related* enhancement for the δ, θ and γ bands in the time windows used for the statistical analysis.

6.2.2.1.1. δ band

For the *ambiguous* task, the enhancement ratio of the single trial δ activity during the *switching* periods compared to the *non-switching* periods was found to be lower in the group of *adolescents* compared to the *adults* group (see Fig. 6.11 (a), left), as indicated by a significant main effect of GROUP ($F(1,28) = 6.61$, $p = .016$, $\eta^2 = .19$).

6.2.2.1.2. θ band

Also, the switching-related enhancement of θ activity in the ambiguous task was less pronounce in the group of *adolescents* than in the *adults* group (see Fig. 6.11 (b), left), as shown by a significant main effect of GROUP ($F(1,28) = 5.93$, $p = .022$, $\eta^2 = .18$).

6.2.2.1.3. γ band

An interaction effect of GROUP × ROI ($F(3,84) = 12.26$, $p = .000$, $\eta^2 = .31$) was found to be significant in the γ band (see Fig. 6.11 (c), left). The post-hoc tests showed that the *switching-related* enhancement was larger over frontal and central regions in the group of *adults* compared to the *adolescents* ($p < .001$ and $p < .05$, respectively).

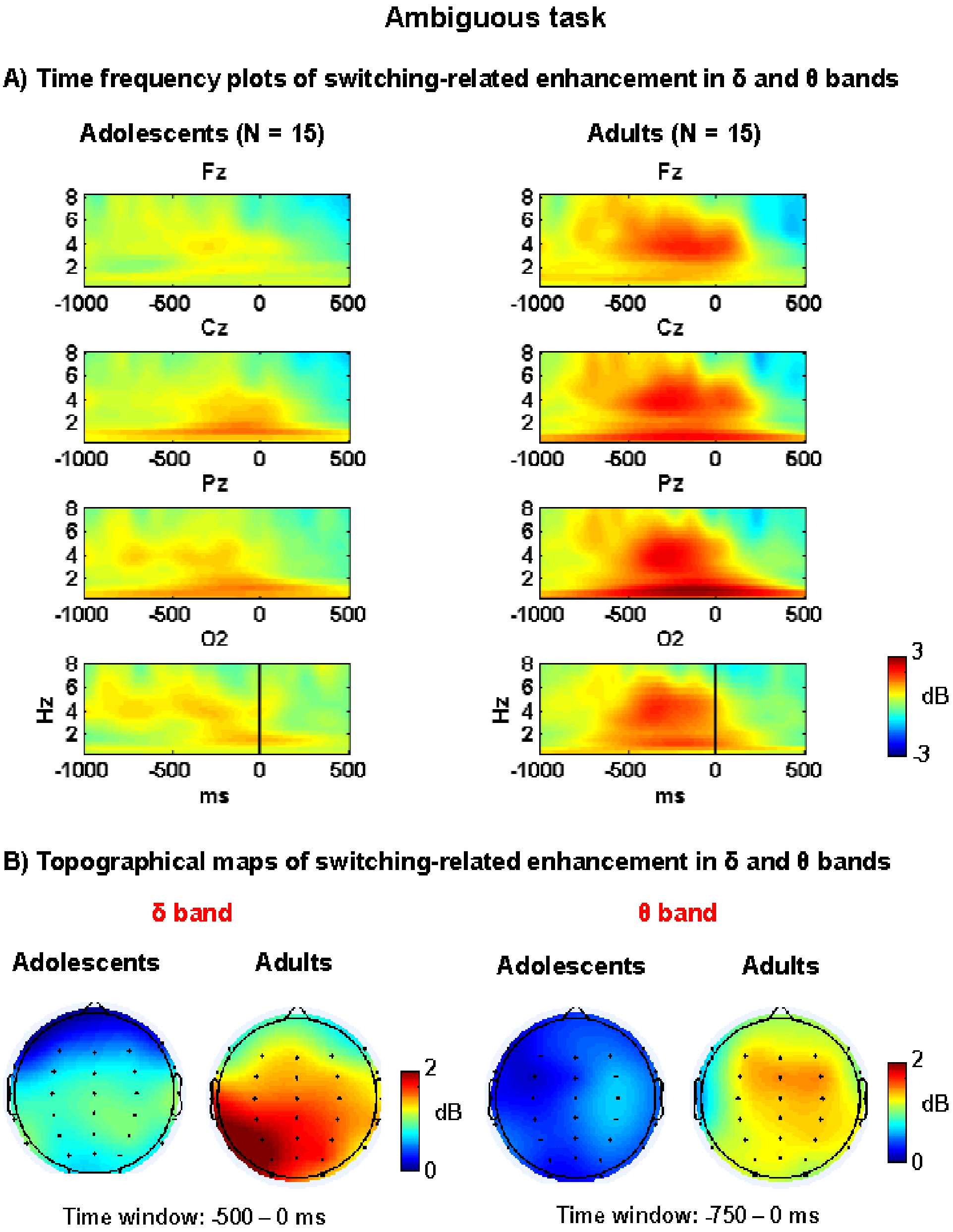


Figure 6.5.: a) Time-frequency plots of the *switching-related* enhancement in the δ and θ bands at the Fz, Cz, Pz and O2 electrodes for *adolescents* (N = 15) and *adults* (N = 15). Abscissa: time in ms. Ordinate: enhancement ratio in dB. The vertical arrow marks the button press (t = 0). b) Topographic head maps of mean values of the *switching-related* enhancement in the time windows used for statistical analysis in the δ and θ bands.

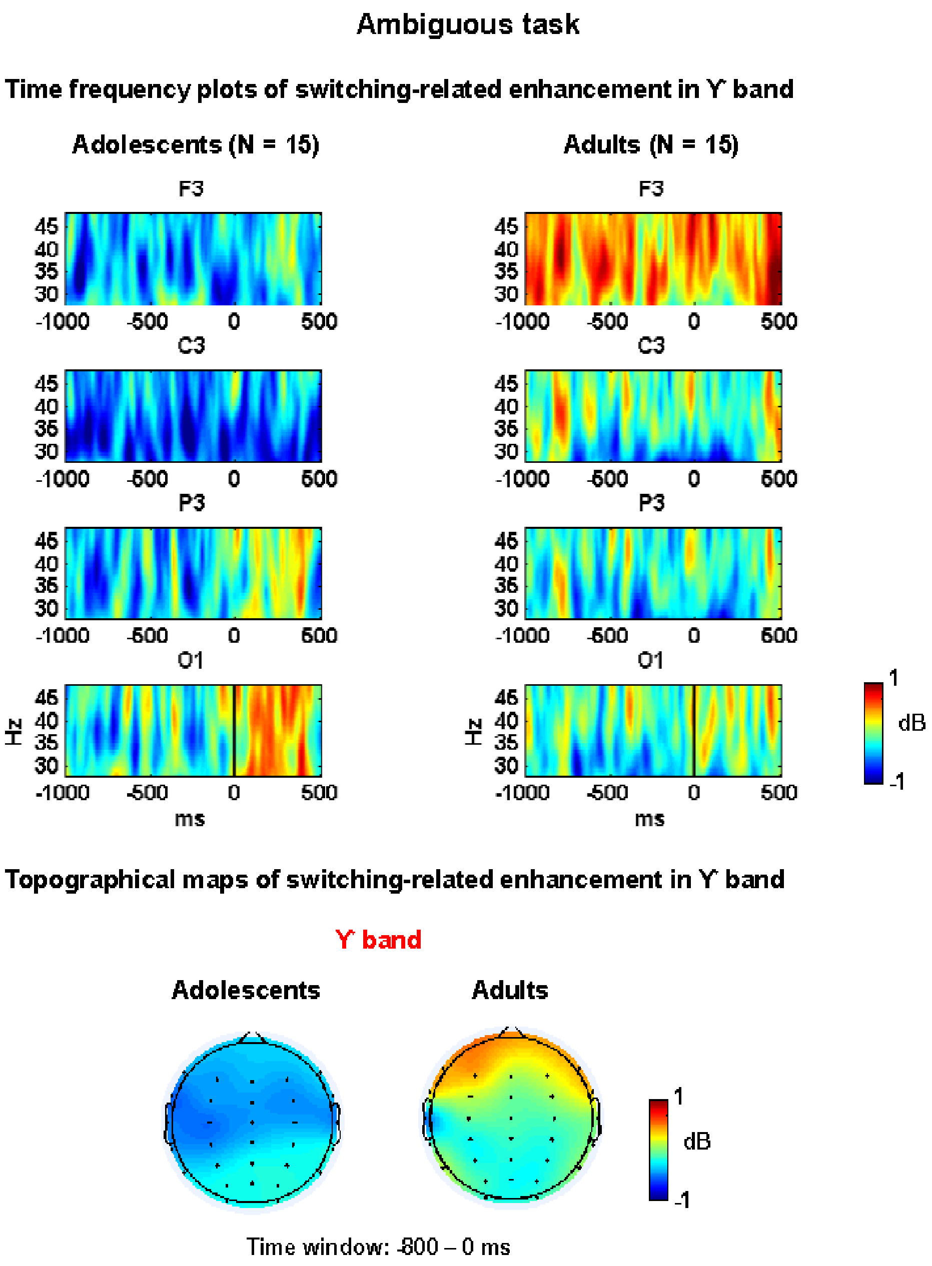


Figure 6.6.: a) Time-frequency plots of the *switching-related* enhancement in the γ band at the F3, C3, P3 and O1 electrodes for *adolescents* (N = 15) and *adults* (N = 15). Abscissa: time in ms. Ordinate: enhancement ratio in dB. The vertical arrow marks the button press (t = 0). b) Topographic head maps of mean values of the *switching-related* enhancement in the time windows used for statistical analysis in the γ band.

6.2.2.2. Unambiguous task

The grand averages of the EEG activity in the *switching* condition filtered in the range of $0.5 - 48\,\mathrm{Hz}$ as well as the single participant averages for both groups during the *unambiguous* task are shown in Fig. 6.7 and Fig. 6.8, respectively.

The switching-related activity can be detected in the groups of interest in both, the grand averages and the single participant averages, particularly over parietal and occipital regions. At almost all regions, the grand averages as well as the single participants averages of the groups seem to have a comparable amplitude deflection size and resemble in their topography the switching-related activity during the ambiguous task.

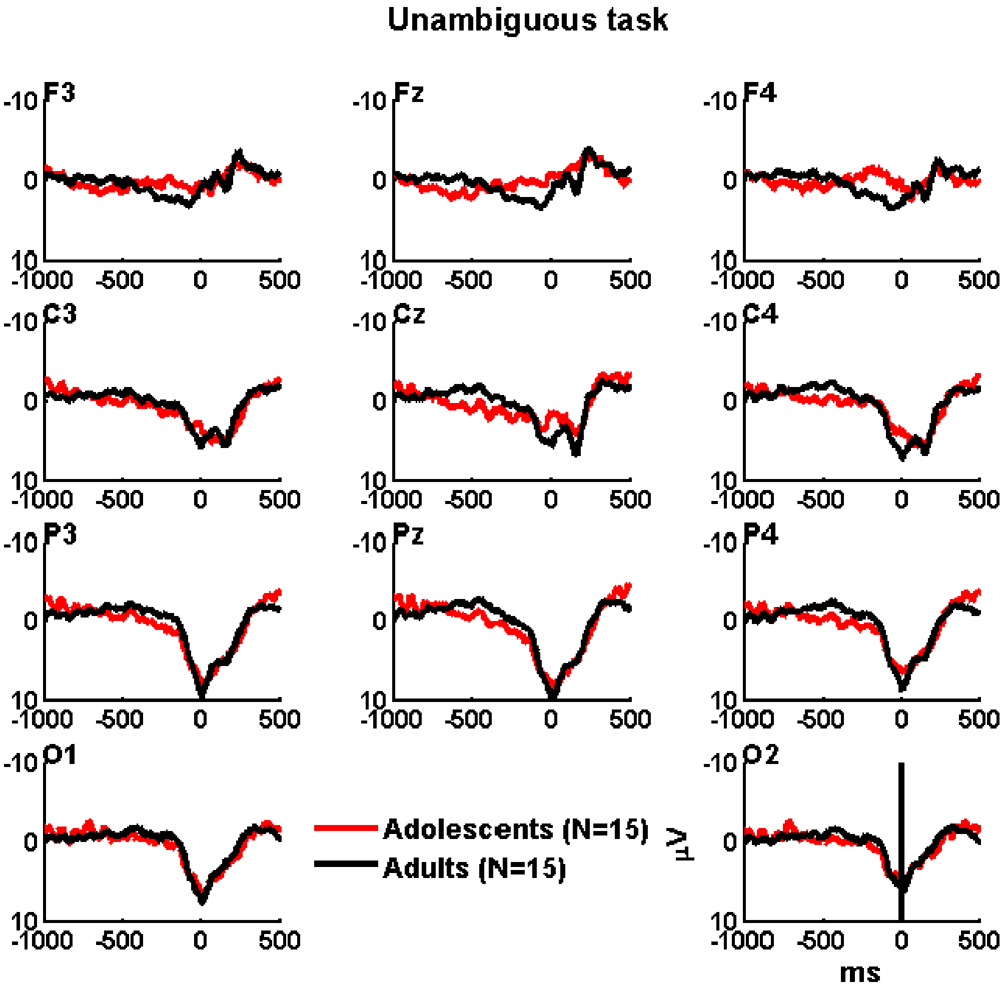


Figure 6.7.: Grand averages of the EEG activity in the *switching* condition in the *unambiguous* task filtered in the range of 0.5 – 48 Hz. Red: *adolescents* (N = 15); Black: *adults* (N = 15). Abscissa: time in ms. Ordinate: amplitude in µV. The vertical arrow marks the button press (t = 0).

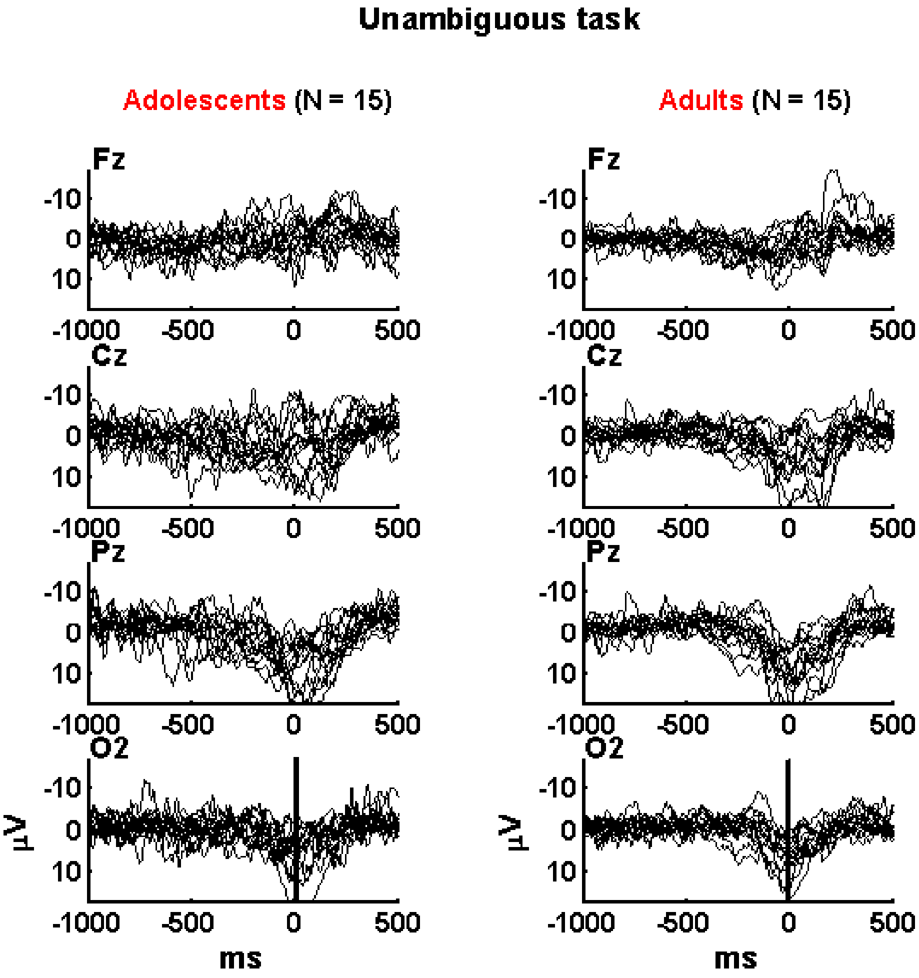


Figure 6.8.: The single participant averages of the EEG activity of the *switching* condition during the *unambiguous* task filtered in the range of 0.5 – 48 Hz for the groups of *adolescents* (N = 15) and *adults* (N = 15). Abscissa: time in ms. Ordinate: amplitude in µV. The vertical arrow marks the button press (t = 0).

Unambiguous task: the switching-related enhancement of single trial activity in the δ, θ and γ frequency bands

The distribution of the *switching-related* enhancement of single trial activity in the δ, θ and γ bands at the midline electrodes for both groups is shown in Fig. 6.9 (a) and Fig. 6.10 (a). The head maps in Fig. 6.9 (b) and Fig. 6.10 (b) depict the topographical distribution of the switching-related enhancement of single trial activity in the δ, θ and γ bands in the time windows used for the statistical analysis.

6.2.2.2.1. δ band

For the *unambiguous* task, the enhancement of the single trial δ activity during the *switching* periods compared to the *non-switching* periods was found to be lower in the group of *adolescents* compared to the *adults* group (see Fig. 6.11 (a), right), as indicated by a significant main effect of GROUP ($F(1,28) = 5.16$, $p = .031$, $\eta^2 = .16$). Furthermore, the *switching-related* enhancement had a centro-parietal maximum, as shown by a significant main effect of ROI ($F(3,84) = 5.94$, $p = .011$, $\eta^2 = .18$). Post-hoc tests revealed that the *switching-related* enhancement was larger at parietal and central regions compared to the frontal ones ($p < .05$ for all comparisons). Furthermore, a significant interaction GROUP × ROI effect ($F(3,84) = 3.70$, $p = .047$, $\eta^2 = .12$) indicated that the switching-related ratio was larger in the group of *adults* compared to the *adolescents* at parietal and occipital regions ($p < .05$ and $p < .005$, respectively).

6.2.2.2.2. θ band

The *switching-related* enhancement of the single trial theta activity during the *unambiguous* task was found to have a fronto-centro-parietal maximum (see Fig. 6.11 (b), right), as shown by a significant main effect of ROI ($F(3,84) = 8.27$, $p = .001$, $\eta^2 = .23$). Follow-up post-hoc tests indicated that the switching-related enhancement was more pronounced at frontal, central and parietal regions compared to the occipital ones ($p < .05$, $p < .005$, $p < .001$).

6.2.2.2.3. γ band

No significant results were found for the gamma band.

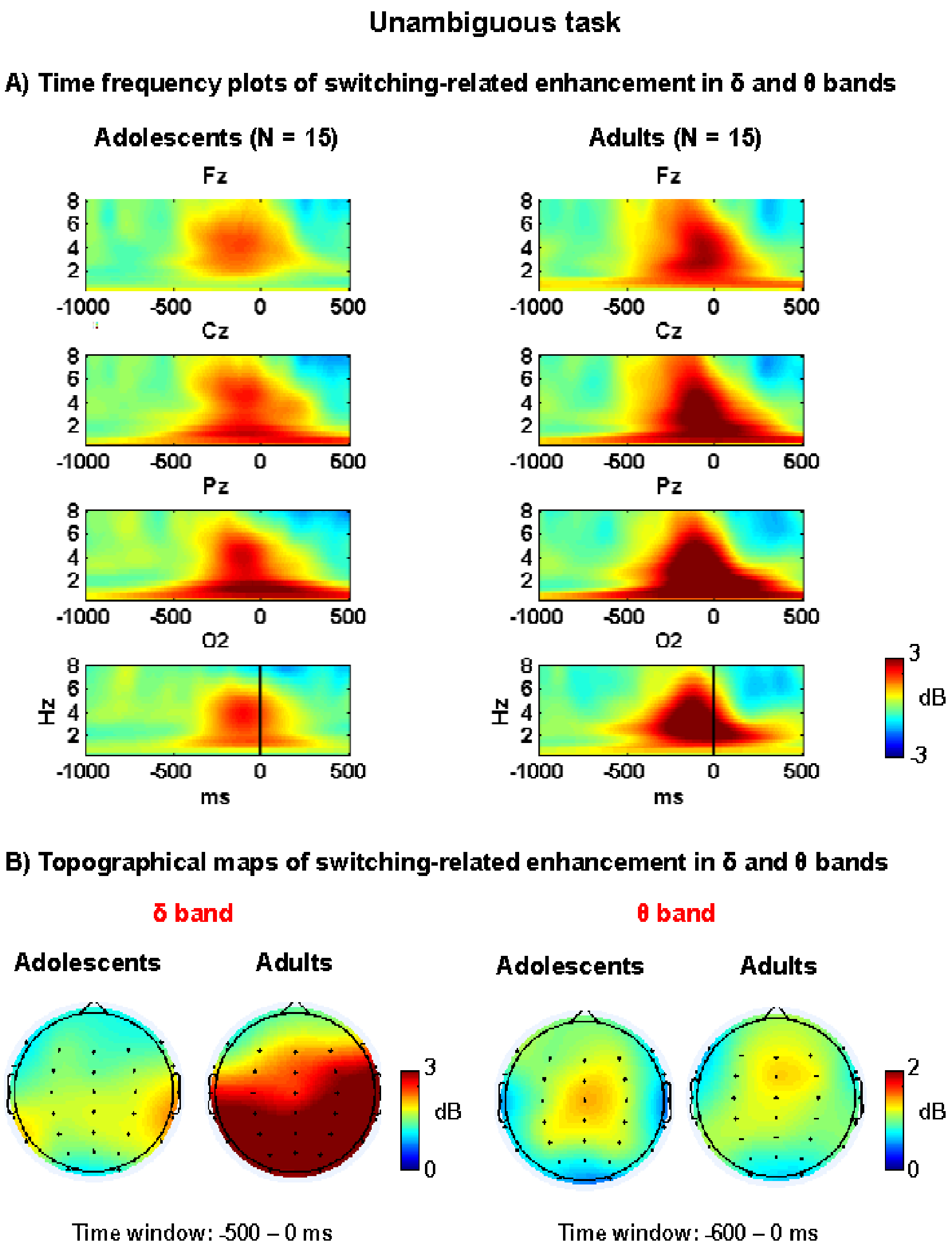
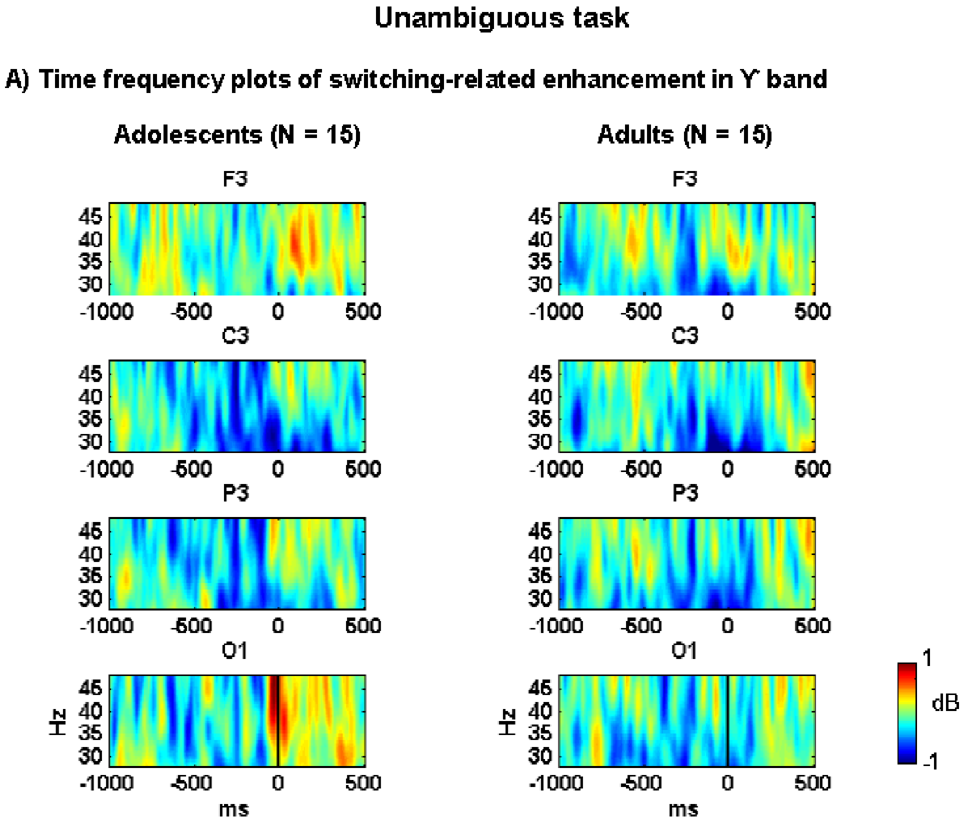


Figure 6.9.: a) Time-frequency plots of the *switching-related* enhancement in the δ and θ bands at the Fz, Cz, Pz and O2 electrodes for *adolescents* (N = 15) and *adults* (N = 15). Abscissa: time in ms. Ordinate: enhancement ratio in dB. The vertical arrow marks the button press (t = 0). b) Topographic head maps of mean values of the *switching-related* enhancement in the time windows used for statistical analysis in the δ and θ bands.



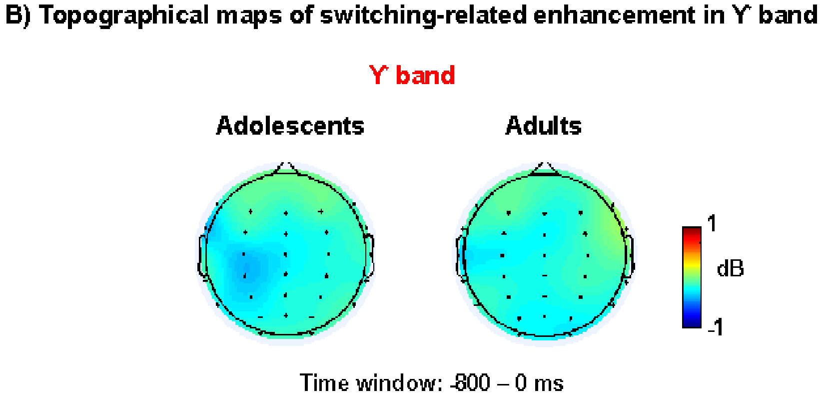


Figure 6.10.: a) Time-frequency plots of the *switching-related* enhancement in the γ band at the F3, C3, P3 and O1 electrodes for *adolescents* (N = 15) and *adults* (N = 15). Abscissa: time in ms. Ordinate: enhancement ratio in dB. The vertical arrow marks the button press (t = 0). b) Topographic head maps of mean values of the *switching-related* enhancement in the time windows used for statistical analysis in the γ band.

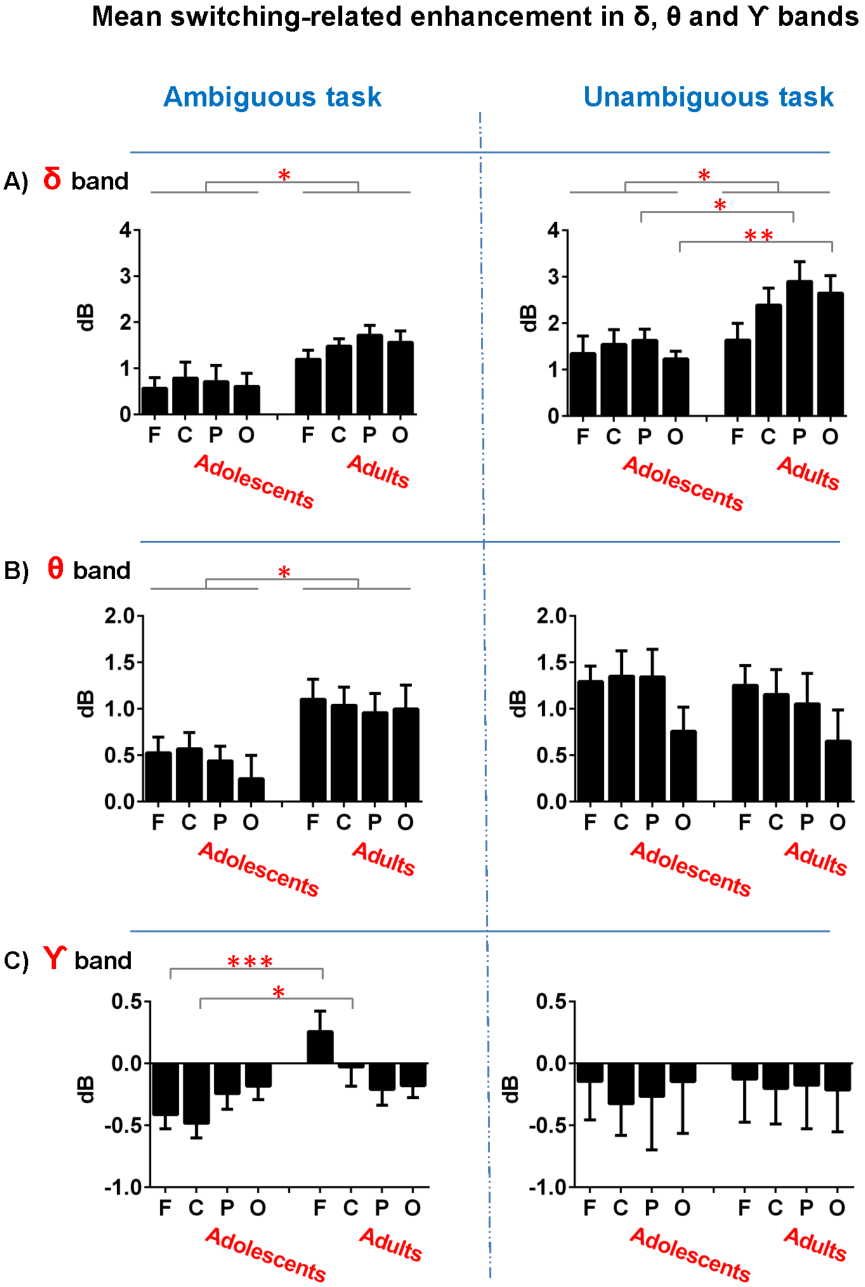


Figure 6.11.: Mean values of the *switching-related* enhancement for the *ambiguous* and *unambiguous* tasks for *adolescents* (N = 15) and *adults* (N = 15) in the (a) δ, (b) θ and (c) γ bands. Abscissa: mean enhancement values in dB. Ordinate: regions of interest (**F** = frontal, **C** = central, **P** = parietal, **O** = occipital). The error bar indicates the standard error. Asterisks indicate the significance niveau: * p≤.05, ** p≤.01, *** p≤.001. For the sake of simplicity, only groups and main interaction effects are shown.

6.2.2.3. Visual oddball task

The grand averages of the EEG activity of the *target* and *non-target* conditions filtered in the range of $0.5 - 48$ Hz as well as single participant averages for both groups during the *visual oddball* task are shown in Fig. 6.12, Fig. 6.14, Fig. 6.13 and Fig. 6.15, respectively.

A broad positive amplitude deflection with a maximum at 500 ms after the *target* onset can be detected in both groups, particularly over central, parietal and occipital regions. No clear distinctions between the groups can be detected at these regions in neither the grand averages nor the single participant averages. For both groups, the positive amplitude deflection is less pronounced at the frontal regions and is furthermore smaller in the group of *adolescents* compared to the group of *adults*.

A similar but less pronounced amplitude deflection peak at about 400 ms after the *non-target* onset can be detected at all regions in both groups. No clear distinctions reflected by this broad amplitude deflection can be detected between groups. The groups appear to differ only in the short positive amplitude deflection peak at about 100 ms after the *non-target* onset. Namely, the short amplitude deflection seems to be larger in the group of *adolescents* compared to the *adults*.

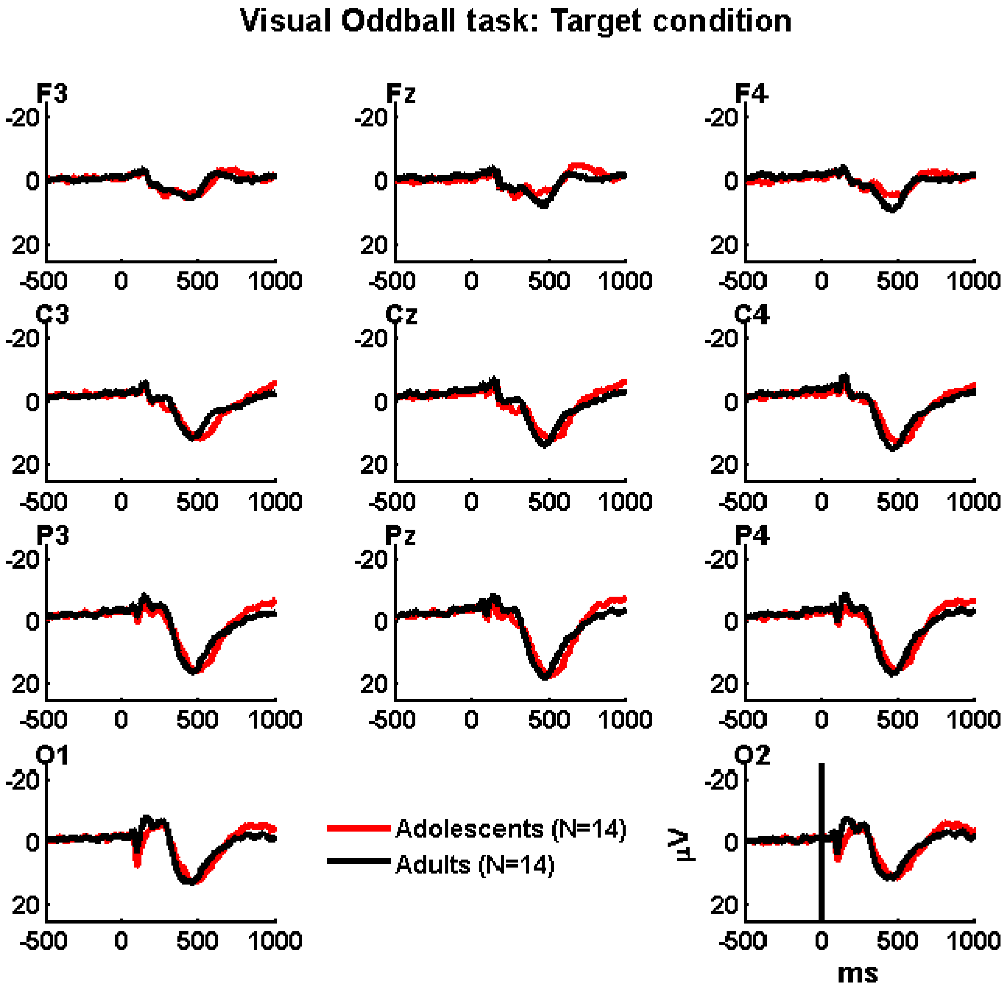


Figure 6.12.: Grand averages of the EEG activity in the *target* condition in the *visual oddball* task filtered in the range of $0.5 - 48\,\mathrm{Hz}$. Red: *adolescents* $(\mathrm{N} = 14)$; Black: *adults* $(\mathrm{N} = 14)$. Abscissa: time in ms. Ordinate: amplitude in µV. The vertical arrow marks the target onset $(\mathrm{t} = 0)$.

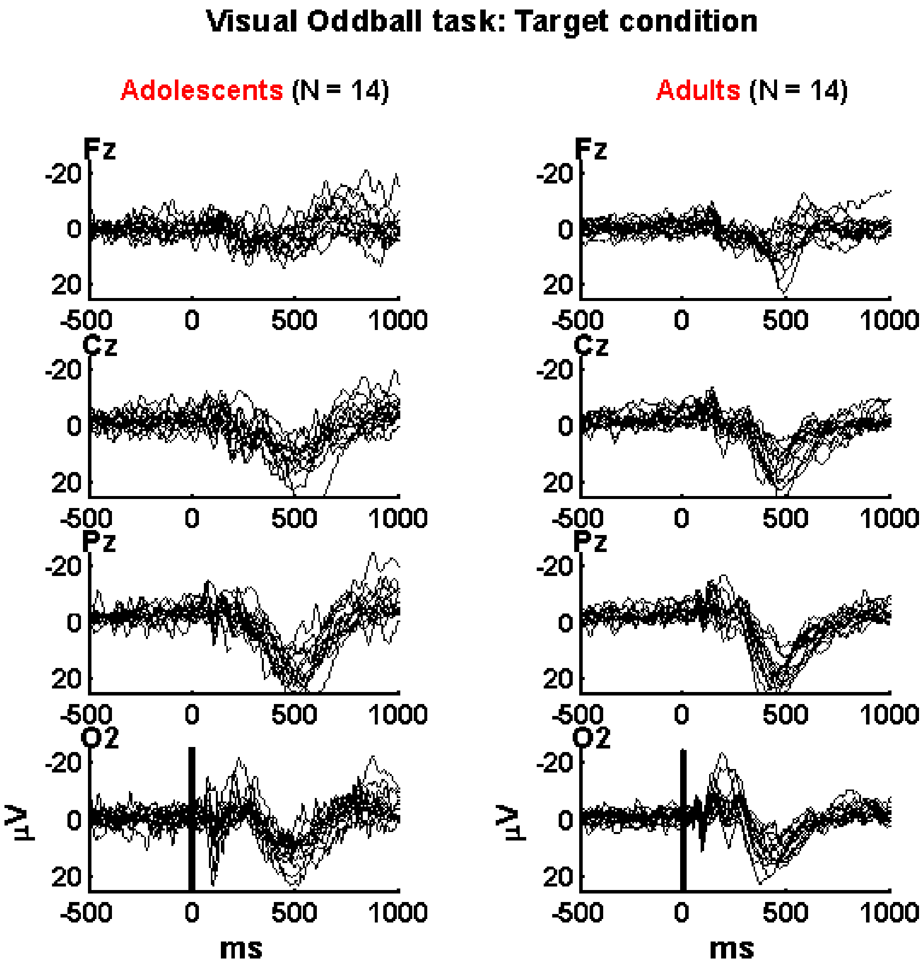


Figure 6.13.: The single participant averages of the EEG activity in the *target* condition in the *visual oddball* task filtered in the range of 0.5 – 48 Hz for the groups of *adolescents* (N = 14) and *adults* (N = 14). Abscissa: time in ms. Ordinate: amplitude in µV. The vertical arrow marks the target onset (t = 0).

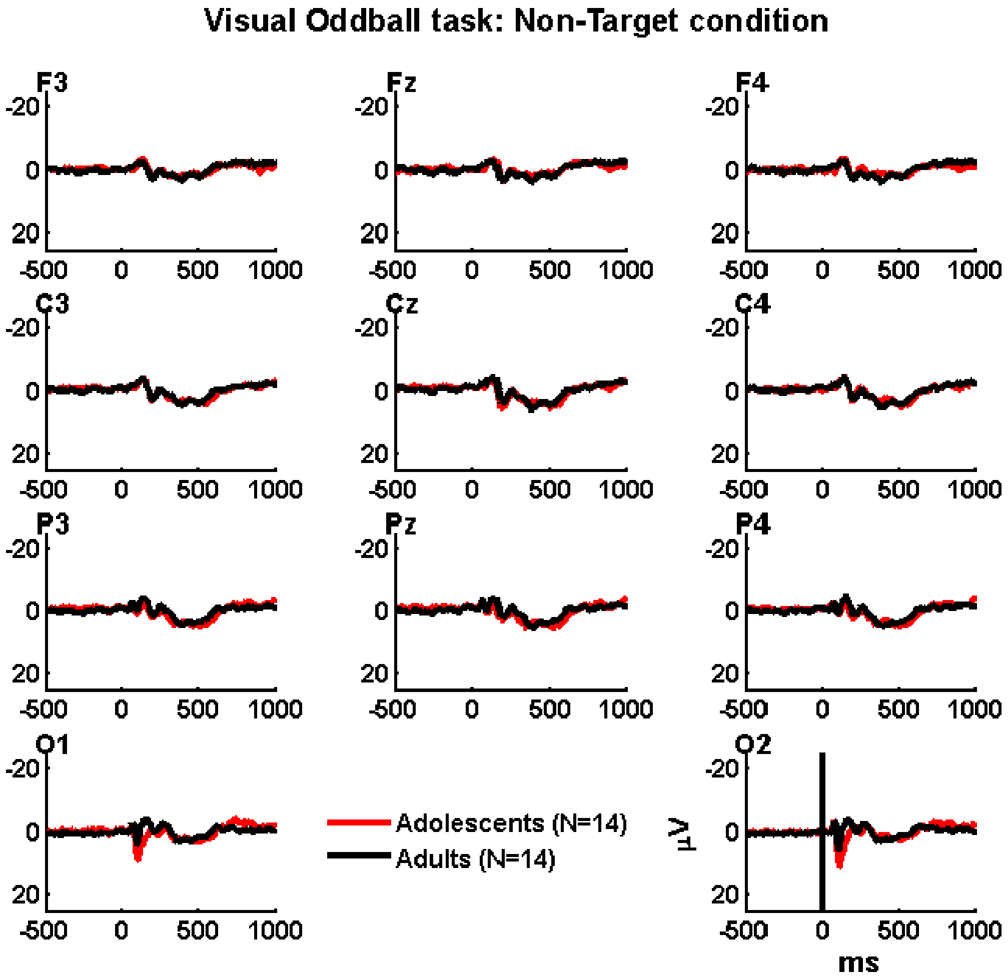


Figure 6.14.: Grand averages of the EEG activity in the *non-target* condition in the *visual oddball* task filtered in the range of $0.5 - 48\,\text{Hz}$. Red: *adolescents* ($N = 14$); Black: *adults* ($N = 14$). Abscissa: time in ms. Ordinate: amplitude in μV. The vertical arrow marks the non-target onset ($t = 0$).

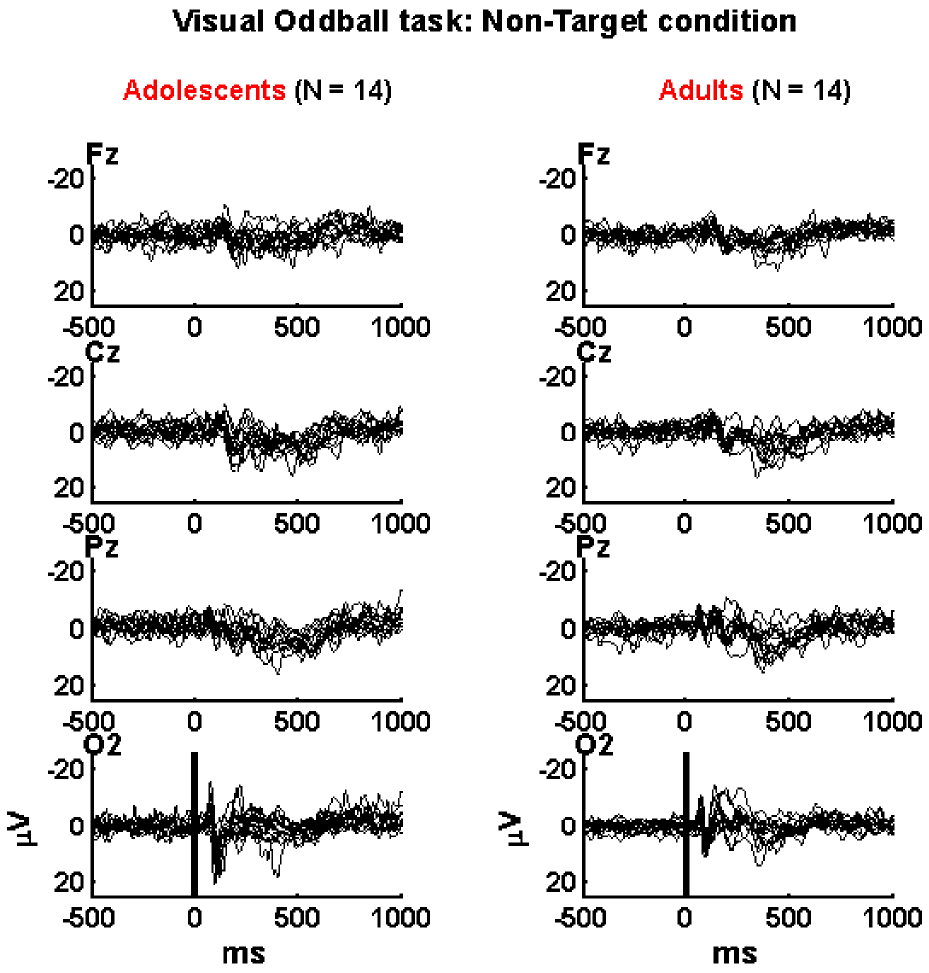


Figure 6.15.: The single participant averages of the EEG activity in the *non-target* condition in the *visual oddball* task filtered in the range of 0.5 – 48 Hz for the groups of *adolescents* (N = 14) and *adults* (N = 14). Abscissa: time in ms. Ordinate: amplitude in μV. The vertical arrow marks the non-target onset (t = 0).

Visual oddball task: task-related enhancement of single trial activity in the δ, θ and γ frequency bands

The distribution of the *target-related* enhancement of single trial activity in the δ, θ and γ bands at the midline electrodes for both groups is shown in Fig. 6.16 (a) and Fig. 6.18 (a). The head maps in Fig. 6.16 (b) and Fig. 6.18 (b) depict the topographical distribution of the target-related enhancement of the single trial activity in the δ, θ and γ bands in the time windows used for the statistical analysis. The distribution of *non-target-related* enhancement for the frequency bands of interest is shown in Fig. 6.17 and Fig. 6.19.

6.2.2.3.1. δ band

In the *late* time window ($300 - 700\,\text{ms}$) after stimulus onset, the overall enhancement of the task-related single-trial δ activity was found to be more pronounced in the group of *adults* compared to the *adolescents* group (Fig. 6.20 (a), right), as shown by a significant main effect GROUP ($F(1, 26) = 4.74$, $p = .039$, $\eta^2 = .15$). The target-related enhancement was found to be significantly larger than the enhancement caused by processing of non-targets, as indicated by a main effect of the factor CONDITION ($F(1, 26) = 96.59$, $p = .000$, $\eta^2 = .79$). The overall enhancement of the event-related δ activity in the late time window was found to have a parietal maximum, as indicated by a significant main effect of ROI ($F(3, 78) = 21.58$, $p = .000$, $\eta^2 = .45$). Post-hoc comparisons showed that the enhancement of the task-related activity was larger at parietal compared to all other regions of interest ($p < .01$). Furthermore, a significant interaction CONDITION × ROI effect ($F(3, 84) = 9.57$, $p = .000$, $\eta^2 = .27$) indicated that the target-related enhancement of δ activity was larger in both groups compared to the non-target enhancement at all regions of interest ($p < .001$ for all comparisons).

6.2.2.3.2. θ band

In the early time window ($0 - 150\,\text{ms}$), the overall enhancement of the event-related θ activity was found to have an occipital maximum, as indicated by a significant main effect of ROI ($F(3, 78) = 7.48$, $p = .002$, $\eta^2 = .22$). Post-hoc tests showed that the overall enhancement of θ activity was larger at occipital compared to fronto-central

($p < .05$) as well as parietal ($p < .01$) regions of interest. A significant interaction effect of GROUP × CONDITION × ROI ($F(3, 78) = 4.49$, $p = .021$, $\eta^2 = .15$) indicated that the event-related enhancement caused by target stimuli was larger compared to the enhancement caused by non-target stimuli at the occipital regions only in the group of *adults* ($p < .05$) (see Fig. 6.20 (b), left).

In the late time window ($300 - 700$ ms), the event-related enhancement of θ activity was found to be more pronounce in the group of *adults* compared to the *adolescents* group, as reflected by a significant main effect of the factor GROUP ($F(1, 26) = 6.50$, $p = .017$, $\eta^2 = .20$). The target-related enhancement was found to be significantly larger than the enhancement caused by processing of non-targets, as indicated by a main effect of the factor CONDITION ($F(1, 26) = 14.99$, $p = .001$, $\eta^2 = .37$). Furthermore, the overall enhancement of the event-related θ activity was larger at anterior compared to posterior brain regions, as shown by a significant main effect ROI ($F(3, 78) = 10.12$, $p = .000$, $\eta^2 = .28$). Post-hoc comparisons showed that the event-related enhancement of θ activity was more notable at frontal, central and parietal regions compared to the occipital ones ($p < .05$ for all comparisons).

6.2.2.3.3. γ band

In the early time window ($0 - 150$ ms), no significant differences were detected.

In the late time window ($300 - 700$ ms), the target-related enhancement of the single-trial γ activity was found to be significantly larger than the enhancement caused by processing of non-targets, as indicated by a main effect of the factor CONDITION ($F(1, 26) = 5.12$, $p = .032$, $\eta^2 = .16$). Furthermore, the overall enhancement of the event-related γ activity was larger at anterior compared to posterior brain regions, as shown by a significant main effect ROI ($F(3, 78) = 9.99$, $p = .000$, $\eta^2 = .28$). Post-hoc comparisons showed that the event-related enhancement of γ activity was more notable at frontal, central and parietal regions compared to the occipital ones ($p < .01$ for all comparisons).

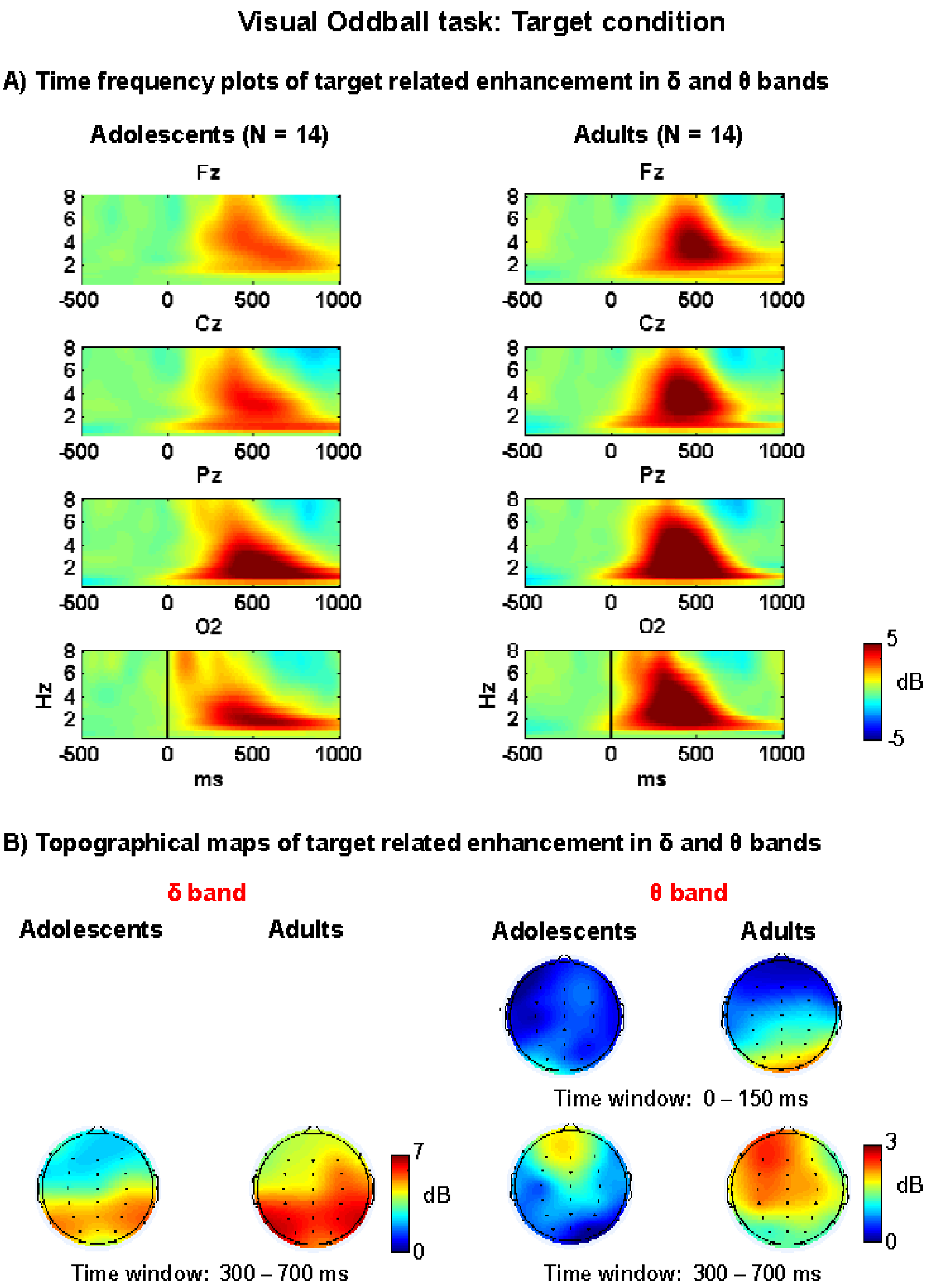


Figure 6.16.: a) Time-frequency plots of the *target-related* enhancement in the δ and θ bands at the Fz, Cz, Pz and O2 electrodes for *adolescents* (N = 15) and *adults* (N = 15). Abscissa: time in ms. Ordinate: enhancement ratio in dB. The vertical arrow marks the target onset (t = 0). b) Topographic head maps of mean values of the *target-related* enhancement in the time windows used for statistical analysis in the δ and θ bands.

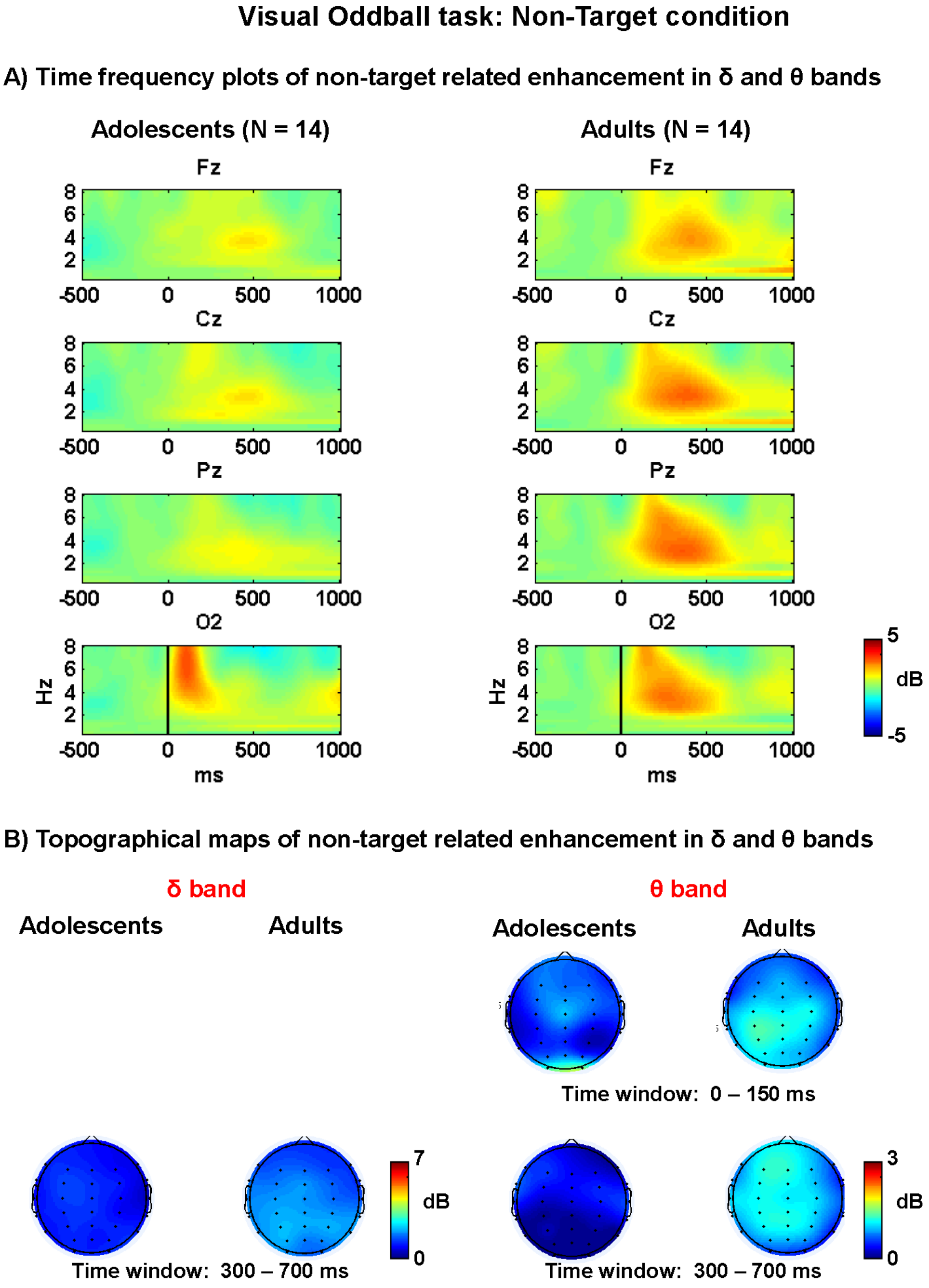


Figure 6.17.: a) Time-frequency plots of the *non-target-related* enhancement in the δ and θ bands at the Fz, Cz, Pz and O2 electrodes for *adolescents* (N = 15) and *adults* (N = 15). Abscissa: time in ms. Ordinate: enhancement ratio in dB. The vertical arrow marks the non-target onset (t = 0). b) Topographic head maps of mean values of the *non-target-related* enhancement in the time windows used for statistical analysis in the δ and θ bands.

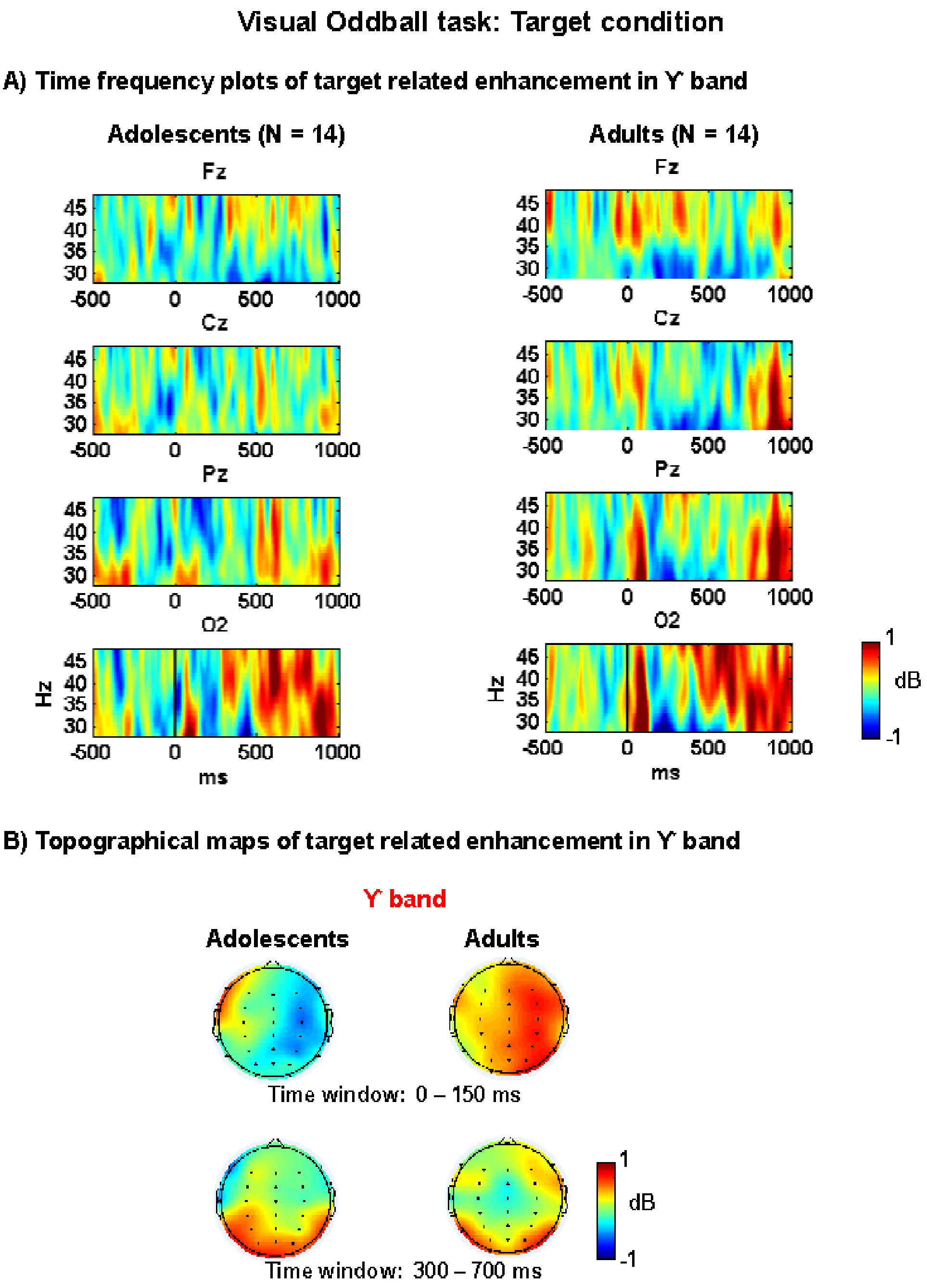


Figure 6.18.: a) Time-frequency plots of *target-related* enhancement in the γ band at the Fz, Cz, Pz and O2 electrodes for *adolescents* (N = 14) and *adults* (N = 14). Abscissa: time in ms. Ordinate: enhancement ratio in dB. The vertical arrow marks the target onset (t = 0). b) Topographic head maps of mean values of the *target-related* enhancement in the time windows used for statistical analysis in the γ band.

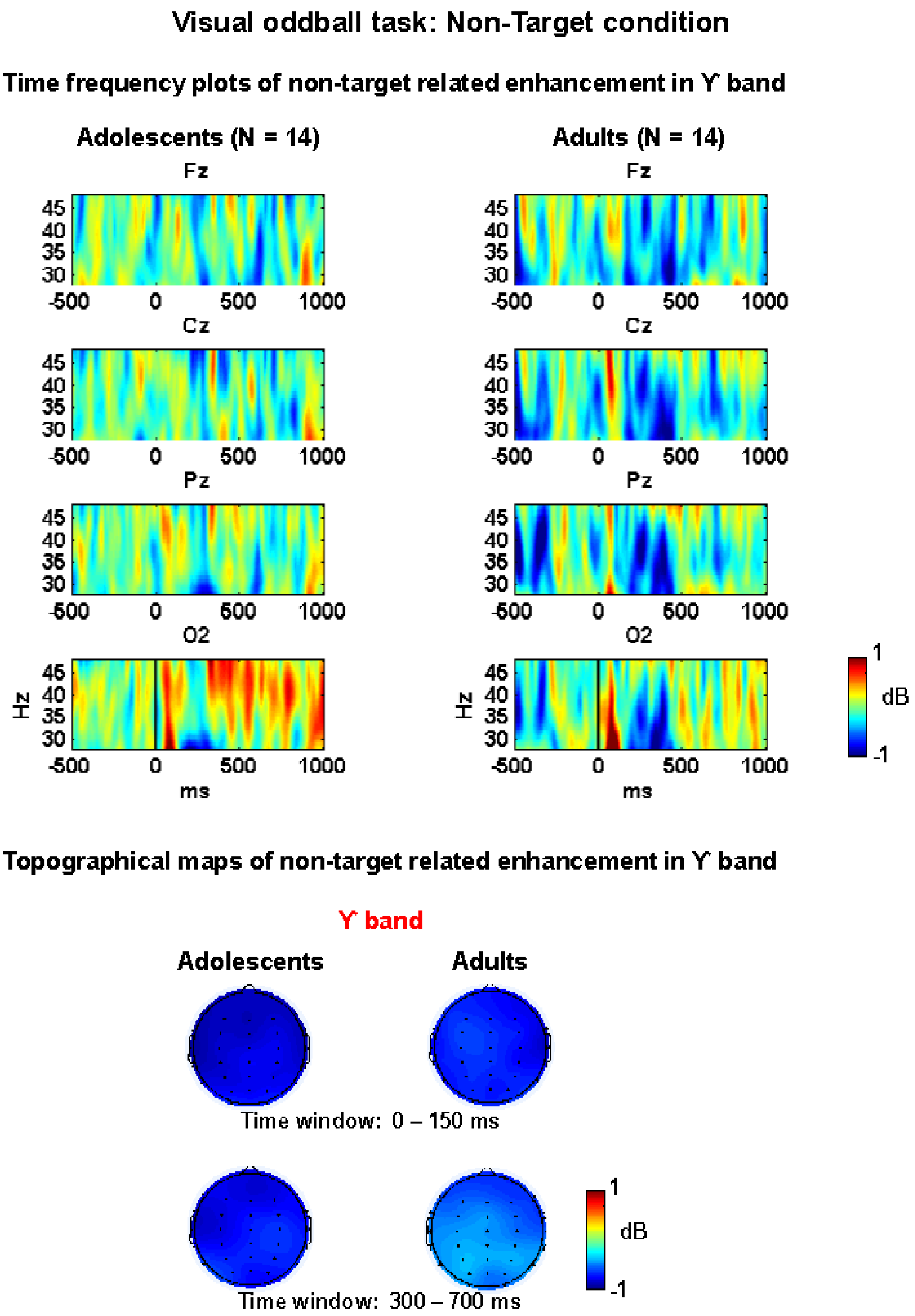


Figure 6.19.: a) Time-frequency plots of the *non-target-related* enhancement in the γ band at the Fz, Cz, Pz and O2 electrodes for *adolescents* (N = 15) and *adults* (N = 15). Abscissa: time in ms. Ordinate: enhancement ratio in dB. The vertical arrow marks the non-target onset (t = 0). b) Topographic head maps of mean values of the *non-target-related* enhancement in the time windows used for statistical analysis in the γ band.

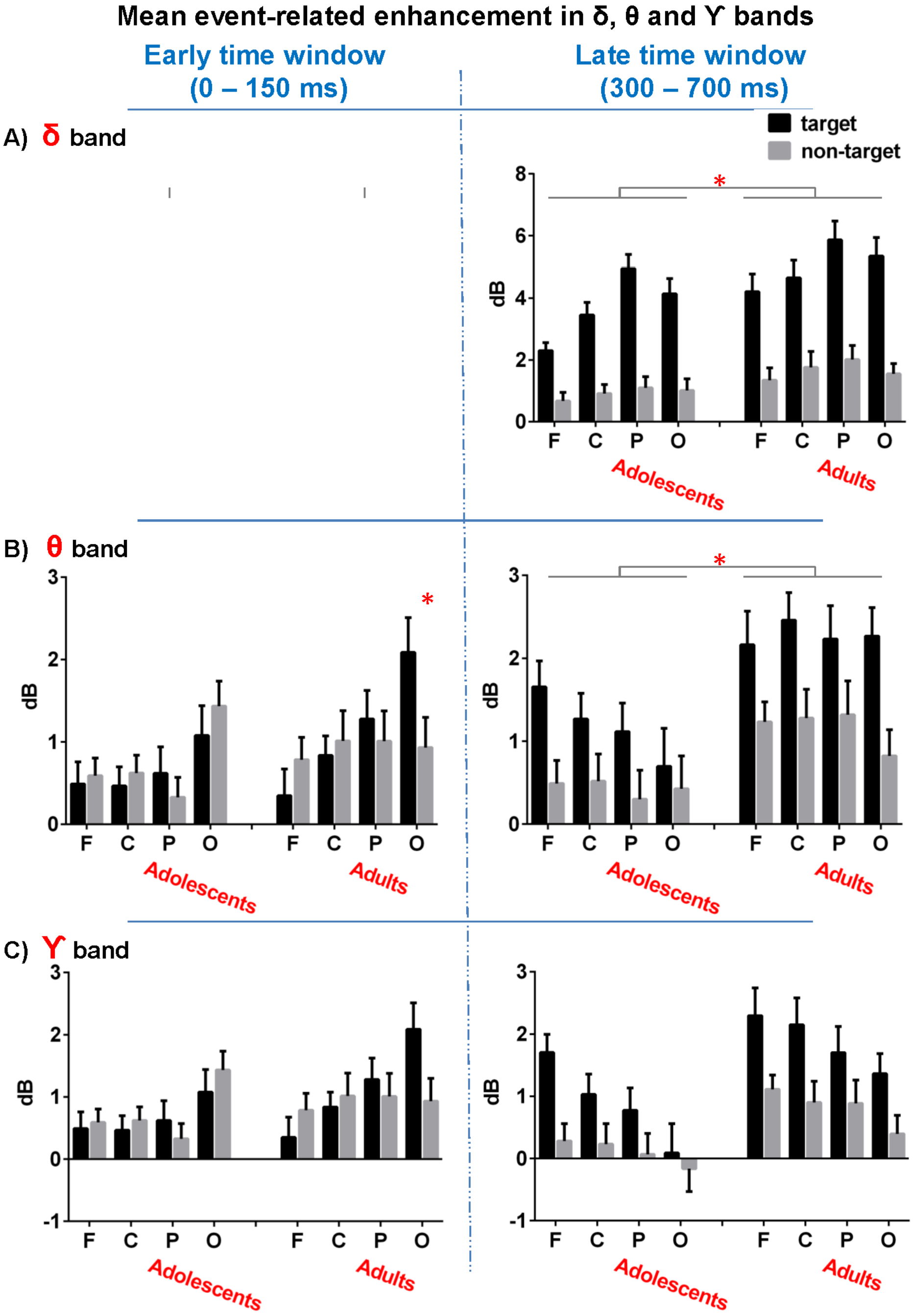


Figure 6.20.: Mean values of the *event-related* enhancement during the *visual oddball* task for *adolescents* (N = 14) and *adults* (N = 14) in the (a) δ, (b) θ and (c) γ bands. Abscissa: mean enhancement values in dB. Ordinate: regions of interest (**F** = frontal, **C** = central, **P** = parietal, **O** = occipital). The error bar indicates the standard error. Asterisks indicate the significance niveau: * $p \leq .05$, ** $p \leq .01$, *** $p \leq .001$. For the sake of simplicity, only groups and main interaction effects are shown.

SECTION 7

Discussion

The present study investigated developmental changes in cognitive-correlates of brain oscillations in the δ, θ and γ frequency bands as well as during the resting state throughout adolescence. As expected, the present study found that δ and θ single-trial amplitudes decrease with age in resting state with open eyes and during prestimulus time periods. As opposed to this, task-related activities were found to increase with age, however, less strictly localized in *adolescents* than in *adults*. The γ activity during resting state, prestimulus intervals and also during more simple tasks as the unambiguous and visual oddball tasks did not depend on age. However, age-related changes were found during the ambiguous task. Interestingly, behavioral data of *adolescents* and *adults* did not differ, despite developmental changes found in the electrophysiological responses.

7.1. Behavioral results

7.1.1. Spontaneous reversal ability

In the present study, any previous experience with ambiguous figures in general was apparent only in the group of *adults*. However, both groups of participants were naive with respect to the ambiguous nature of the SAM pattern and the Necker cube used in the study. The ability to report the two possible interpretations of the ambiguous stimuli spontaneously was similar in the group of *adolescents* compared to *adults*, irrespective of the stimuli used.

This finding is contrary to the hypotheses of Rock *et al.* that in order to reverse a participant has to be aware of the ambiguous nature of the stimulus and to know its possible interpretations [Rock *et al.*, 1994b]. Our results may be more likely consistent with the hypothesis of Mitroff *et al.* that in order to experience reversals spontaneously, mental representation ability rather than prior knowledge about the ambiguous nature of the stimulus and its possible interpretations is required [Mitroff *et al.*, 2006]. The mental representation is defined as the ability to represent the representing relation itself [Perner, 1991]. The mental representation ability develops in 5 - 9 years old children [Mitroff *et al.*, 2006]. Moreover, the development of the mental representation correlates with the development of the ability to reverse spontaneously. In the present study, no difference on the spontaneous reversal ability was found between the groups of *adolescents* and *adults*. Therefore, our results indicate that the mental representation ability might be already developed in adolescents to the same extent as in adults.

Moreover, the spontaneous reversal ability seems to depend on the complexity of the stimulus. In the present study, almost all participants, irrespective of the age group, were able to spontaneously reverse the Necker cube and only approximately half of them were able to experience a perceptual reversal when exposed to the SAM pattern. This finding indirectly supports the assumption about the role of the mental representation ability in experiencing reversals. For more abstract stimuli such as the SAM pattern, it would be more difficult to represent the representing relation between the stimulus and its possible interpretations compared to less abstract stimuli.

7.1.2. Reversal rate for the ambiguous task

In the present study, the group of *adolescents* did not differ from the group of *adults* on the reversal rate (number of reversals per min) during the ambiguous task. Furthermore, the mean reversal rates per minute for both groups (*adolescents*: 8.2, *adults*: 6.8) are smaller compared to the mean reversal rates in the previous study of our group performed with children: The mean reversal rates obtained by Ehlers *et al.* were approx. 13.5 for the group of 11 years old children and approx. 23 for the group of adults [Ehlers *et al.*, in press]. Such different results may be explained by the fact that a mean reversal rate is characterized by a significant interindividual variation and considerable intraindividual stability. In the research history of the multistable phenomenon, the latter was investigated relatively early. In the study performed by Guilford and Hunt in 1931, participants were exposed to an ambiguous figure for three minutes and had to report perceptual reversals three times per day for six days. It was found that there were almost no intraindividual differences in the reversal rates, be it during one day as well as between days. Similar results were obtained by viewing of five different ambiguous figures [Eysenck, 1950]. Furthermore, the variation of the mean reversal rates over time within one individual was found to be significantly smaller than the variation of reversal rates within a group of participants [Guilford and Hunt, 1931]. These findings are likely to be robust and were replicated in later studies [Strüber and Stadler, 1999, Strüber *et al.*, 2000].

7.1.3. Reaction time and accuracy measures for the unambiguous and visual oddball tasks

In the present study, the groups did not differ on error rate or the mean reaction time during the unambiguous and visual oddball tasks. The variability of the individual reaction times was, however, found to be increased for the unambiguous task in the group of *adolescents* compared to the group of *adults*.

The result found on the variability of the individual reaction times is consistent with commonly reported reduction of variability of individual reaction times in childhood and adolescence [Dykiert *et al.*, 2012, Williams *et al.*, 2005, Williams *et al.*, 2007].

Furthermore, in their life span developmental study, Dykiert *et al.* found age-related differences of the variability of reaction times to correlate to the degree of difficulty in tasks. Namely, the variability was found to be more pronounced in more demanding tasks in children and adolescents compared to young adults, whereas it was nearly absent in less demanding tasks [Dykiert *et al.*, 2012]. Our results are in agreement with these findings, the variability of the individual reaction times was significantly increased in the group of *adolescents* only during the unambiguous task which was more complex compared to the visual oddball task.

7.2. EEG data

The theory of the whole-brain-work proposed by Basar postulates that "a brain system responds to external or internal stimuli with those rhythms or frequency components that are among its intrinsic (natural) rhythms [Basar, 2006]. Accordingly, if a given frequency range does not exist in its spontaneous activity, it will also be absent in the evoked activity." (Basar, 2006, p. 135). Furthermore, the author shows that the prestimulus oscillatory activity during task performance is the causal factor for the later brain responses reflected in the evoked activity.

The oscillatory activity undergoes maturational changes not only during the childhood but also later in adolescence until turning into the typical adult pattern. Therefore, evaluation of the spontaneous as well as of the prestimulus EEG activity allows to assess age-dependent maturational changes which can affect the brain responses related to task performance [Kolev *et al.*, 1994, Yordanova *et al.*, 2002, Yordanova and Kolev, 2009].

7.2.1. Age effects in δ, θ and γ frequency bands

7.2.1.1. Age effects during spontaneous EEG activity

According to the present results, the spontaneous single-trial activity in the δ and θ frequency bands was found to decrease with age, whereas no such tendency was found for the γ activity.

The decrease of the δ and θ activity during the spontaneous EEG activity in eyes-open condition is a general finding [Clarke *et al.*, 2001, Cragg *et al.*, 2011, Lüchinger *et al.*, 2011, Matousek and Petersen, 1973, Rodriguez-Martinez *et al.*, 2015, Segalowitz *et al.*, 2010]. While several works describe the decrease of developmental changes of low-frequency bands, little is known about developmental changes of the spontaneous γ activity. Recently, Tierney *et al.* examined the spontaneous γ activity over a wide range of ages (from 3 up to 38 years). The authors found that the spontaneous γ activity decreases, starting from the earliest data obtained (age of 3) through early adulthood. The decrease was found to be most prominent over childhood, whereas a difference between adolescents (14 - 17 years) and adults (18 - 38) was less notable [Tierney *et al.*, 2013]. In the present study, the spontaneous γ activity did not vary as a function of age. One possible explanation could be that in the study of Tierney *et al.* a better signal-to-noise ratio was achieved due to a larger sample of participants. In that study, the EEG data of 38 adolescents was compared to the EEG data of 27 adults, whereas in the present study each group consisted of 12 participants. On the other hand, Yordanova *et al.* reported that the spontaneous γ activity of 9 - 16 years old participants did not show developmental changes [Yordanova *et al.*, 2002]. This is in agreement with our results.

Since the EEG measured on adults could be affected by a lower electrical resistance due to a thicker scull, the possibility that the developmental decrease in the δ and θ activity during the spontaneous EEG observed in the present study may potentially result from differences in scull thickness can not be excluded completely [Segalowitz *et al.*, 2010]. Taking into account that the decrease of θ activity was reported also using the MEG [Puligheddu *et al.*, 2005], the decrease of the spontaneous activity could be more likely attributed to structural changes of the brain tissue throughout adolescence. For example, this decrease may reflect a decline in the number of cortical synapses [Huttenlocher, 1979, Petanjek *et al.*, 2011] which are thought to be reduced throughout adolescence due to the process of synaptic pruning. As pointed out above, there is only few evidence that the spontaneous γ activity changes with age. Taking into account the discrepancy between the results obtained in the present study and the previous findings, it seems to be necessary to perform further studies to clarify developmental aspects of the spontaneous γ activity during adolescence.

7.2.1.2. Age effects reflected in ongoing EEG activity

In the present study, the single-trial activity during the *non-switching* condition of the *ambiguous/unambiguous* tasks as well as the *prestimulus* activity in the *visual oddball* task was found to decrease with age and to have similar topographical distribution in the δ and θ bands as it was shown for the *spontaneous EEG* in the *eyes-open* condition. There is a growing number of studies that report an age-related decrease of θ activity during the prestimulus (baseline) period of perceptual or higher-cognitive tasks [Krause *et al.*, 2001, Liu *et al.*, 2014, Yordanova and Kolev, 1997, Yordanova and Kolev, 1997]. Interestingly, it was not possible to find any studies which report an age-related decrease of the δ activity during the prestimulus period even though the prestimulus δ activity seems to correlate with e. g. reaction-time performance during early adulthood [Winterer *et al.*, 1999].

The age-related decrease of θ and δ activity was found at all electrode sites and for all tasks in the present study. Furthermore, the topographical distribution of the baseline activity was similar to the distribution of the spontaneous EEG in both frequency bands. Therefore, it can be assumed that the age-related decrease of band activity might reflect general structural changes of the developing brain as, for example, the process of synaptic pruning discussed above.

As mentioned earlier, there is almost no evidence on developmental changes of the γ activity. In 2002, Yordanova *et al.* examined the γ activity preceding an evaluation of auditory stimuli. In their study, the EEG data of 114 children and adolescents from 9 to 16 years of age were investigated. One of the findings was that the prestimulus γ activity decreased with age (from 9 to 16). The age-related differences were more prominent at anterior regions than at posterior ones. This is in contrast to the results obtained in the present study. One possible explanation for this discrepancy would be the fact that Yordanova *et al.* compared children and adolescents over a wide age range.

It could be possible that the age-related decrease was largest in the groups of 9 - 12 years old children and only very small in the groups of 13 - 16 years old adolescents, as it was reported by Tierney *et al.* in 2013 for the spontaneous γ activity. Since in our study, the group of *adolescents* (13 - 15 years old) was compared to the group of *adults*, it could be assumed that the γ activity varies less notable between adolescence and early adulthood than between childhood and adolescence.

Taking together, the results obtained in this study for the spontaneous and prestimulus EEG activity in the δ and θ bands reflect maturational changes taking place in the brain throughout adolescence. These findings are also consistent with currently available literature, whereas the maturation of the γ band might be different. The amplitude of the γ oscillations might be already well developed during adolescence. However, further studies on the development of γ activity are required.

7.2.2. Developmental changes reflected in task-related enhancement of single-trial EEG activity in δ, θ and γ frequency bands

According to Basar, the performance of sensory-cognitive tasks is reflected in a synergy between oscillations in different frequency bands [Basar, 2011]. Since the aim of the present study was to clarify the role of top-down effects in sensory-cognitive processing reflected in the δ, θ and γ bands using the developmental approach, the results obtained by the present study for each task will be discussed in the following manner:

- a short overview of top-down correlates will be given for each frequency band, followed by a detailed discussion of the obtained results on the basis of the currently available literature;

- also, a possible interplay of the frequencies of interest and its role in top-down effects during sensory-cognitive processing will be addressed.

7.2.2.1. Ambiguous and unambiguous tasks

Ambiguous patterns such as the SAM might, by means of such high-temporal resolution techniques as the EEG, provide important insights into development aspects of top-down processes underlying coherent perception in an endogenously, self-generating manner without potentially confounding factors caused by a physical change of the stimulus [Basar-Eroglu *et al.*, 1996, Mathes *et al.*, 2014]. For adult participants, top-down processes during processing of ambiguous patterns were found to be reflected in γ, θ and δ oscillations [Basar-Eroglu *et al.*, 1993, Basar-Eroglu *et al.*, 1996, Ehm *et al.*, 2011, Mathes *et al.*, 2006, Mathes *et al.*, 2014, Strüber *et al.*, 2000].

Additionally, developmental aspects of top-down processing of perceptual reversals which occur endogenously were defined more specifically by comparing them with those elicited by exogenously-induced reversals. Cognitive demands required in the first case may differ significantly between the two age groups, whereas in the second case processing may be already at the same level in both groups.

7.2.2.1.1. γ band

Initially, γ oscillations have been proposed to reflect feature binding and integrated object representations in animal models [Gray *et al.*, 1989]. Later, the binding process was also found in humans [Müller *et al.*, 1996]. γ activity in the visual system has been studied intensely in the last 20 years [Basar-Eroglu *et al.*, 1996, Gruber *et al.*, 2008, Karakas and Basar, 1998, Strüber *et al.*, 2000, Tallon-Baudry *et al.*, 1996]. The research has indicated that γ oscillations upon visual stimulation can be divided into two components: an early phase-locked (so-called *evoked*) and a late non-phase-locked (so-called *induced*) component. These components are thought to reflect two different levels of the binding process. Since the *evoked* component has been found mostly to be generated at an early stage of sensory information processing, it might reflect the binding of perceptual information within a local cortical area. The *induced* component has been found to occur during tasks that required attention and top-down integration of features [Rodriguez *et al.*, 1999]. Therefore, this component was supposed to reflect the binding of perceptual information due to top-down (feed-forward) and bottom-up (feed-back) effects in a whole network of cortico-cortical areas [Basar, 2013, Müller, 2000, Müller *et al.*, 2000].

Multistable perception and frontal γ activity in adults

The pioneering study of perceptual ambiguity with adult participants performed by Basar-Eroglu *et al.* in 1996 revealed that the γ oscillations might indicate feature binding of relevant object representations during attentional selection. An exposure of adult participants to the SAM was found to cause an enhancement of γ activity at the frontal regions. The enhancement reached up to 50 % in EEG recordings of both, naive and informed (with respect to the ambiguous nature of the SAM) participants in comparison to spontaneous EEG recordings with no ambiguous patterns presented [Basar-Eroglu *et al.*, 1996]. The topographical distribution of γ activity with a pronounced anterior maximum was thought to be related to such top-down processes as focused attention.

The role of focused attention in experiencing perceptual reversals was later supported by Strueber *et al.* The authors investigated the perceptual reversal phenomenon between participants with high versus low reversal rates using the SAM. It was found that the participants with a high reversal rate showed significantly higher γ activity over the frontal regions compared to the participants with a low reversal rate. The authors concluded that the enhanced γ activity in the group of participants with a high reversal rate may reflect a stronger involvement of attentional *top-down* resources compared to the other group [Strüber *et al.*, 2000]. Top-down control of visual perception seems to be reflected in the enhanced frontal γ activity as it was shown in the study of Mathes *et al.* in 2006. The authors asked participants to bring their reversal rate under voluntary control, either by holding the current perceived interpretation or by reversing back and forth as fast as possible. A participant's intent to hold the currently perceived interpretation of a percept was found to be correlated with more enhanced γ activity over frontal regions as well as a greater deflection of the slow δ component compared to a participant's intent to switch the currently perceived interpretation of a percept [Mathes *et al.*, 2006]. The authors interpreted their findings as an indication for the significance of focused attention for experiencing a perceptual reversal. Furthermore, the modulation of the δ and γ band activity during voluntary control of a perceptual reversal was interpreted to provide an evidence for involvement of a fronto-parietal network in *top-down* regulated attentional processes during multistable perception [Mathes *et al.*, 2006].

Developmental aspects of multistable perception reflected in γ oscillations

In the present study, the γ activity was found to be enhanced over anterior regions during the reversal-related periods compared to the periods of perceptual stability only in the group of *adults*.

The studies discussed above indicate an important role of attentional processes in multistable perception. Attentional processes are known to be coordinated by an activation of the fronto-parietal network [Fuster, 2002]. This network was found to play an important role in attentional top-down processes [Mathes *et al.*, 2006, Weilnhammer *et al.*, 2013]. Earlier research on the development of higher-order cognitive functions emphasized the fact that an improvement of these functions during adolescence relies on protracted maturation of the frontal cortex. Recent research demonstrates that the improvement of higher-order cognitive functions is rather caused by a late maturation of association cortices of each lobe [Luna *et al.*, 2004].

Considering the fact that oscillatory activity measured by the EEG reflects the summation of postsynaptic potentials in the apical dendrites of pyramidal cells, synaptic pruning could be one of the possible factors that affect the proper involvement of the fronto-parietal network during multistable perception. It is worth noting that during adolescence synaptic pruning is most prominent in supragranular layers [Anderson *et al.*, 1995]. These layers are thought to permit communication between different cortex areas and to be the layers where γ oscillations are more prominent [Spaak *et al.*, 2012]. Additionally, developmental changes in the white matter organization of fronto-parietal fiber connections may contribute to reorganization of functional networks which are responsible for the development of higher-cognitive functions [Casey *et al.*, 2008]. Recently, it was shown that maturational changes taking place in the association cortices could result in less synchronized γ activity in adolescents reflected in decreased temporal precision and spatial fine-tuning of neuronal interactions during a cognitive task performance [Uhlhaas *et al.*, 2010]. In addition, less synchronized γ activity during adolescence could depend on changes in several neurotransmitter systems [Buzsaki and Wang, 2012]. GABAergic neurons are thought to be related to the generation of γ and α oscillatory activities, whereas glutamate and acetylcholin may play an important role in regulation of their amplitude and timing [Janiesch *et al.*, 2011]. As shown recently, these neurotransmitter systems change dramatically throughout adolescence [Uhlhaas and Singer, 2011]. Therefore, the diminished enhancement of frontal γ activity in *adolescents* found in our study might reflect immature neuronal processing within the fronto-parietal network and indicate a development of attentional top-down control over feature binding of relevant object representations during multistable perception.

Interestingly, no age-related differences of the γ band modulation were found during the unambiguous task. Furthermore, no enhancement of γ activity was present over anterior brain regions in both groups during the unambiguous task. This finding could indicate that attentional top-down control might be involved in the monitoring of the ambiguous pattern during the unambiguous task to a lesser extent. This is a plausible assumption in light of the fact that perceptual reversals are exogenously-induced in this case. Thus, it could be assumed that less attentional effort might be required in order to maintain and stabilize in the fronto-parietal network the currently perceived interpretation of the ambiguous pattern, so even immature brain structures of adolescents could be able to manage it on adult's level.

Descriptive considerations to right-hemispheric frontal γ enhancement in adults

Lately there has been much discussion whether the activation of a right-hemispheric frontal γ band might reflect attentional top-down process that cause spontaneous perceptual reversals [Rach and Huster, 2014, Sterzer and Kleinschmidt, 2007].
Basar-Eroglu *et al.* in 1996, for the first time, reported a right-hemispheric frontal γ increase during endogenously-induced reversals caused by exposure to the SAM pattern. Later, a selective right-hemispheric frontal activation was found for endogenously-

induced rivalry stimuli by means of fMRI, whereas such activation was absent in the case of unambiguous stimuli [Lumer *et al.*, 1998]. For both, the SAM stimuli and the spinning wheel illusions, a more prominent frontal activation over the right hemisphere was found for the endogenously-induced reversal than for the exogenously-induced [Sterzer and Kleinschmidt, 2007, Ilg *et al.*, 2008].

In the present study, the enhancement ratio (the ratio of reversal-related activity to the activity during perceptual stability) of frontal γ activity seems to be larger over the left hemisphere in *adults* (see Fig. 6.6). However, a separate inspection of the reversal-related epochs and the epochs where perceptual stability was assumed revealed that the frontal γ activity over the right hemisphere was larger for the reversal-related epochs. Therefore, the difference in the enhancement ratio between two hemispheres might be explained by a more enhanced frontal activity over the right hemisphere during perceptual stability than over the left one. This means that the frontal part of the right hemisphere might reflect a stronger activation in both cases – during the reversal-related perception as well as during the perceptual stability.

As no such differences were found for *adults* during the unambiguous task, the finding described above might emphasize the role of the right frontal cortex and top-down attentional control not only in a possible initiation of perceptual reversals but also during maintenance of a currently perceived percept when the visual information is inconclusive. However, this speculation needs further investigations, since in the present study no direct comparisons were made between the periods of perceptual reversal and the spontaneous EEG.

Recent research has shown that activity in the θ and δ bands could influence the modulation of γ oscillations [Basar *et al.*, 1993, Buzsaki and Wang, 2012, Demiralp *et al.*, 2007]. In the following, some functional correlates of θ and δ activities, as well as θ-γ / δ-γ relationships in general and with respect to multistable perception is discussed.

7.2.2.1.2. θ band

High-frequency oscillations are thought to synchronize local assemblies of neurons, whereas the oscillations in the θ and δ band have been linked to the general ability of the brain to transfer and coordinate information over large distances [Von Stein and Sarnthein, 2000]. θ oscillations have been found to be involved in a various number of perceptual and cognitive processes which require a coordinated activity of remote brain regions [Von Stein and Sarnthein, 2000]. Generally, θ oscillations have been related to such cognitive functions as focused attention [Basar-Eroglu *et al.*, 1992], working memory [Sauseng *et al.*, 2010], action monitoring and cognitive control [Cavanagh *et al.*, 2012, Cavanagh and Frank, 2014, Schmiedt-Fehr and Basar-Eroglu, 2011]. Furthermore, recent research indicates that frontal θ activity may be an important mechanism involved in the control of posterior brain regions including early visual areas [Cohen and van Gaal, 2013, Mathes *et al.*, 2014, Volberg *et al.*, 2013].

Multistable perception and frontal θ activity in adults

Frontal θ oscillations related to the perceptual ambiguity were first found in adult participants with a high reversal rate [Nakatani and van Leeuwen, 2005]. The authors concluded that the increased θ activity in the group of participants with a high reversal rate may reflect a stronger involvement of attentional or vigilance resources by exposure to ambiguous stimuli compared to the group of participants with a low reversal rate.
As θ activity is known to reflect different aspects of cognitive event processing even during the same task, Mathes *et al.* investigated the role of top-down influence on multistable perception reflected in frontal θ oscillations during the exposure of participants to an ambiguous stimulus and its disambiguous version. The authors found a transient enhancement of frontal θ activity in both cases. However, the enhancement of the θ oscillations over frontal compared to posterior regions was found to be steeper by viewing the ambiguous stimulus than its diambiguous variant. The authors concluded that the ambiguous stimulus may require more extensive top-down control over sensory brain regions in order to establish a coherent object perception than would be required for the stimulus' diambiguous version [Mathes *et al.*, 2014].

Developmental aspects of multistable perception reflected in θ oscillations

For the ambiguous task used in the present study, θ oscillations were found to be generally enhanced during the reversal-related periods compared to the periods of perceptual stability. The enhancement was smaller in *adolescents* than in *adults*. This finding is consistent with the few existing studies which investigated developmental aspects of event-related θ oscillations throughout late childhood and adolescence [Crowley *et al.*, 2014, Krause *et al.*, 2001, Liu *et al.*, 2014, Müller *et al.*, 2009, Papenberg *et al.*, 2013, Yordanova and Kolev, 1997]. The main outcome of these studies was that task-related θ oscillations have been found to increase with age. The enhancement of task-related θ responses has been associated with an improvement of cognitive abilities during late childhood and adolescence. Furthermore, local phase synchronization (inter-trial coherence) of θ responses was found to increase with age[1].

While the θ activity was found to be only generally enhanced in both groups, the group of *adults* showed more prominent θ activity over frontal regions as can be seen in Fig. 6.6, whereas the θ response in *adolescents* seems to be less localized. As mentioned above, it was recently found that top-down control over sensory brain regions might be required in order to establish a coherent representation of ambiguous stimuli [Mathes *et al.*, 2014]. This top-down control might be represented by an interplay of such higher-order functions as inhibition, updating and monitoring representations in working memory and certainly attention. Each of these functions may play a role in experiencing perceptual reversals as it has been already shown in the behavioral and neuroimaging studies with adults [Long and Toppino, 2004, Reisberg, 1983, Reisberg and O'Shaughnessy, 1984, Slotnick and Yantis, 2005, Strüber and Stadler, 1999, Suzuki and Peterson, 2000]. They were also found to develop during early childhood and to be essential in order to experience perceptual reversals spontaneously [Doherty and Wimmer, 2005,

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[1] This method was not applied to the EEG data obtained for the ambiguous and unambiguous tasks because of the inter-individual variability of reversal rates discussed above in Sec. 7.1.2. The inter-individual variability of reversal rates leads to a widespread number of epochs obtained for each participant. In order to reduce the susceptibility of the ITC measure to noise and therefore to nonrepresentative results, the minimal number of analyzed epochs has to be approximately 30 for each participant and each analyzed condition. It was impossible to obtain this number of artefact-free epochs for each participant in the experimental design as used in the present study.

Wimmer and Doherty, 2011]. The development of these functions has been found to protract into adolescence and even into early adulthood [Anderson *et al.*, 2001, Amso *et al.*, 2014, Leon-Carrion *et al.*, 2004, Luna *et al.*, 2004, Luna *et al.*, 2010] and has been linked to maturational processes like pruning and myelination in the association cortices of the frontal and parietal lobes. Furthermore, a development of frontal θ oscillations related to inhibition and working memory has been shown recently [Liu *et al.*, 2014, Krause *et al.*, 2001, Uhlhaas *et al.*, 2009]. Thus, the decreased θ activity found in the group of *adolescents* might be related to the protracted functional development of these functions and influence top-down control over posterior brain regions.

Recently, a developmental impact of frontal θ activity on perceptual organization was shown by Uhlhaas *et al.* in 2009. In the study, the perception of Mooney faces was examined from late childhood until early adulthood. Developmental changes of the frontal θ activity and fronto-parietal synchronization in the θ band were accompanied by an improvement of neuronal synchronization and an increase of amplitudes in the γ band over parietal brain regions during perceptual organization of the upright Mooney faces. It was suggested that developmental changes found in the θ band could reflect an improvement in the maintenance of task-specific information in working memory as well as in top-down control over the perceptual organization taking place in posterior brain regions, where the increase in γ activity was associated with the construction of coherent object representations [Uhlhaas *et al.*, 2009].

For the unambiguous task, the enhancement of θ activity during the reversal-related periods compared to the periods of perceptual stability was not affected by age. However, the θ response had an anterior maximum in both groups. As the perceptual reversal process in this case is driven by a physical change of the stimulus, it could be assumed that less top-down control over posterior brain regions might be presumably required in order to establish sufficient object binding and that this may account for the comparable increase of θ activity in both groups. Thus, the developmental effects of θ oscillations found during the ambiguous task emphasize the role of top-down regulation of the visual perception when a stimulus is inconclusive or elicits an ongoing conflict between perceptual interpretations.

As can be seen in Fig. 6.6, the distribution of the θ response in the group of *adolescents* is less localized than in *adults*. This is consistent with a various number of fMRI studies, which have revealed that the activation of neural networks critical for task-performance is more diffused in adolescents and becomes more prominent and focused during development [Durston *et al.*, 2006, Durston and Casey, 2006]. The better activation of neural networks is supposed to reflect a better temporal precision in the inter-regional interplay of brain regions underlying a specific task-processing [Yordanova and Kolev, 1997, Uhlhaas and Singer, 2011].

7.2.2.1.3. δ band

δ oscillations have been found to correlate with a various number of cognitive tasks during normal states of wakefulness [Basar *et al.*, 2001, Knyazev, 2012]. It was further found that during cognitive tasks δ oscillations contribute mostly to the well-known P300 component, an evoked brain response to infrequent and unexpected stimuli [Demiralp *et al.*, 2001, Basar-Eroglu *et al.*, 1992, Karakas *et al.*, 2000]. Considering the fact that P300 has been found to be linked with dopaminergic neurotransmission, it was assumed that the enhanced δ oscillations might reflect a participant's motivation and attention to internal processing of certain cognitive events that require signal detection and decision-making processes [Basar-Eroglu *et al.*, 1992, Knyazev, 2012].

Multistable perception and δ activity in adults

Top-down processes involved in experiencing a perceptual reversal may be presumably reflected in slow δ oscillations which were for the first time detected by Basar-Eroglu *et al.* in 1993. Taking into account a posterior distribution of the δ response, it was assumed that this positive wave occurs immediately after a perceptual reversal and belongs to the family of well-known stimulus-locked P300 waves. Because of the similarity between these two brain responses, the δ oscillations are thought to reflect the conscious recognition of a perceptual reversal and, therefore, the closure of the reversal process [Strüber and Herrmann, 2002]. As already mentioned above, the top-down processes involved in experiencing a perceptual reversal become more apparent when participants are instructed to deliberately decrease their reversal rate. In this case, the reversal-related δ response increases, accompanied by an enhancement in the γ band. This presumably indicates the significance of focused attention for the experiencing of a perceptual reversal [Mathes *et al.*, 2006].

Developmental aspects of multistable perception reflected in δ oscillations

For the ambiguous task, δ oscillations were found to be generally enhanced during the reversal-related periods compared to the periods of perceptual stability. The enhancement was smaller in the group of *adolescents* than for *adults*. Moreover, the δ response was almost absent at frontal regions in *adolescents* as well as less focal over posterior brain regions in *adolescents* compared to *adults*. This finding is in agreement with the study by Ehlers *et al.*, where δ oscillations of 11 years old children were compared to adult δ responses. For the children, the authors concluded that unspecific posterior activation of δ oscillations accompanied by a less stable frontal response could result from the immature connectivity patterns within the fronto-parietal network [Ehlers *et al.*, in press]. Furthermore, immature interconnectivity in the cortico-hippocampal network might be one of the reasons for reduced reversal-related δ and γ oscillations in *adolescents*. Basar-Eroglu and Basar showed that the P300 - 40 Hz response upon a cognitive event can be recorded in the cortex as well as in the hippocampus [Basar-Eroglu and Basar, 1991]. As myelination of cortico-hippocampal connections continues throughout adolescence [Benes, 1989], it might account for the results obtained in our study.

Recently, coherent oscillations between parietal and frontal cortices in the δ frequency band have been found to correlate with decision-making processes during a discrimination task [Nacher *et al.*, 2013]. During multistable perception, processing upon a perceptual reversal may involve a decision-making process, reflecting the participant's confidence in having perceived the stimulus as it was shown for the P300 response [Hillyard *et al.*, 1971]. While the decision-making process is known to develop rapidly during childhood, there are evidences that it continues to mature throughout adolescence [Pammi and Srinivasan, 2013]. Therefore, the detected difference between the age groups might reflect less developed decision-making ability in *adolescents* due to the immature connectivity patterns within the fronto-parietal network. A neuroimaging study performed by White *et al.* showed that the fronto-parietal network is modulated by a stimulus' characteristics (like discrimination difficulty) during the decision-making process [White *et al.*, 2012]. During the unambiguous task, the reversal-related δ responses found in both groups were more prominent compared to the δ responses in the ambiguous task. This is in agreement with previous studies [Mathes *et al.*, 2010, Strüber and Herrmann, 2002] and may be due to lower uncertainty during the decision-making process upon an exogenously-induced reversal.

During the unambiguous task, the reversal-related enhancement in the δ frequency band was larger in *adults* than in *adolescents*. As the mean reaction time did not significantly differ between the groups, it is unlikely to assume that the found group difference may be caused by smearing out of the δ response when single trials are averaged. The age-related difference could mean that even a simpler task might reveal a less developed decision-making ability, presumably due to maturational changes taking place in the associative cortices [Blakemore, 2012], in *adolescents* than in *adults*.

Beside decision making, there are other cognitive functions that could account for the age-related differences during multistable perception. In both groups, the unambiguous stimuli caused more enhanced reversal-related δ responses than the ambiguous ones. Given the similar number of perceptual reversals in both tasks, the higher discrimination difficulty might require the participants to allocate more attentional resources in order to detect a perceptual reversal in the ambiguous task [Mathes *et al.*, 2010]. Thus, the less pronounced enhancement of reversal-related activity might be analogous to the decrease of the P300 amplitudes in the case when participants have to pay more attention to the task-relevant stimulus [Polich, 2007]. As the reversal-related enhancement in both tasks was found to be a function of age, it could suggest that allocation of attentional resources might develop throughout adolescence.

From the similar modulation of reversal-related δ responses in *adolescents* and *adults* in both tasks, it might be concluded that similar top-down processes are involved in conscious recognition of perceptual reversals and in the closure of the reversal process [Strüber and Herrmann, 2002].

7.2.2.2. Visual oddball task

For the visual oddball task, a rapid detection of relevant changes during the external sensory stimulation was examined. The test persons had to pay attention to targets that appeared relatively rarely in contrast to non-targets. Due to more salient stimuli, this task can be regarded as simpler than, for instance, the ambiguous or even unambiguous tasks. Since the study of less complex processes can provide important insights for understanding of higher-order processes, the results obtained for the visual oddball task can provide additional information about the role of δ, θ and γ bands in visual perception.

7.2.2.2.1. γ band

Developmental aspects of γ oscillations in the visual oddball task

As discussed earlier, γ oscillations have been found to be related to attentional processing in multistable perception. There is furthermore a bulk of evidence supporting this relationship in a various number of other visual paradigms [Fries *et al.*, 2001, Herrmann *et al.*, 2004, Tiitinen *et al.*, 1993, Yordanova *et al.*, 2002].

During the visual oddball task, no significant differences between the two age groups were found in the early time window (0 - 150 ms), where earlier stages of sensory information processing are known to occur. This finding is in agreement with results obtained by Yordanova *et al.* (2002). In their study, evoked γ responses in the auditory attention task were found to be a function of age only in 9 - 12 years old children, but this effect was not observed in adolescents (14 - 16 years). According to the authors, early target selection in children seems to reflect their sensitivity to the features of an external stimulus. Visually evoked γ responses were also found to be modulated by the features of an external stimulus (e. g. size) to a greater extent in 10 - 12 years old children than in young adults [Werkle-Bergner *et al.*, 2009]. Considering the fact that in the visual oddball paradigm evoked γ responses are detected mostly over occipital brain regions and that the brain matures from posterior areas to the anterior ones, it could be concluded that automatic sensory processing is already fully developed in *adolescents* (and cannot be distinguished from an adult's level).

Also, no age-related differences were found in induced γ responses (late time window: 300 - 700 ms). In both groups, participants had a larger response to targets than to non-targets, with more pronounce responses over anterior brain regions compared to posterior ones.

According to currently available literature, the γ oscillations induced in adults resulting from visual stimulation might, among others, be modulated by task-specific attentional demands [Gruber *et al.*, 1999, Gruber *et al.*, 2008, Fries *et al.*, 2001, Tallon-Baudry *et al.*, 2005, Vidal *et al.*, 2006]. There are no known published data on the development of induced γ oscillations in healthy adolescents, except for the visual grouping study by Uhlhaas *et al.* (2009) discussed above. Taking into account that a more prominent enhancement of the induced γ activity was observed for targets and the fronto-central distribution of responses in the time window corresponding to the P300 component, it could be assumed that selective attention might modulate the induced γ oscillations in the visual oddball task as it was found in the studies cited above.

7.2.2.2.2. θ band

Developmental aspects of θ oscillations in the visual oddball task

During the visual oddball task, the target-related θ oscillations in the early time window (0 - 150 ms) were found to be enhanced compared to non-target ones only in the group of *adults* over occipital brain regions, whereas the target- and non-target-related θ responses did not differ in *adolescents*.

Yordanova *et al.* in 2006 claimed that the early frontal θ response may be functionally associated with attentional processes which allow an early target selection by discriminating the physical characteristics of a stimulus. In their study, early θ responses of 11 years old children to auditory target stimuli differed significantly from the responses to non-target ones. It is worth mentioning that the study of Yordanova *et al.* was designed to be more attentionally demanding compared to the simple oddball task used in our study. This probably is the reason why in our case no difference was found for target and non-target conditions in the early θ responses for *adolescents*.

The target-related oscillations in the late time window (300 - 700 ms) were found to have an anterior distribution in both groups but were less pronounced in the group of *adolescents*.

The anterior distribution of the late θ responses in the time window corresponding to the P300 component is usual for oddball experiments and is thought to be correlated with selective attention [Basar *et al.*, 2000, Basar-Eroglu *et al.*, 1992]. Since selective attention assumes focusing on relevant information while ignoring other, less pronounced θ oscillations in *adolescents* may reflect not completely developed inhibitory control [Leon-Carrion *et al.*, 2004, Luna *et al.*, 2010]. Yordanova and Kolev in 1998 showed that the capacity to produce a stable θ response depends on increasing phase-locking capability with advance in age that reaches maturity beyond the age of 10. Thus, a lower phase-locking of the θ oscillations of *adolescents* may account for the age-related differences.

7.2.2.2.3. δ band

Developmental aspects of δ oscillations in the visual oddball task

While both groups had a posterior maximum, the target-related δ oscillations were found to be less prominent in the group of *adolescents* compared to *adults* in the late time window (300 - 700 ms).

According to Karakas *et al.*, event-related δ oscillations represent the degree of consciousness involved in conscious stimulus evaluation and memory updating [Karakas *et al.*, 2000]. In the visual oddball paradigm, δ oscillations are thought to be related to signal detection and decision-making processes [Basar *et al.*, 2000, Basar-Eroglu *et al.*, 1992]. A discussion of the development of decision-making processes was already given above. The same line of argumentation could also be applied to the age-related differences obtained for the δ oscillations in the visual oddball task.

SECTION 8

Limitations of the study, summary and outlook

8.1. Limitations of the study

As any other study, the present one also had its limitations:

1. The number of artefact-free epochs in studies with children and adolescents is often more limited than in adult studies [Cohen, 2014]. This problem is even more evident in the (endogeneous) *ambiguous* task, because of the high intervariability between participants in experiencing perceptual reversals. It would be of interest to overcome this problem in future studies.
2. Recently, there has been a vivid discussion whether induced γ oscillations found in many studies on visual perception could be caused by miniature saccades during eye movements [Yuval-Greenberg *et al.*, 2008, Yuval-Greenberg and Deouell, 2009]. In

the present study, the EEG data were only checked for eye-blinks and minor blinks. However, if the miniature saccades affected the EEG data, the periods of reversal-related activity and perceptual stability should be affected to a similar extent during the ambiguous and unambiguous tasks. The same can be assumed for the visual oddball task. Therefore, the differential effects of the frontal γ activity found in both, between- and within-group comparisons, would be only marginally affected by the miniature saccades.

3. The statistical analysis was performed using the regions of interest as defined above. Therefore, no statements about a lateralization of the responses can be made.

8.2. General summary

Adolescence is a period of major maturational changes in the brain [Spear, 2000, Uhlhaas *et al.*, 2010]. This late developmental stage is particularly dominated by the maturation of the prefrontal cortex. Interactions between the prefrontal cortex and other brain regions, particularly with the parietal cortex, undergo maturational changes throughout adolescence [Blakemore, 2012, Darki and Klingberg, 2015, Ehlers *et al.*, in press]. If this maturation is completed successfully, it results in a better cognitive performance during decision making, logical thinking and the assessment of potential risks [Spear, 2000].

Maturational changes in neuronal networks may play a significant role for late modifications in brain oscillations and, therefore, reflect the development of higher-order cognitive functions during adolescence [Uhlhaas and Singer, 2011].

In this thesis, developmental changes in the δ, θ and γ frequency bands were investigated during resting and cognitive states in *adolescents* (13 - 15 years) and *adults* (20 - 27 years). Four tasks were conducted to address this issue: the *spontaneous EEG* (with eyes open), the *ambiguous* task, the *unambiguous* task and the *visual oddball* task. The previous finding of δ and θ amplitudes decreasing with age during rest were replicated. Similarly to previous studies, our results also indicate that γ amplitudes during rest do not profoundly differ between *adolescents* and *adults*. This pattern did also account for the amplitude values measured during the cognitive tasks.

According to Basar, the performance of sensory-cognitive tasks is reflected in a synergy between oscillations in different frequency bands [Basar, 2011]. During multistable perception, higher-order cognitive functions have been found to correlate with brain oscillations in the δ, θ and γ frequency bands [Basar-Eroglu *et al.*, 1993, Basar-Eroglu *et al.*, 1996, Ehm *et al.*, 2011, Mathes *et al.*, 2006, Mathes *et al.*, 2014, Strüber *et al.*, 2000]. The anterior maximum of the reversal-related γ and θ oscillations in adults is thought to reflect top-down control over posterior brain regions subserving a coherent visual perception of ambiguous patterns. In the present study, the reversal-related activity in the θ and γ frequency bands was enhanced compared to the periods of perceptual stability. When exposed to ambiguous stimuli, *adolescents* showed a lower and less localized enhancement of reversal-related activity than *adults*. This development is reflected in altered γ and θ oscillations during the performance of the task. For the *unambiguous* task, the reversal-related activity in the γ as well as in the θ bands did not depend on age. As the perceptual reversal process is in this case driven by a physical change of the stimulus, it could be assumed that less top-down control is required in order to establish sufficient object binding; this may account for the comparable increase of the θ activity in both groups. Thus, the developmental effects of γ and θ oscillations found for the *ambiguous* task emphasize the role of top-down regulation of the visual perception when a stimulus is inconclusive or elicits an ongoing conflict between perceptual interpretations [Mathes *et al.*, 2014]. δ oscillations during multistable perception are thought to be related to the closure of a perceptual reversal, reflecting such cognitive processes as signal detection and decision making [Basar *et al.*, 2000, Basar-Eroglu *et al.*, 1993, Strüber and Herrmann, 2002]. In the present study, age-related changes in δ oscillations were found in both, *ambiguous* and *unambiguous* tasks. In both groups, the δ response had a centro-parietal distribution, underlining its functional similarity to the P300 component [Basar-Eroglu *et al.*, 1993, Mathes *et al.*, 2006, Strüber and Herrmann, 2002]. While the decision-making process is known to develop rapidly during childhood, evidence exists that it continues to mature throughout adolescence [Pammi and Srinivasan, 2013]. Therefore, the detected difference between the age groups might reflect a less developed decision-making ability in *adolescents* due to the immature connectivity patterns within the fronto-parietal network, as it was already shown for 11 years old children [Ehlers *et al.*, in press]. Similar topography and age-related differences of task-related δ oscillations were also found in the *visual oddball* task. This was not surprising, as all three cognitive tasks require signal detection and decision-making processes. The age-related differences of the θ activity varied differently across the tasks. The task-related θ activity was found to increase with age only during the *ambiguous* and *visual oddball* tasks, whereas no age-related differences were found during the *unambiguous* task. Considering the fact that during the *unambiguous* and *visual oddball* tasks the perceptual process is driven by a physical change of the stimulus and therefore relies on more salient differences of the stimulus presentation, one would expect rather comparable results during these tasks. One possible explanation for the age-related increase found for the visual oddball task may be that the age-related difference could be more pronounce if the target-related θ activity is compared to the non-target one, probably reflecting an improvement in selective attention. The age-related increase could be less notable if only the target-related θ activity would be compared between the groups. As in the case of the *unambiguous* task, no age-related differences were found for the task-related γ responses during the visual oddball task. As mentioned above, the salience of a perceptual event may account for the comparable results in the tasks. More salient stimuli may require less attentional control which is reflected by frontal γ oscillations.

8.3. Conclusion

The thesis in hand investigated developmental changes in cognitive correlates of brain oscillations in the δ, θ and γ frequency bands during adolescence. The main finding of this study is that functional networks in all these frequency bands undergo maturational changes during adolescence. Moreover, the present study supports previous findings from adult research which have established a functional relationship between δ, θ and γ activities with higher cognitive processes. It was further found that the developmental changes correlated with task difficulty. Only during the *ambiguous* task, which was the most challenging among the tasks used in the present study, the γ oscillations were found to reflect a change in task-related cortical processing during adolescence, whereas no age-related differences of γ responses were detected for either less demanding tasks (the *unambiguous* and *visual oddball* tasks) or the spontaneous γ activity. The spontaneous and prestimulus δ and θ activities were found to decrease with age. This probably reflects general maturational changes taking place in the developing brain. The event-related θ responses were found to increase with age during the *ambiguous* and *visual oddball* tasks and did not depend on age during the *unambiguous* task. In contrast, we founds the event-related δ responses to increase with age for all tasks. The age-related enhancement of the task-related activity in the θ and δ bands may indicate an improvement in higher-order cognitive processes during adolescence.

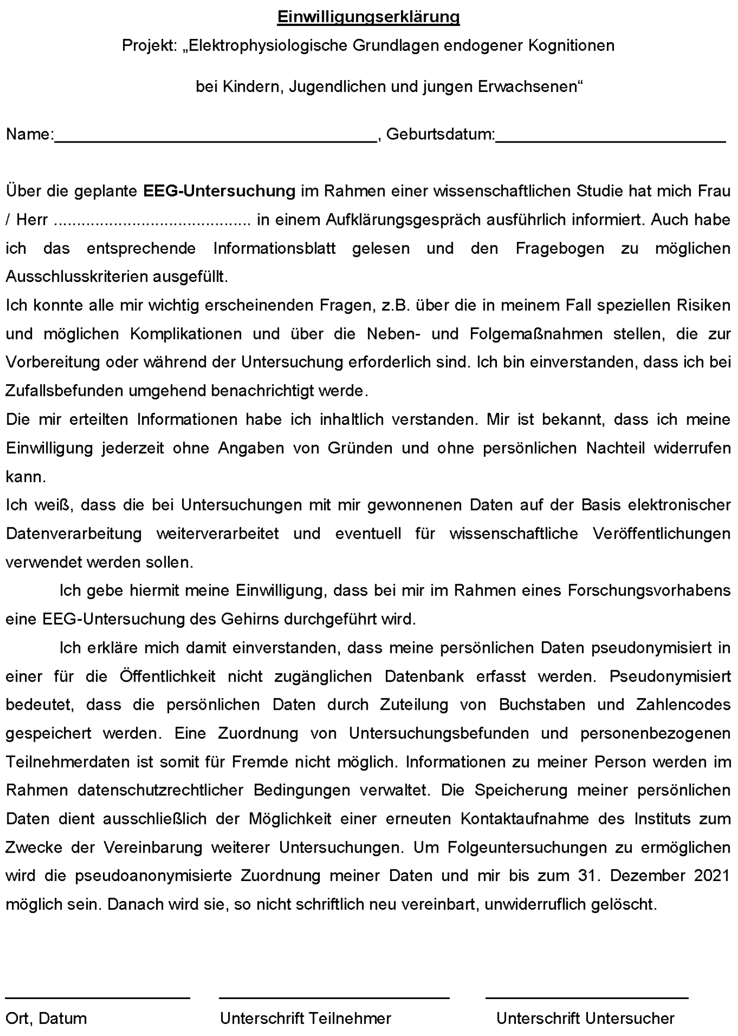
8.4. Outlook

The present study demonstrated that developmental changes in δ, θ and γ oscillatory activities possibly correlate with the development of higher cognitive functions during adolescence. In accordance with the theoretical framework proposed by Basar [Basar, 2011], an interaction of all known frequency bands should be taken into account to investigate integrative functions. For this, α oscillations, which are supposed to be involved in top-down processing during visual perception, have to be investigated [Isoglu-Alkac *et al.*, 2000, Mathes *et al.*, 2010]. Cognitive dysfunctions are a core feature of such mental disorders as schizophrenia that typically develops during adolescence [Pantelis *et al.*, 2003]. Thus, it is crucial to extend our understanding of the mechanism behind the appearance of cognitive functions during normal development in order to understand at which stage of brain development cognitive processes become impaired and what can be done to prevent the onset of such diseases [Uhlhaas and Singer, 2011].

APPENDIX A

Consent forms

On the following pages, the consent forms that were signed by the participants and, in the case of minors by a parent, are provided. Since the participants had German as their main language, the forms were provided in German.



Einwilligungserklärung

Projekt: „Elektrophysiologische Grundlagen endogener Kognitionen

bei Kindern, Jugendlichen und jungen Erwachsenen“

Name:__________________________________, Geburtsdatum:_________________________

Über die geplante **EEG-Untersuchung** im Rahmen einer wissenschaftlichen Studie hat mich Frau / Herr .... in einem Aufklärungsgespräch ausführlich informiert. Auch habe ich das entsprechende Informationsblatt gelesen und den Fragebogen zu möglichen Ausschlusskriterien ausgefüllt.

Ich konnte alle mir wichtig erscheinenden Fragen, z.B. über die in meinem Fall speziellen Risiken und möglichen Komplikationen und über die Neben- und Folgemaßnahmen stellen, die zur Vorbereitung oder während der Untersuchung erforderlich sind. Ich bin einverstanden, dass ich bei Zufallsbefunden umgehend benachrichtigt werde.

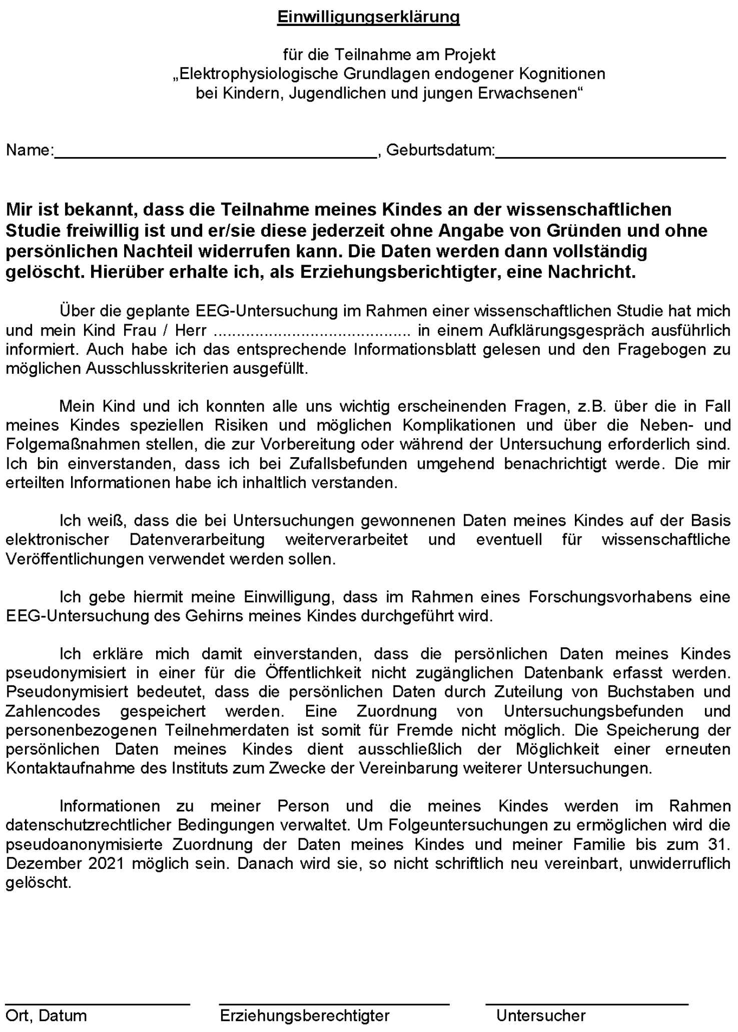
Die mir erteilten Informationen habe ich inhaltlich verstanden. Mir ist bekannt, dass ich meine Einwilligung jederzeit ohne Angaben von Gründen und ohne persönlichen Nachteil widerrufen kann.

Ich weiß, dass die bei Untersuchungen mit mir gewonnenen Daten auf der Basis elektronischer Datenverarbeitung weiterverarbeitet und eventuell für wissenschaftliche Veröffentlichungen verwendet werden sollen.

Ich gebe hiermit meine Einwilligung, dass bei mir im Rahmen eines Forschungsvorhabens eine EEG-Untersuchung des Gehirns durchgeführt wird.

Ich erkläre mich damit einverstanden, dass meine persönlichen Daten pseudonymisiert in einer für die Öffentlichkeit nicht zugänglichen Datenbank erfasst werden. Pseudonymisiert bedeutet, dass die persönlichen Daten durch Zuteilung von Buchstaben und Zahlencodes gespeichert werden. Eine Zuordnung von Untersuchungsbefunden und personenbezogenen Teilnehmerdaten ist somit für Fremde nicht möglich. Informationen zu meiner Person werden im Rahmen datenschutzrechtlicher Bedingungen verwaltet. Die Speicherung meiner persönlichen Daten dient ausschließlich der Möglichkeit einer erneuten Kontaktaufnahme des Instituts zum Zwecke der Vereinbarung weiterer Untersuchungen. Um Folgeuntersuchungen zu ermöglichen wird die pseudoanonymisierte Zuordnung meiner Daten und mir bis zum 31. Dezember 2021 möglich sein. Danach wird sie, so nicht schriftlich neu vereinbart, unwiderruflich gelöscht.

____________________	________________________	______________________
Ort, Datum	Unterschrift Teilnehmer	Unterschrift Untersucher



Einwilligungserklärung

für die Teilnahme am Projekt
„Elektrophysiologische Grundlagen endogener Kognitionen
bei Kindern, Jugendlichen und jungen Erwachsenen“

Name:________________________________, Geburtsdatum:______________________

Mir ist bekannt, dass die Teilnahme meines Kindes an der wissenschaftlichen Studie freiwillig ist und er/sie diese jederzeit ohne Angabe von Gründen und ohne persönlichen Nachteil widerrufen kann. Die Daten werden dann vollständig gelöscht. Hierüber erhalte ich, als Erziehungsberichtigter, eine Nachricht.

Über die geplante EEG-Untersuchung im Rahmen einer wissenschaftlichen Studie hat mich und mein Kind Frau / Herr .... in einem Aufklärungsgespräch ausführlich informiert. Auch habe ich das entsprechende Informationsblatt gelesen und den Fragebogen zu möglichen Ausschlusskriterien ausgefüllt.

Mein Kind und ich konnten alle uns wichtig erscheinenden Fragen, z.B. über die in Fall meines Kindes speziellen Risiken und möglichen Komplikationen und über die Neben- und Folgemaßnahmen stellen, die zur Vorbereitung oder während der Untersuchung erforderlich sind. Ich bin einverstanden, dass ich bei Zufallsbefunden umgehend benachrichtigt werde. Die mir erteilten Informationen habe ich inhaltlich verstanden.

Ich weiß, dass die bei Untersuchungen gewonnenen Daten meines Kindes auf der Basis elektronischer Datenverarbeitung weiterverarbeitet und eventuell für wissenschaftliche Veröffentlichungen verwendet werden sollen.

Ich gebe hiermit meine Einwilligung, dass im Rahmen eines Forschungsvorhabens eine EEG-Untersuchung des Gehirns meines Kindes durchgeführt wird.

Ich erkläre mich damit einverstanden, dass die persönlichen Daten meines Kindes pseudonymisiert in einer für die Öffentlichkeit nicht zugänglichen Datenbank erfasst werden. Pseudonymisiert bedeutet, dass die persönlichen Daten durch Zuteilung von Buchstaben und Zahlencodes gespeichert werden. Eine Zuordnung von Untersuchungsbefunden und personenbezogenen Teilnehmerdaten ist somit für Fremde nicht möglich. Die Speicherung der persönlichen Daten meines Kindes dient ausschließlich der Möglichkeit einer erneuten Kontaktaufnahme des Instituts zum Zwecke der Vereinbarung weiterer Untersuchungen.

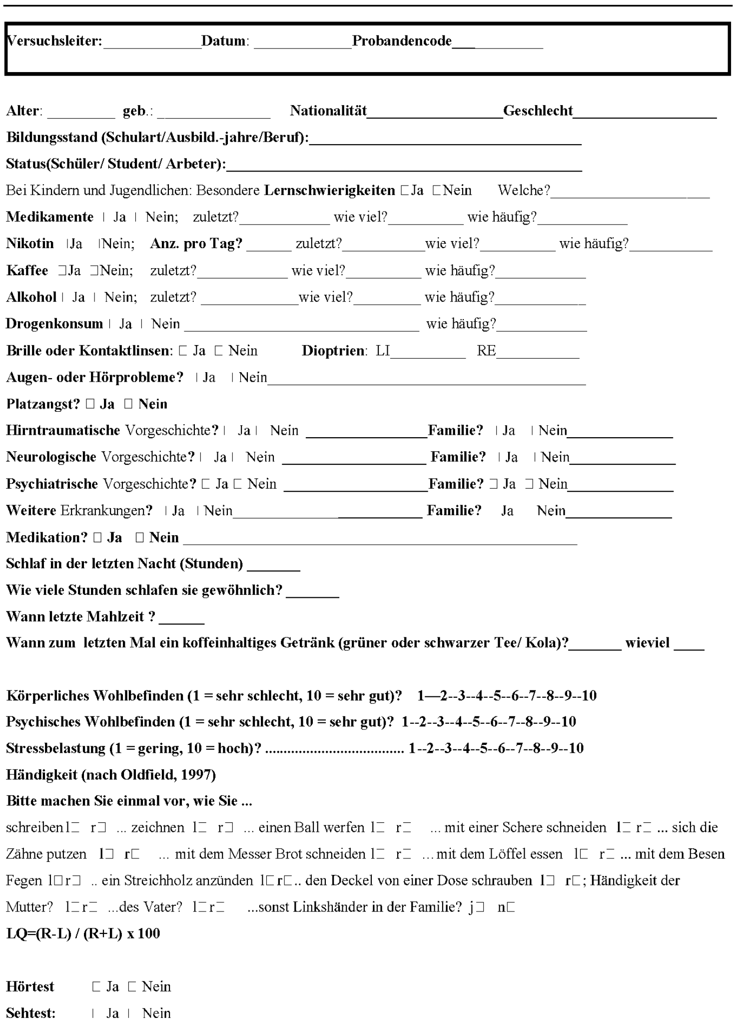
Informationen zu meiner Person und die meines Kindes werden im Rahmen datenschutzrechtlicher Bedingungen verwaltet. Um Folgeuntersuchungen zu ermöglichen wird die pseudoanonymisierte Zuordnung der Daten meines Kindes und meiner Familie bis zum 31. Dezember 2021 möglich sein. Danach wird sie, so nicht schriftlich neu vereinbart, unwiderruflich gelöscht.

____________________	________________________	_____________________
Ort, Datum	Erziehungsberechtigter	Untersucher

APPENDIX B

Questionaire on personal and health details

The questionaire shown on the next page was used to gather data on personal and health details, school performance, as well as on pre-existing condition of neurological and psychiatric diseases of a participant and his/her relatives. Also, a participant was asked to make a self-assessment of physical and mental well-being on a scale from 1 to 10 (where 1 referred to a very bad and 10 to an excellent state) and of their current stress level (in this case, 1 referred to a low and 10 to a high stress level). Furthermore, in order to exclude confounding variables, the participants were asked about their sleeping habits and food and caffeine containing drinks intake.



Versuchsleiter:____________**Datum**: ____________**Probandencode**____________

Alter: ________ **geb**.: ______________ **Nationalität**________________**Geschlecht**__________________

Bildungsstand (Schulart/Ausbild.-jahre/Beruf):__________________________________

Status(Schüler/ Student/ Arbeter):____

Bei Kindern und Jugendlichen: Besondere **Lernschwierigkeiten** ☐Ja ☐Nein Welche?____________________

Medikamente ☐ Ja ☐ Nein; zuletzt?___________ wie viel?_________ wie häufig?___________

Nikotin ☐Ja ☐Nein; **Anz. pro Tag?** ______ zuletzt?__________wie viel?_________ wie häufig?__________

Kaffee ☐Ja ☐Nein; zuletzt?___________ wie viel?_________ wie häufig?___________

Alkohol ☐ Ja ☐ Nein; zuletzt? ____________wie viel?________ wie häufig?___________

Drogenkonsum ☐ Ja ☐ Nein ______________________________ wie häufig?___________

Brille oder Kontaktlinsen: ☐ Ja ☐ Nein **Dioptrien**: LI_________ RE__________

Augen- oder Hörprobleme? ☐ Ja ☐ Nein____

Platzangst? ☐ **Ja** ☐ **Nein**

Hirntraumatische Vorgeschichte? ☐ Ja ☐ Nein _______________**Familie?** ☐ Ja ☐ Nein_____________

Neurologische Vorgeschichte? ☐ Ja ☐ Nein __________________ **Familie?** ☐ Ja ☐ Nein_____________

Psychiatrische Vorgeschichte? ☐ Ja ☐ Nein __________________**Familie?** ☐ Ja ☐ Nein_____________

Weitere Erkrankungen? ☐ Ja ☐ Nein_________________________ **Familie?** Ja Nein_____________

Medikation? ☐ **Ja** ☐ **Nein** ____

Schlaf in der letzten Nacht (Stunden) _______

Wie viele Stunden schlafen sie gewöhnlich? _______

Wann letzte Mahlzeit ? ______

Wann zum letzten Mal ein koffeinhaltiges Getränk (grüner oder schwarzer Tee/ Kola)?_______ **wieviel** ____

Körperliches Wohlbefinden (1 = sehr schlecht, 10 = sehr gut)? 1—2--3--4--5--6--7--8--9--10

Psychisches Wohlbefinden (1 = sehr schlecht, 10 = sehr gut)? 1--2--3--4--5--6--7--8--9--10

Stressbelastung (1 = gering, 10 = hoch)? 1--2--3--4--5--6--7--8--9--10

Händigkeit (nach Oldfield, 1997)

Bitte machen Sie einmal vor, wie Sie ...

schreiben l☐ r☐ ... zeichnen l☐ r☐ ... einen Ball werfen l☐ r☐ ... mit einer Schere schneiden l☐ r☐ ... sich die Zähne putzen l☐ r☐ ... mit dem Messer Brot schneiden l☐ r☐ ... mit dem Löffel essen l☐ r☐ ... mit dem Besen Fegen l☐r☐ .. ein Streichholz anzünden l☐r☐.. den Deckel von einer Dose schrauben l☐ r☐; Händigkeit der Mutter? l☐r☐ ...des Vater? l☐r☐ ...sonst Linkshänder in der Familie? j☐ n☐

LQ=(R-L) / (R+L) x 100

Hörtest ☐ Ja ☐ Nein

Sehtest: ☐ Ja ☐ Nein

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