Chapter 7

Stuck in a Moment: EEG Alpha Power Predicts Perceptual Perseveration

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Abstract

A major question in neuroscience is how the intrinsic state of the neuronal network determines the perception of a complex stimulus and enhances the propensity to either switch or remain attentive to a particular perceptual interpretation. To understand the mechanisms of the spontaneous drive of the brain to explore alternative interpretations of unchanging stimuli, we recorded high-density electroencephalography (EEG) while participants reported the durations of the alternating representations of a bistable perception.

We found that medial occipital and parietal alpha (7–11 Hz) power within the first second after the onset of a representation predicts the fate of its duration. High alpha power promotes the stability of a perceptual representation and suppresses switching to the alternative. An experimentally induced increase in alpha power by means of sleep deprivation mediates in part the concurrent increase in the average duration of individual representations.

The findings support the hypothesis that synchronization of alpha oscillations across a wide neuronal network promotes the maintenance of its current configuration of activity and the corresponding perceptual representation. This concept of stabilization could be a plausible common explanation for a considerable number of findings on alpha across multiple cognitive domains and paradigms. Elevated alpha could also be the key to the poorly understood cognitive deficits, such as the loss of mental flexibility and lapses of responsiveness, that typically accompany sleep deprivation.
CHAPTER 7

Introduction

An important feature of the perceptual system is its flexibility to process identical physical stimuli in different ways, depending on the circumstances. It enables, for example, the maintenance of attention to stimulus properties with expected reward and prevents interference from the competing aspects of the same stimulus. The fate of a newly appearing stimulus with respect to the way it is processed in the brain and modifies behavior is highly dependent on ongoing brain activity (Linkenkaer-Hansen et al., 2001; Palva and Palva, 2012). Even at rest, when faced with an unchanging physical stimulus, the brain continues to explore alternative perceptual interpretations, a property that becomes particularly evident when the stimulus is an ambiguous figure (Blake and Logothetis, 2002; Kornmeier and Bach, 2012; Leopold and Logothetis, 1999; Levelt, 1965).

There have been continued efforts to identify the neuronal correlates of this perceptual flexibility. One of the most likely candidates are the oscillations of neuronal origin, because the numerous combinations of frequency, amplitude, and phase modulation offer a sophisticated and precise neuronal mechanism to entrain diverse neuronal populations that encode the same perceptual object (Buzsáki, 2006). In particular, oscillations in the alpha band activity have been suggested to be important for focused attention by means of inhibition of task-irrelevant brain regions (Cooper et al., 2003; Jensen and Mazaheri, 2010; Klimesch et al., 2007; Mathewson et al., 2011). Alpha activity has also been attributed a role in maintenance of task-relevant items in working memory (Palva and Palva, 2007). Moreover, spontaneous fluctuations in the amplitude of alpha oscillations (Ben-Simon et al., 2008; Linkenkaer-Hansen et al., 2004; Nikulin and Brismar, 2005) in part determine the subject’s ability to process stimuli (Ergenoglu et al., 2004; Hanslmayr et al., 2007; O’Connell et al., 2009; Romei et al., 2010; Thut et al., 2006; van Dijk et al., 2008; Wyart and Tallon-Baudry, 2009). These observations have supported the interpretation that alpha reflects a neural mechanism that sets limits to the visual information that can be passed to higher visual areas, to conscious processing, and to the initiation of behavioral responses (Jensen et al., 2012; Jensen and Mazaheri, 2010; Mathewson et al., 2011; VanRullen and Koch, 2003). The heterogeneity of findings on contribution of alpha in different experimental paradigms renders it unlikely that the role of alpha is limited to one particular cognitive domain, but rather it suggests that alpha might represent a general mechanism involved in controlling perception (Klimesch, 2012).

We here suggest one potential overarching role of alpha. In our framework, a major function of alpha activity is to stabilize the current configuration of neuronal activity and its corresponding perceptual representation. Such stabilization would provide a parsimonious concept that could account for a range of diverging findings, including the observations that high alpha power may render the brain less responsive to incoming stimuli (Haegens et al., 2011), support working memory (Meeuwissen et al., 2011; Palva and Palva, 2007), and inhibit irrelevant activity (Buschman et al., 2012; Cooper et al., 2003; Mathewson et al., 2011).

If alpha plays an active role in stabilizing perception, we expect that its momentary modulation will determine the degree of perceptual stability and that the spontaneous fluctuations in alpha power will affect the perceptual state. In order not to disturb this intrinsic rhythm by
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means of a stimulus-driven experimental paradigm, we took advantage of the spontaneous alternations in perception during a bistable perception with an unchanging stimulus. The proposal that alpha stabilizes perception leads to the testable prediction that high alpha activity should attenuate the likelihood of a transition between two rivaling perceptual representations. The spontaneous alterations between the perceptual representations provide a unique opportunity to investigate how neuronal dynamics modulate perception without changing stimulus properties according to a specific cognitive paradigm (Engel and Singer, 2001; Leopold and Logothetis, 1999; Rees et al., 2002).

A possible functional involvement of alpha power in the stability of a perceptual representation was furthermore experimentally addressed by manipulating alpha power by means of sleep deprivation, which is known to increase eyes-open alpha power (Drapeau and Carrier, 2004). According to our hypothesis, the sleep deprivation-induced increase in alpha power will, on average, increase the duration of individual perceptual representations.

Methods

Participants

Eight healthy adults (five male, age range 20-26 years, all right-handed), naïve to the research question, participated in the experiment after giving informed written consent. The protocol was approved by the Medical Ethics Committee of VU University Medical Center, in accordance with the Declaration of Helsinki. All participants met the following criteria: (I) no self-reported sleep complaints, assessed using standard questionnaires (Buysse et al., 1989; Johns, 1991; Soldatos et al., 2000); (II) non-smoking; (III) no use of medication, including hormonal contraceptives; (IV) no neurological or psychiatric disorders. All had normal or corrected-to-normal vision, followed a regular sleep wake rhythm assessed by actigraphy (Actiwatch, Cambridge Neuro-Technology Ltd., Cambridge, UK) during the week before the experiments and refrained from caffeine and alcohol on the day before and during the experiment.

Protocol

Prior to each assessment day, subjects had a night of normal sleep or a night of total sleep deprivation. The order of the conditions was randomized and counterbalanced across participants. Successful completion of total sleep deprivation was verified using actigraphy, as previously described (Romeijn et al., 2012). This verification is based on visual inspection of the cumulative distribution of immobility bout durations to exclude immobile period longer than 10 minutes, which might correspond to periods of sleep. All the analyses, except those assessing the effect of sleep deprivation on bistable perception, were conducted on the recordings acquired after normal sleep.

At five times during the day (at 10:30, 12:00, 13:30, 15:00 and 16:30), participants viewed a static image of the Necker cube for 4 minutes (Fig. 7.1). Participants were instructed to fixate on the center of the screen and to report perceptual reversals by pressing one of two buttons on a keyboard, where each button was associated with one of the two perceptual representations. The task was programmed in E-Prime® 1.1 (Psychology Software Tools, Pittsburgh, PA). The duration of each individual perceptual representation was defined as the period between two subsequent button presses. Consecutive presses of the same button were discarded. Furthermore, we ex-
Figure 7.1: The viewing of the Necker cube causes the perceptual system to alternate between two rivaling perceptual representations. The onset of each of the alternating representations is reported by use of button presses. The duration of each individual perceptual representation is defined as the time interval between two button presses.

cluded reported durations which could not indicate stable perceptual representations, i.e. durations lasting less than 1.5 s or more than 60 s. Throughout the task, electroencephalography (EEG) was recorded at 1024 Hz, with a Micromed SD-LTM64 recorder (Micromed, Mogliano Veneto, Italy), using a 61-equidistant channel EEG cap (M10, Easy-cap, Munich, Germany), referenced at Cz. Impedance was kept below 10 kΩ.

EEG Preprocessing

All EEG analyses were conducted using FieldTrip (Oostenveld et al., 2011), a toolbox for the analysis of electrophysiological data in Matlab 7.13 (MathWorks, Natick, MA). Noisy channels were interpolated using linear interpolation from the recordings of the neighboring channels for the scalp-level analysis and were not used for the source-reconstruction analysis. Eye-blinks, movement artifacts, and other artifacts were corrected by rejecting noisy independent components (Jung et al., 2000). Artifactual components were automatically identified using various statistical criteria that considered both the temporal and spatial characteristics of the artifacts (Gomez-Herrero et al., 2006). The Matlab source code of the data cleaning pipeline used in this study is freely available online at http://germangh.com/meegpipe. EEG data were high-pass filtered at 0.5 Hz cutoff frequency (4th-order Butterworth filter) and notch-filtered at 50 Hz.

Quantification of Average Alpha Power During Individual Perceptual Representations

For the duration of each individual perceptual representation, EEG recordings were segmented in 1 s long, 50% overlapping time windows, starting at 1 s after the button press and ending, depending on the residual length of the segmentation, between 1.5 s and 1 s before the following button press. The power spectrum in the frequency range between 1 Hz and 30 Hz was estimated with the Welch’s method: the fast Fourier transform was computed on each 1 s long time window and averaged over 14 parietal and occipital electrodes and over the time windows belonging to each individual perceptual representation. Because the alpha peak shows inter-individual variability (Haegens et al., 2014), we defined the limits of the alpha band for our group of participants based on the observed peak in the power spectrum.

Regression of the Duration of Perceptual Representations on their Alpha Power

Regression analysis was used to address the hypothesis that the duration of each individual representation would in part depend on the power of alpha during that representation (Fig. 7.2). Alpha power, computed on the 1 s long, 50% overlapping time windows as described above, was averaged for each of the stable perceptual representation intervals of vari-
Figure 7.2: EEG data were recorded continuously while participants reported the perceived reversal of the representation of the ambiguous Necker cube by pressing a button. In the first analysis, alpha power was computed on the whole period in which a representation was perceived, excluding the periods just preceding and following the button presses (gray areas). In the second analysis, alpha power calculated on a sliding window right after the reversal was used to predict the duration of the following perceptual representation.

The predictive effect of alpha power on the duration of individual perceptual representations was evaluated using linear mixed-effects regression model (LMEM). LMEM partitions the otherwise correlated error terms across the four nested levels (subject-level, day-level, session-level, and at the level of individual perceptual representations) and accounts for the variable number of epochs across sessions (Laird and Ware, 1982; Pinheiro and Bates, 2000; Snijders and Bosker, 2012). Regression coefficients were estimated using maximum likelihood. The significance of the regression coefficient which represented the effect of alpha power on the duration of perceptual representations was evaluated using the Wald test that calculates a z-value as the ratio of the coefficient over its standard error. LMEM were computed using the lme4 package (Bates et al., 2013) in R 2.14 (R Development Core Team, 2010).

Alpha Power Around the Reversals

To investigate how power in the frequency range up to 30 Hz was modulated by the occurrence of the reversal of the perceptual representations, we calculated the time-frequency representation (TFR) of the power in the interval between $-1$ s and $1$ s, centered on the button press. A fast Fourier transform at each frequency $f_0$ between 2 Hz and 30 Hz was computed on sliding time windows whose duration was equal to the lengths of 5 waves at $f_0$ (at 2 Hz, the length of the time window was 2500 ms and at 30 Hz, it was 167 ms) after multiplication with a Hanning taper.

Alpha Power Predicts the Duration of Individual Perceptual Representations

To address the question of how soon after the onset of each individual perceptual representation alpha determined the fate of its duration, alpha power was calculated over sliding windows (500 ms width, 50 ms step size) starting at the reported onset of each individual percep-
Fluctuations in Alpha Power Between the Reversal

We then investigated whether alpha power after the perceptual reversal remained stable, increased or decreased within each individual perceptual representations. The intervals during which a perceptual representation was dominant were divided in 1 s long, 50% overlapping segments, excluding the 2 s around the button press. The time stamp was given by the midpoint of the segment, therefore the segments had time $-1.5 \text{s}$, $-2 \text{s}$, $-2.5 \text{s}$, etc. Alpha power was calculated on each segment and log-transformed. In order to normalize the level of alpha power, such that it was comparable across individual perceptual representations that had different duration, a baseline correction was applied by subtracting the amount of alpha power in the first available segment from the amount of alpha power in each segment. We then averaged over the segments that were at the same distance from the following reversal. Because individual perceptual representations with longer durations were relative rare, to have robust estimates of the amount of alpha power at each time point we only considered segments that were within 25 s from the following reversal.

Source Analysis

Regression of the duration of individual perceptual representations on alpha power was calculated at each brain location on a 1 cm spaced grid using a frequency-domain beamformer (Gross et al., 2001). The analysis was conducted on the average power over the interval between two button presses. The volume conduction model was calculated from a template MRI, distributed with SPM8 and segmented (Litvak et al., 2011) using a 3-level boundary element model (BEM) (Oostendorp and van Oosterom, 1989), each consisting of 1500 vertices. The conductivity for the three compartments (scalp, skull, and brain) was 0.33, 0.0041, and 0.33 S/m, respectively (Rush and Driscoll, 1968). The frequency-domain beamformer is a spatial filter defined by the forward model, the cross-spectral density, and a regularization parameter (Gross et al., 2001). The cross-spectral density (CSD) was computed using multitapering (Mitra and Pesaran, 1999) in the alpha frequency band and the regularization parameter was kept at 5%. Interpolated channels were not used for the computation of the CSD. To obtain a robust estimate of the CSD matrix, we applied a common filter approach, by which the CSD (and therefore the spatial filter) is calculated from all the individual perceptual representations in a session and then the spatial filter is reused on the data from each individual perceptual representation. This procedure returns the estimated alpha activity at each location in the brain for each individual perceptual representation.

The log of the alpha power was used as regressor for the log of the durations of the individual perceptual representations, using an LMEM, with participants, sessions, and individual epochs of perceptual representations as nested levels. The z-value for each location in the brain, which reflects how well alpha power in that location was associated with the interval duration, is then projected onto the cortical surface for illustration purposes.
RESULTS

Figure 7.3: Probability distribution of the durations of individual perceptual representations during Necker cube viewing after normal sleep. The distribution had a positive skew, with a mean value of 8.87 s and a median value of 5.94 s.

Sleep Deprivation 1: Alpha Power

The effect of sleep deprivation on alpha power, which was averaged over the parietal and occipital electrodes (indicated by a marker in Fig. 7.4B), was computed using an LMEM, with the same nesting structure (subject-level, day-level, session-level, and at the level of individual epochs of perceptual representations). The Wald test was used to evaluate significance of the factor ‘sleep deprivation’ on log-transformed alpha power.

Sleep Deprivation 2: Duration of Individual Perceptual Representations

The effect of sleep deprivation on the duration of individual perceptual representations was quantified using three separate tests: (I) whether the distribution of the durations of individual perceptual representations after normal sleep and after sleep deprivation were different was evaluated using a Kolmogorov-Smirnov test implemented in ks.test (Conover, 1971); (II) whether the average duration of individual perceptual representations was longer after sleep deprivation than after normal sleep, was evaluated using LMEM, with four nested levels and sleep deprivation as factor, on the log-transformed duration of the intervals between button presses; (III) whether the relative frequency of particular ranges of durations of individual perceptual representations was affected by sleep deprivation. This test was computed by binning the intervals durations in 2 s intervals, starting with the interval 1–3 s, to form an empirical probability density distribution. For each bin, we computed the probability of observing a perceptual reversal in that time interval, using the Wilson score interval test, implemented in prop.test (Newcombe, 1998; Wilson, 1927).

Sleep Deprivation 3: Mediation Analysis

The possible mediation by alpha power of the effect of sleep deprivation on the average duration of individual perceptual representations evaluated using an LMEM implementation of the Sobel test (Bliese and Hanges, 2004; Krull and MacKinnon, 2001; MacKinnon et al., 2002). Regression coefficient estimates and their standard errors were computed for each path using an LMEM with a nested structure as above (subject-level, day-level, session-level, and at the level of individual epochs of perceptual representations). The Sobel test is defined as the ratio between the estimated ab path and its standard error. The former is computed as the product of a and b and the latter as \[ \sqrt{\frac{a^2}{\sigma_b^2} + \frac{b^2}{\sigma_a^2}} \] (Sobel, 1982). The ratio yields a z-value that can be used to obtain a p-value.

Results

High-density EEG was recorded five times a day for four minutes in eight participants while they viewed a Necker cube image (Fig. 7.1) and reported the alternation between the two bistable representa-
Figure 7.4: Distribution of alpha power after normal sleep in the frequency-, space-, and time-domain. (A) Power spectrum of the EEG recorded over parietal and occipital electrodes in the interval between button presses indicating reversals. The power spectrum shows a clear peak at ~9 Hz, the gray area indicates the frequency boundaries used in the subsequent analysis (7–11 Hz). (B) Topographic distribution of alpha power between perceptual reversals. Alpha power was averaged over the parietal and occipital electrodes indicated by a marker and used in the regression analysis with the subsequent duration of the individual perceptual representation. The same electrodes were used for the subsequent analyses.

Figure 7.5: (A) TFR of the time window around the button press, averaged over the 14 parietal and occipital electrodes indicated in Fig. 7.4B. Alpha power decreases just before the perceptual reversal and increases thereafter. (B) Alpha power after the onset of an individual perceptual representation was predictive of its subsequent duration, quantified by the z-values computed on a 500 ms long sliding window centered in the interval between 0 s and 1 s. The dotted line at 1.96 indicates the z-value threshold at p-value = 0.05.

Stable Perceptual Representations Have Higher Alpha Power

Separate alpha power averages were calculated for each of the reported stable perceptual representation intervals, using Welch’s method, where intervals of variable duration were segmented into 1 s long, 50% overlapping windows. Regression analysis revealed that stable perceptual representations, i.e. of long duration, were characterized by high alpha power, while short-lasting perceptual representations were characterized by low alpha...
RESULTS

power (estimated effect of alpha power
= 0.128 log(s)/log(µV²), s. e. = 0.039,
 z-value = 3.235, p-value < 0.001, r² = 0.20).

Alpha Power at Onset of a Perceptual Representation Predicts the Fate of its Duration

Given the role of alpha in the duration of a perceptual representation, we investigated the phasic changes in alpha power associated with the perceived reversal of the representations of the Necker cube. As reported before (Isoglu-Alkaç et al., 2000; Nakatani and van Leeuwen, 2006; Strüber and Herrmann, 2002), alpha power decreased just before the time of button press (Fig. 7.5A), reaching a minimum during the presumed time of the reversal (Luce, 1986; VanRullen et al., 2006).

We then addressed the question of how soon after the onset of the each individual representation the amount of alpha power could predict the duration of the individual representation. Alpha power was calculated over sliding windows (500 ms width, 50 ms step size) starting at the reported onset of each representation. The alpha power at each sliding window was correlated with the duration of subsequent individual perceptual representation, using LMEM, whereby a high correlation means that alpha power right after the perceptual reversal is predictive of the duration of the upcoming individual perceptual representation. Already in the window centered 200 ms after the reported onset of a perceptual representation, was alpha power significantly predictive of the fate of its duration (Fig. 7.5B) and the peak significance within the first second after the button press was reached already for the window centered 400 ms after its onset (z-value = 3.286, p-value < 0.001).

Fluctuations in Alpha Power Between the Reversal

After showing that alpha after the reversal was predictive of the subsequent duration of the perceptual representation, we investigated whether reversals were preceded by any consistent pattern of fluctuations in alpha power. The intervals during which a perceptual representation was dominant were divided in 1 s long, 50% overlapping segments, again excluding the 2 s around the button press. For each of these segments, defined by their distance in seconds to the subsequent reversal, we calculated alpha power, which was baseline-corrected by taking the difference with the first available segment. We then averaged alpha power based on the distance of the segment to the following reversal, using segments that were within 25 s of the following reversal (i.e. there were at least 80 segments to compute a robust average). We observed that the time course of alpha power relative to the subsequent reversal was relative stable (Fig. 7.6).

Perceptual Stability Involves Occipital Alpha

The frequency-domain beamformer source-reconstruction algorithm (Gross et al., 2001) was applied to identify the brain regions in which alpha power was most strongly associated with the duration of individual perceptual representations. Using multitapering (Mitra and Pesaran, 1999) in the alpha frequency band centered at 9 Hz with 4 Hz frequency smoothing (based on the observed peak in the power spectrum), scalp recordings over the interval between two button presses were transformed into the cross-spectral density (CSD) matrix, which, together with a forward model based on the template MRI distributed
with SPM8 (Litvak et al., 2011), was used to estimate alpha power in each of 2015 voxels of the brain, calculated on a 10 mm spaced grid. The estimated alpha power in each of the voxels was used as regressor of the duration of individual perceptual representations, using the same LMEM approach as applied for the scalp-level analysis reported above. Fig. 7.7 gives a graphical representation of the voxels of which the estimated alpha power significantly predicted the duration of individual perceptual representations ($z$-value $\geq 2.326$, one-sided $p$-value $\leq 0.01$). These were mostly localized in the bilateral medial parts of the higher occipital cortex and in the occipital-parietal junction.

**Alpha Power Partly Mediates Sleep Deprivation-Enhanced Perceptual Stability**

Sleep deprivation has been shown to increase eyes-open alpha power (Corsi-Cabrera et al., 1992; Drapeau and Carrier, 2004; Ferreira et al., 2006; Torsvall and Akerstedt, 1987). We argued that, if alpha functionally contributes to the stability of individual perceptual representations, a sleep deprivation-induced increase in alpha should, on average, increase their durations. Sleep deprivation indeed affected the distribution of durations (Kolmogorov-Smirnov D = 0.089, $p$-value $< 0.001$) that became longer on average (0.251 log(s), s. e. 0.092, $z$-value = 2.728, $p$-value = 0.009). A closer examination of the distribution of the durations of individual perceptual representations, using bin-by-bin (2 s) comparisons with a Wilson score interval test (Newcombe, 1998; Wilson, 1927), revealed that sleep deprivation made short durations less likely to occur (3–5 s, $p$-value = 0.001; 9–11 s, $p$-value = 0.028) and long durations more likely to occur (17–19 s, $p$-value = 0.005; 23–25 s, $p$-value = 0.022; 39–41 s, $p$-value = 0.011).

Mediation analysis was applied to evaluate whether the sleep deprivation-induced rightward shift in the distribution of the durations could be attributed to the sleep deprivation-induced increase in alpha power during the individual perceptual representations (0.202 1/log($\mu V^2$), s. e. 0.077, $z$-value 2.607, $p$-value = 0.009). Mediation was investigated using a linear mixed-effects model implementation of the Sobel test (Bliese and Hanges, 2004; Krull and MacKinnon, 2001; MacKinnon et al., 2002). Following the terminology in mediation analysis literature, the $a$ path corresponds to the effect of sleep deprivation on alpha power, the $b$ path is the effect of alpha power on the duration of individual perceptual representations after partialing out the effect of sleep deprivation, the $c$ path is the unmediated effect of sleep deprivation on the duration of individual perceptual representations and $ab$ is the part of the effect of sleep deprivation on the duration of individual perceptual representations that is mediated by its effect on alpha power (Fig. 7.8). Indeed, the effect of sleep deprivation on the duration of individual perceptual representations was in part mediated by its effect on alpha power (path $ab$, estimate 0.022, s. e. 0.011, $z$-value = 2.059, $p$-value = 0.039; estimate for the $a$ path 0.201, s. e. 0.077; estimate for the $b$ path 0.111, s. e. 0.033) while the unmediated effect (path $c$) was 0.222 (s. e. 0.078).

**Discussion**

The present study addresses the role of EEG alpha oscillations in adjusting the flexibility of the brain to either maintain its current configuration of neuronal activity and the corresponding perceptual representation, or rather switch to a different one. Using a bistable perception
Figure 7.6: The timecourse of alpha power during the individual perceptual representation was relatively stable over time. We excluded recordings within one second of the reversal to avoid transient effects due to the reversal. Alpha power is taken relative to the interval of 1–2s after the reported reversal at the beginning of the individual perceptual representation. Gray areas indicate the standard error of the mean.

Paradigm, we observed that higher alpha power was correlated with longer duration of the individual perceptual representations. The duration that an individual perceptual representation will remain stable can already be predicted from the amount of alpha power observed during the very first second after the emergence of that representation. Intriguingly, perceptual representations could last up to a minute, adding support to previous reports of long-range temporal determination in human brain oscillations with relevance to perception and behavior (Linkenkaer-Hansen et al., 2001; O’Connell et al., 2009; Palva et al., 2013). The association of alpha power with the stability of an individual perceptual representation persisted throughout the duration, and in fact the level of alpha power remained stable in the period between reversals. The estimated generators of the alpha oscillations controlling perceptual stability were localized in the high-level visual cortex, suggesting that alpha oscillations might reflect a mechanism involved in the control of perceptual stability. To substantiate functional involvement of alpha activity, we enhanced it by means of sleep deprivation. Indeed sleep deprivation increased the average duration of an individual perceptual representation and this effect was in part mediated by the concurrently induced increase in alpha power.

Alpha and Perceptual Stability

The strong association between alpha power and perceptual stability found in our study adds to our understanding of the observation that spontaneous fluctuations in alpha power are associated with trial-by-trial variability in cognitive performance (Ergenoglu et al., 2004; Kelly et al., 2009; van Dijk et al., 2008; Wyart and Tallon-Baudry, 2009). In particular, alpha power is high just before or during trials with poorer performance in visual detection tasks (Hanslmayr et al.,
2007; Mathewson et al., 2009; Thut et al., 2006). These observations have supported the interpretation that alpha reflects the inhibition of the processing of visual information in lower visual areas, before the information reaches cortical regions involved in conscious perception and in the initiation of a behavioral response. A beneficial effect of this system is that alpha acts as a filter that prevents the broadcasting of irrelevant information, such as unimportant object’s attributes or distractors (Jensen et al., 2012; Jensen and Mazaheri, 2010; Mathewson et al., 2011; VanRullen and Koch, 2003). In tasks where the relevance of each stimulus is defined by the experimental paradigm, alpha oscillations act on the neuronal populations encoding the distractor, as higher alpha power can be measured in the neuronal populations assumed to encode the irrelevant elements (Bonnefond and Jensen, 2012; Haegens et al., 2011; Händel et al., 2011). This interpretation can be extended to our findings, while keeping in mind that our experimental paradigm differs from those previous observations in a crucial aspect: The dominant representation of the stimulus is not dictated by the protocol, but it fluctuates as perception fluctuates between the two incompatible representations. At any given time, only one perceptual representation is dominant, while the other representation, which is vying for dominance and destabilizing the perceptual state, becomes the distractor. In this perspective, high alpha power is actively suppressing the non-dominant representation, similar to the suppression exerted on the populations encoding the distractor. Consequently, periods of high alpha activity are characterized by a successful suppression of the non-dominant representation and by a more stable, i. e. longer, perceptual durations.

Support for this interpretation comes not only from the association between high levels of alpha activity and longer durations of individual perceptual representations, but also from the observation that alpha activity decreases around the time of the perceptual reversals (Fig. 7.5A) (Isoglu-Alkaç et al., 2000; Nakatani and van Leeuwen, 2006; Piantoni et al., 2010; Strüber and Herrmann, 2002). Because the perceptual reversal precedes the button press by a few hundred milliseconds (VanRullen, 2007), the period during which alpha power is at its minimum may represent the time during which perception becomes unstable and it transitions to the competing perceptual representation. Only after one representation becomes dominant, does alpha resume its role in stabilizing perception. Interestingly, the level of alpha power immediately after the onset of an individual perceptual representation already predicts its duration for up to a minute.

**Attractor Model of Perceptual Stability**

The observation of the relationship between alpha power and the duration of the individual perceptual representations can shed light on the role of spontaneous brain oscillations in controlling perceptual stability, especially in the context of multistable perception. Several models have been proposed to describe the alternation between incompatible perceptual representations in the case of ambiguous stimuli. One of the most influential models, the “cross-inhibition – adaptation” model, proposes cross-inhibition between two competing neuronal populations and a slow adaptation process that slowly attenuates the inhibition to finally allow the other pool to take over and become dominant (Blake, 1989; Blake and Logothetis, 2002; Wilson, 2003). This process
alternates in a limit cycle between the two possible interpretations. The inclusion of the effect of noise as driving factor in multistable perception has led to the proposal of the “noise-driven attractor model” (Braun and Mattia, 2010; Kornmeier and Bach, 2012; Moreno-Bote et al., 2007; Panagiotaropoulos et al., 2013). In this view, noise is the driving force behind transitions between two bistable states. A switch can occur only when noise allows for crossing of the barrier between them. Bistable perception has been conceptualized as a chaotic system where each of the two incompatible representations constitutes an attractor (Braun and Mattia, 2010; Kornmeier and Bach, 2004, 2012). Perception orbits around one attractor until it transitions into the alternative representations. The duration of each alternative representation is stochastic and determined by the distance, in perceptual space, between the two attractors.

We propose that alpha power increases the distance between the two attractors, thereby decreasing the likelihood of a transition to the neuronal configuration encoding the alternative perceptual representation. Support for this interpretation comes from the observation that alpha power is relative stable in the interval between reversal (Fig. 7.6). This stability indicates that perception is entrained in one of the two attractors: As long as alpha power remains at high level, the distance between the two attractors is insuperable and perception remains fixed in one state. When alpha decreases just before the reversal, perception has the op-
portunity to switch to the other attractor state.

In this framework, a major function of alpha activity is to stabilize the current configuration of neuronal activity and its corresponding perceptual representation. Several reports have suggested that alpha oscillations could interfere with the optimal cognitive processing by impeding the responsiveness to environmental stimuli (Hanslmayr et al., 2007; Mathewson et al., 2009; Thut et al., 2006). We contended that a heterogeneous set of findings on the role of alpha oscillations across different cognitive domains might be reconciled by considering alpha power to reflect stabilization of the current configuration, by increasing the distance between multiple attractors in the perceptual state. Periods of high alpha power, therefore, would stabilize perceptions, and spontaneous fluctuations in alpha power would represent a reliable marker of the perceptual stability.

Sleep Deprivation

We experimentally enhanced alpha activity by means of sleep deprivation (Corsi-Cabrera et al., 1992; Drapeau and Carrier, 2004; Ferreira et al., 2006; Torsvall and Akerstedt, 1987). The manipulation led to an increase in the average duration of perceptual representations. Mediation analysis suggests that alpha power contributes to the sleep deprivation-induced perceptual perseveration, supporting a functional role of alpha. These results support the notion that even the experimentally enhanced alpha activity affects the degree of perceptual stability. Increased alpha power, induced by, e.g., sleep deprivation, has a double-edged consequence: on the one hand, alpha promotes perceptual stability and, on the other, diminishes the ability to switch to other, possibly more relevant, representations. This observation provides a fertile theoretical framework which can readily incorporate previous findings of poor performance in sustained attention and cognitive switching after sleep deprivation.

Sustained attention is severely reduced after sleep deprivation (Lim and Dinges, 2008, 2010). Sleep-deprived participants fail to report the presence or change in appearance of the target stimulus (Rakitin et al., 2012; Tucker et al., 2009) and the neuronal signature does not contain traces of the processing of the visual stimulus (Hoedlmoser et al., 2011). In our framework, high alpha power increases of the cost of transition to the brain state required to initiate stimulus evaluation and behavioral responding. This hypothesis would account for two empirical observations. Firstly, the failure to respond to stimuli can mostly been attributed to deficits occurring in the earliest phase of stimulus processing (Tucker et al., 2011). Once the transition to an activated brain state has occurred, the processing of stimulus will proceed unhindered. Secondly, variability in successful task execution increases after sleep deprivation, and periods of relatively high performance only occur in sporadic bouts (Doran et al., 2001). In our framework, the location of the attractors in the state space becomes less stable and the distance between attractors might alternate periods of short distance (where the transition is more likely and performance remains high) with periods of long distance (where performance rapidly deteriorates).

Lower cognitive flexibility and perseveration when switching yields a higher reward are among the most consistently reported yet poorly understood markers of cognitively fatigued (van der Linden et al., 2003) and sleep-deprived individuals (Couyoumdjian et al., 2010; Gottselig et al., 2006; Harrison and Horne, 1999; Herscovitch et al., 1980; Horne, 1988; Killgore
Figure 7.8: Alpha power partly mediates sleep deprivation-induced increase duration of perceptual representations. Sleep deprivation increased the duration of individual perceptual representations (path c). In particular, after sleep deprivation, the stability of individual perceptual representations was less likely to last less than 10 s and more likely to last around 20 s. In agreement with previous work, sleep deprivation increased eyes-open alpha power (path a). Mediation analysis suggested this increase in alpha power contribute to the increase in the duration of individual perceptual representations (path ab).

et al., 2009; Wimmer et al., 1992). As perceptual inflexibility, this cognitive inflexibility is the result of an increased distance between cognitive states. These increased distance between cognitive states, however, become less problematic for those executive functions that profit from maintenance enhancement. These functions may be more robust to interference with sleep deprivation or even profit from it (Altena et al., 2008; Tucker et al., 2010). Future studies should address the possible role of alpha in the perseveration and difficulties with flexibility and task-switching that are among the most characteristic, yet mechanistically elusive, findings after sleep deprivation.

Conclusions

Using the bistable perception paradigm, we here demonstrate that alpha activity reflects the stability of a perceptual representation. Already 200 ms after its reported onset, alpha power had significant predictive value for the duration of an individual representation. The level of alpha power throughout the duration of the individual representation was a consistent marker of the degree of stability of the perceptual system. These findings can be conceptualized within a framework where high alpha power increases the distance, in perceptual space, between multiple attractors, each corresponding to one of the mutually exclusive perceptual alternatives. Such a stabilizing role of alpha may parsimoniously explain both its association with the inability to detect external stimuli, often observed during
CHAPTER 7

sleep deprivation, and its role in optimizing cognitive performance, e.g. in maintaining focus in working memory tasks.

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