

*There are things known and there are things unknown,
and in between are the doors of perception.*

Aldous Huxley, 1954

The role of spontaneous brain activity in perception

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INTRODUCTION

From the moment we are born, until the moment we die, we are trying to understand what is happening within and around us. Appreciating which phenomena have a common cause or identity, and which are separate, is fundamental to reach such an understanding. For example, babies learn very early on, that drinking milk will soothe that unpleasant sensation in their tummies. And that the changing shape of their father's mouth is somehow related to the soothing sound of his voice. In perception, signals with a common cause should be integrated, whereas those with different causes should be segregated. Sensory signals can be integrated over space (such as when we identify a tree based on the leaves, branches and trunk), or over time (such as when we identify words based on a sequence of sounds created by the speaker). They can be integrated within, but also between the senses (such as when the lightshow at a rave seems to add a whole extra dimension to the music). The appropriate integration of stimuli leads to coherent perceptual experiences which allow us to behave in tune with our environment. Inappropriate integration, in contrast, could lead to illusory perceptual experiences, and will leave us out of tune with the material reality of our environment. For example, in the rubber-hand illusion (Botvinick & Cohen, 1998), people sit with one forearm on a table which is then hidden from sight. Next to their own hidden arm, a fake rubber arm is placed. Their real and the fake middle fingers are then stroked simultaneously and synchronously, while the person looks at the fake hand. After a while, through the integration of the visual and touch sensations, their brain mistakenly concludes that it is the rubber hand that must be part of their body, and not their own hand. Although most people are susceptible to this and also other illusions of integration, evidence is accumulating of an increased susceptibility to illusory integration in certain psychiatric conditions such as dyslexia (Hahn, Foxe, & Molholm, 2014), autism (De Boer-Schellekens, Eussen, & Vroomen, 2013; Gelder, Vroomen, & Heide, 1991; Stevenson et al., 2014) and schizophrenia (Zhou et al., 2018). Appropriate sensory integration is thus of utmost importance to our connection to reality and ability to function in the world. Moreover, multisensory integration in particular, has been extensively shown to boost perception (e.g. Sumbly & Pollack, 1954; Van der Burg, Olivers, Bronkhorst, & Theeuwes, 2009; Vroomen & Gelder, 2000), attention (Talsma et al., 2010; Van der Burg, Olivers, Bronkhorst, & Theeuwes, 2008; Van der Burg, Talsma, Olivers, Hickey, & Theeuwes, 2011) and

learning (Shams & Seitz, 2008). To successfully integrate sensory signals, the brain needs to identify signals that originate from the same physical event, and spatiotemporal correlation has often been proposed as the main way it accomplishes this (Burr, Silva, Cicchini, Banks, & Morrone, 2009; Chen & Vroomen, 2013; Parise & Ernst, 2016). These spatio-temporal correlations do not need to be perfect to lead to integration however, nor should they be. In multisensory perception, such as when having a conversation, signals originating from the same event are often carried through different media and pass through different senses (light is carried by photons and sensed through photoreceptors, and sound is carried by air and sensed through mechanoreceptors) which naturally produces a temporal lag between them. Integration will occur despite such a lag, up to a certain point. Similarly, in visuo-spatial integration, such as when tracking a group of players in a soccer match, the individuals are not all in the same spot or moving completely in sync, but we can still integrate over players, up to a certain point. Importantly, what constitutes appropriate integration will in large part depend on the current internal and external contexts of the organism. Since these change continuously over time, it is important that the criteria for integration are flexibly adjusted from moment-to-moment. For example, when painting, one must occasionally switch from local spatial integration to global spatial integration to maintain a high precision of the brushstrokes, while keeping sight of the overall picture. Similarly, when riding our bike, the busier it gets around us, the shorter the lag over which we should integrate auditory and visual signals, since these correspond to the events occurring closest and therefore most relevant to us. Furthermore, independent of which activity we are doing, there will be spontaneous changes in our internal context. In this thesis, I will attempt to uncover the brain dynamics that might reflect these changes in internal context and underlie moment-to-moment variability in temporal and spatial integration. To date, most of the evidence has been gathered by repeatedly observing the behavior of interest under multiple experimental conditions and then comparing the average values of the observed behavior in each condition. Variability across observations in the same condition is considered to be a nuisance and is removed through averaging. This effectively isolates the factors that are manipulated from those contextual factors that give rise to the moment-to-moment variability. Precisely those contextual factors that are averaged out, however, might

be crucial in determining whether an integrated perceptual experience ensues after a stimulus meets a sensory organ or whether different aspects of the stimulus are experienced separately. An alternative approach can be found in the analysis of single trials, which allows uncovering systematic relations between fluctuations in integration and contextual factors that occur on a short timescale. As a proxy for the internal context, I will focus on the analysis of pre-stimulus, ongoing brain activity as measured with the electroencephalogram (EEG), and link three of its parameters (power, frequency and the slope of the power spectrum) to fluctuations in spatial and temporal integration. The main aim of this doctoral thesis is to advance our understanding of how spontaneous, or background, brain activity relates to the integration vs. segregation of information across time and space.

SPONTANEOUS ELECTRICAL BRAIN ACTIVITY AND PERCEPTION

The temporal structure of ongoing EEG activity is characterized by the coexistence of rhythmic oscillatory activity and arrhythmic scale-free activity, indicative of processes or patterns that are repeated across scales of analysis (He, 2014). Oscillations are recurring patterns of brain activity that adhere to a regular temporal beat. The power spectrum of any one particular oscillation contains a peak at the frequency of that temporal beat. For instance, the “alpha” oscillation, which I will discuss more extensively below, shows a peak in the power spectrum around 10 Hz, since it repeats approximately 10 times per second. The power spectrum of scale-free activity in contrast, does not show peaks at any particular frequency, since its pattern of repetition is not dominated by any particular timescale or frequency. Rather, patterns are repeated across a wide range of timescales, much like the pattern of a Romanesco broccoli plant is repeated across spatial scales (see fig. 1A). The power spectrum of such scale-free activity is characterized by a $1/f^\chi$ power-law shape. That is, power decreases exponentially as a function of frequency, where the power-law exponent (PLE) χ determines the slope of that decline. In a typical EEG power spectrum, both oscillatory and

scale-free dynamics are readily apparent (see fig 1B). In the following two sections, I will describe these two aspects of spontaneous brain activity and how they relate to, mainly temporal, but also to spatial integration.

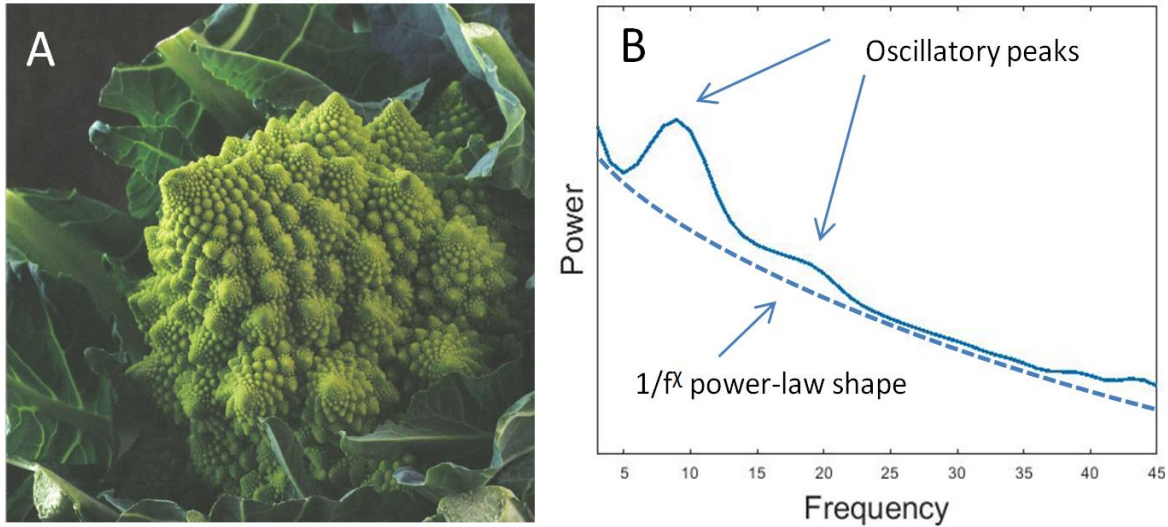


Figure 1.1 $1/f^x$ power-law scaling A. Romanesco broccoli displaying spatial scale-free $1/f^x$ power-law scaling. B. EEG power spectrum showing both scale-free and oscillatory activity.

OSCILLATIONS

The oscillations that we measure at the scalp in the EEG reflect the synchronized fluctuations of post-synaptic potentials generated by inhibitory and excitatory activity across large neuronal populations (Nunez & Srinivasan, 2006). Oscillations in five canonical frequency bands have been linked to specific aspects of cognition and perception. Delta oscillations (0.5 – 3.5 Hz) have been observed to vary most often in the context of basic motivational and survival-related processes such as appetite, pain or sexual arousal (Knyazev, 2012). Theta oscillations (3.5 – 7 Hz) correlate with performance on tasks testing constructs such as memory, attention and cognitive control (Ward, 2003). Alpha oscillations (8 – 13 Hz) have been extensively studied and seem to be intimately linked to visual, auditory and somatosensory perception and attention (Clayton, Yeung, & Kadosh, 2017). Beta oscillations (15 – 25 Hz) are relevant for motor-related processing (Jenkinson & Brown, 2011) and have also been implicated in perceptual processes (Hipp, Engel, & Siegel, 2011). Finally, gamma oscillations (30 – 70 Hz)

have been related to a broad range of processes including feature integration, stimulus selection, attention, memory and consciousness (Jensen, Kaiser, & Lachaux, 2007; Singer & Gray, 1995). One explanation for the differentiation of functions according to frequency is the observation that the frequency of an oscillation is inversely related to the distance across which synchronization takes place. In general, the more “local” a process is, and thus the smaller the distance at which neural synchronization takes place, the higher the frequency at which the relevant neural population can oscillate (von Stein & Sarnthein, 2000). This relationship is largely due to the limitations imposed by axon conduction delays (Voss & Clarke, 1976). Although oscillations in each of the frequency bands described above seem to be related in one way or another to uni- and multi-sensory perceptual integration, evidence has been mounting that especially alpha oscillations play a pivotal role in perception (Brüers & VanRullen, 2018; Clayton et al., 2017). This evidence will be discussed below.

Alpha oscillations

The most prominent peak of the power spectrum is commonly found between 8 and 13 Hz. This peak in the frequency domain corresponds to the alpha oscillations that can readily be seen in the time-domain EEG signal and which is the most pronounced over occipital and parietal areas of the brain. Because of their prominence they were the first feature of the EEG to be described by its inventor Hans Berger (1929). Initially, alpha was thought to reflect a state of relaxation or idling, since alpha increased in power when people closed their eyes. However, a more complex picture has emerged in recent years, and different aspects of alpha oscillations have been proposed to underlie a broad range of neurocognitive functions such as temporal perceptual integration, memory maintenance, inhibition of irrelevant information, and top-down attention (Clayton et al., 2017). It has also become clear that there is not one single process that generates these alpha waves. Broadly speaking, we can identify two classes of processes involved in the generation of alpha waves observed at the scalp. First, alpha oscillations are generated by a range of interconnected processes in the thalamus (Ohmoto et al., 1978; Goldman, Stern, Engel, & Cohen, 2002). Second, alpha oscillations have also been shown to originate from the cortex itself (e.g. Lopes da Silva,

1991). Moreover, multiple cortical generators of alpha can co-exist and covary with one and the same behavioral variable. The existence of such a multiplicity of alpha rhythms makes it unsurprising that so many functions seem to be related to alpha activity. It is therefore not straightforward to achieve a one-to-one mapping of brain function to any aspect of these oscillations (e.g. Benwell et al., 2018). Nevertheless, for all the many functions that have been ascribed to alpha oscillations, there is one central theme to most current theories which is that alpha reflects fluctuations in the balance of cortical excitation vs. inhibition and plays an active role in shaping perception (Foxye & Snyder, 2011; Jensen & Mazaheri, 2010; Klimesch, Sauseng, & Hanslmayr, 2007; Mathewson et al., 2011; VanRullen, 2016). On a short time-scale, the alpha oscillations themselves reflect rhythmic fluctuations between more and less excitable states of the cortex. Excitability is highest at the trough of the wave and lowest at its peak (Buzsáki & Draguhn, 2004; Dugue, Marque, & VanRullen, 2011; Lindsley, 1952). Not only the alpha oscillation itself reflects a fluctuation between higher and lower levels of excitability; at a time-scale superseding the length of the alpha cycle itself, so do periods of higher and lower alpha power, (Romei et al., 2008; Samaha, Gosseries, & Postle, 2017), with higher alpha power indicating lower excitability and vice versa.

Alpha phase and frequency

Dustman and Beck (1965) were among the first to suggest that alpha waves reflect an excitability cycle in the human cortex. They conducted a reaction time study where participants were instructed to respond to single flashes of light as quickly as possible. Reaction times were found to be reliably faster when the stimulus light was flashed during the trough of the alpha wave and slower when it was flashed at the peak of the alpha wave. These results were interpreted as evidence for alpha reflecting an excitability cycle, and this has been corroborated by several other studies since (Busch, Dubois, & VanRullen, 2009; Dugue et al., 2011; Mathewson, Gratton, Fabiani, Beck, & Ro, 2009). For example, Busch, Dubois, and VanRullen (2009) presented short light flashes at participant's individual detection threshold. They found that the probability of detection depended on the phase of low alpha/theta oscillations just before stimulus onset. Such results suggest that perception may cycle periodically between moments of

weaker inhibition/higher excitability (when stimuli at threshold are consciously perceived) and moments of stronger inhibition/lower excitability (during which the same stimuli are more likely to go undetected). The idea that alpha oscillations reflect a cycling between more and less excitable states of the cortex, where stimuli are more or less likely to be perceived speaks to the question of whether perception is discrete or continuous. In an attempt to shed some light on this question VanRullen and Koch (2003) and later VanRullen (2016) proposed that neuronal oscillations, and more specifically low-frequency rhythms such as alpha oscillations provide the structural basis for behaviorally observed fluctuations in perception. More specifically, they proposed that it is the length of the alpha cycle that determines the length of a visual perceptual frame. An important question when assuming discrete perception is what happens to the sensory information that arrives in between each frame; that is, during the phase of low excitability. One suggestion is that it is deferred to the next frame, thereby creating ripples in the temporal structure of perception with some percepts being “pushed” forward in time, away from their actual time of existence towards the future. Another consequence is that sequential stimuli that fall into the same cycle will be perceived as having occurred simultaneously, and any order-information is lost. Evidence for this idea has been provided by Varela, Toro, Roy John, and Schwartz (1981). They presented three participants with two flashes of light with an unvarying SOA, but at different phases of the ongoing alpha rhythm. They found that the probability of the stimuli being judged as simultaneous or sequential depended on the phase at which the flashes were presented. At one particular phase they would be judged as simultaneous, and at the opposite phase they were perceived as sequential. More recently, Milton and Pleydell-Pearce (2016) presented two flashes of light with synchronous or asynchronous onsets. At a certain phase of the alpha cycle, participants were more likely to correctly perceive asynchronous stimuli than at the other, near-opposite phase.

If alpha oscillations create periodic “windows of excitability”, then the frequency of the alpha rhythm should predict the length of this window and the temporal resolution of perception. Samaha and Postle (2015) tested this by relating the temporal resolution of visual perception with the frequency of the alpha rhythm. The temporal resolution of visual perception was measured as the inter-

stimulus interval (ISI) at which two successively presented, spatially overlapping light flashes could be discriminated from a single flash, known as the two-flash fusion threshold. Faster alpha frequencies predicted more accurate flash discrimination, both between and within participants. To test whether frequency modulation of alpha supports top-down control over temporal integration, Wutz, Melcher, and Samaha (2018) recorded magnetoencephalography (MEG) data while observers performed two tasks, one requiring visual integration over time (the missing element task or MET) and the other requiring visual segregation over time (the odd element task or OET). In the MET, an array of elements is presented in two successive frames, separated by a short interstimulus interval (ISI). When superimposed, the elements in both frames occupy all but one of the positions in the array and the observer's task is to identify this empty position. The task becomes easier as the ISI decreases and the two frames become perceptually integrated. In the OET, one-half of one of the elements is presented in the first frame and the other half is presented in the second. Here, the observer's task is to identify the location of this odd element. In contrast to the MET, this task becomes easier as ISI increases and the frames are perceptually segregated. When participants switched between the MET and OET, the peak frequency of alpha oscillations decreased and increased, respectively. Finally, using a similar paradigm, Ronconi, Busch, and Melcher (2018) were able to simultaneously modulate performance on the temporal integration and segregation tasks by entraining alpha oscillations to 2 Hz above or below each individual's peak frequency. When entraining to a higher frequency, thereby shortening the windows of excitability, accuracy improved on the segregation task, but worsened on the integration task. When entraining to a lower frequency the opposite pattern of results was found.

Taken together, the above-mentioned studies have provided converging evidence for the notion that alpha oscillations determine the temporal resolution of visual perception. In addition, some evidence has been found to indicate a similar relation between beta oscillations and somatosensory perception (Baumgarten, Königs, Schnitzler, & Lange, 2017; Baumgarten, Schnitzler, & Lange, 2015; however, see (Baumgarten, Schnitzler, & Lange, 2017)). A crucial question regarding these perceptual cycles is whether they only occur within the limited scope of the sensory cortical area or whether they affect integration of

information across multiple brain areas and sensory cortices modalities. Studying multisensory perception, which requires the involvement of multiple sensory cortices for processing a stimulus, therefore affords us with a unique opportunity to address this question. Some work has already been done in this respect. For instance, Cecere, Rees, and Romei (2015) presented participants with a simultaneous beep and flash and then after a varying interval with a second beep. When the time between the first beep and the flash, and the second beep is shorter than ~ 100 ms, a second illusory flash is often observed. This phenomenon is known as the sound induced flash illusion (Shams, Kamitani, & Shimojo, 2000). Cecere et al. (2015) found a positive correlation between the size of the time window in which this illusion could occur and the individual alpha frequency (IAF). In a second experiment, participants performed the same task while the experimenters applied transcranial alternating current stimulation (tACS) to entrain the alpha oscillations to participants' IAF or to either 2 Hz above or below their IAF. Compared to IAF tACS, IAF-2 Hz and IAF+2 Hz tACS, respectively, enlarged and shrunk the temporal window of illusion. Keil and Senkowski (2017) replicated this study and also showed a negative correlation between the length of the window for the illusion and the IAF. These results seem to suggest that the perceptual cycles created by alpha oscillations are more than just a local phenomenon, as they can affect the integration of information across multiple sensory systems. What is actually measured in the Cecere et al. (2015) study, however, is visual perception (an illusory flash is or is not perceived) and does not necessarily imply multisensory perception in the sense that one unified multisensory stimulus is perceived. Rather, sound is shown to induce visual perception and the duration of this effect is modulated by the frequency of alpha oscillations. Supporting this interpretation, Keil and Senkowski (2017) localized the effect to the calcarine fissure, the area in and around which the primary visual cortex is located (Belliveau et al., 1991). Although these studies show that alpha oscillations provide windows of opportunity for multisensory interactions, it would be premature to conclude on the basis of these results alone that alpha oscillations create perceptual cycles that affect processing throughout the entire brain.

Another question that arises regarding these putative perceptual cycles is whether they are a fundamental aspect of our everyday perception, or whether

they manifest themselves only at (near)threshold levels. In other words, are perceptual cycles involved in fully segmenting our percepts into discrete temporal frames, or does this only happen for stimuli that are presented precisely at the perceptual threshold. Alpha oscillations do not represent a fluctuation between zero and maximal excitation but are, instead, the result of a balance of excitation and inhibition around an optimal level. Because of this, we do not experience full-blown hallucinations at the trough of an alpha cycle, and neither do we go completely blind at its peak. Perceptual processing appears to continue more or less normally throughout the entire alpha cycle. What we *do* see is a modulation in the relative probability of detecting stimuli (Busch et al., 2009; Dugue et al., 2011; Dustman & Beck, 1965; Mathewson et al., 2009), and only when they are at threshold. To make a case for a theory of perceptual frames beyond local boundary phenomena, it would at least be necessary to show an effect of slow neural oscillations on supra threshold integrated multisensory percepts. In chapter 3 I will present the results of a study that was conducted in part to test this very question.

Alpha power

In the previous paragraph we saw that the alpha cycle reflects rhythmic changes between higher and lower levels of excitation and that the phase and frequency of alpha oscillations can affect the timing and probability of perceiving visual stimuli. At a longer time-scale, we can observe periods of higher and lower alpha *power* that also indicate periods of lower and higher cortical excitability, respectively. This association was demonstrated by Romei et al. (2008) who applied transcranial magnetic stimulation to visual cortex. They found that individuals were more likely to report a phosphene (perception of a flash without light entering the eye) as a result of stimulation during periods of low alpha power than during periods of high alpha power. This evidence for a negative association between excitability and alpha power confirmed previous studies reporting that stimuli preceded by strong alpha power are less likely to be detected (Ergenoglu et al., 2004; Hanslmayr et al., 2007; Thut, Nietzel, Brandt, & Pascual-Leone, 2006) or will be perceived with less intensity (Babiloni et al., 2006). Furthermore, when alpha power is low participants are more susceptible to multi-sensory illusions (Lange, Keil, Schnitzler, van Dijk, & Weisz, 2014) and more

likely to perceive visual stimuli when none were presented (Iemi, Chaumon, Crouzet, & Busch, 2017). These findings also support the hypothesis that low alpha power is associated with higher cortical excitability.

Alpha power has been shown to affect temporal aspects of perception. For example, van Viegen, Charest, Jensen, and Mazaheri (2017) presented participants with a tone, which was followed by a flash that was presented 1 or 1.5 seconds later. Participants had to indicate whether the length of the interstimulus interval was 1 or 1.5 second. They found that the tone always elicited alpha and beta suppression over parietal and occipital electrodes, but that the long intervals were more likely to be incorrectly perceived as short intervals when alpha and beta power were less suppressed. They concluded that higher alpha and beta power led to a subjective compression of time. Baumgarten, Schnitzler, and Lange (2016) presented two supra-threshold tactile stimuli at SOA's varying from 0 to 100 ms. Participants indicated whether they perceived one or two stimuli. Intermediate SOA's were titrated per participant to result in 50% perception of one stimulus and 50% perception of two stimuli. They found that low contra-lateral alpha power over occipital and somatosensory cortices predicted the veridical perception of two stimuli. Alpha power thus seems to modulate the temporal resolution of perception. Further evidence for this conclusion was provided by Leonardelli et al. (2015) who presented participants with a tactile stimulus to the cheek, at varying SOAs with the simulated sound of a flying mosquito approaching that same location. Participants had to indicate whether they felt that it was the mosquito that touched them or not, and these responses were taken to indicate integrated vs. segregated percepts, respectively. When comparing trials with SOA's where participants experienced maximal ambiguity (where they were approximately equally likely to perceive the stimuli as integrated or segregated), higher pre-stimulus alpha power predicted an integrated percept whereas lower alpha power predicted a segregated percept.

Taken together, these results suggest that when excitability is low, cortical processing is biased towards temporally integrated perception. When excitability is high, cortical processing is biased towards temporally segregated perception. The goal of the task at hand determines whether each of these biases is desirable or not. In the studies described above, the goal of the task does not clearly describe whether integration or segregation would be desirable, but it could be ar-

gued that in a simultaneity judgement (SJ) task, the nature of the question posed to the participants “are these stimuli simultaneous or not?” implies that participants should try to temporally integrate the stimuli and then report whether they were successful or not. The goal of the task (integration vs. segregation) is therefore somewhat ambiguous. In the case of a temporal order judgement (TOJ) task, where the goal of the task is to segregate the constituent stimuli to be able to report their temporal order, the upregulation of alpha would always be detrimental. This interpretation is supported by data showing that audiovisual temporal windows of integration inferred from two-alternative forced choice (2AFC) SJ tasks are on average wider than those found in 2AFC-TOJ tasks (Stevenson & Wallace, 2013). In chapter 3 I will test whether alpha power modulates temporal order information additionally to perceived simultaneity using an audiovisual TOJ task.

The involvement of alpha oscillations in the structuring of perception goes beyond the temporal domain, and although the role of alpha oscillations in spatial attention has been extensively studied, only a limited amount of work has been done on how oscillations impact the perception of individual stimulus features. Romei, Thut, Mok, Schyns, and Driver (2012) did so by presenting participants with hierarchical stimuli which consisted of large (global) “H”, “D” and “S” letters comprised of smaller (local) “H”, “D” and “S” letters in an adaptation from the classical Navon task (Navon, 1977). The combinations could be congruent (e.g. a global “H” comprised of local “H’s”) or incongruent (e.g. a global “H” comprised of local “D’s”). Just before stimulus presentation, they stimulated left and right parietal cortices with TMS at 10 Hz. Right parietal 10 Hz stimulation significantly impaired global processing without affecting local processing, while left parietal 10 Hz stimulation impaired local processing with a minor trend to enhance global processing. These results fit with those from an EEG study where the lateralization of pre-stimulus alpha power depended on whether participants were preparing to report the local or global level information of a similar hierarchical stimulus (Volberg, Kliegl, Hanslmayr, & Greenlee, 2009). Fast responses to local targets were associated with high alpha amplitude over right centro-parietal cortex and fast responses to global targets with high alpha amplitude over left centro-parietal cortex. These two studies converge with evidence regarding hemispheric asymmetry in the processing of global vs. local features

(Gable, Poole, & Cook, 2013; Lamb, Robertson, & Knight, 1990; Martinez et al., 1997; Robertson, Lamb, & Zaidel, 1993; Robertson, Lamb, & Knight, 1988; Volberg & Hübner, 2004). Crucially, these studies show that this asymmetry is already visible during the pre-stimulus stage. In this account, the left and right hemispheres are specialized in processing local or global features, respectively, and alpha oscillations are assumed to simply indicate the inhibition of the hemisphere specialized in the “wrong” level. However, the existence of such a mechanism does not preclude the possibility that fluctuations in alpha power go beyond the mere up- or down-regulation of certain specialized areas. Quite possibly the level of excitability, as indexed by alpha power, might flexibly tune the cortex to the relevant hierarchical level. In this scenario, we should be able to observe differences in alpha power between local or global conditions irrespective of lateralization. Indeed, there is evidence supporting this idea. Fründ, Busch, Körner, Schadow, and Herrmann (2007) presented participants with gratings of varying spatial frequency and measured EEG across the scalp. They found that higher spatial frequencies evoked stronger alpha power over occipitoparietal areas than lower spatial frequencies. In a similar vein, Flevaris, Martínez, and Hillyard (2014) showed participants a bistable moving image in which perception spontaneously alternates between dissociated fragments and a single, integrated object. Alpha power always decreased before a switch, but a greater decrease in alpha (8–12 Hz) was observed when participants switched from a fragment percept to an object percept than when they switched from an object percept to a fragment percept. Similar to Fründ et al. (2007), higher alpha power was associated with local perception and lower alpha power with global attention. The effects found by Fründ et al. (2007) and Flevaris et al. (2014) were bilateral and existed over occipitoparietal areas, whereas the lateralized effects discussed above were apparent mainly over centro- and temporo-parietal areas (Romei et al., 2012; Volberg et al., 2009). Although the poor spatial resolution of EEG precludes drawing any conclusions based on these diverging topographies, they do suggest the possibility that the hemispheric asymmetries observed in the processing of global versus local stimuli exist at stages beyond primary sensory ones. Studies using fMRI have supported this possibility. For example, Sasaki et al. (2001) used functional MRI to map activity in the human occipital cortex during local and global attention. Instead of lateralized activation, they found that

global and local attention are mapped consistently with the maps of retinotopy and spatial frequency tuning in multiple visual cortical areas. In contrast, Martinez et al. (1997) mapped activity in a more anterior set of slices including temporo-parietal, but not occipital regions, and did find evidence for a lateralization depending on global vs. local attention. A combined ERP/PET study provides converging evidence that the lateralization of global versus local processing occurs not at the earliest sensory, but rather at later stages (Heinze, Hinrichs, Scholz, Burchert, & Mangun, 1998). Participants were shown hierarchical stimuli consisting of large letters comprised of smaller letters. When attention was divided between global and local levels, the N2 component (260-360 ms post-stimulus) to local targets was larger over the left hemisphere, and the N2 to global targets was larger over the right hemisphere. There were no differences observed for the sensory-evoked P1 component (90- to 150-msec latency). In contrast, during selective attention to either global or local targets, asymmetries in the N2 component were not observed, but the P1 components were enlarged for global versus local attention. PET data showed bilaterally increased regional cerebral blood flow in the posterior fusiform gyrus but neither these nor the P1 component showed any tendency toward hemispheric difference for global versus local attention. These suggest that global vs. local perception is only asymmetric at higher stages of perceptual processing and not at the earliest stages of visual cortical analysis. The function of alpha power in spatial integration therefore seems to go beyond the selective inhibition of task-irrelevant areas. How alpha power is involved in visual spatial integration is a question I will further address in chapter 5.

SCALE FREE BRAIN ACTIVITY

The aperiodic, non-oscillatory part of the power spectrum is often referred to as “1/f noise”. However, the fact that this background activity has a $1/f^x$ distribution tells us that this noise is not unstructured. As described above, the $1/f^x$ power-law component of the EEG power spectrum indicates the presence of scale-free dynamics; processes or patterns that are repeated across scales of analysis. This can be referred to as “self-similarity”, which is when the signal has a similar shape across different time-scales. This self-similarity in brain activity, as in the

rest of nature, tends to be not exact, but rather approximate and statistical. For example, when using the Fourier transform, it is the statistical relation between the measured signal and a sinusoidal kernel that is invariant to the frequency of that oscillation. $1/f^x$ scaling is characteristic of signals with long-range temporal correlations; since certain patterns of activity repeat over time, the signal correlates with itself (is autocorrelated) over varying temporal lags. This is a sign of redundancy and indicates the presence of a history-effect, or memory in the temporal structure of brain activity. The $1/f^x$ power-law shape of the aperiodic component of the EEG power spectrum therefore tells us that there are patterns in ongoing background brain activity that repeat across timescales and over time. Such scale freedom is not specific to brain activity and can be observed in a broad scala of both living and non-living complex systems. For example, it can be seen in the temporal structure of stock market fluctuations (Baillie, 1996), the time interval between the R peaks of the electrocardiogram (Kobayashi & Musha, 1982), fluctuations in pitch and loudness of music and speech, the frequency of occurrence of earthquakes of different sizes (Gutenberg & Richter, 1944) and the structure of organisms such as a fern or the Romanesco broccoli plant (see fig. 1A). Furthermore, $1/f^x$ distribution of the power spectrum characterizes the temporal dynamics of brain activity at multiple observational levels. It can be seen in the fluctuations of neuronal membrane potentials (Destexhe, Rudolph, & Paré, 2003; El Boustani et al., 2009), local field potentials (Milstein, Mormann, Fried, & Koch, 2009), electrocorticograms (ECoG; Manning, Jacobs, Fried, & Kahana, 2009; Miller et al., 2014; Miller, Sorensen, Ojemann, & den Nijs, 2009), EEG and MEG signals (Dehghani, Bédard, Cash, Halgren, & Destexhe, 2010) and fMRI (Bullmore et al., 2001; Ciuciu, Varoquaux, Abry, Sadaghiani, & Kleinschmidt, 2012; He, 2011). At the same time, cognitive behavioral measures also show power law distributions (Gilden, 2001; Kello et al., 2010). For example, Gilden, Thornton, & Mallon (1995) asked participants to repeatedly reproduce spatial or temporal intervals from memory. Sequences of the errors in both spatial and temporal replications followed a $1/f^x$ distribution. While the pervasiveness of power laws in cognition may be novel to many, there are two classic examples of such power laws in cognitive science that are very well known; Stevens' law (Stevens, 1957) and Zipf's law (Zipf, 1949). Stevens' law, which applies specifically to psychophysics, states that the physical magni-

tude of a stimulus (S) is proportional to its perceived intensity (I) raised to a power α , $S \propto I^\alpha$. Zipf's law applies to linguistic effects such as word frequency and letter sequences in lexicons (Kello & Beltz, 2009), but can also be applied to many other data sets such as population ranks of cities in various countries (Auerbach, 1913). The fact that both behavior and brain activity show $1/f^\alpha$ scaling suggests a possibly meaningful relationship between parameters of scale free activity and behavior.

Concepts in the study of scale-free brain activity

Self-Organized Criticality

An influential model of $1/f^\alpha$ processes is the “self-organized criticality” theory (Bak, Tang, & Wiesenfeld, 1987). The term criticality comes from thermodynamics, where the critical point is the end point of a phase equilibrium curve, where phase boundaries vanish. The liquid-vapor critical point, for example, is the point where a liquid and a vapor can exist simultaneously. Self-organized criticality refers to the tendency of complex natural systems to spontaneously produce structures or behavior that can be modelled with a $1/f^\alpha$ shaped function. When applied to the brain, the theory states that its activity is poised at the critical point between order and disorder, continuously transitioning between these two phases, one in which activity will rapidly decay, and another where activity will amplify and spread (Chialvo, 2010). In this conceptualization, the subcritical state is associated with a more predictable signal with stronger long-range temporal correlations (self-similarity over time), is more stable, and less easily perturbed. The supercritical state, in contrast, is associated with weaker long-range temporal correlations, is less stable and more easily perturbed (Chialvo, 2006).

Stochastic resonance

Another way to understand how changes in $1/f^\alpha$ scaling could impact perception and cognition is through the concept of stochastic resonance; a phenomenon in which noise enhances the response of a non-linear system (such as the brain) to a weak signal. In their seminal paper the physicists Wiesenfeld and Moss (1995) describe how the presence of noise in dynamical systems can enhance the detection of weak signals. The concept was first proposed to explain

the 100.000-year periodicity of the earth's ice ages (Benzi, Sutera, & Vulpiani, 1981). A general dynamical mechanism was proposed to explain this phenomenon whereby large environmental fluctuations could greatly amplify small periodic perturbations. The relationship between the signal-to-noise ratio and the amount of noise in a dynamical system is not linear, but has an inverted u-shaped form; adding noise to the system raises the signal-to-noise ratio multiplicatively, as the weak signal starts to break the threshold due to the increasing noise, until the optimum level of noise is reached. Then, as noise increases beyond the optimum level, the signal-to-noise ratio starts to decline again as the increasing noise randomizes the signal beyond detectability. In a neural context, stochastic resonance has been well established through experiments using controlled addition of external noise (Collins, Imhoff, & Grigg, 1996; Douglass, Wilkens, Pantazelou, & Moss, 1993; Levin & Miller, 1996). For example, Collins et al. (1996) applied subthreshold tactile stimuli to participants' finger tips accompanied by noise at one of seven intensity levels. As the noise level increased, detection rate increased and then decreased again, showing the inverted U-shape characteristic of stochastic resonance effects. Extending such results from perception to cognition, Usher & Feingold (2000) delivered auditory noise at six levels of intensity while participants performed single-digit arithmetical multiplications. They found that performance was optimal at intermediate levels of noise, again suggesting that SR was involved. Similarly, Simonotto et al. (1997) added different levels of noise to images and found that participants' perceptive contrast threshold was lowest at intermediate amounts of noise. Interestingly, different levels of noise enhanced contrast at different spatial frequencies. This hints at a possible role for stochastic resonance in the selection of the spatial scope of integration in visual perception. Most studies on stochastic resonance in perception and cognition have involved measuring how the nervous system and behavior are affected by adding external noise. However, this approach overlooks the fact that there is already a clear presence of noise in the nervous system itself (Faisal et al., 2008; Pinneo, 1966). Evidence for intrinsic stochastic resonance, where no external noise is added to the system, but existing internal noise is exploited instead, has almost exclusively been obtained from simulation studies (Czaplicka, Holyst, & Sloot, 2013; Kawaguchi, Mino, Momose, & Durand, 2011; Mino & Durand, 2010; Rudolph & Destexhe, 2001b, 2001a; Stacey & Du-

rand, 2000). To study intrinsic stochastic resonance in humans, and relate it directly to behavior, the $1/f^\alpha$ scaling exponent could help us quantify the amount of noise present in the system (Voytek et al., 2015). A flatter EEG power spectrum indicates weaker long-range temporal correlations and a more random signal.

Power Spectral Density

There are several measures to quantify scale-free aspects of EEG activity. Most of these, such as multi-scale entropy (Costa, Goldberger, & Peng, 2002), detrended fluctuation analysis (Peng et al., 1994) or the Hurst exponent (Hurst, 1951) attempt to measure either the complexity or long-range temporal correlations of the signal. These are time-domain analysis methods and require the repetition of analysis steps at different time-scales. The PSD, in contrast, is the frequency domain representation of the raw EEG fluctuations at all time-scales simultaneously. The scale-free, broadband component of the PSD can be approximated by a straight line on a double-log scale (Haller et al., 2018; He, Zempel, Snyder, & Raichle, 2010; Miller et al., 2009), and can be characterized by its slope and offset. Interestingly, there is evidence that the PSD slope reflects characteristics of brain activity that are highly overlapping with characteristics picked up by the complexity measures mentioned above, with flatter PSD slopes indicating increased complexity (Miskovic, MacDonald, Rhodes, & Cote, 2019; Sheehan, Sreekumar, Inati, & Zaghoul, 2018; Waschke, Wöstmann, & Obleser, 2017). The offset of the PSD is best characterized from electrophysiological data measured with ECoG or iEEG, since the offset of the PSD based on EEG measurements can find itself significantly influenced by non-brain activity related factors such as scalp thickness, skin-type and humidity among others. The PSD slope can be successfully inferred from EEG data as well as ECoG and iEEG measurements. Both the offset and the slope of the PSD have been shown to vary in functionally and physiologically meaningful ways.

PSD Offset

Manning et al. (2009) recorded local field potentials and single-neuron activity in 20 neurosurgical patients during a virtual navigation task. They found a

population of neurons which varied their firing in proportion to power at specific frequency bands. This is consistent with findings such as those reviewed by Fries, Nikolić, and Singer (2007) that report strong correlations between neuronal firing and narrowband oscillatory power. However, in addition, Manning et al. (2009) observed an even larger population of broadband-shift neurons, which varied their firing with the offset of the power spectrum. In other words, these neurons' firing rate depended on the overall power present at *all* frequencies. The broadband power was almost exclusively positively correlated with single-neuron firing, and thus seems to provide a robust estimate of neuronal firing. Fluctuations in the broadband offset can occur in response to sensory stimuli and may also be linked to the fMRI blood oxygen level-dependent (BOLD) response. Winawer et al. (2013) measured ECoG and the BOLD response to a flickering visual stimulus. They found that ECoG responses could be separated into two components; one that was synchronous with the flickering visual stimulus, whose temporal response rose and fell when the stimulus came on and off, respectively (i.e. a steady state visual evoked potential; van der Tweel & Verduyn Lunel, 1965) and another component consisting of a broadband increase in the response power during the periods when the stimulus was on, spanning frequencies from below 10 Hz to above 100 Hz. The characteristics of the fMRI response corresponded to the characteristics of the broadband response, and not to those of the stimulus-locked response. This emphasizes the importance of the scale-free broadband signal as a potential link between the macroscale and microscale features of cognition as reflected by different neurophysiological measures. The offset of the aperiodic signal is dynamic and varies with behavior. Miller et al. (2012), for example, measured ECoG activity in humans while they performed simple motor tasks. They found a modulation of the broadband offset of the power spectrum that followed the dynamics of individual fingers, with somatotopically specific responses for different fingers.

PSD Slope

The slope of the power spectrum has been linked to both state and trait characteristics of cognition. Sheehan, Sreekumar, Inati, & Zaghoul (2018), for instance, captured intracranial EEG recordings as participants performed a paired-associates verbal memory task. They found that a flatter PSD slope pre-

dicted better performance, both within and across participants. Podvalny et al. (2015) showed that the power law exponent of the $1/f^x$ component of the power spectrum was significantly reduced upon visual stimulation. In other words, when compared to resting-state recordings, the slope of the scale free component of the power spectrum was flattened during visual stimulation. Similarly, He et al. (2010) recorded the electrocorticogram during quiet wakefulness and the performance of a simple task where participants were instructed to press a button either in a visually cued or self-paced manner. The authors reported a significant flattening of the slope while participants performed the task compared to quiet wakefulness. Notably, a similar relationship was observed in the fMRI signal, where the PSD slope decreased during performance of a visual detection task, compared to rest (He, 2011). An investigation of the power spectra of people diagnosed with schizophrenia revealed that PSD slope was a better predictor of schizophrenia than power measurements derived from specific oscillatory bands or even from behavioral responses on a selective attention task (Peterson, Rosen, Campbell, Belger, & Voytek, 2018), with the slope being significantly steeper for this patient group. The studies reviewed above seem to indicate that flatter PSD slopes are related to task engagement and better performance in general. However, this does not seem to always be the case. The PSD slope has also been found to flatten with age (Voytek et al., 2015; Waschke, Woestmann, & Obleser, 2017). Moreover, flatter slopes predicted decreased working memory performance and slower and more variable RTs. In fact, the PSD slope was found to be the mediating factor in the decline of working memory performance with age (Voytek et al., 2015). Two interpretations of the PSD slope might help reconcile these results. First, Gao, Peterson, & Voytek (2017) proposed a model explaining PSD slope in terms of the balance between excitatory and inhibitory activity. Their model was based on evidence that synaptic input fluctuations can be accurately modeled by a summation of two stochastic processes representing excitatory and inhibitory inputs (Alvarez & Destexhe, 2004). Since these inputs have different rates of decay, with excitatory inputs decaying faster, they can be differentiated in the frequency domain and computationally inferred from the postsynaptic potentials measured at the scalp. When the faster, excitatory activity increases, power in the higher frequencies will increase relative to the lower frequencies and result in a flatter PSD slope.

Both computational modelling (e.g. Lam et al., 2017) and empirical studies (e.g. Cools & D’Esposito, 2011) have implied that performance might often be related to excitatory activity in an inverted u-shaped manner. Such results stress the importance of a balance between excitatory and inhibitory activity, which echoes the theory of self/organized criticality explained above. The PSD slope, as an indicator of the ratio of excitatory to inhibitory activity would then be expected to show a non-linear relationship to behavior as well. Second, the PSD slope flattens as the strength of long-range temporal correlations is reduced, indicating an increase in the randomness or noisiness of the signal. In the context of stochastic resonance, with intermediate levels of noise resulting in the highest signal-to-noise ratio, a non-linear relationship between the PSD slope and behavior would also be expected. Viewed from both these frameworks, modulations of the PSD slope would be expected to have paradoxical, and possibly baseline dependent consequences for behavior. How the PSD slope is involved in audiovisual temporal integration is a question I will further address in chapter 5.

THE RELATION BETWEEN SCALE-FREE AND OSCILLATORY ACTIVITY

Although the scale-free and oscillatory components of the power spectrum can be modeled separately (Haller et al., 2018), and can each be successfully linked to different behavioral characteristics, this doesn’t mean they are independent. Becker, Van de Ville, & Kleinschmidt (2018), for example, showed an increase in the power of alpha oscillations to cause a reduction in the PSD slope for frequencies between 0.12 and 4.8 Hz. In a similar vein, Miller et al. (2010) analyzed ECoG data and found that the broadband offset of the PSD was modulated by narrow-band oscillations in the lower frequencies up to 20 Hz. Additionally, the amplitude fluctuations of narrow-band oscillatory activity exhibit scale-free dynamics as well. For example, these so-called long range temporal correlations of alpha oscillations have been shown to predict timing-error dynamics (Smit, Linkenkaer-Hansen, & de Geus, 2013) and be modulated by sensorimotor stimulation (Linkenkaer-Hansen, Nikulin, Palva, Kaila, & Ilmoniemi,

2004). As a final example of the interrelatedness of scale-free and oscillatory activity, noise can induce synchronization in populations of oscillating neurons by providing a random but correlated input to disparate neurons causing synchronous phase resetting and thereby leading the population to synchronize (Ermentrout, Galán, & Urban, 2008).

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METHODS

In this chapter, I will give a general introduction to the experimental methods. First, I will discuss the behavioral paradigms (consisting of an audiovisual temporal order judgement task and a Navon task) and their analyses. Second, I will discuss the aspects of the EEG that I've attempted to relate to behavior in these tasks and their analyses. These include power spectral density, instantaneous frequency and the slope of the power spectrum. Third, I will explain the method of jackknife replications that allowed linking behavior to these EEG measures on a single-trial basis. Finally, I will briefly explain the statistical method of cluster-based permutation testing which was used to assess the statistical significance of the results.

BEHAVIORAL PARADIGMS AND ANALYSES

TEMPORAL ORDER JUDGEMENTS

In a temporal order judgement (TOJ) task, an individual is presented with two stimuli that can be distinguished from each other by a specific feature. For example, in a visual TOJ, one stimulus might be presented on the left side and the other on the right. In an audiovisual TOJ, one will be presented in the auditory modality and the other in the visual modality. The task of the individual is to respond which of the two stimuli was presented first (or last). By presenting the stimuli at a varying interval or stimulus onset asynchrony (SOA), and fitting a psychometric function to the data, the shortest temporal offset between the stimuli that can be perceived is inferred. It is assumed that the stimuli that are presented at intervals that are shorter than this “just noticeable difference” (JND) are integrated and therefore cannot be assigned to two different instances that occur one after the other. In other words, a TOJ can provide an estimate of the time window over which information is integrated. Data from such experiments commonly provide us with two independent parameters. The JND, which we described above, reflects temporal sensitivity, and the point of subjective simultaneity (PSS) describes the SOA at which the two stimuli appear to be simultaneous to the observer. It is worth noting that the JND and PSS do not reflect in a straightforward way how *accurately* the observer perceives the stimuli. Ra-

ther, they tell us something about their temporal bias (PSS) and sensitivity (JND). An observer with a large bias might have very good temporal sensitivity while performing less accurately than an observer with a small bias and very poor temporal sensitivity. Consequently, if temporal sensitivity is the latent variable of interest, as it is here, accuracy is not a suitable metric, whereas the JND is.

Fitting psychometric functions

To fit a psychometric function to the TOJ data described in Chapters 3 and 4, I employed the Palamedes toolbox (Kingdom & Prins, 2009). A logistic function produced the best fits and was used for all analyses. One manually set parameter can have great impact on the resulting fits; the lapse rate. Lapses are incorrect responses given due to inattention or disengagement from the task. Lapses can bias the estimation of slope and threshold, especially if they occur at the extreme ends of the psychometric curve (Wichmann & Hill, 2001). The effect of lapses can be minimized in at least three ways. First, lapse rate can be included as a free parameter (Wichmann & Hill, 2001). Some of the variation will then be expressed in the lapse rate instead of the slope or threshold. Second, lapse rate can be estimated and constrained to be equal between conditions. If it is reasonable to assume that incorrect responses at high intensities can only be due to lapses of attention, the lapse rate can be estimated from performance at these intensities and fixed at that value. Third, and the method we chose, lapse rate can be constrained to a low non-zero value. While estimates of threshold and slope are affected when the assumed value of the lapse rate is different from the actual lapse rate, they are so systematically, thereby not affecting the differences among parameter estimates for different conditions (Prins, 2010). A lapse rate fixed at zero should be avoided (Hall, 1981), since the presence of a lapse when the lapse rate is fixed at zero has a much stronger effect on slope estimation than the absence of a lapse when the lapse rate is fixed at a small, non-zero value (Kingdom & Prins, 2016). Due to a lack of experimental data to back up these suggestions, I verified the effect of fixing lapse rate at 0.02 vs. fixing it at 0, and simulated behavioural data for two hypothetical participants (HPs); HP 1 with a steep slope that asymptotes at 0 and 1, and HP 2 with a shallow slope where asymptote is

not reached at any side of the curve. I then compared the effect of one single “flash first” (incorrect) response at an extreme SOA of 350 ms, with a fixed lapse rate of 0 and of 0.02 for both HPs. The results are displayed in Table 1. For HP 2, a lapse affects the JND estimate similarly, whether lapse rate is fixed at 0 or 0.02. For HP 1, a lapse rate set to 0.02 reduces the effect of a lapse on the JND estimate from 2,3 to 0,2 ms. It seems that fixing the lapse rate to a small non-zero value can help mitigate the biasing effects of lapses at the extremes of the curve in participants that reach asymptote, without reducing the sensitivity of the slope to variations at the extremes in subjects who do not reach asymptote. Therefore, this method appears to successfully avoid introducing noise to the data due to momentary lapses of attention.

JND	LR fixed at 0		LR fixed at 0.02	
	+0 lapse	+1 lapse	+0 lapse	+1 lapse
HP 1 (asymptotes)	59	61,3	58,8	59
HP 2 (does not asymptote)	179,3	182,2	176,6	179,5

Table 1. JND estimates for hypothetical participants with **(top)** a steep slope that asymptotes at 0 and 1 and **(bottom)** a shallow slope that does not reach asymptote at either side. In blue, lapse rate is set to 0. In green lapse rate is set to 0.02. The JND is estimated for both hypothetical participants and with both lapse rate settings in the case of no lapse and one lapse.

NAVON TASK

In a typical Navon task (Navon, 1977), participants are presented with visual hierarchical letters and are instructed to identify either the small or the large letter as quickly as possible. The letters can be either congruent (the large letter is made up of letters with the same identity) or incongruent (the large letter is made up of letters with a different identity; see figure 1). Instructions can prompt observers to report the global or the local letter. In incongruent trials, the local level can interfere with identification of the global letter and vice versa, which lengthens reaction times. Local interference is calculated by subtracting

the mean reaction time in the congruent global condition from the incongruent global condition. Global interference is calculated by subtracting the mean reaction time in the local congruent condition from local incongruent condition. Navon (Navon, 1977) devised these stimuli to test his idea that global structuring of a scene precedes local analysis, and found evidence in the fact that global interference was stronger than local interference. In Chapter 5, I use these stimuli to probe the relation between ongoing brain activity and spatial integration based on the assumptions that, global interference will increase and local interference decrease as the visual scene is integrated over a larger area and that local interference will increase and global interference decrease as the visual scene is integrated over a smaller area.

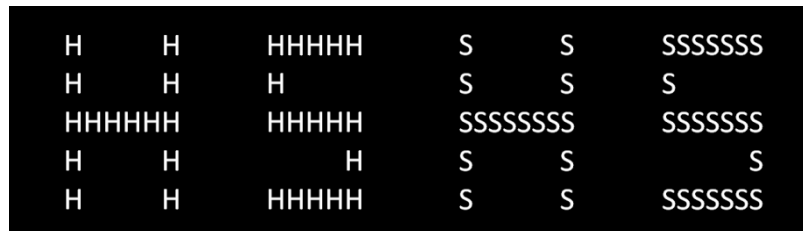


Figure 1. Navon stimulus set. Stimuli can be either congruent (1st and 4th) or incongruent (2nd and 3rd).

EEG ANALYSES

One way to measure ongoing brain activity is by recording so-called resting state activity. Here, participants are instructed to look straight ahead to a fixation point or to remain still with their eyes closed. Their EEG data is then analyzed, for the extraction of specific parameters, such as power, complexity, phase locking and so forth. The parameters of interest can then be correlated to behavioural traits of interest across participants. An important benefit of resting state recordings is the relatively long continuous data that can result from them. Also, one could argue that this resting state brain activity is really spontaneous, in the sense that there is no external stimulation evoking any activity. There are also considerable drawbacks of this approach, however. For instance, it is not possi-

ble to investigate how this spontaneous activity interacts with task-performance within an individual, which makes it harder to gain any mechanistic insight into the behaviour of interest. Moreover, even though individuals are asked to do nothing, our minds are always working and it is challenging to acquire knowledge about what the participant is actually doing while at rest (Diaz et al., 2013). A different approach to relating background activity to behaviour is by measuring brain activity in the pre-stimulus interval, right before the stimuli are presented. Even though the individual is not resting, and some aspects of activity are most probably task-related (such as arousal related activity for example), evoked activity (that is; activity that is directly elicited by the stimulus, such as an event-related potential, or an evoked oscillation) is kept to a minimum. The analysis of pre-stimulus EEG activity thus allows for the analysis of spontaneous activity on a trial-by-trial basis.

In the studies reported in this dissertation we measured spontaneous ongoing brain activity with EEG for the following reasons (Cohen, 2014a). First, cognition and the underlying brain dynamics are fast, and EEG has a very high temporal resolution that can capture this activity in real time. Therefore, EEG activity can reveal patterns over very short to very long time-scales. Second, EEG directly measures neural activity. Unlike the signals measured by methods such as fMRI and PET, the voltage fluctuations that give rise to the EEG directly reflect biophysical processes that take place at the level of neural populations. Oscillations that are visible in the EEG are direct reflections of oscillations in neural populations (however, see below). Third, the temporal dynamics of EEG have a large capacity for the representation and processing of information. The signal from even one single electrode is so complex that we need to summarize it using methods such as a Fourier transform, or entropy analysis to extract certain features from the data. The Fourier transform, for instance, gives us information in multiple domains such as frequency, power and phase angle, which in turn can interact with each other. For example, the phase of one oscillation at a lower frequency may determine the amplitude of an oscillation at a higher frequency. Adding the dimension of space, when recording from multiple electrode sites, interactions between electrodes in any of these aforementioned parameters can occur, allowing us to glean interactions across networks as well. This multid-

mensionality of the information contained in the EEG gives us access to at least a fraction of the dimensions of brain activity that are relevant for cognition and allows us to formulate psychological hypotheses that are inspired by known physiological processes. There are, however, some limitations inherent to the EEG that should be noted (Ward, 2003). One mayor limitation arises from the fact that the activity recorded at the scalp is the summation of activity across multiple large populations of neurons. This leads to a poor spatial resolution which in turn limits our ability to link specific brain functions to specific EEG characteristics. Moreover, it is difficult to distinguish whether signals arise from one or from multiple sources. Related to this, EEG only records the dendritic field potentials of the cortical pyramidal neurons. Therefore, it does not directly take into account activity that arises from different structures. Despite the fact that EEG in essence summarizes activity across a large number of subunits of activity, the information contained in the EEG is still so rich and complex that in order to analyze it and make it understandable for our limited human minds, we need to summarize it even further. Depending on which method we choose to do this, we will gain access to different aspects of the EEG. The measures I use in this thesis nearly all rely on the Fourier theorem, which states that each signal can be expressed as a combination of different sine waves each defined by its own amplitude, frequency and phase (Fourier, 1822).

A powerful aspect of the Fourier theorem is that it can be used to decompose *any* signal into a combination of sine-waves, even signals that are not composed of sinusoidal or even periodic activity. This also comes with an important caveat. Namely, the fact that a sine wave at a certain frequency is part of the frequency spectrum of a (neural) signal does not mean that there are actually cell groups exhibiting a periodic phenomenon at that frequency (making such an assumption was aptly termed a “Fourier fallacy” by Jasper (1948)). If, for example, we Fourier transform a white noise signal, we will find equal power at all frequencies. Likewise, if we Fourier transform a pink noise signal we will find a spectrum with a power-law distribution, where power is inversely proportional to the frequency. In neither of these scenarios actual sinusoidal oscillations are present in the signal.

POWER

When applying the Fourier transform to EEG data, the input to the transform consists of a time series of voltage values. The Fourier transform then decomposes the EEG time series into a voltage by frequency spectral representation (the power spectrum). The spectrum shows the amount of energy (expressed as voltage) present at each frequency. The higher the sample rate, the higher the maximum frequency that can be considered. The longer the time-series, the finer the frequency resolution of the spectrum will turn out to be. A typical power spectrum of EEG data will be composed of its offset, an aperiodic and a periodic (oscillatory) component. The aperiodic component of the power spectrum will look like the power spectrum of pink noise and have a $1/f^\chi$ power-law distribution, with power declining as frequency increases, and the power-law exponent χ indicating the steepness of that decline. The periodic component is made up of peaks where power in narrow bands rises above the $1/f^\chi$ (Haller et al., 2018; He, 2014). Physiologically, a peak in the spectrum indicates an oscillation, which reflects the synchronized fluctuations of the post-synaptic potentials of a group of neurons. An increase of this peak would indicate that more neurons are synchronized to this particular oscillation. In chapters 3 and 5 we used EEG power to predict behavior on the TOJ and Navon tasks, respectively.

Power Law Exponent

When modeling the aperiodic part of the power spectrum with the power law function $1/f^\chi$, the power-law exponent χ in the formula is what defines the steepness of the decline of power with increasing frequency. The higher χ , the steeper the decline. Flatter slopes indicate a higher ratio of autocorrelation on shorter time scales (reflected in power at higher frequencies) to autocorrelation on longer time scales (reflected in power at lower frequencies). To estimate the power-law exponent, we applied the “fitting oscillations & one over f” (FOOOF) algorithm, developed by (Haller et al., 2018). FOOOF isolates the aperiodic component of the spectrum and estimates its exponent by fitting an exponential function in the semi-log power domain (frequency on a linear x-axis, power on a log y-axis). This is equivalent to fitting a linear function in the log-log domain. In

chapter 4, we used this power-law exponent to predict behavior on the TOJ task, on a trial-by-trial basis.

INSTANTANEOUS FREQUENCY

Most EEG analyses assume that a neural oscillator's frequency is approximately stationary over time, or changes only slowly. In reality, however, this is almost never the case. Cohen (2014b), for example, demonstrated how signals coming from both real and computational neural networks exhibit temporal fluctuations in peak frequency over time. This "frequency sliding" modulates the spike timing dynamics of individual neurons, where decreases in oscillation frequency decrease spike threshold and increase spike timing variability. Frequency sliding has also been shown to predict the temporal resolution of visual integration within and across participants (Samaha & Postle, 2015). The quantification of frequency sliding involves computing the frequency of an oscillation from time point to time point; its "instantaneous frequency". The concept of instantaneous frequency goes somewhat against the way we usually think about what frequency means; the number of cycles of an oscillation occurring within a certain span of time. How then, can we conceive frequency at one single point in time? Apart from the number of cycles per unit time, frequency can also be defined as the speed of an oscillation (how fast it is cycling). The higher this speed, or angular velocity, the higher the frequency. The angular velocity at each time point is given by the phase angle time series. From this phase angle time series we can thus infer instantaneous frequency at each data point and investigate how its fluctuations are related to behavior.

JACKKNIFE REPLICATIONS

The goal of the experiments described in Chapters 3 and 4 of this dissertation is to shed light on the relationship between moment-to-moment fluctuations in brain activity and the integration of audiovisual stimuli over time. The analysis

of single trials is imperative to achieve this goal. However, the JND is not defined at a single-trial level. It is derived from a psychometric function that is fit to the data from many trials at all conditions. Similarly, the power law exponent, which we employed in Chapter 4, is derived from a function fit to the slope of the power spectrum. Although this could theoretically be done using the spectra of single trial data, it would result in exceedingly bad fits and thus noisy estimates. To overcome this problem, we applied jackknife correlations (Quenouille, 1949; Stahl & Gibbons, 2004; Tukey, 1958). In jackknife correlations, the metrics of interest (EEG parameters and the JND in our case) are computed iteratively over all trials while one trial is left out at each iteration (and reinserted at the next iteration). This results in variables which contain as many values for the statistic as there are trials. Since the resulting statistic at each trial reflects the effect of that trial being left out, the direction of variance is inverted. Additionally, since the effect is scaled by the number of trials, the variance is compressed. This inversion and compression of variance resulting from the jackknife procedure is illustrated in figure 2A. It is apparent that the jackknife variable mirrors the original variable and is scaled down by the number of trials. As figure 2B shows, the original and jackknife variable are perfectly correlated, but the sign of the correlation is negative. As a consequence, any correlation of a jackknife variable with a non-jackknife variable will have a sign that is inverted from the true relationship. As a solution, both measures can be subjected to the jackknife procedure, thereby restoring the correct sign of the resulting correlation. For the mathematical proof of the equivalence of the conventional and jackknife correlations we refer to (Richter, Thompson, Bosman, & Fries, 2015). For a detailed explanation of how to apply this procedure to link psychophysical data with EEG data, see (Benwell, Keitel, Harvey, Gross, & Thut, 2017). Crucially, this method unlocks additional inferential dimensions by allowing the estimation of ensemble metrics such as the JND at the single trial level. In the case of measures such as the power-law exponent, it allows for a more sensitive estimate of the power-law exponent at the single trial level than could be achieved by estimating single trial power-law exponents directly. Jackknife replications therefore enabled us to test the relationship between fluctuations in EEG parameters and temporal sensitivity on a short, moment-to-moment time scale.

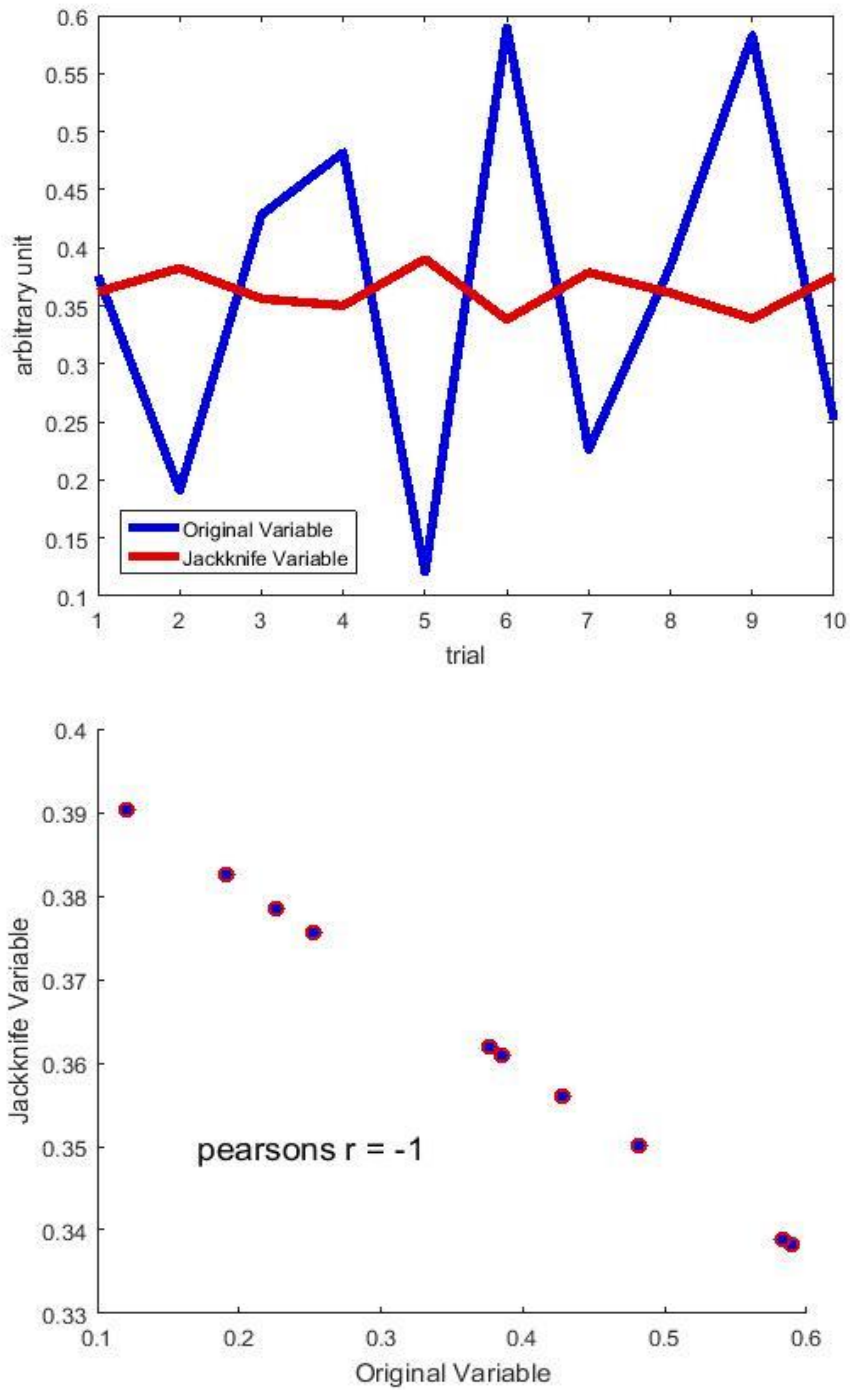


Figure 2. Illustration of a jackknife variable. **A.** A random variable with 10 values is shown in blue. The same variable after calculating a jackknife statistic (the mean in this example) is shown in red. **B.** Scatter plot of the relation between the original and the jackknife variable. Note the perfect correlation with a negative sign.

CLUSTER-BASED PERMUTATION TESTING

In each of the experiments described, multiple comparisons were tested. Since the probability of a type I error increases as more comparisons are tested, appropriate steps need to be taken in order to reduce the risk of such an error. The most popular correction for multiple comparisons is the Bonferroni correction (Bonferroni, 1936), which simply adjusts the stringency of the criterion to reject the null hypothesis proportionately to the number of comparisons. For example, if two comparisons are made, the level of stringency for each is doubled. Such a correction is not suitable to our data for at least three reasons (Cohen, 2014a). First, a Bonferroni correction assumes independence between the tests. This is not the case for our analyses because neighboring (and thus partially dependent) time points, frequencies and electrodes were correlated with the same measure across trials. Second, the large amount of comparisons (e.g. 36.800 comparisons in the analysis described in Chapter 3) would lead to a criterion so stringent that it would be unlikely that any true effects would be deemed statistically significant. Third, the number of comparisons depends on arbitrary decisions made by the experimenter, not on the actual information present in the data. For example, in Chapter 3, we chose to examine frequencies from 1 to 45 Hz in steps of 2 Hz. If we would have chosen to do this in steps of 1 Hz instead, thereby doubling the number of comparisons, the statistical criterion for significance would be twice as stringent, despite the same data being queried and thus little unique information being added. One method to overcome the limitations presented by this type of correction for multiple comparisons is to employ non-parametric permutation testing instead. Non-parametric permutation testing corrects for multiple comparisons based on the information present in the results rather than the number of comparisons, and provides corrected significance criteria that are sensitive enough to detect effects in correlated multidimensional data (Cohen, 2014a). The specific type of non-parametric permutation testing we applied was the cluster-based variant specifically for application to EEG or MEG data as described by Maris & Oostenveld (2007) and implemented in the FieldTrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011). A cluster-based correction assumes that since the data are autocorrelated,

as is indeed the case for EEG data, a finding is large enough if neighboring data-points (in time, frequency and/or space) also show the same effect. Individual data points (each representing one statistical comparison) that show a significant effect are considered to be false positives when they are not part of a cluster of significant effects. The “strength” of a cluster can be calculated, for example, by summing the t-values across the data points in the cluster. This cluster statistic is then compared to the distribution of cluster statistics that would be expected under the null hypothesis to determine the probability that this cluster statistic could have been obtained by chance. The null distribution is not created based on assumptions such as with parametric tests, but rather is created in a data driven manner. The data is randomly permuted (shuffled), and then, as with the observed data, statistical tests are performed on each data point and cluster statistics are calculated. This is done iteratively for hundreds or thousands of permutations and the null distribution is then built from the maximum cluster statistic from each iteration. The location of the original real cluster statistic on this null hypothesis distribution indicates how probable such an observation would be if the null hypothesis were true. Hence, in a two-tailed test and with an alpha level of 5%, if a given negative or positive cluster has a cluster statistic lower or higher than 97.5% of the respective null distribution cluster statistics, then this is considered a significant effect.

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SPONTANEOUS NEURAL OSCILLATIONS PREDICT THE TEMPORAL SENSITIVITY OF MULTISENSORY PERCEPTION FROM TRIAL TO TRIAL¹

¹London, R. E., Benwell, C. S. Y., Cecere, R., Quak, M., Thut, G., and Talsma, D. (in preparation). Spontaneous neural oscillations predict the temporal sensitivity of multisensory perception from trial to trial.

ABSTRACT

Pre-stimulus EEG oscillations, especially those in the alpha range, can affect the integration of individual stimulus features into a coherent percept. The effects of alpha power have often been explained in terms of alpha's inhibitory functions, whereas the effects of alpha frequency have bolstered theories of discrete perceptual cycles, of which the length is determined by the frequency of alpha. Such studies have typically employed visual detection paradigms with near-threshold or illusory stimuli. It is therefore unclear to what extent the results can be generalized to more general temporal integration in perception and to situations that involve above-threshold stimulation. In this study, we recorded electroencephalography (EEG), while measuring audio-visual temporal discrimination sensitivity in a temporal order judgement (TOJ) task using above-threshold auditory and visual stimuli. We then tested whether pre-stimulus oscillations predict audio-visual temporal discrimination sensitivity on a trial-by-trial basis. By applying a jackknife procedure to link single-trial pre-stimulus oscillatory power and instantaneous frequency to psychometric measures, we identified a posterior electrode cluster in the alpha frequency band prior to stimulus presentation where power co-varied with the temporal sensitivity of audiovisual discrimination. We also identified a cluster where higher instantaneous frequency within the alpha-band was predictive of higher temporal discrimination sensitivity. A follow-up analysis revealed that these effects were linked and that the effect of instantaneous frequency could be explained by power modulations in the lower alpha band. These results show that temporal sensitivity for above-threshold multisensory stimuli changes spontaneously from moment to moment and is likely related to fluctuations in cortical excitability.

INTRODUCTION

A fundamental aspect of perception is the integration of sensory signals to form meaningful percepts within and across modalities. Whether two signals from different sensory modalities are integrated depends, among other factors, on their temporal proximity. The shorter the time between them, the higher the chance they will be integrated (Lewald & Guski, 2003; Meredith, Nemitz, & Stein, 1987; Senkowski, Talsma, Grigutsch, Herrmann, & Woldorff, 2007).

Exactly how close in time these signals need to be for integration to occur depends on several factors. Accordingly, temporal sensitivity is highly variable both within and between individuals. For example, in people diagnosed with schizophrenia, autism or dyslexia, audiovisual temporal sensitivity appears to be reduced compared to healthy controls (De Boer-Schellekens, Eussen, & Vroomen, 2013; Foucher, Lacambre, Pham, Giersch, & Elliott, 2007; Hairston, Burdette, Flowers, Wood, & Wallace, 2005; Martin, Giersch, Huron, & van Wassenhove, 2013; Stevenson et al., 2017, 2014; Wallace & Stevenson, 2014). Even in the healthy population, the temporal sensitivity of integration differs markedly across individuals (Stevenson, Zemtsov & Wallace, 2012). Within individuals, temporal sensitivity is modulated by factors such as stimulus complexity (Stevenson & Wallace, 2013), stimulus intensity (Fister, Stevenson, Nidiffer, Barnett, & Wallace, 2016) and spatial relation (Lewald & Guski, 2003). Previous experience and training (Lee & Noppeney, 2011; Navarra et al., 2005; Powers, Hillock, & Wallace, 2009), attention (Donohue, Green, & Woldorff, 2015; Talsma, Senkowski, & Woldorff, 2009) and cognitive load (Dean et al., 2017) also have an impact.

Most of the studies discussed above have focused on phasic activity of the nervous system. Recently, however, it has been found that spontaneous oscillatory EEG activity can affect temporal discrimination sensitivity in unisensory auditory, tactile and visual perception (Baumgarten, Schnitzler, & Lange, 2016; Bernasconi, Manuel, Murray, & Spierer, 2011; Ronconi, Busch, & Melcher, 2018; Samaha & Postle, 2015). In the multisensory domain, the relation between tonic brain activity and multisensory integration has increasingly been studied as well

(Cecere, Rees, & Romei, 2015; Grabot, Kösem, Azizi, & Wassenhove, 2017; Keil & Senkowski, 2017; Leonardelli et al., 2015; Yuan, Li, Liu, Yuan, & Huang, 2016).

For example, Cecere et al. (2015) used the sound-induced flash illusion in combination with EEG and transcranial alternating current stimulation (tACS) to show that peak alpha-frequency around stimulus presentation causally determined the temporal window of audiovisual integration. Their findings were corroborated by (Keil & Senkowski, 2017) based on an analysis of pre-stimulus activity alone. These results are informative regarding the temporal characteristics of auditory influences on visual perception, but the question remains whether they are representative of general multisensory perceptual processes since they rely on the illusory perception of a flash. Not all participants report this illusion and whether they do so might even depend on the power of their alpha oscillations (Cecere et al., 2015; Lange, Oostenveld, & Fries, 2013; however see Keil & Senkowski, 2017). Furthermore, the effect of oscillations on the temporal sensitivity of perception may be so subtle that it only becomes apparent when the stimuli are around threshold or even illusory.

To test more directly whether spontaneous pre-stimulus activity affects audiovisual temporal sensitivity, we asked participants to make temporal order judgements on supra-threshold audio-visual stimuli. We employed a “jackknife” procedure adapted for linking psychophysical data to single-trial EEG parameters (Benwell, Keitel, Harvey, Gross, & Thut, 2017). This leave-one-out procedure allowed us to examine cross-trial co-variation of pre-stimulus oscillatory parameters in EEG with temporal discrimination sensitivity estimates obtained from psychometric curves. In this manner, we tested whether the power of pre-stimulus oscillations (2 to 45 Hz) was predictive of the temporal sensitivity of multisensory integration. Furthermore, to extend the results of Cecere et al. (2015) and (Keil & Senkowski, 2017), we tested whether the instantaneous frequency of pre-stimulus oscillations in the alpha range positively correlated with individuals’ audio-visual temporal sensitivity.

METHOD

PARTICIPANTS

Forty-three volunteers participated in this experiment for monetary compensation. Two participants were excluded due to their estimated sensitivity measure exceeding the maximum SOA of 350 ms. One participant was excluded due to not completing the experiment. Analyses were carried out on the data of the remaining 40 participants (30 female, 2 left handed, median age: 23, age range: 18 – 32). Participants reported having normal audition and normal or corrected-to-normal vision and no history of neurological disorder or recent use of psychoactive substances. The experiment was approved by the Ethics Committee of Ghent University and participants gave informed consent prior to the start of the experiment.

APPARATUS AND STIMULI

Participants were seated in a dimly lit, sound-proof and electrically shielded chamber, with their head stabilized by a chinrest at 50 cm from a 24-inch LCD monitor (BenQ XL2411; 120 Hz refresh rate). The task was an audiovisual temporal order judgement task (TOJ) in which participants were presented with a visual flash and an auditory beep, and then asked to judge which of the two had been presented first (See figure 1). The experiment had one single within-participants factor which was the stimulus onset asynchrony (SOA) between the flash and the beep. The SOA had 12 levels (-350, -216, -133, -88, -50, -16, +16, +50, +88, +133, +216 and +350 ms) where negative SOAs indicate that the beep was presented first and positive SOAs that the flash was presented first. Each SOA was presented 70 times giving a total of 840 trials, divided over 35 blocks of 24 trials each. SOA was randomized per block with each condition presented twice within each block. The task was implemented using the E-prime 1.2 software package (Schneider, Eschman, & Zuccolotto, 2002) on an HP Compaq desktop computer running Microsoft Windows XP. This setup allowed for the timing of stimulus presentation to be at a resolution of ≤ 1 ms which was confirmed with an oscilloscope. The visual stimulus was a solid white circle (lumi-

nance of 270 cd/m^2) subtending a visual angle of 1.95° . It was presented at 5° below a central fixation cross subtending 0.46° on a black background and for a duration of 16.6 ms. The auditory stimulus was a 1850 Hz tone presented at 72 dB(A) with a duration of 16 ms (plus 3 ms fade-in and 3 ms fade-out) delivered by two loudspeakers (Logic3 Screenbeat ES20). The loudspeakers were placed symmetrically, to the left and right of the monitor.

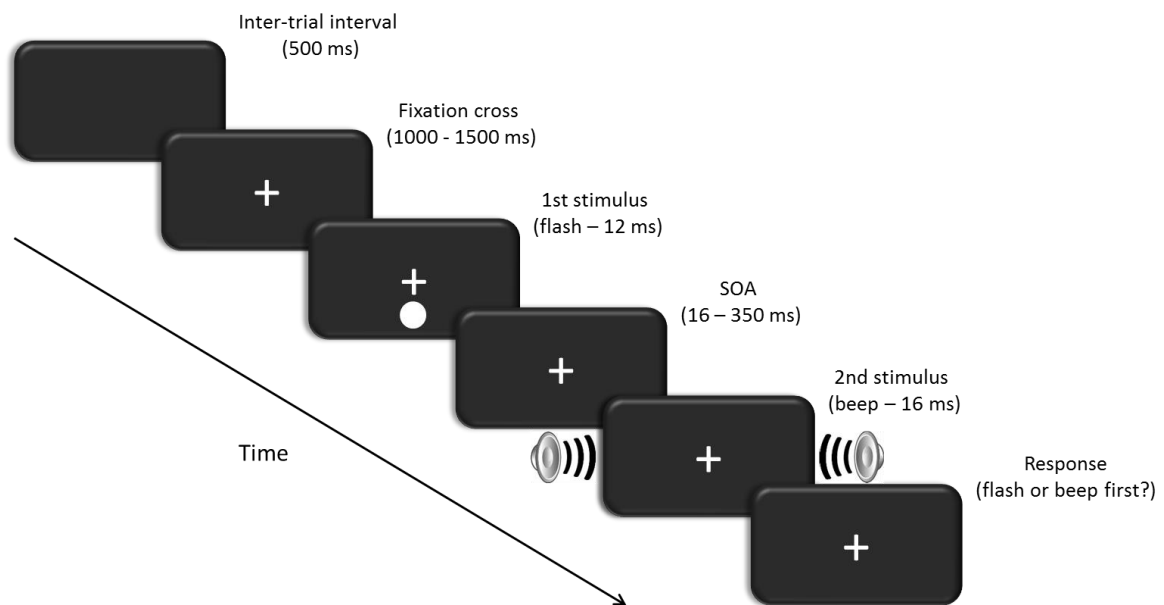


Figure 1. Schematic representation of one experimental trial. After an inter trial interval of 500 ms, a fixation cross appeared on the screen for a random duration between 1000 ms and 1500 ms. Then the first stimulus (in this case a flash) was presented and after the SOA the second stimulus (in this case a beep) was presented. The fixation cross remained on the screen until participants had responded which of the two they had perceived first.

PROCEDURE

The experiment started with the recording of 5 minutes of eyes-open resting state EEG and a seven-minute passive observation task with the sequential presentation of 50 instances of the visual stimulus and 50 instances of the auditory stimulus. Since the EEG data collected during this session are beyond the scope of the current project, they will not be reported here. The TOJ task then started after two practice blocks of 12 trials (one for each SOA) during which the

experimenter was present to ensure participants understood the instructions. Each trial started with the presentation of a central fixation cross. Participants were instructed to fixate this cross throughout the task. After a random interval of 1000-1500 ms, the first stimulus (a flash or a beep, depending on the condition) was presented. After a random delay, chosen amongst the 12 possible SOAs, the second stimulus was presented. Participants were instructed to judge which stimulus (auditory or visual) had been presented first. The task was not speeded, and there was no time limit, but participants were instructed not to think about the answer for too long. Participants pressed the “g” key when they had perceived the auditory stimulus first, and the “h” key when they had perceived the visual stimulus first. After the response, a black screen was presented for 500 ms after which the next trial started. In the practice session, participants received feedback after each trial. During the experimental session no single trial feedback was given, but after each block their mean accuracy for that block was presented. Between blocks there was a self-paced break during which participants were encouraged to rest for a short moment. The total duration of the experiment was approximately 50 minutes.

ELECTROPHYSIOLOGICAL RECORDING AND PRE-PROCESSING

The electroencephalogram (EEG) was recorded at 1024 Hz with a Biosemi ActiveTwo system (Biosemi, Amsterdam, Netherlands) with 64 Ag–AgCl scalp electrodes positioned according to the standard international 10–20 system. Additional electrodes were positioned at the outer canthi of both eyes and directly above and below the right eye to acquire horizontal and vertical electrooculograms (EOG), respectively. Preprocessing was done with custom scripts incorporating functions from the EEGLAB toolbox (Delorme & Makeig, 2004). Data was high-pass filtered using a Hamming windowed sinc FIR filter with the lower edge of the pass band at 0.5 Hz and a cutoff-frequency of 0.25 Hz. Data was low-pass filtered using a Hamming windowed sinc FIR filter with the upper edge of the pass band at 45 Hz and a cutoff-frequency of 50.6 Hz. In preparation for independent component analysis (ICA), data was then cut into 2-second epochs starting 1500 ms before the first stimulus and ending 500 ms after the first stimulus. The epoch mean was subtracted and trials containing unique or

very large artefacts were manually discarded. Electrodes exhibiting excessive noise were removed and interpolated. In six participants, this was the case for one electrode and in two participants for two electrodes. Data was then re-referenced to the average of all electrodes (excluding external electrodes) and ICA was run with the EEGLAB “runica” function. Subsequently the filtered continuous data was re-epoched in preparation for time-frequency analysis to 4-second-long epochs starting 2500 ms before the first stimulus onset until 1500 ms after the first stimulus onset (exceeding the -1500 to +500ms window of interest to avoid filter artifacts at the edges). As before, the epoch mean was subtracted, bad electrodes were eliminated and the data was re-referenced to the average of all electrodes except the EOG and mastoid electrodes. Then the previously obtained ICA weights were applied to this dataset and components reflecting eye movements or blinks and muscle artefacts were projected out of the data. The number of components that was removed per participant ranged from 1 to 10 with a median of 3 (the median is reported here because its more robust against outliers) . Then, eliminated electrodes were interpolated and trials containing artefacts were manually discarded. The percentage of trials that was discarded per participant ranged from 2% to 39%, with a median of 9%. Finally, in order to improve topographic localization, a Laplacian transform was applied through the use of Matlab script accompanying (Cohen, 2014).

BEHAVIORAL ANALYSIS

We were interested in the minimum amount of time between the auditory and visual stimuli that was needed in order for each participant to be able to correctly judge the order in which the stimuli had been presented in 75% of the trials. This psychophysical measure of temporal sensitivity is referred to as the “just noticeable difference” (JND) and was derived using the Palamedes toolbox for Matlab (Prins & Kingdom, 2018). First, a logistic function was fit to the proportion of “flash-first” responses as a function of SOA. Guess rate and lapse rate were fixed at 0.02 for each participant. The logistic function is given as:

$$F_L(x; \alpha, \beta) = \frac{1}{1 + \exp(-\beta(x - \alpha))}$$

with x denoting the SOA, α the value of x at which the function evaluates to 0.5 and β the slope or steepness of the function. Second, the difference along the x -axis in milliseconds between 25% and 75% “flash first” responses on the y -axis was divided by two to obtain the JND in milliseconds:

$$JND = \frac{F_L^{-1}(.75) - F_L^{-1}(.25)}{2}$$

Lower JND values indicate higher temporal sensitivity whereas higher JND values denote lower sensitivity. Since observations from multiple trials are required to fit a function and derive the JND, this metric is not definable on a single-trial basis. However, it was precisely our aim to investigate how moment-to-moment fluctuations in EEG parameters and temporal sensitivity co-varied across trials. We tackled this challenge by applying a method developed by (Benwell et al., 2017) which adapts a “jackknife” procedure (Quenouille, 1949; Richter, Thompson, Bosman, & Fries, 2015; Stahl & Gibbons, 2004; Tukey, 1958) to link single-trial variability in oscillatory activity to psychometric measures such as the JND (see Jackknife analysis below). Another measure that can be derived from the logistic function is the point of subjective simultaneity (PSS). Although this measure is not pertinent to our research question and was not further analyzed in relation to the EEG, we derived it for each participant to offer a more complete description of the behavioral data. The PSS corresponds to the value of the SOA for which the function evaluates to 0.5 and is interpreted as the SOA where the stimuli appear to the observer as arriving simultaneously. The PSS is given as:

$$PSS = F_L^{-1}(.5)$$

ELECTROPHYSIOLOGICAL ANALYSES, WITHIN PARTICIPANTS

EEG Power

A time-frequency representation of the single-trial data was obtained by convolving the preprocessed data with a complex wavelet using the “mtmconvol” option of the “ft_freqanalysis” function from the Fieldtrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011). A sliding window with a length of 500 ms was employed to segment the data. The window was shifted forward in steps of 20 ms. Each segment was multiplied with a Hanning taper to avoid edge artefacts. The value of oscillatory power at each data point therefore included activity from 250 ms before and 250 ms after that time point. Since we were expressly interested in stochastic, stimulus-unrelated activity, we restricted our power analysis to the time points ranging from 750 ms to 250 ms before stimulus onset to ensure that no stimulus related activity was included. Oscillatory power was thus obtained for each trial at 25 time points in 20 ms steps and 21 frequencies ranging from 2 to 45 Hz in 2 Hz steps for 64 electrodes. Finally, the resulting power values were converted to decibels.

Instantaneous alpha frequency (InstAF)

The InstAF was extracted for each data point during a one-second period preceding the onset of the first stimulus using the method described by Cohen (2014). First, one-second long epochs were created immediately preceding the onset of the first stimulus. To avoid edge artefacts, each epoch was reflected on both sides; it was flipped horizontally and concatenated to the beginning and end of the original epoch. The data was filtered in the time domain using a plateau-shaped 8-to-13 Hz band-pass filter with 15 % transition zones and a filter order of 896 points and the analytic signal was computed using the Hilbert transform. The phase-angle time series was then unwrapped and its first temporal derivative multiplied by the sampling rate and divided by 2π to obtain instantaneous frequency in Hz. Noise in the data can cause small jumps in the phase-angle time series (“phase slips”) which in turn produce large artefactual frequency peaks and troughs. To attenuate these, the instantaneous-frequency

time series was median-filtered ten times using ten filter orders ranging from 10 to 400 ms in length, before averaging the ten filtered time series. Finally, the one-second period was segmented into 32 segments of 31,25 ms each. For each trial the average instantaneous frequency was calculated for each of these segments. InstAF for each trial at 32 time points and 64 electrodes was thus entered into the subsequent analysis.

Jackknife analysis of behavior in relation to EEG power and InstAF

In order to test whether moment-to-moment fluctuations in pre-stimulus EEG characteristics co-varied with moment-to-moment fluctuations in temporal sensitivity, we implemented a two-level analysis. At the participant level, a single-trial analysis was done where we computed a jackknife Spearman correlation across trials between (i) the JND and EEG power at all time points, frequencies and electrodes and between (ii) the JND and InstAF at all time points and electrodes. At the group level these results were subjected to cluster-based permutation tests, to test whether any clusters of data points showed a systematic relationship (i.e. positive or negative correlation) across participants.

Single-trial jackknife correlations at the participant level. As stated above, the aim of these analyses was to obtain correlations across trials between EEG power and temporal sensitivity and between InstAF and temporal sensitivity. Since our measure of sensitivity, the JND, is an ensemble metric which cannot be obtained at the single-trial level, the application of jackknife correlations was required. We computed jackknife EEG power by iteratively averaging over all trials while leaving one trial out at each iteration. This method enabled us to use a single-trial analysis and test the relationship between fluctuations in EEG parameters and temporal sensitivity on a short, moment-to-moment time scale. For the mathematical proof of the equivalence of the conventional and jackknife correlations we refer to (Richter et al., 2015). For a detailed explanation of how to apply this procedure to link psychophysical data with EEG data, see (Benwell et al., 2017). We used Spearman's rho (ρ_s) to correlate EEG power and InstAF with the JND across trials. For EEG power, this procedure was repeated at all

electrodes, frequencies and time points resulting in a $64 \times 23 \times 25$ matrix of ρ 's per participant. For InstAF, we repeated the procedure for all time points and electrodes resulting in a matrix of 64×32 ρ 's per participant. Importantly, we controlled for possible non-stationarities in power and frequency over the course of the experiment by partializing out trial order (Pearson, 1915). This precluded the possibility that a spurious correlation would arise due to co-occurring but unrelated EEG and behavioral non-stationarities over the course of the experiment (Benwell et al., 2018).

Group-level analysis. Subsequently, we tested whether any of the correlations obtained at the participant level showed a systematic deviation from zero across participants. Dependent sample t-tests against 0 were performed on the Spearman ρ 's at each data point across participants. To control for multiple comparisons, a cluster-based permutation-testing routine developed by Maris and Oostenveld (2007) was implemented. This was done separately for correlations of behavior with EEG power and InstAF. All data points were selected for which the t-value had a probability lower than 5% of having occurred by chance. These were then clustered based on adjacency in the temporal, spectral or spatial domain for EEG power and in the temporal and spatial domain for InstAF. For the EEG power analysis, this procedure was done separately for positive and for negative t-values (two-tailed test). For the InstAF analysis, a one-tailed test was employed and only negative t-values were clustered (we hypothesized that higher InstAF would be associated with a smaller JND based on Cecere et al. (2015) and Keil and Senkowski (2017)). For each cluster, the sum of t-values was then calculated and the maximum of these cluster-level statistics was taken. To create a reference distribution against which to test the value of this cluster-level statistic, 1000 permutations of the data were conducted using the "ft_statistics_montecarlo" function from the fieldtrip toolbox (Oostenveld et al., 2011). Each iteration yielded a maximum cluster level statistic and over iterations a null distribution of maximum cluster level values was constructed. The p value of the effect was then estimated as the proportion of elements in the null distribution exceeding the observed maximum cluster-level test statistic.

ELECTROPHYSIOLOGICAL ANALYSES, INDIVIDUAL DIFFERENCES

To test whether individual peak alpha frequency (IAF) and individual alpha power (IAP) could predict temporal sensitivity across individuals, we calculated IAF during the pre-stimulus period for each participant. Then, we calculated alpha power at each participant's IAF. Both these measures were then correlated with the JND across participants using a Spearman correlation. We corrected for multiple comparisons with a Bonferroni correction. For each participant the individual alpha peak was estimated from the following centro-parietal electrodes; TP7, CP5, CP3, CP1, CPz, CP2, CP4, CP6, TP8, P9, P7, P5, P3, P1, Pz, P2, P4, P6, P8, P10, PO7, PO3, POz, PO4, PO8, O1, Oz, O2, Iz. The frequency range of interest was 8-13 Hz. This individual-differences analysis was carried out on the same data epochs as the within participant analysis described above. Each segment was multiplied with a Hanning window and the data was zero padded to obtain a frequency resolution of 0.25 Hz. In order to determine IAF, an automated estimation routine was utilized developed by Corcoran, Alday, Schlesewsky, and Bornkessel-Schlesewsky (2018). This provided us with an objective and replicable method to pick the electrode from which the IAF was inferred and discard participants that did not exhibit a clear alpha peak. The method is described in detail in Corcoran et al. (2018). First, the power spectrum is smoothed using a Savitzky-Golay filter. This is a least-squares polynomial curve-fitting procedure originally developed in chemistry to detect spectral peaks amidst noisy conditions (Savitzky & Golay, 1964). The first- and second-order derivatives of the fitted function are then analyzed for evidence of a peak in the alpha band region (8-13 Hz). A peak was considered to be valid when the highest power value was at least 1 standard deviation from the mean and was at least 20 % higher than other peaks in the same spectrum. As a measure of the quality of each peak, the area under the peak was defined and divided by its frequency span. Only participants for which at least three electrodes yielded a peak were maintained in order to exclude those where the detected alpha peak was spurious. The electrode with the largest value was chosen to provide the IAF estimate for that participant. Thirty-three participants satisfied this condition and the following electrodes were used for peak detection (1 per participant; see figure 8A); PO4, PO4, PO3,

O2, POz, POz, PO7, P5, Oz, Pz, POz, O1, POz, PO4, P6, Oz, POz, POz, O2, PO7, PO8, PO4, PO8, PO7, POz, PO7, P3, CPz, PO7, POz, PO3, PO8.

RESULTS

BEHAVIORAL RESULTS

Participants completed an audio-visual TOJ task. They were presented with a beep and a flash at varying SOAs, and were asked to indicate which stimulus had been presented first. A psychometric function was then fitted to the proportion of “flash-first” responses.

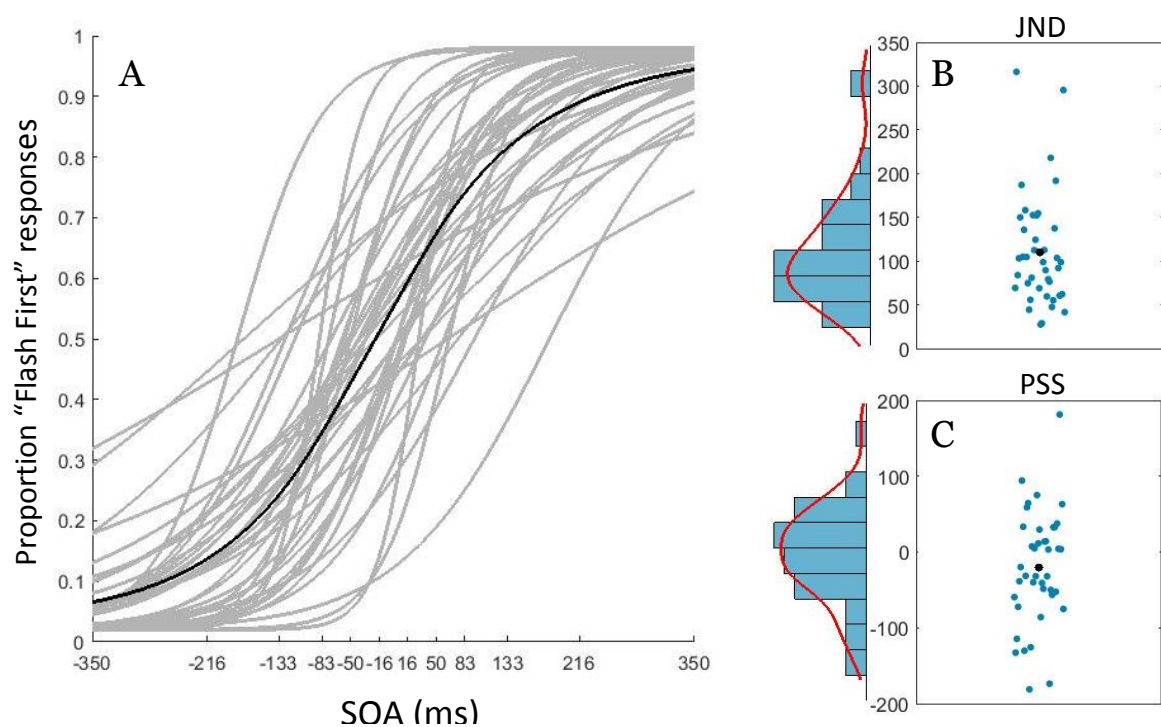


Figure 2. Behavioral results. **(A)** Psychometric functions fitted to each participant’s data are displayed in grey. The psychometric function fitted to the group averaged data is displayed in black. **(B)** The JND’s derived from the psychometric function of each participant are displayed in blue. The average JND is displayed in black. **(C)** The PSS’s derived from the psychometric function of each participant are displayed in blue. The average PSS is displayed in black.

Figure 2A shows the fitted functions for each participant as well as a function fit to the average data of all participants in black. As an index of temporal audio-visual discrimination sensitivity, our primary measure of interest, we derived the JND from this function. Across all participants the mean JND was 110 ms, with a standard deviation of 64 ms, which is typical of the large individual differences habitually observed in such paradigms (e.g. Stevenson et al., 2012; see figure 2B). Additionally, we derived the point of subjective simultaneity (PSS). On average the PSS was -21 ms (audio-leading), however this deviation from 0 was not statistically significant (the 95% confidence interval ranged from -44,41 ms to 3,11 ms, see figure 2C).

EEG RESULTS

Pre-stimulus alpha power predicts temporal sensitivity

We tested if the power of spontaneous fluctuations during the pre-stimulus interval predicted the temporal sensitivity of audio-visual perception on a trial-by-trial basis. Figure 3A shows the strength and direction of the relationship between EEG power and the JND. One significant positive cluster ($p = .018$) was present in the alpha frequency range from 650 to 250 ms preceding stimulus onset. The cluster was restricted to posterior electrodes (see figure 3B). Figure 3C shows for each participant the correlation between power and the JND averaged over the points in the cluster. For 33 out of 40 participants (82,5%), higher power was accompanied by worse temporal sensitivity. This was not a spurious finding caused by coexisting, but independent, changes in alpha power and JND over the course of the experiment (due to fatigue, boredom and/or decreased motivation; see Benwell et al., 2018), as the results are controlled for trial order. Therefore, these data suggest a functional role of alpha oscillatory power in the temporal sensitivity of audio-visual perception on a short, trial-to-trial time scale.

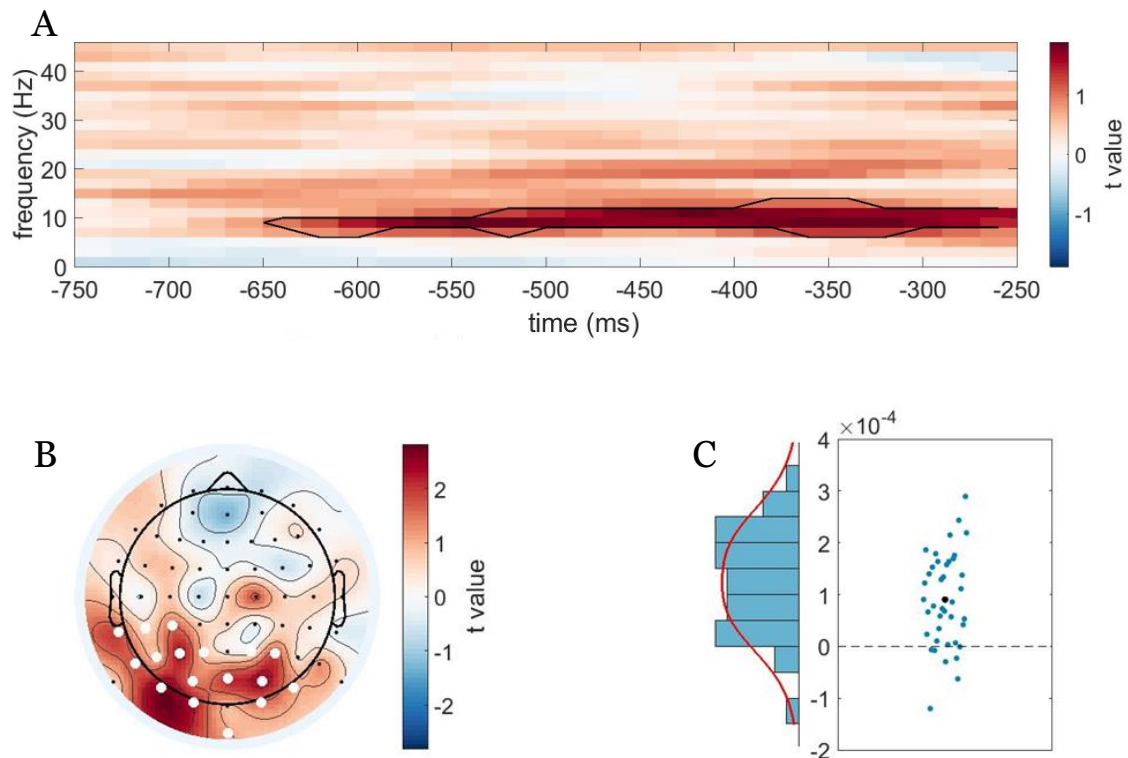


Figure 3. EEG oscillatory power predicts the temporal sensitivity of audio-visual perception. **(A)** Time-frequency representation of t-values averaged over all electrodes included in the cluster. Onset of the first stimulus (auditory or visual) is at 0 seconds. Positive t-values (in red) indicate that higher power is accompanied by a higher JND (worse temporal sensitivity). Negative t-values indicate that higher power is accompanied by a lower JND (better temporal sensitivity). One positive cluster survived multiple comparisons and is outlined in black. **(B)** Topographical representation of the t-values averaged over all time-frequency points included in the cluster. Electrodes that were included in the cluster are highlighted in white. **(C)** Average correlations for each participant between EEG power in the cluster and the JND. Each blue dot represents one participant. The black dot indicates the group mean, and the black dotted line indicates a correlation of 0.

Pre-stimulus instantaneous alpha frequency predicts temporal sensitivity

We tested whether higher instantaneous frequency of alpha oscillations during the 1000 ms pre-stimulus period was associated with higher temporal sensitivity of audio-visual perception on a trial-by-trial basis. Figure 4A shows the strength of the relationship between alpha instantaneous frequency and the JND in the only significant (negative) cluster. The time segment where higher alpha instan-

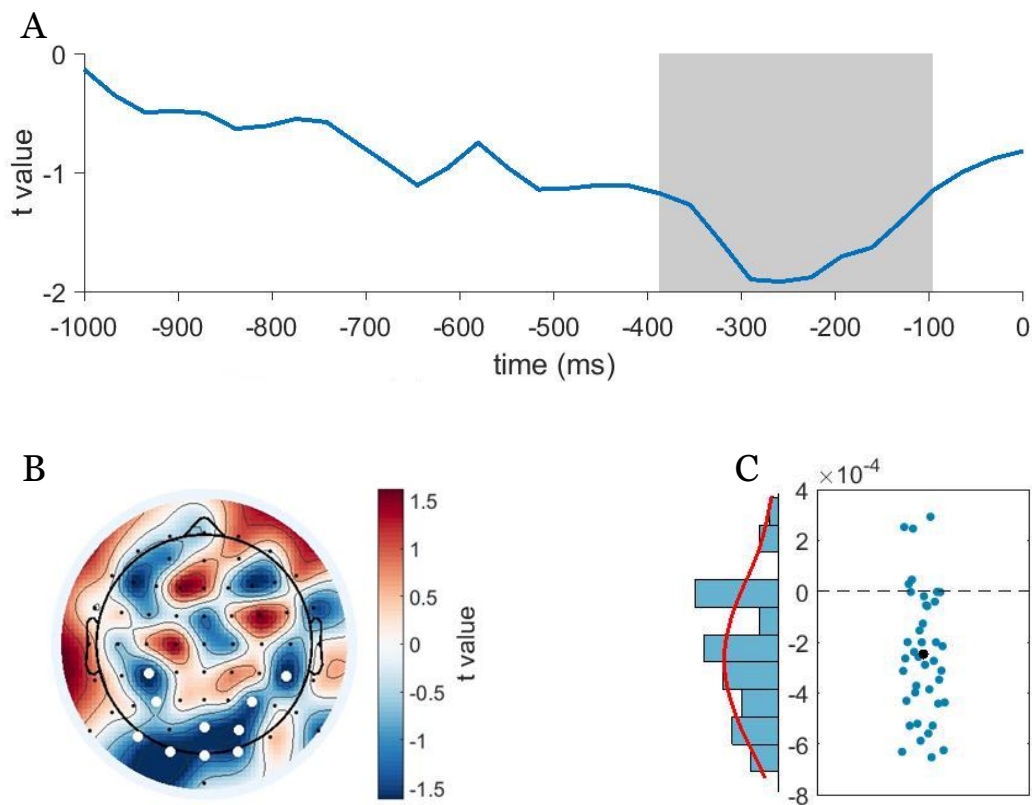


Figure 4. EEG instantaneous alpha frequency predicts the temporal sensitivity of audio-visual perception. **(A)** t-values over time, averaged over all electrodes included in the cluster. Onset of the first stimulus (auditory or visual) is at 0 seconds. Negative t-values indicate that higher instantaneous frequency is accompanied by a lower JND (higher temporal sensitivity). One negative cluster survived multiple comparisons and is marked with a grey box. **(B)** Topographical representation of the t-values averaged over all time points included in the cluster. Electrodes that were included in the cluster are highlighted in white. **(C)** Average correlations for each participant between EEG instantaneous frequency in the cluster and the JND. Each blue dot represents one participant. The black dot indicates the group mean and the dotted line indicates a correlation of 0.

taneous frequency significantly predicted a lower JND (and thus better temporal sensitivity) is marked with a grey box ($p = .03$). This cluster was present from 375 ms to 94 ms before stimulus onset. Only posterior channels were part of this cluster (see Fig. 4B). Figure 4C shows for each participant the correlation between alpha instantaneous frequency and the JND averaged over the points in the cluster. For 35 out of 40 participants (87.5%), higher instantaneous alpha frequency was accompanied by better temporal sensitivity. Again, this was not a spurious finding caused by coexisting, but independent, changes in alpha instan-

taneous frequency and JND over the course of the experiment (due to fatigue, boredom and/or decreased motivation; see Benwell et al., 2018), given that we controlled for trial order. Therefore, these data again are in line with the existence of a functional role of alpha oscillatory frequency in the temporal sensitivity of audio-visual perception on a short, trial-by-trial time-scale.

Alpha frequency and power effects appear to be driven by the same process.

A question that arises is whether the power and frequency effects are connected, and if so, how? One scenario in which these effects may result from the same underlying process is if the driving force of both effects were an asymmetric power modulation (see figure 5). When measuring the instantaneous (alpha) frequency of a scalp-level signal such as the EEG, it is important to keep in mind that it likely includes multiple oscillatory sources, even when it is bandpass filtered around the frequency band of interest (Benwell et al., 2018; Clayton et al., 2017), and that the instantaneous frequency and power of a signal are not independent (Nelli, Itthipuripat, Srinivasan, & Serences, 2017). The instantaneous frequency of such a summated signal will gravitate towards the instantaneous frequency of the oscillatory source with the highest power. When there are multiple oscillators at different frequencies, an increase in the power of one oscillator can shift the instantaneous frequency of the scalp-level signal towards its own without any changes in the instantaneous frequencies of the underlying oscillators. Therefore, an increase in lower alpha power would automatically lead to a decrease in instantaneous alpha frequency (see figure 5). This pattern would be in line with our results; the InstAF relation with the JND is negative, whereas the power relationship is positive. If the power effect were mostly driven by upper-alpha, then this could not explain the negative relation we found between InstAF and the JND, nor could an effect of power at peak alpha frequency. In order to unpack our results and see if the scenario described above could explain both the power and frequency effects, we conducted a follow-up analysis using a higher frequency resolution of 1 Hz. First, in order to compare lower alpha and upper alpha across participants we accounted for individual differences and aligned participant's spectra on their IAF. We included frequencies up to two Hz

above and below IAF. Then we reran the analysis as explained before, correlating power with the JND across trials, while controlling for trial order. If the power and frequency effects resulted from the same process, we would expect to see the strongest effect of power in the lower alpha band. This is exactly what we found. Power at one Hz below the alpha peak was most predictive of the temporal reso-

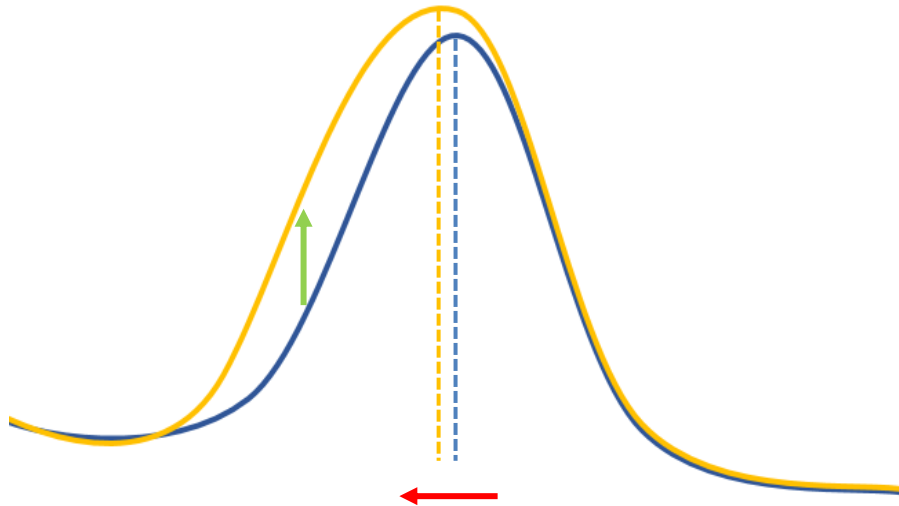


Figure 5. Toy model depicting the scenario where a modulation of lower-alpha power could lead to a concurrent modulation of InstAF. The power spectrum in yellow shows an increase in mostly lower-alpha power compared to the blue spectrum. This increase in lower-alpha power pulls the InstAF measurement of the signal towards the lower alpha range, where more power is now present.

lution of integration (see figure 6A). It is of course still possible that the instantaneous frequency effect is only partially due to fluctuations in lower-alpha power, and that it also has an independent component to it. To check if this was the case, we correlated InstAF and the JND across trials for each time point and electrode as we did before. To avoid inclusion of post-stimulus effects due to temporal smearing our power data only run from 740 to 240 ms pre-stimulus, and we cut the instantaneous frequency data to match it. Crucially, we repeated the analysis five times, each time controlling for alpha power at one of the five individualized alpha frequencies. The relation between InstAF was not affected

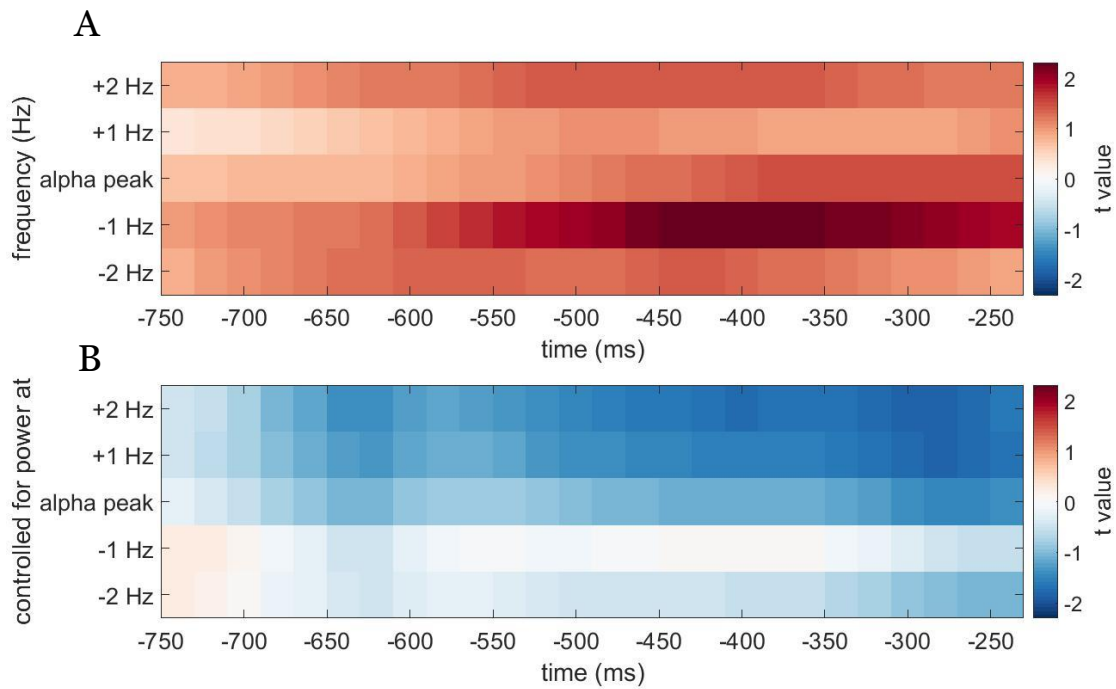


Figure 6. The predictive value of instantaneous alpha frequency for the temporal sensitivity of audio-visual perception can be explained by fluctuations in lower-alpha power. **(A)** Time-frequency representation of t-values averaged over all electrodes included in the cluster. **(B)** Time-frequency representation of t-values averaged over all electrodes included in the cluster.

much when controlling for power at upper alpha-frequencies, but when controlling for power at alpha peak minus one, where the strongest effect for alpha power was found, the instantaneous frequency effect seemed to vanish (see figure 6B). The results of this follow-up analysis appear to suggest that instead of dealing with two separate effects, it is one and the same process, reflected by a modulation of lower-alpha frequency, that predicts the temporal resolution of audiovisual integration in our paradigm.

Neither IAF nor IAP predicts individual differences in temporal sensitivity.

At the group level we found that trial-by-trial variations in both alpha power and alpha instantaneous frequency predicted the temporal sensitivity of multisensory perception. Subsequently, we tested whether alpha power and frequency could also predict performance across individuals, and thereby help explain the

large inter-individual variability in JND's habitually found in such paradigms. We calculated individual alpha peak frequency (IndAF) during the pre-stimulus period for each participant. We then calculated alpha power at this frequency for each participant (IndAP) to correlate these measures with the JND across participants using a Spearman correlation. Seven participants were excluded from these analyses, because an alpha peak was not identified by our peak-finding algorithm, leaving a total of 33 participants included in this analysis. Figure 7 shows that neither IAF (Fig. 7B; $\rho_s(31) = -0.21$, $p = 0.12$, one-tailed) nor alpha power (Fig. 7C; $\rho_s(31) = 0.03$, $p = 0.85$, two-tailed) was predictive of an individual's JND.

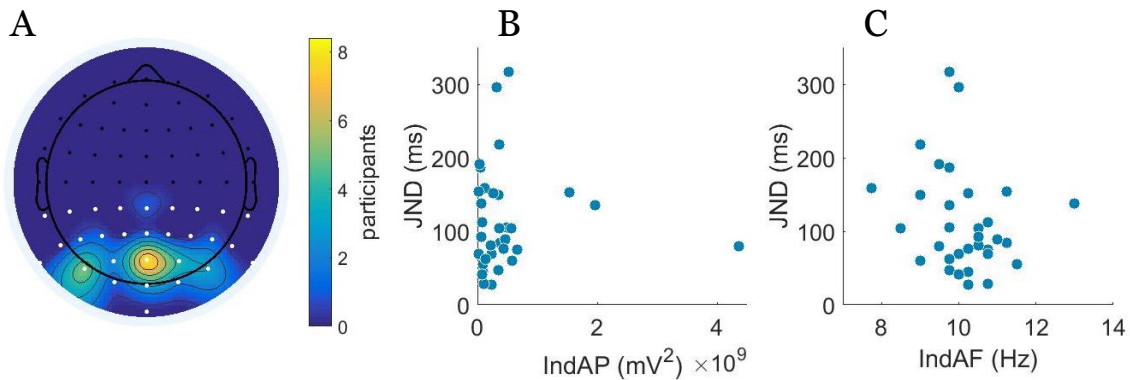


Figure 7. Individual alpha power and individual alpha frequency did not predict temporal sensitivity of audio-visual perception across participants. **(A)** Heat map showing the number of participants for which each electrode was selected to measure IAF and IAP. The electrodes that were entered into the peak picking algorithm are marked in white. **(B)** No systematic relation was shown between IAP and JND. **(C)** No systematic relation was shown between IAF and JND.

DISCUSSION

This study used a temporal order judgement (TOJ) task to examine the role of spontaneous, ongoing oscillations in the temporal sensitivity of audiovisual integration. Pre-stimulus power at a wide range of frequencies was tested, and we found that specifically alpha power had significant predictive value over performance on a single-trial level. Higher power in this frequency band predicted worse temporal sensitivity. The instantaneous frequency of alpha oscillations

(InstAF) was also measured and higher InstAF was found to predict better temporal sensitivity from trial to trial. At first glance, the latter result seemed to support an account of audiovisual temporal integration in terms of the theory of perceptual cycles (VanRullen, 2016). A follow-up analysis revealed, however, that the correlation between InstAF and the JND could be explained by power modulations in the lower alpha band. These results suggest that, in our task, the cycle of alpha oscillations does not determine the length of time over which the auditory and the visual stimulus are integrated. Rather it seems to be alpha power that affects performance. These results provide novel insight into the neural basis of the temporal resolution of multisensory integration. We show that not only task conditions (Stevenson & Wallace, 2013; van Eijk, Kohlrausch, Juola, & van de Par, 2008) and individual differences (Stevenson, Zemtsov, & Wallace, 2012; Wallace & Stevenson, 2014) affect the temporal sensitivity of audiovisual integration, but that spontaneous brain activity does so as well, on a trial-to-trial basis. The effect of alpha power likely reflects the impact of fluctuations in excitability on the mechanisms driving integration. In showing this, we extend existing evidence that higher alpha power is indicative of a tendency towards temporal integration (Baumgarten et al., 2016; Leonardelli et al., 2015; Peterson & Voytek, 2018). Furthermore, our pattern of results highlights the need for caution when interpreting analyses involving instantaneous alpha frequency, since asymmetric shifts in alpha power such as we see here, can lead to epiphenomenal relationships between InstAF and behavior. Such asymmetric power shifts may turn out to be common, as evidence for the existence of multiple, variable alpha rhythms is mounting. These rhythms are believed to originate from both cortical and sub-cortical sources that together give rise to the rhythm measured at the scalp (Benwell et al., 2018; Clayton, Yeung, & Kadosh, 2017; Klimesch, Doppelmayr, Schimke, & Pachinger, 1996).

DECREASED ALPHA POWER PREDICTS INCREASED TEMPORAL SENSITIVITY

Alpha oscillations have not only been shown to play a role in a variety of processes, they also originate from multiple sources, reflecting the complex result of both thalamocortical and corticocortical interactions in visual cortex (Clayton et

al., 2017). We found that from trial to trial, higher alpha power predicted worse temporal sensitivity in an audiovisual TOJ. This effect was driven mostly by power in the lower-alpha band as compared to power in the mid- or upper-alpha band and the effect was most pronounced over occipito-parietal electrodes. There is some evidence that activity in the lower- and mid-alpha band reflects expectancy and alertness, with power decreasing as alertness increases, and that upper alpha band activity reflects cognitive performance in certain tasks, with alpha power rising as performance improves (Klimesch, Doppelmayr, Russegger, Pachinger, & Schwaiger, 1998). Even though this evidence is limited and comes mostly from studies into memory maintenance, the idea that alpha band activity reflects expectancy and alertness fits well with evidence that pre-stimulus alpha oscillations index excitability of the cortex, with higher alpha power indicating lower excitability (Romei et al., 2008; Sauseng, Klimesch, Gerloff, & Hummel, 2009). In studies where participants are asked to detect a weak stimulus, lower pre-stimulus alpha power commonly leads to higher detection rates (as reviewed in Iemi, Chaumon, Crouzet, & Busch, 2017). Notably, this is the case whether the stimulus is real or illusory. Thus, lower pre-stimulus alpha power does not necessarily lead to more accurate perception (e.g. Lange, Oostenveld, & Fries, 2013). Iemi et al. (2017) addressed this issue with signal detection theory. They hypothesized that if decreased alpha power indicates increased baseline excitability, not only the signal but also the noise would elicit a larger response. This would lead to more hits, but also to more false alarms, thereby shifting the criterion towards the more liberal side, but leaving sensitivity unchanged. Indeed, they found that in a near-threshold visual stimulus detection task, decreased alpha power made observers more likely to report the presence of a stimulus, whether the stimulus was present or not. In a discrimination task, they found that alpha power did not affect performance, in accordance with the idea that perceptual bias, but not sensitivity is affected by alpha oscillations. Other studies where visual perceptual discrimination sensitivity was measured have also shown to be unaffected by alpha power shifts (Bays, Visscher, Dantec, & Seitz, 2015; Hanslmayr et al., 2007; Lou, Li, Philiastides, & Sajda, 2014; Wutz, Weisz, Braun, & Melcher, 2014). Our data do not mirror these results. We find that pre-stimulus alpha power does predict discrimination sensitivity. Similar results have been reported by Leonardelli et al. (2015) who presented participants with an audio-tactile pair

of above-threshold stimuli with variable SOA's while recording MEG. When comparing brain activity between identically timed pairs with different perceptual outcomes they found that on trials where participants perceived one integrated audio-tactile stimulus, pre-stimulus alpha power had been higher compared to trials where participants perceived the stimuli as separate. On a comparable note, Baumgarten, Schnitzler, & Lange (2016) presented participants with one or two short, above-threshold tactile stimuli. When the time between the stimuli was such that the percept varied from 1 to 2 on a trial-by-trial basis, decreased pre-stimulus alpha power predicted veridical perception of 2 stimuli. In other words, in a tactile temporal discrimination task (Baumgarten et al., 2016), in an audio-tactile temporal discrimination task (Leonardelli et al., 2015), and in our audiovisual temporal discrimination task, lower alpha power predicted higher temporal sensitivity and segregated perception, while higher alpha power predicted lower temporal sensitivity and integrated perception. Our study and those by Baumgarten et al. (2016) and Leonardelli et al. (2015), differ in at least three characteristics from the visual discrimination tasks where alpha power did not affect perceptual sensitivity (Bays et al., 2015; Hanslmayr et al., 2007; Wutz et al., 2014). First, they are not unisensory visual tasks, but either multisensory (our study and Leonardelli et al., 2015) or do not involve the visual modality at all (Baumgarten et al., 2016). Second, a pair of above-threshold stimuli is presented instead of near-threshold stimuli. And third, they involve temporal discrimination, whereas the mentioned visual tasks involve discrimination based on visual features such as orientation (Bays et al., 2015), identity (Hanslmayr et al., 2007) or numerosity (Wutz et al., 2014). Temporal discrimination differs in a fundamental manner with these visual feature criteria in that they require perception to be updated on a short time-scale. There is evidence that alpha power actually promotes stability as opposed to the flexibility required for this fast updating. For example, when viewing a Necker cube, perception spontaneously alternates between two rivalling perceptual interpretations (Necker, 1832). The onset of each of the alternating percepts can be reported with button presses. In this paradigm, higher alpha power correlates with a longer duration of each of the rivalling percepts and thus higher perceptual stability (Piantoni, Romeijn, Gomez-Herrero, Werf, & Someren, 2017) and reductions in alpha power predict an impending switch from one percept to the other (Strüber & Herrmann,

2002). Based on these studies, Piantoni et al. (2017) proposed that alpha oscillations do not purely inhibit cortical activity but stabilize the current configuration of neuronal activity and its corresponding perceptual interpretation. Despite the lack of spatial specificity of the EEG, it is interesting to note that the relation between alpha power and temporal sensitivity in our experiment is most pronounced over occipito-parietal areas, which mirrors the topographies of the relationship between alpha power and perceptual stability in Piantoni et al.'s (2017) study. In temporal discrimination tasks such as ours, higher excitability would lead to an improvement of sensitivity due to a greater perceptual flexibility to adapt to new information on short time-scales.

Another possible interpretation of our results could simply be that as participants got tired over the course of the experiment, their performance decreased, while their alpha power increased. Alpha power is known to increase with fatigue and at the same time, both alpha power and fatigue tend to increase over the course of an experiment (C. S. Benwell et al., 2018; Kasten, Dowsett, & Herrmann, 2016; Mathewson et al., 2015; Simon et al., 2011). We controlled for trial order in our analyses, and a spurious correlation due to these factors can therefore be ruled out. Alternatively, the periodic waxing and waning of sustained attention to the task, accompanied by fluctuations in alpha power may underlie our results. Macdonald, Mathan, & Yeung (2011) measured alpha power and participants' introspective judgements of attentional state while they performed a visual detection task. For trials in which subjects reported lowered attentional state, pre-stimulus alpha was higher. Then, the authors investigated the time course of this relationship. Using a window-based classification procedure, the authors found that attentional state judgements smoothed over 7 min were most significantly correlated with pre-stimulus alpha power. This suggests that slow fluctuations in the state of attention in the order of minutes are reflected in spontaneous alpha power. The lower attentional state could lead to worse task performance, which would be more likely to lead to lower than higher temporal sensitivity (due to the nature of our task, temporal sensitivity and veridical observation are not necessarily related). This possibility does not negate explanations on a more mechanistic level however.

Studies using other temporal discrimination paradigms have produced results that are in line with ours. For example, van Viegen, Charest, Jensen, and Mazaheri (2017) presented participants with a tone and then after 1 or 1.5 seconds a flash. They found that the tone always elicited alpha and beta suppression over parietal and occipital electrodes, but that the long intervals were more likely to be incorrectly perceived as short intervals when alpha and beta power were less suppressed. They concluded that higher alpha and beta power led to a subjective compression of time, which can also be interpreted as stronger integration over time. And in a multisensory time-estimation task, van Driel, Knapen, van Es, & Cohen (2014) tested how phase coupling between auditory and visual sensory regions was related to interference effects from one modality to the other. They found that when participants had to judge the duration of a visual target, the duration of an auditory distractor interfered more in those participants with stronger alpha phase coupling between auditory and visually responsive electrodes. As in our study, stronger alpha synchronization was indicative of cross-modal temporal integration. Taken together, the evidence suggests that when excitability is low, and alpha synchronization is high, the cortex leans towards temporally integrated perception, and that when excitability is high, and alpha synchronization is low, the cortex leans towards temporally segregated perception.

INCREASED ALPHA FREQUENCY DOES NOT PREDICT INCREASED TEMPORAL SENSITIVITY

Evidence has been mounting that the length of the cycle of alpha oscillations determines the length of time over which stimuli are integrated (Cecere et al., 2015; Keil & Senkowski, 2017; Ronconi et al., 2018; Samaha & Postle, 2015). These findings support the idea of discrete windows of perception or perceptual cycles (VanRullen, 2016). In this study we attempted to replicate such results using multisensory above-threshold stimuli. Although we did find the expected pattern, with higher alpha frequency predicting better temporal sensitivity on a trial-by-trial basis, a follow-up analysis revealed that this effect could be attributed to an asymmetry in alpha-power modulations, as described above. Therefore, despite our initial positive finding, with results in line with those of

Ronconi et al., (2018) and Samaha & Postle (2015), we cannot conclude that the length of the cycle of alpha oscillations determines the length of time over which multisensory, above-threshold stimuli are integrated. One reason for our differing pattern of results could be that whereas the integration of uni-sensory veridical and illusory stimuli occurs mostly in the sensory cortices themselves, activity relevant to the TOJ task occurs at least partially in higher association areas (Binder, 2015; Love, Petrini, Pernet, Latinus, & Pollick, 2018; Watkins, Shams, Tanaka, Haynes, & Rees, 2006). Furthermore, our pattern of results stresses the need of accounting for individual differences in peak alpha frequency, as well as systematic shifts in both alpha frequency and power over the course of an experiment. Importantly, in light of the increasing popularity of instantaneous frequency as a measure in EEG research (Babu Henry Samuel, Wang, Hu, & Ding, 2018; Samaha & Postle, 2015; Shen, Han, Chen, & Chen, 2018; Wutz, Melcher, & Samaha, 2018), our results caution against an interpretation of such effects in terms of genuine frequency shifts involving one oscillator, without controlling for the possibility of asymmetric power shifts over multiple oscillators.

INDIVIDUAL ALPHA FREQUENCY NOR POWER PREDICT INDIVIDUAL DIFFERENCES IN TEMPORAL SENSITIVITY

Even though alpha power predicted performance on a trial-by-trial basis, we did not find any relation between alpha power and temporal sensitivity across participants. Nor did we find a relation between alpha frequency and temporal sensitivity across participants. This is in contrast to findings from Cecere et al. (2015), Samaha & Postle (2015), and Keil & Senkowski (2017) who found a positive relation between alpha frequency and temporal sensitivity across participants. Again, an important difference between their tasks and ours is that they both involve some form of visual detection with an implicit temporal factor. In our task, the temporal factor is explicitly probed and a discriminatory response is required. Similar to our results, in the same tactile temporal discrimination task as described above (Baumgarten et al., 2016) this relationship was absent across participants (Baumgarten, Schnitzler, & Lange, 2017), despite a within-participant relation between alpha frequency and temporal sensitivity (Baumgarten et al., 2016). One reason this relationship was absent in our data could be

that the TOJ task is a much harder and cognitively demanding task than the sound induced flash illusion used by Cecere et al. (2015) and Keil & Senkowski (2017). At an individual level, many more factors affect the JND than just the speed and power of oscillations, and might do so more strongly. This is readily apparent when looking at the sizes of the JND exhibited by our participants which ranged from 28 to 316 ms (see fig. 3). It is unlikely that the main factor underlying such a broad range of JND's could be found in the subtle differences in peak frequency between participants. It might be the case that peak frequency and/or power do matter, but that factors such as self-confidence, conscientiousness or decision-related processes play a much bigger role. When conducting analyses within participants, these factors are neutralized, enabling the subtler influence of oscillatory characteristics to come to light, but when correlating across participants they are drowned out.

LIMITATIONS

One of the main limitations of our study stems from the inherent spatial imprecision of the EEG. The fact that any number of sources could contribute to the signal measured at the scalp at any moment makes it impossible to distinguish between true shifts in InstAF and shifts in the relative power of multiple sources with differing, but stable, InstAF's. Fortunately, as we have shown, by centering the power spectra on each individual's alpha peak frequency and controlling for alpha power at each sub-frequency included in the alpha band, the chance of mistaking an asymmetric power shift for an InstAF shift can be reduced. Another important limitation concerns the fact that our analysis only includes the oscillatory parameters of the power spectrum without accounting for the underlying a-periodic activity that constitutes the $1/f$ slope and offset of the spectrum. Since the $1/f$ offset and slope have both been found to be behaviorally and physiologically relevant (Manning, Jacobs, Fried, & Kahana, 2009; Palva et al., 2013; Peterson, Rosen, Campbell, Belger, & Voytek, 2017; Voytek et al., 2015; Winawer et al., 2013), and power within a certain frequency band does not necessarily imply oscillatory power (He, 2014), this could lead to a conflation of the oscillatory and aperiodic parameters of the power spectrum (Haller et al., 2018). Another limitation is that the response mappings were not counterbalanced

within participants; they always used their left hand to indicate “sound first”, and their right hand to indicate “flash first”. A potential response bias could therefore have affected our measures of the PSS (García-Pérez & Alcalá-Quintana, 2013). Any effect on our measure of interest; the JND, would not be expected (Morgan, Dillenburger, Raphael, & Solomon, 2012). In the future however, the mapping between the hand and response should be counterbalanced to avoid any possible influence of response bias. A statistical limitation of our analysis of individual differences in IndAF and temporal sensitivity was that we only applied frequentist statistics. Our analysis did not provide evidence to reject the null hypothesis, but, having used frequentist statistics, this does not allow us to conclude that no relationship between IndAF or IndAP and temporal sensitivity is present. In order to do so, a Bayesian analysis would be recommended. Also, despite evidence suggesting that an inverted U-shaped relationship between alpha power and optimal performance exists, with intermediate levels of alpha power being optimal (Linkenkaer-Hansen, 2004; Rajagovindan & Ding, 2010; Zhang & Ding, 2010) we limited ourselves to testing linear relationships between EEG and behavioral parameters. Our results do not preclude the possibility of such an inverted u-shaped relationship existing.

CONCLUSION

In this study we tested whether spontaneous, pre-stimulus EEG activity predicted behavioral performance on an audio-visual temporal order judgement task. We found that lower pre-stimulus alpha power predicted higher temporal sensitivity on a trial-by-trial basis. Higher pre-stimulus alpha frequency also seemed to predict higher temporal sensitivity, but this effect could be attributed to an asymmetry in the effect of alpha power. This pattern of results encourages careful consideration of asymmetric power effects and individual differences in alpha frequency when interpreting results of instantaneous alpha frequency analyses. We did not find any systematic relationship between individual alpha frequency or individual alpha power and temporal sensitivity across participants. Taken together with previous work, our findings suggest that modulations in alpha power reflect the brain’s tendency for temporal integration vs. segregation on a trial-by-trial basis.

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THE SLOPE OF THE EEG POWER
SPECTRUM SYSTEMATICALLY FLATTENS
WITH TIME ON TASK, BUT DOES NOT
PREDICT THE TEMPORAL SENSITIVITY
OF AUDIOVISUAL PERCEPTION ¹

¹London, R. E., and Talsma, D. (in preparation). *The slope of the EEG power spectrum systematically flattens with time on task, but does not predict the temporal sensitivity of audiovisual perception.*

ABSTRACT

The appropriate integration and segregation of sensory signals is fundamental to the formation of meaningful percepts and temporal proximity is an important cue that two signals should be integrated. The main question motivating this study was whether the power spectrum density (PSD) slope, reflecting aperiodic activity, of pre-stimulus EEG activity predicted the temporal sensitivity of audiovisual integration in an audiovisual temporal order judgement task. A shallower PSD slope has been proposed to reflect an increased ratio of excitatory to inhibitory activity and shorter and weaker autocorrelation across time. Based on previous work indicating that higher cortical excitability leads to increased temporal sensitivity, and the notion that a system with weaker autocorrelation over time shows greater entropy and thus greater capacity for fast information processing, we would expect that a shallower slope would be predictive of higher temporal sensitivity. We did not find evidence in support of this hypothesis, within or between participants. Since the PSD slope is a relatively novel way to analyze EEG activity, we also described how the PSD slope varied over the scalp and over the course of the experiment. We found that the PSD slope was most steeply negative-going over posterior electrodes and flattened out towards the front of the scalp. We also found that the slope flattened out significantly over the course of the experiment, in two focal bilateral parietal clusters. More studies linking behavior to the PLE are needed to establish its functional significance. When conducting such studies, time-on task effects should be taken into account, to avoid spurious correlations between the PSD and slope and behavior from arising.

INTRODUCTION

The appropriate integration and segregation of sensory signals, both within and across modalities, is fundamental to the formation of meaningful percepts. Temporal proximity is an important cue that two signals might come from the same event and should be integrated. The shorter the time between them, the higher the probability of integration (Meredith, Nemitz, & Stein, 1987). There is, however, some flexibility in this respect; stimuli perceived by different senses are often transmitted with different speeds through their respective media and by the nervous system from receptor to sensory cortex. An auditory and a visual stimulus created by the same event, such as a car accident, will reach the auditory and visual sensory cortices at different points in time. The nervous system absorbs these lags, which allows these stimuli to be appropriately integrated. Exactly how close in time the signals need to be for integration to occur depends on several factors. Temporal sensitivity is modulated by stimulus-related factors such as stimulus complexity (Stevenson & Wallace, 2013), intensity (Fister, Stevenson, Nidiffer, Barnett, & Wallace, 2016) and spatial relation (Lewald & Guski, 2003). Accordingly, temporal sensitivity is highly variable within, but also across individuals (Baumgarten, Schnitzler, & Lange, 2017; Cecere, Rees, & Romei, 2015; Samaha & Postle, 2015; Stevenson, Zemtsov, & Wallace, 2012). Importantly, however, the appropriate temporal sensitivity of integration will to a high degree depend on the current internal and external contexts of the organism. Since these contexts change continuously over time, it is important that the temporal sensitivity of integration is flexibly adjusted from moment-to-moment.

A question that remains to be answered concerns the neural processes that allow for such fast modulations of temporal sensitivity. Due to its high temporal resolution, EEG is the method of choice to search for such fast neural modulations (Cohen, 2011). The analysis of single trials, which considers the variance within participants (Pernet, Sajda, & Rousset, 2011), has recently allowed us to uncover systematic relations between fluctuations in temporal sensitivity and neural processes that occur on such a short time-scale. Using this approach, we were able to show that the power of EEG alpha oscillations predicts the temporal sensitivity of audiovisual integration from trial to trial (London et al., in

prep.). This is in line with other work revealing a crucial role of alpha oscillatory activity in the temporal sensitivity of perceptual integration (e.g. Cecere, Rees, & Romei, 2015; Leonardelli et al., 2015; Samaha & Postle, 2015). EEG activity, however, is composed not only of periodic oscillatory activity but also of aperiodic activity (He, 2014). Whereas oscillations can be identified as narrow-band bumps on the EEG power spectrum, this aperiodic activity is apparent in the characteristic $1/f^\chi$ power-law shape of the spectrum. That is, power decreases exponentially as a function of frequency, where the power law exponent (PLE) χ determines the slope of that decline.

Although the aperiodic component of the power spectrum has received far less attention than the periodic, oscillatory component, evidence is growing that its slope can vary in meaningful ways (e.g. Freeman & Zhai, 2009; He, Zempel, Snyder, & Raichle, 2010; Peterson, Rosen, Campbell, Belger, & Voytek, 2017; Podvalny et al., 2015; Voytek et al., 2015). For example, healthy aging is associated with a flattening of the slope (Voytek et al., 2015; Waschke, Wöstmann, & Obleser, 2017), and in people diagnosed with schizophrenia, the slope is significantly steeper than in healthy controls (Peterson et al., 2017). In fact, in the Peterson et al. (2017) study, it was found that the slope was better at distinguishing between the patient and control group than alpha oscillatory power or even behavior itself. Not only does the slope vary across individuals due to psychiatric conditions or age, it also varies with behavior. For example, He et al. (2010) recorded the electrocorticogram during quiet wakefulness and the performance of a simple task where participants were instructed to press a button either in a visually cued or self-paced manner. The authors reported a significant flattening of the slope while participants performed the task compared to quiet wakefulness. A similar relationship was observed in the fMRI signal, where the PLE decreased during performance of a visual detection task, compared to rest (He, 2011). Moreover, Palva et al. (2013) showed that the PLEs of the power spectra derived from the EEG and those derived from the temporal structure of behavioral performance were highly correlated across time-scales. These studies suggest that the PLE of the power spectrum reflects physiologically relevant processes that could be exploited by the brain to adjust behavior from moment-to-moment, for example, through changing the temporal sensitivity of perceptual integration.

The slope of the power spectrum has been linked to functionality in at least two ways. Gao, Peterson, & Voytek (2017) developed a computational model demonstrating that the slope of the power spectrum reflects the balance between excitatory and inhibitory activity. Specifically, the model produced power spectra with shallower slopes, as the ratio of excitatory to inhibitory activity was increased. Based on this idea, a shallower slope would be predictive of better temporal sensitivity. He (2014) speculated that since a reduced power-law exponent (a shallower slope) indicates shorter and weaker autocorrelation across time (i.e. less predictability of the signal over time), it could reflect more flexibility vs. stability and thus a greater capacity for online information processing. From this perspective, we would predict that if the slope of the power spectrum is indeed a key factor in the temporal sensitivity of perceptual integration, that a shallower slope would be predictive of better temporal sensitivity. To date, however, no studies that we are aware of have employed measures of aperiodic EEG activity to predict behavior on a short, single-trial time scale.

Here, we combined two novel EEG-analysis approaches (Benwell, Keitel, Harvey, Gross, & Thut, 2017; Haller et al., 2018) to test the prediction that a shallower slope of the power spectrum will be associated with higher temporal sensitivity of perceptual integration on a trial-by-trial basis. We re-analyzed the data collected for the experiment described in chapter 3, where we presented participants with an audiovisual temporal order judgement task. In the present study, we tested whether the slope of the power spectrum of pre-stimulus EEG activity predicted the temporal sensitivity of audiovisual integration on a trial-by-trial basis. Additionally, we tested whether the slope of individuals' average power spectra could explain the vast individual differences commonly found in temporal sensitivity. For both the within-participants as individual-differences analyses, we expected a flatter slope to be predictive of higher temporal sensitivity.

METHOD

PREVIOUSLY DETAILED METHODS (SEE CHAPTER 3)

Forty-three volunteers participated in this experiment for monetary compensation. Two participants were excluded due to their estimated sensitivity measure exceeding the maximum SOA of 350 ms. One participant was excluded due to not completing the experiment. Analyses were carried out on the data of the remaining 40 participants (30 female, 2 left handed, median age: 23, age range: 18 – 32). Participants reported having normal audition and normal or corrected-to-normal vision and no history of neurological disorder or recent use of psychoactive substances. The experiment was approved by the Ethics Committee of Ghent University and participants gave informed consent prior to the start of the experiment.

ELECTROPHYSIOLOGICAL ANALYSES, WITHIN PARTICIPANTS

EEG Power Law Exponent

A power spectral density (PSD) representation of the single-trial data was obtained by applying a fast Fourier transform (FFT), as implemented in Matlab's "fft" function (Mathworks, USA) and taking the squared absolute of the output. To match the data that was analyzed in Chapter 3, we restricted our analysis to 750 ms to 250 ms pre-stimulus. The data was multiplied with a Hanning window to avoid edge artifacts, and zero padded to achieve a frequency resolution of 1Hz. We proceeded to calculate single-trial jackknife estimations of the PSD by iteratively averaging the PSD over trials while leaving one trial out at each iteration. This mitigated the noisiness of the PSD's calculated over short time series and facilitated the fitting of a power-law function to the spectrum at the next step of the analysis, while still preserving the variance structure of power values at each frequency across trials. The jackknife single-trial PSD ranging from 3 to 45 Hz was entered into the next step of the analysis. The power-law exponent (PLE), defining the slope of the aperiodic part of the PSD, was obtained with the "fitting oscillations & one over f" (FOOOF) algorithm (Haller et al., 2018) for the jack-

knife PSD at each electrode and trial. For details on the workings of the algorithm, we refer to Haller et al. (2018). In essence, the algorithm decomposes the PSD into periodic and non-periodic activity and then fits an exponential function to the aperiodic signal in the $\log(\text{power})$ by $\text{linear}(\text{frequency})$ space. The function is given by:

$$L = b - \log(F^\chi)$$

where L is the aperiodic signal, b the offset, F frequency in Hz, and χ the power-law exponent. The power-law exponent χ controls the slope; the higher χ , the more steeply negative-going the slope is. Lower or negative χ 's reflect flatter or positive going slopes, respectively. We calculated χ for each trial at each electrode.

Single-trial analysis of time-on-task effects on the PLE and temporal sensitivity

First, we tested for systematic drifts in the PLE and the JND over the course of the experiment. We obtained Spearman's rho (ρ_s) by correlating the jackknife single-trial JND with trial order and the jackknife single-trial PLE at each electrode with trial order. At the group level we tested for any systematic deviation from zero among the participant-level correlations by performing one-sample t-tests against 0 on the Spearman ρ_s 's. For the PLE – trial order relationship this procedure was repeated at all electrodes, resulting in 64 ρ_s 's per participant. The family-wise error rate was controlled with a False Discovery Rate (FDR) correction. The FDR applies a common corrected threshold to all p -values which is defined using the Holm-Bonferroni method (Holm, 1979). Here all uncorrected p -values are sorted from low to high. Then, the lowest is compared to the Bonferroni statistical threshold of $0.05/N$ (64 in our case), the next lowest to $0.05/N-1$, and so on for all p -values. The largest (weakest) p value to reach significance using this method is then chosen as the corrected significance threshold for all comparisons.

Single-trial analysis of temporal sensitivity in relation to the PLE

Next, we tested whether moment-to-moment fluctuations in the PLE of pre-stimulus EEG co-varied with temporal sensitivity. At the participant level, we computed Spearman's rho (ρ_s) between the jackknife JND and the jackknife PLE across trials. This procedure was repeated at all electrodes, resulting in 64 ρ_s 's per participant. We controlled for non-stationarities in the PLE and behavior over the course of the experiment by partializing out trial order (Pearson, 1915). This prevented any spurious correlation from arising due to co-occurring but unrelated EEG and behavioral non-stationarities over the course of the experiment (e.g. Benwell et al., 2018). At the group level we tested for any systematic deviation from zero among the participant-level correlations by performing one-sample t-tests against 0 on the Spearman ρ_s 's at each electrode across participants. As before, the family-wise error rate was controlled with a False Discovery Rate (FDR) correction.

Electrophysiological analyses, individual differences

Finally, we tested whether the PLE across participants covaried with the JND across participants. This individual-differences analysis was carried out on the same data epochs as the within-participant analysis described above. We calculated the average PLE at each electrode for each participant and the average JND of each participant. Then we obtained Spearman's rho (ρ_s) by correlating these two variables across participants at each electrode. The family-wise error rate was controlled with a False Discovery Rate (FDR) correction as before.

RESULTS

BEHAVIORAL RESULTS

Participants completed an audio-visual TOJ task. They were presented with a beep and a flash at varying SOAs, and were asked to indicate which stimulus had been presented first. A psychometric function was then fit to the proportion of “flash-first” responses. The behavioral results are reported in detail in Chapter 3 (see figure 3.2). In summary, the mean JND was 110 ms, with a standard deviation of 64 ms.

EEG RESULTS

Slope topography

For each participant, we estimated the PLE for each trial and electrode. Figure 4.1 shows the PLE averaged over trials and participants. The slope is steepest (high PLE's) over posterior areas and flattens out (lower PLE's) towards more frontal areas.

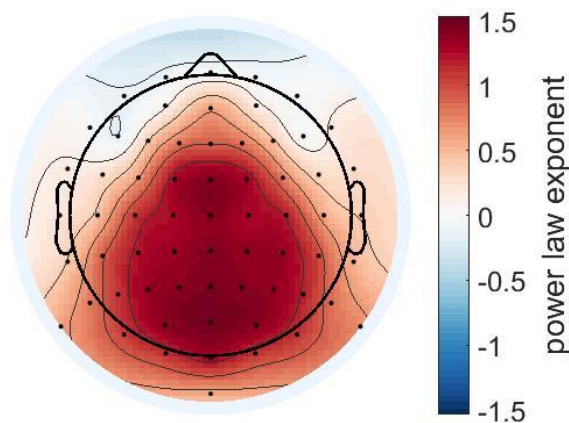


Figure 1. Topography of the power law exponent averaged over trials and participants. The color red indicates a positive PLE, which leads to a negative-going slope. The color blue indicates a negative PLE, which leads to a positive-going slope.

Time-on-task effects on PLE and temporal sensitivity

We tested whether our measures of temporal sensitivity (the JND) and of the slope of the PSD (the PLE) drifted systematically over the course of the experiment. Figure 4.2A shows the relationship between trial order and the PLE at each electrode. Over the course of the experiment, the slope of the PSD flattens out over two bilateral parietal areas (PLE becomes less positive). Three electrodes within two focal areas over left and right parietal cortex showed an effect that was significant at the FDR corrected alpha level of 0.002. Figure 4.2B shows the correlation between the PLE and trial order for each participant averaged over the significant electrodes. Figure 4.3 shows the correlation between the JND and trial order for each participant. There was no systematic relation between time-on-task and temporal sensitivity across participants ($t = 1,357$, $p = .182$).

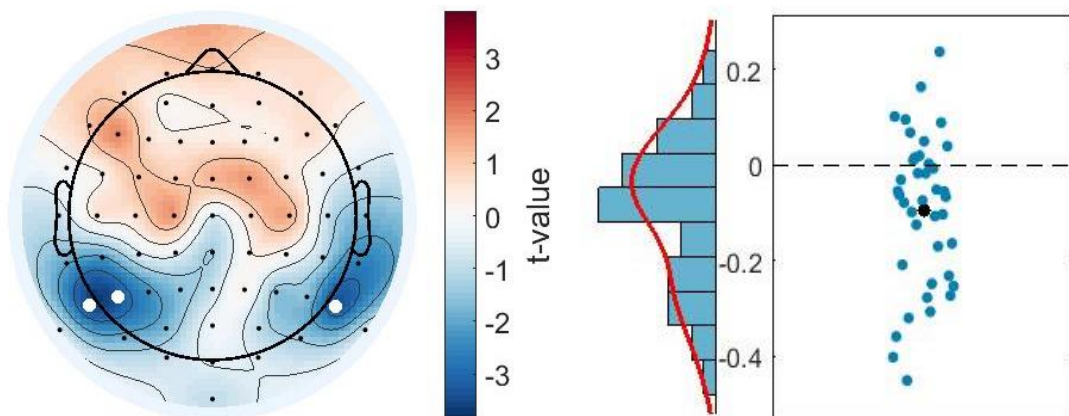


Figure 2. Time-on-task effects on the PLE. **(A)** Topography of t-values representing the consistency of the correlation between PLE and trial order across participants. Electrodes marked in white were significant at an alpha of .002. **(B)** Correlation between PLE and trial order for each participant averaged across the significant electrodes. Each blue dot represents one participant. The black dot indicates the group mean.

The PLE does not predict temporal sensitivity within or across participants

Our main question was whether the PLE could predict performance on the audiovisual TOJ task on a trial-by-trial basis. Figure 4.4A shows the consistency of the relationship between trial order and the PLE at each electrode. We ex-

pected a flatter slope to be predictive of a smaller JND. No evidence was found for such a systematic relationship between the slope of the PSD and the temporal sensitivity of audiovisual integration. Finally, we tested whether there was any relationship between the average PLE at each electrode and the average JND across participants. As for the within participant comparisons, we expected a steeper PSD slope to be predictive of a larger JND (a positive correlation between the PLE and the JND). Figure 4.4B shows this correlation at each electrode. None of the electrodes showed a significant effect after FDR correction.

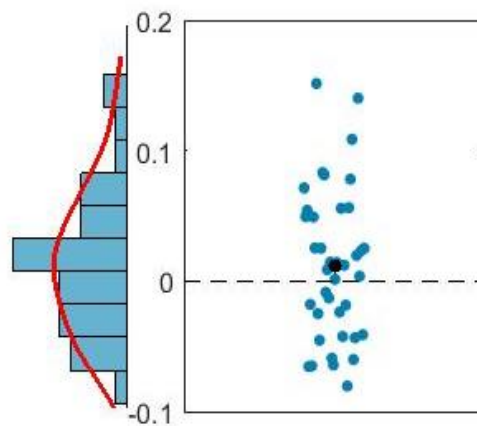


Figure 3. Time-on-task effects on the JND. Correlation between JND and trial order for each participant. Each blue dot represents one participant. The black dot indicates the group mean.

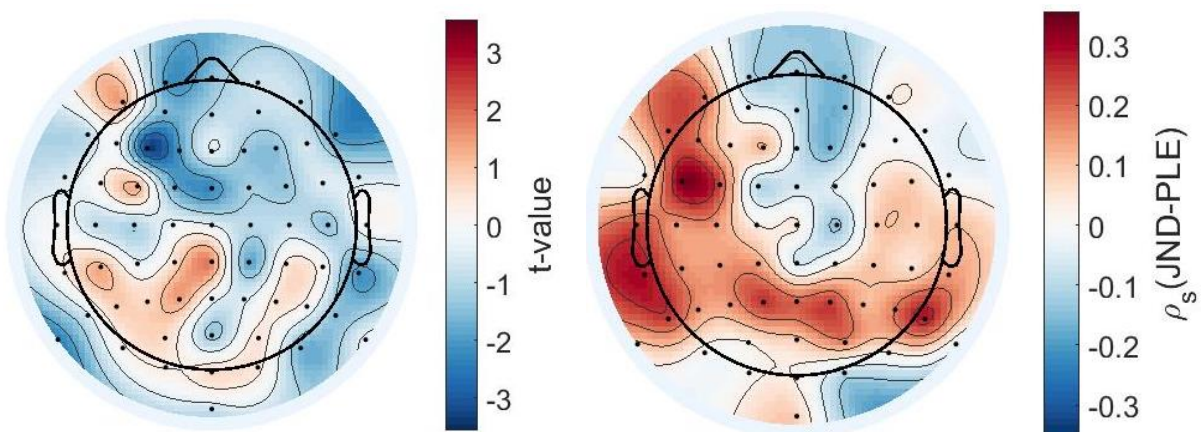


Figure 4. The PLE does not predict temporal sensitivity of audiovisual integration. **(A)** Topography of t-values for the within-participant analysis of the predictive value of the pre-stimulus PLE for the JND on the subsequent trial **(B)** Topography of across participant correlations between the PLE and JND.

DISCUSSION

The main question motivating this study was whether the slope of the power spectrum of pre-stimulus EEG activity predicted the temporal sensitivity of audiovisual integration in an audiovisual temporal order judgement task within and across participants. We expected flatter slopes to be predictive of higher temporal sensitivity, since these are indicative of a higher ratio of excitatory to inhibitory activity (Gao et al., 2017) and shorter and weaker autocorrelation across time (He, 2014), possibly facilitating the encoding of sensory information with higher temporal precision. We did not find evidence in support of our hypothesis, within or across participants. Since the PSD slope is a relatively novel way to analyze EEG activity, we also described how the PSD slope varied over space and over the course of the experiment. We found that the PSD slope was most steeply negative-going over posterior electrodes and flattened out towards the front of the scalp. We also found that the slope flattened out significantly over the course of the experiment, in two focal bilateral parietal clusters.

THE PSD SLOPE DOES NOT PREDICT TEMPORAL SENSITIVITY WITHIN OR BETWEEN PARTICIPANTS

The few studies that have investigated the predictive value of PSD slope for behavior have provided us with diverging results. Voytek et al. (2015) analyzed a combination of ECOG and EEG data and described how the PSD slope flattened with age, and how a flatter slope was predictive of worse performance on a visual working memory task. This finding was replicated by Waschke et al. (2017) who also found that PSD slope flattened with age. Sheehan, Sreekumar, Inati, & Zaghoul (2018) captured intracranial EEG recordings as participants performed a paired-associates verbal memory task. In contrast to Voytek et al. (2015) they found that a flatter PSD slope predicted better performance, both within and across participants. Peterson et al. (2017) presented evidence of a steeper PSD slope for patients with schizophrenia together with worse performance on a fast-paced selective attention task. He et al. (2010) recorded the electrocorticogram and found that the PSD slope was flatter during performance of a simple task

where participants were instructed to press a button either in a visually cued or self-paced manner than during quiet wakefulness. Similarly, Podvalny et al. (2015) analyzed ECOG data of participants engaged in visuo-motor tasks and described a flattening of the PSD slope associated with neural activation related to the task. In summary, on the one hand, a flatter slope is related to aging (Voytek et al., 2015; Waschke et al., 2017) and worse visual working memory performance (Voytek et al., 2015). On the other hand, a flatter slope is related to better performance on a fast-paced attention task (Peterson et al., 2017) and a verbal memory task (Sheehan et al., 2018), and is also related to task-engagement (He et al., 2010; Podvalny et al., 2015). Meanwhile, we do not find any evidence of an effect of PSD slope on the temporal sensitivity of multisensory integration (see figure 4.4). How can we understand these diverging results?

Mathematically, the flattening of the PSD slope indicates shorter and weaker autocorrelation in the time-domain (Wiener, 1930). As the shape of the frequency spectrum flattens, the signal becomes less and less predictable in the time domain. A flatter PSD slope has also been shown to be highly predictive of increased entropy (Sheehan et al., 2018), a measure of signal complexity and capacity for information (Shannon, 1948). Structurally, a flatter spectrum is thought to reflect a heightened ratio of excitation to inhibition (Gao et al., 2017). It could be the case that such a state is beneficial for tasks where a high sensitivity to change is needed, and not beneficial for tasks where a high level of stability is required. Although at first glance it seems counter-intuitive, this idea fits well with Voytek et al.'s (2015) results. The memory task they used was a simple visual change-detection task that measures visual short-term memory. Participants were presented with an array of colored squares which they held in memory for 900 ms. Then another array appeared and they had to indicate whether any square had changed compared to the memory they held of the first array. Detection of a change was therefore contingent on their ability to maintain a stable percept of the first array during the memory interval. The memory task employed by (Sheehan et al., 2018), in contrast, involved encoding lists of words that were to be recalled at a later stage. Since the information participants had to memorize was more complex, it may have been the case that the increased information carrying capacity of the signal indicated by the flatter PSD slopes and

increased entropy related to good performance was the decisive factor. Regarding our own results, one explanation could be that a larger ratio of activity at shorter time-scales to activity at longer time-scales might also indicate a larger ratio of local to distributed processing (Garrett, Kovacevic, McIntosh, & Grady, 2010; von Stein & Sarnthein, 2000). Since our task required reporting on the temporal information carried by sensory signals from disparate cortices, it seems likely that some distributed processing would be needed. This idea is supported by the fact that audiovisual temporal order judgement tasks involve widespread brain activity in a collection of areas including frontal, parietal and occipito-temporal cortices (Binder, 2015). Whereas the sensory signals of the visual and auditory stimuli must be segregated in time, their temporal order can only be determined by relating them to each other through a distributed higher-order process. Any positive effect of a shallower PSD slope on the temporal sensitivity of perception could thus have been cancelled out by its negative effect on such a higher-order distributed process.

The heightened excitability and lower predictability associated with flatter PSD slopes could also be interpreted as an increase in noise. Voytek et al. (2015) concluded that it was an increase in noise, reflected by flatter PSD slopes, that was responsible for the decrease in cognitive capabilities as we age. This seems to go against the evidence presented by others discussed above since they report flatter slopes to be associated to better task performance or task engagement (He et al., 2010; Peterson et al., 2017; Podvalny et al., 2015; Sheehan et al., 2018). Noise, however, is not necessarily a bad thing, and evidence is mounting that it might also be beneficial to behavior (McDonnell & Abbott, 2009) or even a fundamental necessity for flexible and adaptive behavior (Ghosh, Rho, McIntosh, Kötter, & Jirsa, 2008; Pinneo, 1966). One process through which noise might be beneficial is stochastic resonance. This concept refers to the process where random noise can aid the detection of below-threshold stimuli, by “lifting” these signals above the threshold (Wiesenfeld & Moss, 1995). Interestingly, in non-linear systems, such as the brain, the signal to noise ratio is often maximal at non-zero levels of noise (Benzi, Sutera, & Vulpiani, 1981). Since the relation between noise and signal-to-noise ratio follows an inverted U-shape, this framework could help us understand why a flatter PSD slope would be beneficial in

certain tasks, but detrimental or neutral in others. In our paradigm, for example, the stimuli were well above threshold. This could be a reason why we did not find any evidence that the slope of the PSD predicted the temporal sensitivity of audiovisual integration.

PLE TOPOGRAPHY AND TIME-ON-TASK EFFECTS

As an addition to the analysis designed to test our experimental hypothesis, we described how the PLE varied across the scalp and over the course of the experiment. We found that the PLE was steepest over posterior and central areas, and flattened out towards lateral and frontal areas (see figure 4.1). To our knowledge no other EEG studies have reported the topography of the PLE. Previous studies have shown that the power spectra of spontaneous fMRI signals also follow a power-law distribution (Bullmore et al., 2001; Fox, Snyder, Vincent, & Raichle, 2007). Therefore, He (2011) investigated the power spectra of spontaneous fMRI signals and their power-law exponent for different networks. The PLE was steepest for the visual regions, default network and dorsal anterior cingulate cortex which is consistent with the topography that we report here (Jann, Kottlow, Dierks, Boesch, & Koenig, 2010).

Additionally, we found the PLE to drift systematically over the course of the experiment. Two focal bilateral clusters survived correction for multiple comparisons where the slope flattened significantly as time went on. The clusters were located over left and right temporo-parieto-occipital cortex and left parietal cortex. This change over time is likely related to fatigue due to the sustained attention required by the task. It is interesting to note that a flattening of the slope is seen not only to be linked to task-engagement (He et al., 2010; Podvalny et al., 2015) and improved performance on some tasks (Gao et al., 2017; Sheehan et al., 2018), but also to aging and fatigue. In this context, it is important to remember that the PSD is a second order statistic; different underlying processes may produce a similar PSD. For example, He et al. (2010), compared fluctuation in the EEG with fluctuations in the Dow-Jones index and earth seismic waves. They found that all three processes exhibited power-law scaling with very similar slopes. When examining the nested frequency patterns in each of these processes, the results differed markedly, demonstrating that differing underlying pro-

cesses may result in similar PSD slopes. Similarly, a flatter slope might indicate an increase in local and faster processing (Garrett et al., 2010), but it might also indicate an increase in randomness or noise, and random uncorrelated series of samples are among the least complex (e.g. Costa, Goldberger, & Peng, 2002). It is therefore possible that in the cases of aging and fatigue a flatter slope might indicate a non-functional reduction in information content of the signal, while in within participant task modulations it is indicative of a functional adaptation to the task at hand.

In contrast, there was no systematic relation of time-on-task on temporal sensitivity across participants (see figure 4.3). It is possible that performance was not affected by fatigue or learning, or that both had effects which canceled each other out. Although at the group level there was no effect of time-on-task on performance, for some participants there was quite a strong correlation between trial order and the JND. Possibly, some participants experienced a stronger learning effect and others a stronger effect of fatigue. Taken together, these time-on-task data patterns suggest that, in order to reduce measurement noise, and avoid the emergence of spurious correlations between variables due to systematic drifts of behavior and EEG parameters over the course of the experiments, it is important to control for time-on-task in single-trial analyses of the PLE.

CONCLUSION

The aperiodic component of the power spectrum holds great promise as a measure that can help us learn more about how behavior emerges from brain activity. To date, however, most studies have focused on relating different measures of this non-oscillatory activity to each other and to other measures of brain activity such as oscillatory power and the BOLD response. Our study was among the first attempting to link the PSD slope to behavior. We did not find any predictive value of the PSD slope for temporal sensitivity in an audiovisual temporal order judgement task. We did show, however, that there is a significant effect of time-on-task on the PSD slope. More studies linking behavior to the PLE and other measures of aperiodic activity are needed to establish the functional meaning of these characteristics of brain activity and to determine which

aspects of behavior they can help us understand. When conducting such studies, it is important to take into account the time-on task effects for the slope of the PSD, to avoid spurious correlations between the PSD and slope and behavior due to a combination of a systematic flattening of the slope over the course of the experiment, and the possible effects of learning and fatigue on behavior.

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SPONTANEOUS ALPHA AND BETA OSCILLATIONS BIAS VISION TOWARDS LOCAL SPATIAL PERCEPTION ¹

¹London, R. E., and Talsma, D. (in preparation). Spontaneous alpha and beta oscillations bias vision towards local spatial perception.

ABSTRACT

Visual perception offers us such a wealth of information, and having flexible biases towards distinct aspects of the visual scene can help us limit perception towards those features that matter to us most at each moment. One important characteristic of visual information is that it is hierarchical and perception can be biased towards a specific level within this hierarchy. Studies have shown that this bias is achieved through the differential activation of left versus right parietal cortices for local versus global biases, respectively. Other studies have shown that this lateralization is true for more central areas, but not for occipital areas. Here we examined anticipatory biasing, during the pre-stimulus interval, and asked whether a similar pattern could be found. Previous studies have focused on specific brain areas or electrode clusters and on specific frequency bands. Also, most, if not all studies on the role of oscillations in perceptual bias of local vs. global features have tested mean differences in power between conditions without considering spontaneous fluctuations in the power of oscillatory activity. We measured EEG while participants performed a Navon task with hierarchical letters and tested whether power at any cluster of channels differentially predicted reaction times for global versus local incongruent trials. We found that higher pre-stimulus alpha and low-beta power predicted a local bias on a trial-by-trial basis. This effect was maximal over right centro-parietal cortex, but extended over both hemispheres. It did not include electrodes over occipital areas. Taken together with previous work, our findings suggest that modulations in alpha and low-beta power reflect global vs. local perceptual bias from moment-to-moment.

INTRODUCTION

Imagine going for a hike in the mountains. While you walk on flat terrain, you will effortlessly place your feet on the path while looking around. You have a global idea of what your surroundings look like and can act according to this global image. As the path gets steeper and rockier, you must look at the path in more detail to see where the rocks are. Based on these local details, you can avoid stepping on a rock. If you are lucky, you might see an interesting rock, and then must examine this rock in even more detail to check if there is a fossil in it. This situation illustrates the importance of spatial integration at an appropriate level. A local perceptual scope will emphasize the perception of high spatial frequency features, such as the lines of a fossil on a rock, whereas a global perceptual scope will emphasize the perception of low spatial frequency features, such as the general outline of the mountain path (Broadbent, 1977; Flevaris, Bentin, & Robertson, 2011; Flevaris & Robertson, 2016; Hübner, 1997).

Evidence has been mounting that brain activity related to the processing of global versus local features is lateralized, with right parietal cortex being more strongly involved in global processing and the left parietal cortex being more strongly involved in local processing (Gable, Poole, & Cook, 2013; Lamb, Robertson, & Knight, 1990; Martinez et al., 1997; Robertson, Lamb, & Zaidel, 1993; Robertson, Lamb, & Knight, 1988; Volberg & Hübner, 2004; Weissman & Woldorff, 2005). Other studies have expanded on this work and provided evidence that differential activity for global vs local perception is indeed lateralized for areas later in the processing stream, but not for early areas (Craddock, Martinovic, & Müller, 2015; Heinze, Hinrichs, Scholz, Burchert, & Mangun, 1998; Martínez, Di Russo, Anllo-Vento, & Hillyard, 2001; Rokszin, Gyóri-Dani, Nyúl, & Csifcsák, 2016). For example, Heinze, Hinrichs, Scholz, Burchert, & Mangun (1998) showed participants hierarchical stimuli consisting of large letters comprised of smaller letters. They found that the N2 component (260-360 ms post-stimulus) to local targets was larger over the left hemisphere, and the N2 to global targets was larger over the right hemisphere. While the sensory-evoked P1 event-related potential (ERP) components (90- to 150-msec latency) in the extra-striate cortex were enlarged for global versus local attention, there were no

hemispheric differences observed for this effect. Similarly, Martinez et al. (2001) presented their participants with high and low spatial frequency checkerboard patterns while recording EEG. They reported that high SF stimuli elicited an early negative difference potential (ND120) starting at about 100 ms, whereas low SF stimuli elicited a positivity (PD130) in the same latency range. This early effect was not lateralized. Starting at 150 ms, both high and low spatial frequency checkerboards elicited a broad selection negativity which was larger over the left hemisphere for high spatial frequency patterns and over the right for low spatial frequency patterns. Studies using fMRI have supported the idea that differential processing for local and global features is lateralized only at later processing stages. For example, Sasaki et al. (2001) used functional MRI to map activity in the human occipital cortex during local and global attention. Instead of lateralized activation, they found that global and local attention are mapped consistently with the maps of retinotopy and spatial frequency tuning in multiple visual cortical areas. In contrast, Martinez et al. (1997) mapped activity in a more anterior set of slices including temporo-parietal, but not occipital regions, and did find evidence for a lateralization depending on global vs. local attention.

The studies described above have all measured activation in response to hierarchical stimuli with attention to the local or global level, or to patterns with high or low spatial frequencies. It has been shown, however, that if we can anticipate the visual demands of a situation, we can bias our visual system towards the right scope of perception. Robertson, Lamb, & Zaidel (1993), for instance, observed that response times to one target level can be shortened by increasing the probability for that level. Responses are also faster when the target level is varied in a blocked instead of a random fashion (Hübner, 1997). The processes related to global or local processing thus already start to take place before stimulus onset. The question remains, however, how these preparatory processes bias visual perception towards local or global perception. Some research has already focused on brain activity during the pre-stimulus period. Flevaris, Martínez, & Hillyard (2013) showed participants a bistable moving image in which perception spontaneously alternates between dissociated fragments and a single, integrated object. Alpha oscillatory power always decreased before a switch, but a greater decrease in alpha (8–12 Hz) was observed when participants switched

from a fragment percept to an object percept than when they switched from an object percept to a fragment percept. Similarly, Volberg, Kliegl, Hanslmayr, & Greenlee (2009) presented participants with hierarchical stimuli and a pre-cue and then analyzed EEG alpha oscillations. They analyzed four centro-posterior electrode clusters and divided the trials in three bins based on reaction times (slow, intermediate and fast). Volberg et al., found that pre-stimulus alpha power decreased more compared to baseline after local vs global cues in the left hemisphere and that in the right hemisphere it decreased more after global vs local cues. They found this effect exclusively for the centro parietal cluster for fast reaction times, however. Romei, Thut, Mok, Schyns, and Driver (2012) presented participants with hierarchical stimuli which consisted of large (global) letters comprised of smaller (local) letters in an adaptation from the classical Navon task (Navon, 1977). The combinations could be congruent (e.g. a global “H” comprised of local “H’s”) or incongruent (e.g. a global “H” comprised of local “D’s”). Just before stimulus presentation, they stimulated left and right parietal cortices with TMS at 10 Hz. Right parietal 10 Hz stimulation significantly impaired global processing without affecting local processing, while left parietal 10 Hz stimulation impaired local processing with a minor trend to enhance global processing, thus providing evidence for a causal role of alpha oscillations in biasing visual perception towards global or local features. In summary, the limited knowledge we have regarding the characteristics of pre-stimulus activity in the biasing of visual perception appears to indicate that alpha oscillations are an essential neural correlate of a mechanism that is involved in inhibiting the hemisphere that is specialized for the scope that is not appropriate.

The studies by Romei et al. (2012) and Volberg et al. (2009), however, have focused on specific brain areas or electrode clusters. Romei et al. (2012), for instance, only stimulated the parietal cortices. Results from earlier work have reported neural correlates of processes involved in global vs. local perception that are widespread across the cortex. Therefore, it would be premature to conclude that the processes involved in preparing the brain to focus on local or global features are limited to specific areas. Additionally, Romei et al. (2012) and Volberg et al. (2009) focused only on alpha oscillations. From the perspective where alpha oscillations index cortical excitability (Klimesch, Sauseng, &

Hanslmayr, 2007; Romei et al., 2008), this is a sensible choice. Not only alpha oscillations have been linked to cortical excitability, however. Samaha, Gosseries, & Postle (2017) measured the EEG while administering near-threshold TMS to occipital and parietal cortices. Weaker alpha power predicted phosphene perception due to occipital stimulation, whereas weaker low beta-power predicted phosphenes due to parietal stimulation. This suggests that alpha oscillations may index excitability over occipital cortex, while low beta oscillations index excitability over parietal regions.

Flevaris et al. (2013) did analyze several frequency bands, but with an important gap in the chosen bands. More specifically, they analyzed frequencies from 8 to 12 Hz (alpha band), from 16 to 30 Hz (beta band), and from 30 to 50 Hz (gamma band) and did not report any relation between beta band activity and local vs. global perception. The gap between alpha and beta bands (between 12 and 16 Hz) overlapped with the frequencies that Samaha et al. (2017) had shown to index parietal cortical excitability. The fact that Flevaris et al. (2013) did not find evidence for a role of beta oscillations in biasing vision towards local or global perception, therefore, could be due to this gap in the analysis. In summary, the present knowledge about the electrophysiological correlates of pre-stimulus biasing of the scope of perception has been narrowly defined to specific brain areas or electrode clusters and alpha frequency oscillations. In this study we attempted to cast a wider net and examined whether the power of pre-stimulus oscillations could predict how strongly visual perception was biased towards the correct perceptual scope in a classic Navon task. We presented participants with hierarchical stimuli; global letters made up of smaller local letters. The local letters could have the same identity as the global letter or a different one, and participants were instructed to respond to either the global or local letter as fast as possible. In the trials where the global and local letters had different identities, it was crucial for optimal performance to bias the visual system towards the appropriate target level. Therefore, we tested whether power at any cluster of channels differentially predicted reaction times for global versus local incongruent trials, from trial-to-trial. We expected higher power of low-frequency oscillations to be associated with a local bias (negative relation between power and reaction times for local trials and a positive or weaker negative

relation between power and reaction times for global trials), and we expected more posterior effects to be less lateralized than more anterior effects.

METHOD

PARTICIPANTS

Thirty-nine volunteers participated in this experiment for monetary compensation (30 female, 1 left handed, median age: 22, age range: 18 – 32). These participants all took part previously in the temporal order judgement task reported in chapters 3 and 4. Participants reported having normal audition and normal or corrected-to-normal vision and no history of neurological disorder or recent use of psycho-active substances. The experiment was approved by the Ethics Committee of Ghent University and participants gave informed consent prior to the start of the experiment.

APPARATUS AND STIMULI

Participants were seated in a dimly lit, sound-proof and electrically shielded chamber, with their head stabilized by a chinrest at 50 cm from a 24-inch LCD monitor (BenQ XL2411; 120 Hz refresh rate). The task was a classic Navon task (Navon, 1977) in which participants were presented with hierarchical stimuli consisting of large global letters, made up of smaller local letters (see Figure 1 for a schematic representation of the stimuli and trial procedure). The letters used for both global and local levels were “S” and “H”. Stimuli could be congruent (global and local letters had the same identity) or incongruent (global and local letters had a different identity). Participants were instructed to identify the global or local letter as fast as they could by pressing the respective keys on the keyboard. The experiment had three factors; Letter (S or H), Congruency (Congruent or Incongruent) and Target level (Global or Local). Letter and Congruency were varied randomly and Target level was varied from block to block. When collapsing over Letter, there were 48 trials in each condition, for a total of 192 divided over 8 blocks of 24. Each large letter was made up of 64 smaller letters. The letters were presented in white (luminance of 270 cd/m²) on a black background with the global letter subtending a visual angle of 11.40° high and 5.42° wide, and the local letters 0.97° high and 0.48° wide. Stimuli were presented centrally until a response had been made. The task was implemented using the

E-prime 1.2 software package (Schneider, Eschman, & Zuccolotto, 2002) on an HP Compaq desktop computer running Microsoft Windows XP.

PROCEDURE

The experiment started with the recording of 5 minutes of eyes-open resting state EEG and a seven-minute passive observation task with the sequential presentation of 50 instances of the visual stimulus and 50 instances of the auditory stimulus. Since the EEG data collected during this session are beyond the scope of the current project, they will not be reported here. Subsequently they completed a temporal order judgement task, which is reported in chapter 3. Then, the Navon task started with four practice blocks of 16 trials each, two in the Global condition and two in the Local condition, during which the experimenter was present to ensure participants understood the instructions. Each

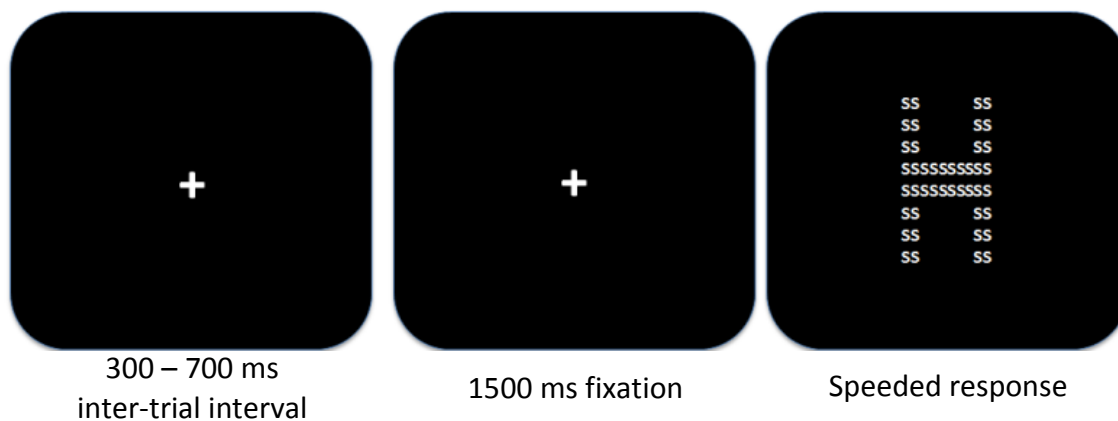


Figure 1. Schematic representation of the task and stimuli, time from left to right. After an inter trial interval of 300 to 700 ms, a fixation cross appeared on the screen for 1500 ms. Then the hierarchical letter stimulus was presented and participants had to report the letter at the instructed target level (blocked) with a key press as fast as possible.

block in the practice and experimental session started with the Target Level instructions. The Target Level was alternated from block to block and the first block was always Global. Each trial started with a fixation cross presented centrally in white on a black background. Participants were instructed to fixate this cross throughout the task. After an interval of 1500 ms the hierarchical letter stimulus appeared on the screen until participants indicated the identity of the

letter at the correct target level by pressing the corresponding key as fast as possible. Then after a randomly varying interstimulus interval, during which a fixation cross was presented, the next trial started. No feedback was given during practice nor experimental blocks. Between blocks there was a self-paced break during which participants were encouraged to rest for a short moment. The total duration of the experiment was approximately 15 minutes.

ELECTROPHYSIOLOGICAL RECORDING AND PRE-PROCESSING

The electrophysiological recording and pre-processing was identical to the study described in chapter 3.

BEHAVIORAL ANALYSIS

Reaction times on trials with correct responses were subjected to an ANOVA for repeated measures with Target level (Local / Global) and Congruency (Congruent / Incongruent) as within-participants factors.

EEG ANALYSES

EEG Power

The method for calculating EEG power values was identical as the one applied in the study described in chapter 3. For the current study, oscillatory power was obtained for each trial at 26 time points in 20 ms steps from 750 to 250 ms before stimulus presentation and 22 frequencies ranging from 2 to 45 Hz in 2 Hz steps for 64 electrodes.

Single-trial correlations at the participant level. For this analysis we analyzed only the incongruent trials, since on these trials the selection of the correct target level and inhibition of the incorrect target level is crucial for reaction times. Then, for each Target level, we calculated Spearman's rank correlations between reaction times on incongruent trials and power at each electrode, frequency and time point. We then calculated the difference in correlations between the local and global conditions (Local minus Global), since this difference indicates if

power at any data point differentiates between successful biasing toward one or the other Target level.

Group-level analysis. Subsequently, we tested whether any of the correlations obtained at the participant level showed a systematic deviation from zero across participants. Dependent sample t-tests against 0 were performed on the Spearman ρ 's at each data point across participants. To control for multiple comparisons, a cluster-based permutation-testing routine developed by Maris and Oostenveld (2007) was implemented. All data points were selected for which the t-value had a probability lower than 5% of having occurred by chance. These were then clustered based on adjacency in the temporal, spectral or spatial domain. This procedure was done separately for positive and for negative t-values (two-tailed test). For each cluster, the sum of t-values was then calculated and the maximum of these cluster-level statistics was taken. To create a reference distribution against which to test the value of this cluster-level statistic, 1000 permutations of the data were conducted using the “ft_statistics_montecarlo” function from the fieldtrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011). Each iteration yielded a maximum cluster level statistic and over iterations a null distribution of maximum cluster level values was constructed. The p value of the effect was then estimated as the proportion of elements in the null distribution exceeding the observed maximum cluster-level test statistic.

RESULTS

BEHAVIORAL RESULTS

We subjected the behavioral data to a repeated measures ANOVA with the factors Scope (Local / Global) and Congruency (Congruent / Incongruent). The data showed higher RT's for Local vs. Global trials (443 ms vs. 525 ms; $F(1,38) = 181.626$, $P < .0005$), and a stronger interference effect of Global information with Local information than vice versa (75 ms vs. 16 ms; $F(1,38) = 176.629$, $P < .0005$), see figure 2. This pattern of results replicates previous findings and is in

line with the idea that the global structuring of a visual scene precedes analysis of local features (Navon, 1977).

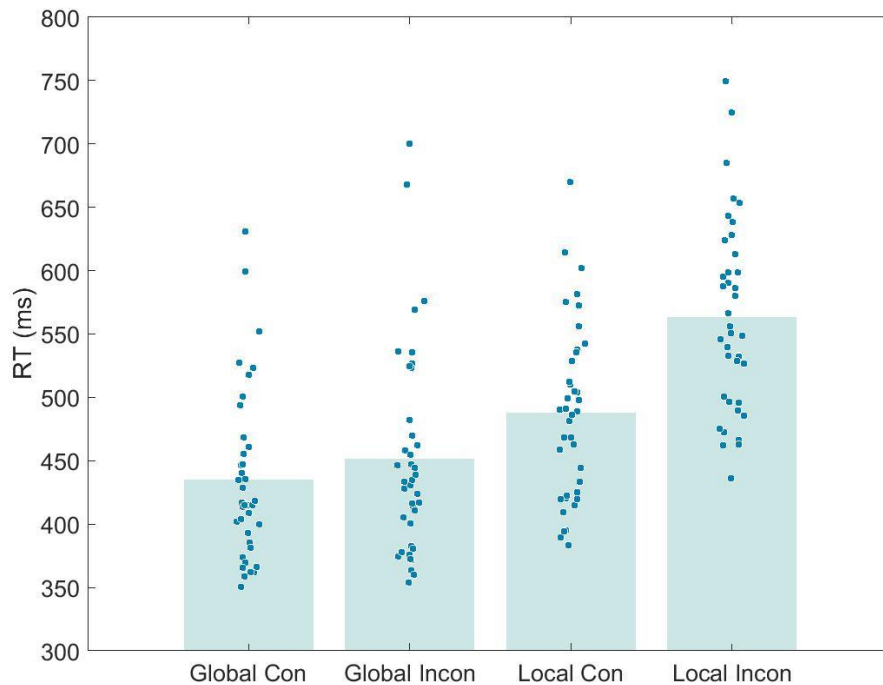


Figure 2. Behavioral results. Mean RT's for each participant in each condition are represented by the blue dots. Condition group-means are represented by the bars.

EEG RESULTS

We tested if the power of spontaneous fluctuations during the pre-stimulus interval could differentiate between a Global vs. Local bias in visual perception. To this end, we analyzed only the incongruent trials. Figure 3A shows the strength and direction of the relationship between EEG power and RT for local incongruent trials minus global incongruent trials. One significant positive cluster ($p = .018$) was present in the alpha frequency range from 750 to 570 ms preceding stimulus onset in frequencies ranging from 9 to 17 Hz (alpha to low beta). The cluster was widespread, covering nearly the entire scalp, with maximal values over central right electrodes (see figure 3B). Thirty-three out of 39 participants (84,6%) showed this effect, whereas one participant (2,6%) showed no difference

and five (12,8%) showed an opposite effect (see Figure 3C). Since we tested the difference in correlation between power and RT in global vs. local trials, the effect we found does not necessarily imply opposing effects of EEG power on RT

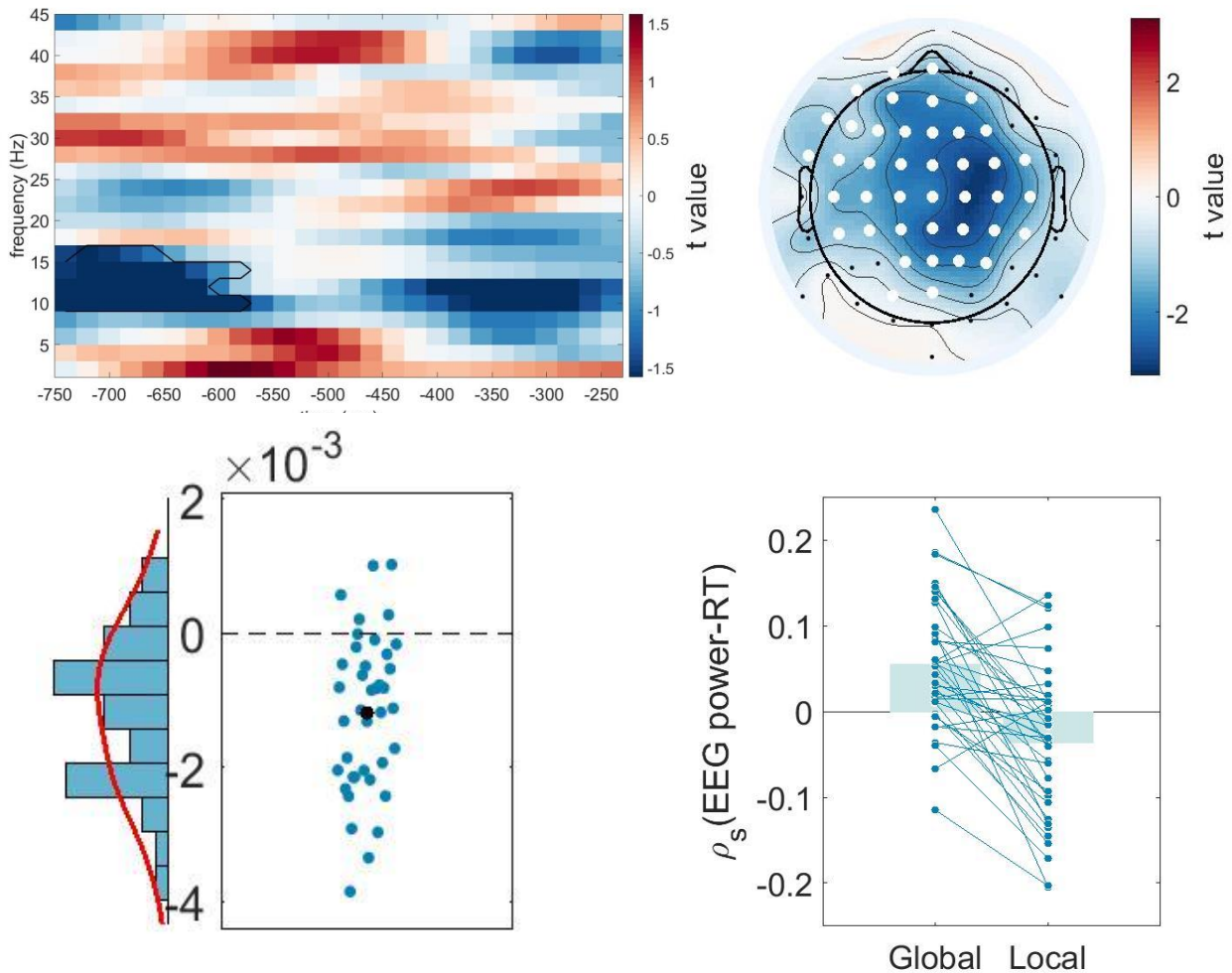


Figure 3. Higher power in alpha and low beta frequencies enhances local integration, but worsens global integration. **(A)** Time-frequency representation of t-values averaged over all electrodes included in the cluster. Onset of the stimulus is at 0 milliseconds. Positive t-values (in red) indicate a more positive correlation between power and RT for Local vs. Global trials. Negative t-values (in blue) indicate a more negative correlation between power and RT for Local vs. Global trials. One negative cluster survived correction for multiple comparisons and is outlined in black. **(B)** Topographical representation of the t-values averaged over all time-frequency points included in the cluster. Electrodes that were included in the cluster are highlighted in white. **(C)** Local vs. Global correlation between EEG power in the cluster and RT for each participant. Each blue dot represents one participant. The black dot indicates the group mean, and the black dotted line indicates a correlation of 0. **(D)** Average correlation between EEG power in the cluster and RT plotted for each participant, separately for Global and for Local trials. Bars represent group means, and observations of the same participant are linked by a line.

depending on the scope of integration. To visualize this relationship and provide a more intuitive understanding of the result, we plotted the values for the local and global incongruent data from the significant cluster separately (see figure 3D). From this visualization, it is apparent that on average, higher power in the alpha and low beta frequencies predicted faster RT's in Local trials, but slower RT's in Global trials. This was not a spurious finding caused by coexisting, but independent, changes in alpha power and JND over the course of the experiment (due to fatigue, boredom and/or decreased motivation; see Benwell et al., 2018), as the results are controlled for trial order. Therefore, these data suggest a functional role of alpha and low beta oscillatory power in modulating the bias of visual perception between global and local features on a short, trial-to-trial time scale, with an opposing effect of oscillatory power for Local vs. Global spatial integration.

DISCUSSION

During a classic Navon task (Navon, 1977), we tested whether the power of spontaneous fluctuations during the pre-stimulus interval could differentiate between a Global vs. Local bias in visual perception. We found a large cluster, spanning parieto-occipital to frontal electrodes over both hemispheres, where stronger alpha and low-beta oscillatory activity was associated with a bias towards the local Target level. These results, for the first time, provide evidence that neural oscillations covary with perceptual bias from moment-to-moment.

Results from previous studies have implied a differential specialization of the left and right parietal cortices for the processing of local vs. global targets respectively (Lamb, Robertson, & Knight, 1990; Romei, Thut, Mok, Schyns, & Driver, 2012; Volberg, Kliegl, Hanslmayr, & Greenlee, 2009). While our results do suggest a lateralization in accordance with the idea that the right hemisphere is specialized for the processing of global features, it does not provide evidence for the specialization of the left hemisphere for local features, since the cluster of electrodes where greater alpha and low-beta power predicts faster performance for local vs. global stimuli extends over both hemispheres. The effect was maxi-

mal over right central electrodes, and electrodes over early sensory areas were not included. This suggests that anticipatory perceptual biasing acts through differential activation in more anterior regions related to spatial attention (e.g. Shulman et al., 2010) or advanced stages of visual perception (Heinze, Hinrichs, Scholz, Burchert, & Mangun, 1998). Importantly, since the appropriate target level was cued in a blocked fashion, any covariation between power and behavior uncovered in this study was due to spontaneous, moment-to-moment fluctuations in brain activity.

Similar to Flevaris et al. (2013), we found that stronger oscillations in the alpha range predicted a bias towards the local target level. However, whereas their effect was found over occipital areas and was not lateralized, we found this effect over central areas with maximal strength over the right hemisphere, although we did not test for lateralization. Additionally, however, the significant cluster we found included oscillations in the low beta range (up to 17 Hz). The fact that our findings involved alpha and low-beta frequency oscillations is in line with results presented by Smith, Gosselin, & Schyns (2006). They showed participants small samples of Dali's painting *The Slave Market with Disappearing Bust of Voltaire* to induce conscious perceptions. This painting shows an ambiguous image where two nuns are depicted that, if globally integrated, form the image of the bust of Voltaire. A local bias would therefore make perception of the nuns more likely and a global bias the perception of Voltaire. Smith et al. (2006) measured EEG and found that centro-parietal beta oscillations supported perceptual moments underlying the conscious perception of the nuns, whereas theta oscillations supported the perception of Voltaire. Providing causal evidence for a similar relation between beta oscillations and perceptual bias, Romei, Driver, Schyns, & Thut (2011) found that when stimuli were incongruent and when distractors were salient, pre-stimulus rhythmic TMS stimulation over right parietal cortex at 20 Hz significantly enhanced performance for local, but not global targets, whereas stimulation at 5 Hz benefited global target perception, but not local. Both alpha and beta frequencies have been associated with cortical inhibition of the occipital and parietal cortices, respectively (Romei et al., 2008; Samaha, Gosseries, & Postle, 2017). One interpretation of these results and ours could therefore be that the two hemispheres have differential roles in

local versus global processing and that alpha and low-beta oscillations bias visual perception towards the appropriate level by inhibiting the hemisphere corresponding to the other level (Romei et al., 2012). Romei et al. (2012) found that 10 Hz TMS over right parietal cortex disrupted global processing without disrupting nor enhancing local processing, whereas 10 Hz TMS over left parietal cortex disrupted local processing without disrupting nor enhancing global processing. In our results in contrast, although the biasing effect of alpha and low-beta power towards the local target level we found was indeed strongest over the right hemisphere, it was also present over the left hemisphere. Similarly to Romei et al. (2012), Volberg et al. (2009) found a reversed pattern where high alpha power over right centro-parietal cortex was associated with fast responses to local trials and high alpha power over left centro-parietal cortex with fast responses to global trials. These results seem, at least partially, contradictory to ours. Comparing these results, and attempting to reconcile them is complicated by several factors, however. First, there is a limited amount of studies into the role of (pre-stimulus) oscillations in global vs. local perception, some of which report results based on a very small number of observations per condition (e.g. Romei et al., 2011, 2012; Volberg et al., 2009). Second, these studies have used different paradigms, have focused on different frequency bands, and compared different topographical areas, either a priori or post-hoc. Third, they have employed stimuli differing in size, spatial frequency and content. This third point is especially important in the light of studies that have provided evidence that the classically assumed hemispheric tendencies of left/right hemisphere being specialized towards local/global perception can be abolished or even reversed depending on stimulus characteristics such as saliency (Mevorach, Humphreys, & Shalev, 2006a, 2006b), spatial frequency (Flevaris, Bentin, & Robertson, 2011) and stimulus category (Fink et al., 1997). In going forward with this line of questioning, it seems thus of utmost importance to design a series of experiments to replicate previous findings using a uniform set of stimuli and analysis methods.

Another explanation for our results and those of Romei et al. (2011) and Smith et al. (2006) could be that oscillations at different frequencies tune the cortex towards global or local perception. So instead of thinking about alpha oscillations as shutting down a certain area, and avoiding its participating in the

processing of a stimulus, it may instead tune that area to the processing of certain stimulus features and not others. In support of this perspective, Fründ, Busch, Körner, Schadow, & Herrmann (2007) presented participants with gratings at different spatial frequencies and found that, whereas low frequency gratings elicited a stronger gamma response, high frequency gratings brought about a stronger alpha response. Similarly, Flevaris, Martínez, & Hillyard (2013) showed participants a bi-stable moving image in which perception spontaneously alternates between dissociated fragments and a single, integrated object. Alpha oscillatory power always decreased before a switch, but a greater decrease in alpha (8–12 Hz) was observed when participants switched from a fragment percept to an object percept than when they switched from an object percept to a fragment percept.

LIMITATIONS AND FUTURE DIRECTIONS

Due to our choice of analyzing only incongruent trials, we were not able to directly measure local vs global interference, since this is defined as the difference between congruent and incongruent trials. Since interference effects are not defined on a single-trial basis, we could use a jackknife procedure (see chapters 3 and 4, and (Benwell, Keitel, Harvey, Gross, & Thut, 2017) to estimate interference effects on a single-trial basis. Relating EEG power to interference effects would constrain the possible explanations for our results and enable us to test our interpretation of alpha and low beta as inhibitory mechanisms.

The multiple functions that have been ascribed to alpha oscillations besides inhibition further widens the space of possible explanations (Clayton, Yeung, & Kadosh, 2017). Adding a different measure of excitability would help to gain converging evidence for an explanation terms of inhibition of task-irrelevant areas and further constrain the space of possible explanations. For example, the power spectral density slope is also thought to index the balance between excitation and inhibition (Gao, Peterson, & Voytek, 2017) and can be inferred from the same EEG data.

Since we performed a cluster-based permutation test to correct for multiple comparisons, and the significance of our effect is based on the entire cluster,

we cannot test whether this effect is lateralized or not, since this test would involve comparing values within the cluster and then performing another statistical test on these. This would lead to circularity (Sassenhagen & Draschkow, 2019). In a future analysis, we will conduct a separate analysis and test whether the extent of lateralization of EEG power at any frequency is predictive of the bias of visual perception to the global or local level.

CONCLUSIONS

In this study we tested whether pre-stimulus EEG activity predicted global vs. local perceptual bias in a classic Navon task using hierarchical letter stimuli. Our results show, for the first time, that spontaneous oscillations predict visual perceptual bias on a trial-by-trial basis, with higher pre-stimulus alpha and low-beta power predicting a local bias. This effect was maximal over right centro-parietal cortex, but extended over both hemispheres. We did not find any systematic relationship between EEG power and global vs local perceptual bias over occipital areas. Taken together with previous work, our findings suggest that modulations in alpha and low-beta power reflect global vs. local perceptual bias from moment-to-moment.

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SUMMARY AND CONCLUSION

Perception is the way we acquire knowledge about the world. To understand the meaning of what we perceive, it is fundamental to appreciate which phenomena have a common cause or identity and should be integrated, and which are separate and should be segregated. Appropriate sensory integration is, therefore, of the utmost importance to our connection to reality and ability to function in the world. For temporal integration, this has been proposed to occur through the spatiotemporal correlation between stimuli (e.g. Parise & Ernst, 2016). These spatio-temporal correlations do not need to be perfect to lead to integration. In multisensory perception, signals originating from the same event are often carried through different media and pass through different senses which naturally produces a temporal lag between them. Integration will occur despite such a time difference, up to a certain point. Similarly, in visuo-spatial perception, information over different areas needs to be integrated to form a coherent understanding of the visual scene. One important characteristic of visual information is that it is hierarchical, and perception can be biased towards a specific level within this hierarchy. Flexibly integrating at the appropriate level of the visual scene can help us limit perception to those features that matter to us most at each moment. What constitutes appropriate integration, and which is an appropriate time period or hierarchical level over which to integrate perception will in large part depend on the current internal and external contexts of the organism. These change continuously over time, both in a goal-directed and spontaneous manner. In this dissertation I have attempted to capture spontaneous fluctuations in this internal context by recording the EEG during the pre-stimulus period. Then, I used three frequency-domain measures; power, instantaneous frequency and the slope of the power spectrum, to predict the time and space over which visual and audiovisual integration occurred. In three studies linking pre-stimulus EEG activity to behavior on a single-trial basis, we investigated how EEG power and alpha instantaneous frequency predicted the temporal sensitivity of audiovisual integration (**Chapter 3**), how the slope of the power spectrum predicted the temporal sensitivity of audiovisual integration (**Chapter 4**) and how EEG power predicted visual perceptual bias to global vs. local features (**Chapter 5**). The main conclusions that emerged from this work are summarized below.

PRE-STIMULUS ALPHA POWER, BUT NOT FREQUENCY, PREDICTS THE TEMPORAL SENSITIVITY OF AUDIOVISUAL INTEGRATION.

Recent studies have produced evidence that spontaneous oscillatory activity can affect the temporal integration of individual stimulus features into a coherent percept (e.g. Cecere, Rees, & Romei, 2015; Samaha & Postle, 2015). Such studies have typically employed visual detection paradigms with near-threshold or illusory stimuli, and the majority have shown significant effects in the alpha band. These effects have often been explained in terms of alpha power as an index of the balance between excitation and inhibition, with higher alpha power accompanying lower cortical excitability (Romei et al., 2008; Samaha, Gosseries, & Postle, 2017). Effects of alpha frequency have bolstered theories of discrete perceptual cycles, of which the length is determined by the frequency of alpha (VanRullen, 2016). In **Chapter 3**, we recorded the EEG, while measuring audiovisual temporal discrimination sensitivity in a temporal order judgement task using above-threshold auditory and visual stimuli. We applied a jackknife procedure to link single-trial pre-stimulus oscillatory power and instantaneous alpha frequency to our psychometric measure of temporal sensitivity; the just noticeable difference. We found that lower pre-stimulus alpha power predicted higher temporal discrimination sensitivity on a trial-by-trial basis. Higher pre-stimulus alpha frequency also seemed to predict higher temporal sensitivity, but this effect could be attributed to an asymmetry in the effect of alpha power. We did not find any systematic relationship between individual alpha frequency or individual alpha power and temporal sensitivity across participants. The fact that we did not find a significant relation between instantaneous alpha frequency and the temporal sensitivity of audiovisual integration suggests that the theory of perceptual cycles cannot be generalized to include supra-threshold audiovisual perception. Moreover, since other studies reporting an effect of instantaneous alpha frequency do not report having controlled for alpha power (Samaha & Postle, 2015; Wutz et al., 2018), our results call for caution when interpreting the reported effects of those studies. Taken together with previous work (Baumgarten, Schnitzler, & Lange, 2016; Leonardelli et al., 2015), our findings suggest that modulations in alpha power reflect the brain's tendency for temporal integra-

tion vs. segregation on a trial-by-trial basis, and is likely related to fluctuations in cortical excitability.

NO EVIDENCE THAT THE PSD SLOPE PREDICTS THE SENSITIVITY OF AUDIOVISUAL INTEGRATION.

To follow up on **Chapter 3**, and seek confirmation for our interpretation of the results in terms of alpha as an index of excitation/inhibition balance, in **Chapter 4** we re-analyzed the data from **Chapter 3** using a different measure of the excitation/inhibition balance; the PSD slope (Gao, Peterson, & Voytek, 2017; Haller et al., 2018). Most studies using this measure have focused on relating different measures of non-oscillatory activity, such as entropy or detrended fluctuation analysis, to each other and to other measures of brain activity such as oscillatory power and the BOLD response (e.g. Sheehan, Sreekumar, Inati, & Zaghoul, 2018; Winawer et al., 2013). A shallower PSD slope has been proposed to reflect an increased ratio of excitatory to inhibitory activity and shorter and weaker autocorrelation across time (Gao et al., 2017; He, 2011, 2014). We tested whether the power spectral density (PSD) slope of pre-stimulus EEG activity predicted the temporal sensitivity of audiovisual integration. Our study is among the first attempting to link modulations of PSD slope to modulations in behavior (He, Zempel, Snyder, & Raichle, 2010; Podvalny et al., 2015; Voytek et al., 2015), and the first to do so on a single-trial basis. Based on the results from **Chapter 3**, which we interpreted as higher cortical excitability leading to increased temporal sensitivity, and the notion that a system with weaker autocorrelation over time shows greater entropy and thus greater capacity for fast information processing (He, 2014; Peterson & Voytek, 2018), we expected that a shallower PSD slope would predict higher temporal sensitivity in the temporal order judgement task. We did not find evidence in support of this hypothesis, within or between participants. It is difficult to draw conclusions from a null finding, but this is even further complicated by the fact that the PSD has not yet been extensively researched. More studies into the PSD slope are needed to establish its functional significance. A study using TMS to probe excitability while recording EEG,

such as conducted by Romei et al. (2008), to test whether PSD slope indeed indexes the balance between excitatory and inhibitory activity as suggested by Gao et al. (2017) would be an important step towards a better understanding of this measure.

PARAMETERS OF APERIODIC AND PERIODIC SPONTANEOUS EEG ARE INTERRELATED AND DRIFT SYSTEMATICALLY WITH TIME-ON-TASK.

Since the PSD slope is a relatively new EEG parameter to study, in **Chapter 4** we also described how the PSD slope varied over the scalp and over the course of the experiment. We found that the PSD slope was most steeply negative-going over posterior electrodes and flattened out towards the front of the scalp. We also found that the slope flattened out significantly over the course of the experiment, in two focal bilateral parietal clusters. When conducting studies relating the PSD slope to behavior, time-on task effects should therefore be taken into account, to avoid spurious correlations between the PSD and slope and behavior. In **Chapter 3** we found that higher pre-stimulus alpha frequency predicted higher temporal sensitivity, but we also noticed that alpha power and instantaneous frequency were inversely related across most channels and time points. This spurred us to conduct a follow-up analysis, where we ran the same analysis, relating instantaneous alpha frequency to behavior, only this time we controlled for alpha power at peak alpha frequency and two Hz above and below. This revealed that the relation between instantaneous alpha frequency and behavior was actually a reflection of a modulation of power below peak frequency. These additional analyses conducted in **Chapters 3** and **4** clearly demonstrate that, when linking frequency domain measures such as the ones used here to behavior, the fact that these measures show certain interdependencies, and drift systematically with time on task, need to be taken into account (Benwell et al., 2018).

PRE-STIMULUS ALPHA POWER BIASES VISUAL PERCEPTION TOWARDS LOCAL FEATURES.

In **Chapters 3** and **4**, we investigated how spontaneous pre-stimulus activity predicted the time over which visual and audiovisual integration occurred. The involvement of oscillations in the structuring of perception goes beyond the temporal domain, however. Only a limited amount of work has been done on how pre-stimulus oscillations impact the perception of individual stimulus features (Flevaris, Martínez, & Hillyard, 2013; Romei, Driver, Schyns, & Thut, 2011; Romei, Thut, Mok, Schyns, & Driver, 2012; Volberg, Kliegl, Hanslmayr, & Greenlee, 2009). A factor complicating the interpretation of these studies and how they relate to each other is that they tested effects narrowly defined to specific brain areas or electrode clusters and focused on specific frequency oscillations. Romei et al. (2011, 2012) showed that alpha and beta TMS over right parietal areas was detrimental to global perception and that alpha TMS over left parietal cortex was detrimental to local perception. Flevaris et al. (2013) showed a symmetrical relation over occipital areas where alpha power biased perception towards local features. Finally, Volberg et al. (2009) showed that fast responses to local features were associated with high alpha amplitudes in the right centro-parietal cortex, whereas fast responses to global forms were associated with high alpha in left centro-parietal cortex. These results support a similar view of anticipatory biasing of perception to the local or global level as the one currently held based on experiments that investigated activity in response to the stimuli. In this view, the global vs. local bias is achieved through the differential activation of left versus right parietal cortices for local versus global biases, respectively, and that this lateralization is true for more central areas, but not for occipital areas. In **Chapter 5** we attempted to cast a wider net and include all electrodes and frequencies in the analysis. This allowed us to attempt to replicate the results from the studies discussed above together in the same experiment. We linked behavior to raw EEG power directly and on a trial-by-trial basis, instead of comparing differences to baseline activation between the conditions, and examined whether the power of pre-stimulus oscillations could predict how strongly visual perception was biased towards the correct perceptual scope in a classic Navon task. We found that higher pre-stimulus alpha and low-beta power predicted a

local bias on a trial-by-trial basis. This effect was maximal over right centro-parietal cortex, but extended over both hemispheres. We did not find any systematic relationship between EEG power and global vs local perceptual bias over occipital areas. As previous work has shown (Flevaris et al., 2013; Romei et al., 2011, 2012; Volberg et al., 2009), our findings show that alpha and low-beta oscillations predict a local perceptual bias. Unlike Romei et al. (2012) and Volberg et al. (2009), however, this is the case for both hemispheres, although the effect appears stronger over the right than left hemisphere. This suggests that even if alpha and low-beta oscillations modulate perceptual bias by shutting down the areas dedicated to processing the irrelevant target level, this might not be the whole story. Additionally, these oscillations may tune both areas to the processing of certain stimulus features and not others.

LIMITATIONS

As discussed above, parameters of aperiodic and periodic spontaneous EEG are interrelated. An especially important relation can be seen between the PSD slope and power at specific oscillatory frequencies, especially the alpha band (Becker, Van de Ville, & Kleinschmidt, 2018; Haller et al., 2018). Methods exist to account for PSD slope when measuring oscillatory power and vice versa (Haller et al., 2018). Unfortunately, in neither **Chapters 3** and **5**, where we measured power, nor in **Chapter 4**, where we measured the PSD slope we took this interdependency into account. Another important limitation of our studies is that we only tested for linear relationships, while it is well known that dynamic systems often display non-linear behavior (He & Zempel, 2013; Schoner & Kelso, 1988). This might be a reason why we did not find a significant effect of PSD slope on temporal sensitivity, for example.

FUTURE DIRECTIONS

It is notable that alpha oscillations play a role in both temporal and spatial perception. While high alpha power seems to go along with a tendency to integrate over larger temporal segments, it is also indicative of a tendency to integrate over smaller, more local spatial areas. In other words, higher alpha power predicts worse temporal, but better spatial resolution. Could it be the case that there is a trade-off between spatial and temporal resolution, modulated by alpha power, where the senses can be biased towards the fast perception of large global features or the slower perception of smaller local features? This is an idea worthy of consideration for further inquiry. If proven correct, it could provide a mechanistic explanation for theories and results from the relatively disparate visuospatial and temporal research-domains.

CONCLUSION

In this dissertation I have attempted to capture spontaneous fluctuations in the brain's tendency to integrate over shorter or longer time periods and over more local or global spatial hierarchical levels and relate these tendencies to spontaneous fluctuations in pre-stimulus brain activity from moment to moment. While fluctuations in alpha power predicted the temporal sensitivity of audiovisual integration and fluctuations in alpha and low-beta power predicted the strength of the perceptual bias towards global vs. local features, the slope of the PSD did not predict the temporal sensitivity of audiovisual integration. These results provide evidence that alpha and low-beta oscillations allow us to flexibly modulate perceptual integration over space and time on a short time scale.

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SUMMARY

Appreciating which phenomena have a common cause or identity, and which are separate, is necessary to make sense of what we perceive. Signals with a common cause or identity should be integrated, whereas those with different causes or identities should be segregated. It has been suggested that spatiotemporal correlation is the way that signals originating from the same physical event are identified (Burr, Silva, Cicchini, Banks, & Morrone, 2009; Chen & Vroomen, 2013; Parise & Ernst, 2016). These spatio-temporal correlations do not need to be perfect to lead to integration however, and integration will occur across temporal lags, or spatial distances, up to a certain point (e.g. Lewald & Guski, 2003). The size of these windows of integration vary under the influence of changing internal or external contexts (De Boer-Schellekens, Eussen, & Vroomen, 2013; Fister, Stevenson, Nidiffer, Barnett, & Wallace, 2016; Vroomen & Keetels, 2010). In this dissertation, I attempted to uncover the brain dynamics that might reflect changes in the internal context and how these might underlie the moment-to-moment variability in temporal and spatial integration.

In the first empirical chapter we tested whether pre-stimulus oscillations predicted audio-visual temporal discrimination sensitivity. We found that lower pre-stimulus alpha power predicted higher temporal sensitivity on a trial-by-trial basis. These results provide novel insight into the neural basis of the temporal resolution of multisensory integration. We show that not only task conditions (Stevenson & Wallace, 2013; van Eijk, Kohlrausch, Juola, & van de Par, 2008) and individual differences (Stevenson, Zemtsov, & Wallace, 2012; Wallace & Stevenson, 2014) affect the temporal sensitivity of audiovisual integration, but that spontaneous brain activity does so as well, from moment to moment. In showing this, we extended existing evidence that higher alpha power is indicative of a tendency towards temporal integration (Baumgarten, Schnitzler, & Lange, 2016; Leonardelli e.a., 2015; Peterson & Voytek, 2018). Moreover, we show that temporal sensitivity for above-threshold multisensory stimuli changes spontaneously from moment to moment and is likely related to fluctuations in cortical excitability. Higher pre-stimulus alpha frequency also seemed to predict higher temporal sensitivity, but this effect could be attributed to an asymmetry

in the effect of alpha power. This pattern of results stresses the importance of accounting for individual differences in peak alpha frequency, as well as systematic shifts in both alpha frequency and power over the course of an experiment.

In the second empirical chapter, we followed up on the first chapter to see if we could find evidence in favour of our interpretation of the results in terms of the balance of excitation versus inhibition. To do this, we analysed the same data, but now using the slope of the power spectrum as an index of the balance of excitation versus inhibition. A shallower PSD slope has been proposed to reflect an increased ratio of excitatory to inhibitory activity and shorter and weaker autocorrelation across time (Gao, Peterson, & Voytek, 2017; Haller e.a., 2018; He, 2014). Therefore, we expected that a shallower slope would be predictive of higher temporal sensitivity. We did not find evidence in support of this hypothesis, within or between participants. We did find that the PSD slope was most steeply negative-going over posterior electrodes and that the slope flattened out significantly over the course of the experiment, in two focal bilateral parietal clusters. More studies linking behavior to the PLE are needed to establish its functional significance.

In the third and last empirical chapter, instead of measuring audiovisual integration over time, we investigated visual integration over space. One important characteristic of visual information is that it is hierarchical and perception can be biased towards a specific level within this hierarchy. We measured EEG while participants performed a Navon task with hierarchical letters and tested whether power at any cluster of channels differentially predicted reaction times for global versus local incongruent trials. We found that higher pre-stimulus alpha and low-beta power predicted a local bias on a trial-by-trial basis. This effect was maximal over right centro-parietal cortex, but extended over both hemispheres. Our findings show that modulations in alpha and low-beta power reflect a global vs. local perceptual bias in visual perception. This was the first study showing that spontaneous oscillations could predict such a bias from moment to moment.

In this dissertation I have attempted to capture spontaneous fluctuations in the brain's tendency to integrate over shorter or longer time periods and over more local or global spatial hierarchical levels and relate these tendencies to

spontaneous fluctuations in pre-stimulus brain activity from moment to moment. temporal sensitivity of audiovisual integration and fluctuations in alpha and low-beta power predicted the strength of the perceptual bias to global vs. local features, the slope of the PSD did not predict the temporal sensitivity of audiovisual integration. These results provide evidence that alpha and low-beta oscillations allow us to flexibly modulate perceptual integration over space and time on a short time scale.

Baumgarten, T. J., Schnitzler, A., & Lange, J. (2016). Prestimulus Alpha Power Influences Tactile Temporal Perceptual Discrimination and Confidence in Decisions. *Cerebral Cortex*, *26*(3), 891–903.

Burr, D., Silva, O., Cicchini, G. M., Banks, M. S., & Morrone, M. C. (2009). Temporal mechanisms of multimodal binding. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1663), 1761–1769.

Chen, L., & Vroomen, J. (2013). Intersensory binding across space and time: A tutorial review. *Attention, Perception, & Psychophysics*, *75*(5), 790–811.

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Fister, J., Stevenson, R. A., Nidiffer, A. R., Barnett, Z. P., & Wallace, M. T. (2016). Stimulus intensity modulates multisensory temporal processing. *Neuropsychologia*, *88*, 92–100.

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Wallace, M. T., & Stevenson, R. A. (2014). The construct of the multisensory temporal binding window and its dysregulation in developmental disabilities. *Neuropsychologia*, 64, 105–123.

SAMENVATTING

Het besef van welke verschijnselen eenzelfde oorsprong of identiteit hebben en welke niet is cruciaal om te kunnen begrijpen wat we waarnemen. Signalen met eenzelfde oorsprong of identiteit moeten worden geïntegreerd en signalen van verschillende oorsprong of identiteit moeten afzonderlijk van elkaar waargenomen worden. Gesuggereerd wordt dat spatiotemporele correlaties van belang zijn om signalen die van eenzelfde gebeurtenis afkomstig zijn te kunnen identificeren (Burr, Silva, Cicchini, Banks, & Morrone, 2009; Chen & Vroomen, 2013; Parise & Ernst, 2016). Deze correlaties hoeven echter niet perfect te zijn en er is een marge van imperfectie waarbinnen signalen toch geïntegreerd kunnen worden. (e.g. Lewald & Guski, 2003). Hoe gevoelig perceptie is voor zulke imperfecties in spatiotemporele correlaties hangt af van interne en externe omgevingsfactoren van het organisme (De Boer-Schellekens, Eussen, & Vroomen, 2013; Fister, Stevenson, Nidiffer, Barnett, & Wallace, 2016; Vroomen & Keetels, 2010). In deze dissertatie heb ik gepoogd licht te werpen op de hersenactiviteit die deze interne context reflecteert en hoe fluctuaties in deze context ten grondslag liggen aan snelle variaties in de temporele gevoeligheid van integratie en de spatiale neiging om kleine, locale kenmerken waar te nemen of grote, globale kenmerken.

In het eerste empirische hoofdstuk hebben we onderzocht of pre-stimulus oscillaties de temporele gevoeligheid van audiovisuele integratie konden voorspellen. We vonden dat alpha oscillaties met een lagere power een hogere temporele gevoeligheid voorspelden van moment tot moment. Deze resultaten geven een nieuwe kijk op de brein mechanismen die aan de temporele gevoeligheid van audiovisuele integratie ten grondslag liggen. We laten hiermee ook zien dat niet alleen taak kenmerken (Stevenson & Wallace, 2013; van Eijk, Kohlrausch, Juola, & van de Par, 2008) en individuele verschillen (Stevenson, Zemtsov, & Wallace, 2012; Wallace & Stevenson, 2014) maar ook spontane hersenactiviteit van invloed is op de temporele gevoeligheid van audiovisuele integratie. Dit convergeert met ander bewijs voor het idee dat hogere alpha power een indicatie is voor een tendens tot integratie (Baumgarten, Schnitzler, & Lange, 2016; Leonardelli e.a., 2015; Peterson & Voytek, 2018). Bovendien laten

we zien dat temporele gevoeligheid spontaan varieert van moment tot moment en dat dit waarschijnlijk in verband staat met de balans tussen excitatoire en inhibitoire corticale activiteit. Daarnaast leek het ook alsof een hogere alpha frequentie een hogere temporele gevoeligheid voorspelde, maar dit effect bleek te kunnen worden verklaard door een assymetrie in het effect van alpha power. Dit laat zien hoe belangrijk het is om te controleren voor individuele verschillen in alpha frequentie en systematische verschuivingen in alpha frequentie en power gedurende het experiment.

In het tweede empirische hoofdstuk wilden we onderzoeken of onze interpretatie van de resultaten uit hoofdstuk 3 op basis van de balans van excitatoire versus inhibitoire activiteit ondersteund konden worden door nog een andere maat te gebruiken voor deze balans. We hebben dezelfde data nogmaals geanalyseerd, maar nu met de helling van het power spectrum als index voor de ratio van excitatoire to inhibitoire activiteit. Een minder steile helling van het power spectrum wordt gedacht een aanwijzing te zijn voor een hogere ratio excitatoire tot inhibitoire activiteit en zwakkere temporele autocorrelaties (Gao, Peterson, & Voytek, 2017; Haller e.a., 2018; He, 2014). Op basis hiervan verwachtten we dat een minder steile helling voorspellend zou zijn voor een hogere temporele gevoeligheid van audiovisuele integratie. We vonden echter geen bewijs voor deze hypothese. Wel toonden we aan dat de helling van het power spectrum minder steil werd, al naar gelang het experiment vorderde in twee bilaterale parietale clusters. Er is meer onderzoek nodig om te begrijpen hoe de helling van het power spectrum precies gelinkt is aan perceptie.

In het derde en laatste empirische hoofdstuk hebben we geen audiovisuele temporele integratie gemeten, maar visuele integratie over de ruimte. Een belangrijk kenmerk van visuele informatie is dat deze hiërarchisch is. Perceptie kan een tendens hebben naar het waarnemen van lokale of globale kenmerken van een visuele scene. We hebben EEG metingen gedaan terwijl proefpersonen een klassieke Navon taak met hiërarchische letters uitvoerden. We vonden dat een hogere power van alpha en beta oscillaties een tendens tot het waarnemen van lokale kenmerken voorspelde. Dit verband was het sterkste voor centro-parietale elektroden, maar strekte zich uit over beide hemisferen. Dit was de eerste studie waarin werd aangetoond dat spontane hersenactiviteit de

tendens van visuele waarneming van locale of globale kenmerken kan voorspellen van moment tot moment.

In deze dissertatie heb ik getracht spontane fluctuaties in de tendens van het brein tot integratie over kortere of langere momenten en over locale of globale kenmerken te beschrijven en deze in verband te brengen met snelle en spontane veranderingen in hersenactiviteit. Terwijl fluctuaties in alpha power de temporele gevoeligheid van audiovisuele integratie voorspelde, en fluctuaties in alpha en beta power de tendens tot het waarnemen van locale versus globale kenmerken voorspelde, was er geen gelijkaardige voorspelling mogelijk op basis van de helling van het power spectrum. Deze bevindingen vormen bewijs dat alpha en beta oscillaties ons toestaan om op flexibele en snelle wijze perceptuele integratie over tijd en ruimte te moduleren.

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- Peterson, E. J., & Voytek, B. (2018). The trade-off between neural computation and oscillatory coordination. *bioRxiv*, 309427.
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- Wallace, M. T., & Stevenson, R. A. (2014). The construct of the multisensory temporal binding window and its dysregulation in developmental disabilities. *Neuropsychologia*, *64*, 105–123.

Data Storage Fact Sheet for Chapters 3 and 4

% Name/identifier study
% Author: Raquel London
% Date: 10-feb-2019

1. Contact details

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2. Information about the datasets to which this sheet applies

* Reference of the publication in which the datasets are reported:
Chapters 3 and 4 of PhD dissertation:
Chapter 3: Variability of spontaneous neural oscillations predicts the temporal sensitivity of multisensory perception from trial to trial.
Chapter 4: The slope of the EEG power spectrum systematically flattens with time on task, but does not predict the temporal sensitivity of audiovisual perception.

* Which datasets in that publication does this sheet apply to?:
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- research group file server
- other (specify): researcher hard drive back up

* Who has direct access to the raw data (i.e., without intervention of another person)?

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- responsible ZAP
- all members of the research group
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- file(s) containing processed data. Specify: Matlab data files

- file(s) containing analyses. Specify: Matlab analysis scripts

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Data Storage Fact Sheet for Chapter 5

% Name/identifier study
% Author: Raquel London
% Date: 10-feb-2019

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If a response is not received when using the above contact details, please send an email to data.pp@ugent.be or contact Data Management, Faculty of Psychology and Educational Sciences, Henri Dunantlaan 2, 9000 Ghent, Belgium.

2. Information about the datasets to which this sheet applies

* Reference of the publication in which the datasets are reported:
Chapter 5 of PhD dissertation: Spontaneous alpha and beta oscillations bias vision towards local spatial perception.

* Which datasets in that publication does this sheet apply to?:
All data from the reported experiment (behavioral and EEG)

3. Information about the files that have been stored

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