

# **The Diverse Role of Alpha Oscillations in Visual Object Processing**

Dissertation submitted for the degree of  
*Doctor of Philosophy*

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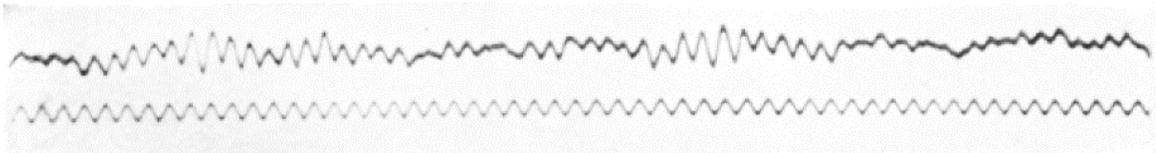
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# 1 Preface

In 1924, Hans Berger, driven by his search for the “psychic energy” of the brain [1], put together a machine called “electroencephalograph”, and managed to measure for the first time electric activity arising from the brain through the skull [2]. What he saw was a wavy activity pattern, roughly sinusoid of shape, waxing and waning, repeating itself cca. 10 times every second. After him, it is sometimes called “the Berger rhythm”, but these wave patterns today are more well-known as alpha waves, due to their primacy in the family of brain oscillations.



**Figure 1.1** The electroencephalogram of man, as measured by Hans Berger in 1924. The top trace is the EEG, the bottom trace is a reference waveform with a frequency of 10 Hz. From [2], image enhanced using Microsoft Word.

Berger did not know back then how lucky he was. It is arguably not always the case in science, but the importance of these waves that he discovered was inherently related to the mere fact that he could actually measure them. In order for neuroelectric activity to be measurable from outside the skull, two main prerequisites should be met: the spatial alignment of the electric fields and the temporal (in-phase) synchrony of their fluctuations. The spatial alignment requirement is met due to the organization of cortical tissue: the somatodendritic axes of cortical neurons – especially pyramidal cells – are perpendicular to the surface of the cortex, and the fields arising from their postsynaptic potentials (and possible other potentials, see e.g. [3]) are thus aligned appropriately to be summated into a field potential that also reaches the scalp surface. The temporal synchrony prerequisite is more interesting, because synchronization of the activity of neurons arguably requires some kind of communication between them. Of course, synchrony can arise through simple physical interactions [4], but in the last decades it has become clear that neural oscillations and their patterns of synchronization are the main governing principles of the temporal organization of information processing and communication in the brain [1, 5]. That is, oscillations in the EEG, including those in the alpha band, are not epiphenomenal fluctuations that we can measure due to their large amplitude, but they are inherently meaningful and important.

Ironically, though, since their discovery alpha oscillations have become a nuisance for a lot of researchers, as they had become preoccupied with another kind of synchrony: synchrony with sensory events. As measurement technology has become more advanced, EEG activity waveforms that are synchronized to external events, i.e. event-related potentials (ERPs), have become easier to measure and quantify, and alpha activity that is not time-locked to stimulation was mostly averaged out or was regarded as background noise, a sign of “idling”. Methodology that enables the efficient characterization of the diverse oscillatory signals that can be acquired by M/EEG have only become available with the advent of microcomputers (see e.g. [6]). By today, alpha activity, and oscillations in general, have come back to the focus of research: a regimen of methods to quantify oscillatory signals have become available [7], which also led to a huge body of experimental results and competing theories on the role and nature of alpha oscillations [8–13].

In this dissertation, I will first describe some principles of object encoding and attention in the visual system, then will continue with summarizing our current knowledge on the role of alpha oscillations in sensory processing and attention. Then, I will present original research that provides novel insight about how alpha oscillations contribute to visual attention and visual expertise in the case of complex natural objects.

## 2 Introduction

### 2.1 Attention and stimulus encoding in the visual system

The brain consists of approximately 100 billion neurons, with an estimated number of 200 trillion synapses between them [1]. Synapses, the elaborate structures of the dendrites and soma can all be regarded as minute biophysical computing units, which, working together, constitute the enormous computing power of the brain. However, to achieve adaptive behavior, the brain faces the daunting task of extracting the behaviorally relevant portion from the enormous amount of complex and structured, but also uncertain information available in the environment, which also has to be done within a limited time. With this in mind, considering brain functions as resource allocation problems is an important perspective.

Visual attention is the strategy to tackle this resource allocation problem in the case of visual perception [14–17]. It is clear that instantaneous and full analysis of a complex visual scene is not feasible, as demonstrated by everyday experiences like looking for a key on a cluttered table or a face in a crowd. This practically means that visual stimuli will compete for the representational resources of the brain, and this competition can manifest on multiple levels from visual analysis to motor output [14]. Focusing on the ventral visual stream, the chain of areas responsible for detailed shape representations and visual object recognition, receptive fields can be considered the scarce resource that stimuli compete for. Receptive fields are small and respond to simple visual features at the input stage of the ventral stream (V1), and become progressively larger and have more and more complex response properties in higher-level areas, up to the extreme of ventral temporal cortical areas representing complex natural objects like faces [18], body parts [19], animals, everyday objects or visual words [20] with spatial receptive fields that cover a large portion of the visual field ( $\sim 20\text{-}25^\circ$ , [14]). The key idea is that if multiple objects are present in a receptive field (which is quite probable in the case of the aforementioned large receptive fields in the ventral temporal cortex), then the processing resources available should be divided between them. Attention, according to the biased competition theory, can resolve this competition by suppressing the processing of irrelevant stimuli, freeing up representational resources for the attended stimulus almost to a degree as if the irrelevant stimulus was not even there.

Both these competitive interactions and the way attention can resolve them are well captured by the more general neurocomputational principle of response normalization, which states that responses in the cortex (on multiple levels of its organization) are normalized so that overall activity across a neural population (the normalization pool) remains constant [21, 22]. This mechanism can ensure that cortical activity has an upper bound, avoiding pathological overactivation, while also optimizing the dynamic range of neural coding [21, 22]. It appears that lateral inhibitory connections have a prominent role in normalization and biased competition, but there is more and more evidence that feedback pathways also influence the process [23, 24].

Another aspect of optimal resource allocation concerns the representations (or “filters”) that the cells in the visual cortical hierarchy implement. The organization of the visual system is governed by information theoretic principles. In particular, it realizes the representational structure that is most energy efficient and adaptive given the statistical structure of the visual environment. For example, the Gabor-like receptive fields of V1 can be acquired by a computational approach applied to a large set of natural images, trying to find a basis set (“receptive fields”) that is maximally sparse (i.e., the representation of the most probably occurring images requires the least number of representational elements to be active) [25, 26].

In a slightly different formulation, the visual system (or the whole brain [27]) attempts to predict the input patterns by trying to infer the underlying cascade of hidden causes that might have created them, thereby construing itself as a generative model of the environment [28]. These models have compelling explanatory power both theoretically and practically. They apply not only to the structure of the visual system, but also its functioning and plasticity: perceiving a stimulus entails inverting this generative model as neural activity cascades up the visual hierarchy, and also modifying model parameters as manifested in the plasticity phenomena of the visual system such as perceptual learning and the formation visual expertise.

Most importantly to the subject of this dissertation, predictive coding models highlight the importance of feedback connections in the visual cortical hierarchy [29, 30]. In order for hierarchical generative models to work, each level of the hierarchy should pass a prediction to the lower level. According to the predictive coding account of the visual system, this occurs through feedback connections. In turn, the lower level should return a prediction error, which in the visual system corresponds to feedforward connections. Based on this prediction error, the parameters on the higher level are updated so that future prediction errors would decrease, and this logic applied iteratively

throughout the whole hierarchy until convergence gives rise to perception and stimulus representations that are optimal in the sense laid out above. Recent research has led to important insights regarding how these principles are realized in the physiological mechanisms underlying attention and object perception, to which we return later in this section.

Several characteristics of the higher level visual system also emerge if we consider the consequences of these principles. Probably the primary parameter to describe a visual stimulus is its category – for example, human faces, buildings or visual words clearly have highly distinct “underlying causes” (basic visual components and organization) and also different implications for adaptive behavior. Reflecting these inherent discrete classes of stimuli in the visual world, the highest levels of the visual hierarchy have a modular organization, with distinct areas encoding frequently occurring and/or behaviorally relevant visual categories. For example, high-level encoding of face stimuli (supported by a broader network of visual areas) involves a circumscribed area in the ventral temporal cortex, called Fusiform Face Area (FFA) [18], while there is another region called Visual Word Form Area (VWFA) specifically involved in the processing of printed words [20, 31]. These two categories and their respective brain networks are probably among the most researched model systems in the research of object perception. The development of these areas probably builds on some innate liabilities and, relatedly, more abstract gradients in the representational space of potential high-level objects[32, 33], but experience and the acquisition of visual expertise is arguably highly important in this process.

Considering exemplars within one category, predictive coding models posit that the most probable (or frequent) ones will be recognized most effectively: after stimulus category is recognized, these stimuli will match the “first guesses”, or a priori predictions of the system, which means that the feedback loops described above will converge faster. This is in accordance with the norm-based encoding scheme faces are thought to be represented in the visual system [34, 35]. At the expense of being fast for the more frequent ones, perceiving rare, peculiar exemplars or ones presented in unusual circumstances or orientations can be substantially slower. These phenomena are used in the research of visual expertise: for example, for faces presented upside-down, both electrophysiological and behavioral responses are slower [36–38], and also, visual expertise for text during reading makes us less effective unusual formats or reading conditions [39].

Besides and despite this specialization, it is also remarkable how robust object recognition can be. For example, partially occluded or noisy images of objects can still be recognized [40, 41]. As a

consequence of the coding strategies laid out above, signals that match the representational dictionary of the visual system will be amplified, and in turn, those that are orthogonal to them will be suppressed. Thus, in the case of noisy or partial input, the system will perform pattern completion and converge to the closest potential interpretation of the input. An example from daily experience for this is pareidolia, our liability to see, for example, faces on household objects or on the surface of Mars. A more extreme example is the notion that sensory deprivation can induce hallucinations, which is potentially related to the overactivation of top-down predictions due to the lack of bottom-up input [42, 43]. In a condition called Charles Bonnet syndrome, a surprisingly large number (10-20%) of psychologically normal visually impaired people (e.g. elderly people suffering from macular degeneration) experience complex, vivid hallucinations, especially during time periods of relative inactivity [44–46].

To sum up, the brain makes use of its limited representational resources both through learning robust optimal stimulus encoding strategies especially for frequent specimens of behaviorally important stimulus categories, and also by attention that boosts behaviorally relevant stimulus representations among concurrently present competitor stimuli.

## 2.2 Alpha oscillations: from idling through inhibition to active processing

The first functional property of alpha oscillations was the so-called alpha blocking response, which was demonstrated already by Berger [2] and later confirmed by Adrian and Matthews [47]. Alpha blocking is the reduced amplitude of alpha oscillations upon the opening of the eyes, compared to large-amplitude alpha waves in the baseline, eyes-closed state. On the simple premise of associating higher alpha activity with the lack of input, one could infer that alpha oscillations could indicate a resting or idling state of the cortex. In the second half of the XX. century, when efficient and cheap computing and also multielectrode scalp measurements have become more and more available, research on alpha oscillations continued to expand from this starting point. Based on these measurements, it was established that the blocking response related to the opening of the eyes, which is measured best over the posterior scalp and originates from the visual cortex, is generalizable to other cortical areas and other functions: alpha power decreases in the visual cortex upon visual stimulation (light flashes with closed eyes, compared to pre-stimulation), drops in the auditory cortex during auditory stimulation and also over motor areas preceding movement [48]. This disappearance of oscillatory activity was named event-related desynchronization, abbreviated as ERD, and is interpreted as active processing in a local patch of the cortex that is concerned with the function investigated [6, 48].

Thus, areas which are task-relevant produce alpha ERD. Areas that are irrelevant to the task at hand remain idle, as indicated by alpha amplitude staying on high levels – or even increasing compared to baseline, which is termed event-related synchronization (ERS). ERS is observed, for example, over motor areas in a visual task, and over visual areas and non-engaged motor areas preceding and during voluntary movement onset [49, 50]. Following desynchronization, a rebound power increase is also often observed, which can surpass baseline levels [49] – this is sometimes called re-synchronization. (It should be noted that in the first 300 ms after stimulation a short phasic increase in spectral power is often present, but this corresponds to the evoked response that is phase-locked to stimulus onset, while the modulations described above are all changes in the strength of ongoing “background” oscillations due to stimulation, which are not phase-locked to the stimulus; i.e., they are induced power modulations.)

Importantly, alpha ERD and ERS are not restricted to the domain of sensory stimulus processing and motor processes, and it is clear that even stimulus-induced alpha responses are profoundly influenced by top-down processes [10]. For example, in working memory (WM) tasks – in accordance with the previously mentioned results – encoding, and also the retrieval of the memory items is associated with alpha ERD. Based on the idling hypothesis, one would expect that the maintenance of sensory information in memory would also be accompanied by an ERD, but Klimesch and colleagues [51] observed that, especially if subjects have to avoid the intrusion of memory items from previous trials, i.e. high interference, alpha oscillations displayed ERS in the memory maintenance period. This, and various other results, has led to the hypothesis that ERS does not simply reflect a passive baseline state of idleness, but active, top-down inhibition [8].

How alpha oscillations are related to top-down processes most profoundly appears in the field of attention research. In particular, the alpha ERD in the cortical area corresponding to the task-relevant modality (e.g. auditory vs. visual) has been shown to occur *before* the stimulus, as far as the subject knows which kind of stimulation to expect [52]. The same was demonstrated within the visual modality first for the deployment of attention to either visual hemifield, that is, after a cue that indicated that a target stimulus would appear e.g. in the left visual hemifield, alpha power decreased over the visual cortex in the right hemisphere, while it increased in the left hemisphere [53]. This result has been replicated (and extended) in a huge variety of experiments. For example, it has been shown that this ERD/ERS patterning can be used to track the retinotopic locus of spatial attention beyond the binary distinction of visual hemifields with remarkable accuracy [54]. Importantly, several of these experiments specifically addressed the issue of ERS being a process related to active suppression rather than the return of baseline excitability state (e.g. [54, 55]). Only a few studies have attempted to show whether and how the suppressive role of alpha oscillations extends to non-spatial varieties of attention. Snyder and Foxe [56] have shown that attending to the color or motion direction of a moving dot field modulates alpha oscillations in the dorsal and ventral aspects of the visual system in a way that is compatible with the suppression account. More recent results indicated that the temporal dynamics of covert spatial orienting [57] and temporal expectation [58] is also closely tracked by alpha oscillations. To conclude, a huge body of research demonstrates that the inhibition account has a compelling explanatory power, especially in the case of visuospatial attention.

Despite all this, it has also become clear that the relation between alpha activity and inhibition is far from general, and unfortunately, the exact boundary conditions of when an alpha power modulation measured on the scalp might indicate inhibition or suppression are only subject to speculations. Palva and Palva [11], for example, argue for the active role of alpha oscillations in general, including the working memory scenario (ERS depending on load and interference) from which the inhibition account was derived [51]. As mentioned above, WM-related ERS is interpreted in the inhibition framework as suppression of competing representations, for example those lingering from the previous trial. In contrast, the active processing account posits that alpha oscillatory network spanning the sensory and frontoparietal cortices actively organizes neural activity in a way that is essential for the maintenance of the representations of the memory items [11]. This function of alpha oscillations – and low-frequency oscillations in general – arises from the physiological mechanisms that cause the primary information processing activity of neurons – spiking – to occur at preferred phases of oscillations [59]. The timing of spikes is essential for coordinated neural computing, therefore neural oscillations are the primary organizers of brainwide dynamic neural ensembles that make complex computations underlying adaptive perception and behavior possible [1, 5, 60]. The updated version of the inhibition hypothesis, the inhibition-timing hypothesis [8] also takes this into account as a possible mechanism of selective inhibition.

Recent research has provided evidence for a computationally and neurophysiologically circumscribed role for alpha oscillations in the networks of attentional and visual areas. Buschman and Miller [61] demonstrated in macaques that the flow of information dominantly occurs in the gamma band from parietal to frontal areas during bottom-up, stimulus-driven attention, while beta oscillations convey top-down information in the direction of frontal areas from the parietal cortex. In the visual cortical hierarchy, in supragranular layers where feedforward connections originate gamma oscillations are most common, while infragranular layers send feedback connections to lower areas and produce alpha/beta oscillations [62–64]. These observations suggest that alpha/beta and gamma oscillations would be the preferred channels for feedback and feedforward communication in the visual hierarchy, respectively. This hypothesis was tested and validated in the macaque using invasive recordings [65, 66], and also in humans using MEG [67]. These findings have profound implications on the interpretation of noninvasive recordings from human subjects.

To sum up, the different theories debate how the amplitude and phase dynamics of alpha oscillations affect cortical circuits. Also, other frequencies on the spectrum could be also interesting targets for investigating the neural processes of visual object perception and attention (Box 2.1). However, they do agree that alpha oscillations mark an essential component of brain function, being a main orchestrator of coordinated activity that provides the neurocomputational background for fundamental aspects of the human mind such as attention and consciousness [8, 9, 11], and therefore the alpha band is a good candidate to focus our analyses on.

### **Box 2.1 The oscillatory architecture of the brain**

This dissertation focuses on alpha oscillations, which are usually the largest amplitude oscillations in the human brain. Of course, it is impossible to adjudicate between frequency bands, as they are equally important in forming the oscillatory architecture of the brain. Our hypotheses were nevertheless focused on alpha oscillations because they are especially prominent in the visual system which is the main subject of this work, and are frequently implicated in attentional processes. In order to be a little more comprehensive, here I promptly traverse the whole spectrum, also mentioning some possible connections to the attention and object perception. Note that the boundaries of the frequency bands are somewhat arbitrary, and may vary between individuals, species, arousal levels or cortical states.

The beta frequency band, ranging from around 12-15 Hz up to 30 Hz is the closest relative of the alpha band. Attentional effects are frequently found to extend up into the beta band, and beta also appears equally important as alpha as a channel for feedback communication in the visual hierarchy [1]. Beta oscillations are most prominent in sensorimotor cortices, their desynchronization response is observable there in preparation for limb movements [2]. Frontal beta activity is theorized to be related to reward and motivational factors [3–5]. A general theory suggests that beta-band activity might be related to the maintenance of the current sensorimotor set, or signalling the status quo [6]. Theta-band (4 Hz to 7-8 Hz) activity frequently modulates the phase and amplitude of higher frequency oscillations [7–9]. It is the most dominant frequency band in visual evoked responses. Theta oscillations most dominate the frontal cortex, especially its medial part, and the hippocampus [10]. Frontal theta is found to be important in cognitive control, conflict and error monitoring [11, 12], while hippocampal theta is implicated in long term memory and navigation [13]. The Delta band (<3 Hz) is most prevalent during sleep, and

is also involved in motivation-related processes and error monitoring [14, 15]. Gamma-band activity (>30-40 Hz), among LFP and EEG signals, is thought to most closely reflect neural activity, especially in the high gamma band (>100 Hz), which is directly related to multiunit activity [16]. Accordingly, unlike lower frequency oscillations, the attentional modulation of gamma activity can mostly be interpreted as an index of changing intensity of neural activity (e.g., [17]). Relatedly, the gamma band is the main frequency of feedforward communication in the visual system [18].

Also importantly, the present work focuses on the scalp-measured oscillatory power, which reflects locally synchronous neural activity in the brain. However, the phase of the oscillations is also important, and can have different functional relevance if measured relative to, a stimulus, the phase at the same frequency at a different cortical location, or the phase at a different frequency at the same or another location. As mentioned above, amplitude can be also modulated by the phase of another oscillation. Also, some researchers propose that there are other parameters that can be used to characterize oscillatory activity in the brain that might have great physiological relevance, like the slope of the power spectrum [19], or the nonsinusoid features the oscillations display [20, 21]. So, it is clear that focusing on alpha power is looking at a small slice of the potential hypothesis space that the analysis of brain oscillatory activity offers.

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## 2.3 Motivations and goals

In this dissertation, I venture to show two facets of how alpha oscillations constitute an important cornerstone in the neural machinery of visual object processing in humans. The two facets correspond to the two resource allocation problems laid out in the Introduction (Section 2.1): I. Resolving instantaneous competition for computing resources by attention; II. Optimizing the use of neural resources by specialization to frequent and important stimuli by visual expertise. Two experiments were conducted under controlled fixation conditions, but were designed so that they would provide information on how the mechanisms in question would work in real-world vision: operating on complex visual objects in dynamic spatiotemporal context.

Attention in everyday circumstances is quite different from how it is studied in the lab. Laboratory experiments mostly involve simple, artificial stimuli separated in both space and time, while in the wild, complex stimuli in dynamic, cluttered scenes are rapidly sampled by eye movements. This scenario requires dynamic object-based attention. **Given the known role of alpha oscillations in spatial and feature-based attention, we hypothesized that they would similarly contribute to object-based attention.** In the first experiment, this question was investigated using complex natural stimuli (words and faces) presented in spatial overlap (as in a cluttered natural scene) in relatively fast-paced sequences (mimicking temporal context during natural vision).

At first, both the hypothesis formation and the interpretation of the object-based attention experiment was mainly based on the inhibitory account of alpha oscillations that dominates most of the literature on attention. However, simply taking alpha oscillations as a signal of attentional inhibition did not perfectly align with every aspect of the results acquired, also in agreement with several lines of more recent research pointing to the more nuanced (and less straightforward) interpretations on the possible role of alpha activity in the visual system. This led to the following question: **could we relate alpha oscillations to expert object processing in the visual system?**

The role of alpha oscillations in expert object processing was investigated using visual words as model stimuli. Although the main perspective on reading and word recognition has arguably been from that of neurolinguistics, understanding the visual cortical processing of printed words, the interfacing and interactions of the visual system with higher level lexico-semantic subprocesses of reading is of hallmark importance. Studying visual word recognition by comparing neural responses to words with those evoked by pseudowords or other objects has been a fruitful approach, but subtle

manipulations affecting mainly the visual properties of text while leaving its content and overall “legibility” relatively unaffected has remained an important, less traversed avenue in current research. The second study included in this dissertation takes this approach: letter spacing, a key configural property of words, was manipulated to probe the neural correlates of visual expertise for orthography.

The spatial context of natural reading was mimicked by displaying flanker words around the target word. In this case, no further measures were taken towards more ecological validity within this experiment. However, another experiment was also conducted, where participants read lines of text with the same spacing manipulation in a natural way, with freely moving eyes [J2]. This natural reading experiment is not included (but is shortly described) in this dissertation, but fixation-triggered responses from it will be compared to event-related potentials acquired in the present work, and the implications will be discussed to better assess how these mechanisms might be relevant during natural reading.

Understanding the visual cortical processes underlying reading and word recognition can also provide a deeper understanding of reading disorders like dyslexia.

**The goals of the dissertation can be summarized as follows:**

*First, I will show that in accordance with its already established role in spatial attention, alpha oscillations are also at play when attention selects complex natural objects (faces and words) in cluttered visual scenes where relevant and irrelevant visual elements overlap in space.*

*Second, I will demonstrate on the case of printed word stimuli that the way the visual system optimizes its processing mechanisms to frequently encountered and/or important stimulus configurations – termed visual expertise – is also reflected in alpha oscillations. I will show how visual expertise molds the ERP responses as well, and relate the modulations to those observed during natural reading*

*Finally, I will discuss the practical and theoretical implications of the findings. I will attempt to interpret the results from the two experiments in a common framework, and will explore the potential overlaps between the cortical network mechanisms of the two investigated phenomena, and give some examples how these issues could be addressed in further experiments.*

## 2.4 Methods

The present work is based on EEG experiments with visual stimulus presentation conducted on human participants. The results were analyzed in terms of Event-Related Potentials and neural oscillations as characterized by wavelet-based methods. Statistical methods involve conventional parametric tests and mass univariate tests using Monte Carlo methods for type I error control. The methods of each experiment are also described in the respective Methods sections, but here I provide an overview of the EEG and statistical methods used and discuss some general methodological considerations and their relevance to the current work in more detail.

As already hinted at in the Preface, scalp EEG measures temporally synchronous postsynaptic potentials that are thought to originate primarily from the principal pyramidal cells with dendrites perpendicular to the cortical surface [68], besides other sources [3]. As for instrumentation, an active electrode system was used (actiCAP, Brain Products, München, Germany) to measure EEG, which has higher signal-to-noise ratio owing to the preamplification circuitry in the sensors themselves [69]. These systems, in theory, permit high impedance recording, and owing to this, a 20 k $\Omega$  impedance threshold was used during the preparation of the first experiment. However, as we learned that some noise sources (low frequency noise from sweating in particular) are stronger in high impedance recordings even in the case of active electrode systems [69], we decided to use a lower impedance threshold of 5 k $\Omega$  during the preparation phase of our newer experiments (including the experiment in Chapter 4 of this work), matching more conventional thresholds applied with passive recording systems in the literature [70]. We decided to do so because a) the noise sources of question might become particularly stronger after longer periods of recording, and our experiments are usually long, b) reaching the lower impedances also does not take too much extra time relative to the whole experiment, especially as weighed against c) the potential benefits of lower impedance recording even in the case of active electrode systems [69]; and, finally d) studying non-sensitive neurotypical populations permitted us to do so. All other measurement parameters and general preprocessing methods were conventional in the field, and are described in detail in the Methods sections of the respective chapters.

Event-Related Potentials (ERP) are also analyzed [70], but the primary focus of this work is oscillatory activity in the alpha band. While ERP is only sensitive to activity that is phase-locked to the event of interest, frequency domain analyses permit the characterization of both the former (evoked) and also non-phase-locked (induced) signal components. Time-frequency representations

were obtained using wavelet convolution with complex Morlet wavelets [7] as implemented in the MATLAB Wavelet Toolbox. The wavelets applied were short (the bandwidth parameter was set to 1), which favors temporal resolution at the expense of frequency resolution. Although larger frequency resolution is favorable, for example, for characterizing oscillations in the lower and upper alpha subbands, in this research we were more interested in the temporal dynamics of the alpha modulations, and also, in the object based attention experiment, the interstimulus interval was short, and longer wavelets would have made our analysis more sensitive to evoked activity, while non phase-locked modulations were of primary interest.

While temporal resolution, as compared to fMRI, is usually listed as a benefit of using EEG for cognitive neuroscience, spatial resolution is arguably a shortcoming of it. Due to volume conduction, all the electrodes pick up signals from all points of the brain, and the boundaries of the different compartments of the skull also cause further spatial smearing in the signal [68, 70]. While a plethora of more and more sophisticated source imaging methods have become available in the last decades, most of them requires individual subject MRI, and larger electrode coverage is also advisable for their effective application. Therefore, we decided to use the surface Laplacian method (also known as Scalp Current Density or Current Source Density mapping). This method, with a few assumptions and simplifications about the structure of the skull, approximates the current flowing through the dura mater, i.e. estimates an underlying configuration of current sinks and sources for a given topographic potential distribution [68, 70–72]. Practically, this means that far-field signals are suppressed, and the current density estimate at each electrode will be more sensitive to neural activity in the cortical area directly below the sensor. The surface Laplacian has been shown to improve not only the spatial resolution of EEG, but also its sensitivity to genuine temporal differences [73].

Apart from standard paired t-tests and analysis of variance, this work makes use of mass univariate testing with type I error control by cluster-based permutation tests, as laid out in [74] and implemented in the FieldTrip MATLAB toolbox [75]. Permutation tests make no assumption about the distribution of the tested quantities as parametric tests do. Owing to this, and to the fact that a multitude of tests have to be performed, these tests are more powerful than simple parametric tests. For permutation tests, the null hypothesis is that the conditions in the experiment are exchangeable with respect to the statistic tested. In the paired one-sample case, this is practically tested by calculating the same statistic multiple times so that the signs of the individual values are reversed at each iteration. This yields a null distribution to which the observed statistic is compared – if the

observed statistic is more extreme than the 95% of the null distribution, the null hypothesis of exchangeability is rejected.

In the case of multiple tests, for example when multiple time and/or frequency and/or channel samples should be tested, the problem of inflated type I errors ensues. One solution for this is clustering neighboring significant results together, and calculate a cluster statistic from the individual test values. For example, the t-values for neighboring significant test can be summed, which yields the cluster statistic. Calculating the cluster sum statistics in each permutation yields a null distribution of the cluster statistic in this case, and comparing to this null distribution achieves type I error control at the desired  $\alpha$  level.

This framework is versatile, because the analysis pipeline can be adapted to specific questions at several points (, while keeping in mind the utterly important caveats [76, 77] ). Designing an analysis pipeline always entails arbitrating several tradeoffs. Similarly to other methods, one has to decide what hypotheses should actually be tested. In the group-level analyses conducted in this work, the original input data format was subjects  $\times$  channels  $\times$  time  $\times$  conditions. (Oscillatory frequencies and arbitrary more dimensions could be taken into account analogously to methods described here.) The most straightforward way to analyze this is to conduct repeated measures ANOVAs with respect to the condition(s, with appropriate factor structure) at each channels  $\times$  time data point, wherein neighborhood in channels  $\times$  time space can be used to form clusters to correct for multiple comparisons. An important limitation during interpretation of the results is that it is fallacious to rely on the contours defined by the significant clusters acquired from analyses like this. Put differently, where the significance threshold is crossed in space or time provides no statistical support for inferences about where in space or when in time the effect in question occurred.

Alternatively, any set of linear combinations can be formed from the channels  $\times$  time matrix to define a constrained hypothesis set, and these can be either tested in a mass univariate framework (where, again, a neighborhood structure can be defined). These linear combinations can correspond to, for instance, channel averaged (pooled) time series, or average topographic distributions in time windows – this corresponds to a conventional Region of Interest (ROI) analysis. As another option, the linear combinations can entail contrasts. With appropriately defined contrasts, specific hypotheses about response patterns within the channels  $\times$  time matrix (and their interactions with experimental conditions) can be tested (e.g. lateralization or temporal fluctuation) – this step can be also regarded as conducting a repeated measures (factorial) ANOVA on spatiotemporal regions of

interest. For example, (as also described in Section 4.2.4,) the second study in this work focused on parieto-occipital alpha oscillations, hence spatial ROIs (electrode pools) were formed bilaterally. Lateralization of effects were also of interest, thus a lateralization contrast was added to the spatial ROI set. Multiple tests were conducted along the temporal and the newly derived 3-element spatial dimension; temporally adjacent samples and data from the left and right electrode pools were considered neighboring, but the lateralization contrast was considered to be isolated during clustering.

Quite obviously, the more *a priori* constraints are imposed on the hypothesis set, the more sensitive the analysis will become for the hypothesized effect, but, in turn, it will become less sensitive or even blind to other effects. A little less obviously, even if a highly focused ROI analysis is conducted, it is not only possible but also highly advisable to “take a step back” to observe and appraise the broader context of the effect during interpretation, potentially including also that part of the data that is *not covered at all* by the statistical analysis [78]. Continuing the above example, Figure 4.3A displays the results of the statistical analysis that was conducted (showing significant effects on the time series of the two electrode pools, corrected for multiple testing). In addition, Figure 4.3B shows the effect on all the 64 electrodes separately as topographic distributions, to show that the effect actually conformed to our expectations, and displays a physiologically plausible topography.

As implied above, not forming ROIs but testing on each electrode leaves the stage open for arbitrary possible effects, but at the cost of reduced sensitivity. In an ideal case, this could be mitigated by defining a ROI on an independent dataset. However, data collection is usually costly, so alternative strategies are desirable, for example, under certain boundary conditions, ROIs can be defined using contrasts that are orthogonal to the effect under investigation [79, 80]. An essential prerequisite for such strategies is that they should not increase the Type I error rate – any circularity easily leads to serious Type I error inflation and consequently, false results.

In the first study described in this dissertation, a two-step analysis pipeline was used that included such a ROI definition step. The initial hypotheses to be tested were not constrained along the spatial dimension, but temporal windows of interest were defined, so multiple tests were conducted on all the channels and in each of the five time windows. The ROIs for the next analysis step are defined so that channels are selected where the number of significant time windows for the current main effect of interest are largest, and their contralateral pairs are also selected. From the resulting

symmetrical channel sets, one pool is defined for each hemisphere. The second step involves space (hemisphere factor: left and right) and time (sequence factor: 5 time windows of interest) as repeated measures factors in an ANOVA, and the interactions of these factors with the current main effects of interest are tested. For example, the effect of category (face vs. word) was tested on all channels in each time window separately ( $64 \times 5 = 320$  tests), with cluster-based correction. Then, a bilateral pool was defined based on this, using which the category  $\times$  hemisphere, category  $\times$  sequence and category  $\times$  hemisphere  $\times$  sequence interactions were assessed (, but *not* the main effect of category).

The important point to note is that the effects tested at the second step correspond to dimensions along which multiple tests were conducted independently in the first step, (and also, no effect tested at the first step is probed again in the second,) and this rule avoids circularity and type I error inflation. This intuition was tested using Monte Carlo methods. For simplicity, the data of one time window (S6) was extracted from the attentional experiment, and the above analysis was conducted with only the hemisphere factor in the second step. Using permutation of the two conditions, null data was generated ( $N=9999$ ), and the same two-step pipeline was run on all the 9999 permuted datasets. From this, the empirical type I error rate was estimated:  $\alpha_{MC}=0.049$ , 95% CI: [0.045 0.053]. This supports that the two-step procedure used in the first study does not inflate the false alarm rate of the analysis. Here, if we consider again the limitation in the interpretation of mass univariate results on spatiotemporal data – that the spatiotemporal significance patterns are not significant spatiotemporal patterns – it appears that this strategy can be a good step to remedy this problem as well.

In summary, the two studies in this dissertation used conventional EEG methods with regard to recording and preprocessing, while the logic of statistical inference required more consideration. Being aware of the several methodological problems that surfaced in the last decade in the field of psychology and neuroscience (e.g. [77, 81–84]), the need for statistical methods to be both powerful and strictly valid was always considered a priority during this work.

## 3 Alpha oscillations in object-based attentional selection

### 3.1 Introduction

A remarkable ability of the visual system is that it can deal with the clutter of visual objects in our environment. Given its limited processing capacity, this can only be achieved via attentional selection, that is, assigning priorities to parts of visual information that are relevant according to behavioral goals [14]. In neurophysiological terms, this implies that neural processes related to high-priority visual information – attended regions of space, features or objects – should be facilitated [85–87]. Conversely, it can be advantageous to suppress the neural representation of irrelevant items (distractors) [88–91]. These inhibitory processes are especially important for efficient attentional selection when several objects are simultaneously present, which frequently occurs during everyday visual experience [92, 93].

A prominent neural signature of attentional distractor suppression is enhanced oscillatory activity in the alpha frequency band [8, 12, 13], which can be measured in human subjects non-invasively by means of electroencephalography (EEG). It is well-established that during spatial attentional tasks, the representation of the unattended visual space is inhibited through enhanced alpha activity in the corresponding parts of the visual cortex [53–55, 94, 95]. More recently, it has been shown that this generalizes to feature-based attention: Snyder and Foxe [56] demonstrated that anticipatory alpha band power increases can be localized more ventrally when the motion of the presented dot field was task-relevant, as compared to more dorsal sources when attending the color of the same dots.

However, when the visual system is faced with the visual clutter of multiple objects, the units of attentional selection are whole objects [96]. On what level of the visual hierarchy object-based selection operates is an outstanding question in recent research. The findings thus far support the assumption that, besides well-established modulations in category-specific areas in the ventral temporal cortex, object-based attention relies on top-down feedback signals biasing the activity of earlier visual areas based on high-level object knowledge [97–99]. However, whether inhibitory

processes involving alpha oscillations are invoked in object-based attentional selection remains an important unresolved question.

To address this question, we designed a paradigm using word, face and composite word-face stimuli. In each trial, either the word or the face component was cued to be attended, the other being task-irrelevant. To maximize the engagement of object-based selection mechanisms and to minimize the involvement of spatial attention, all stimuli were presented foveally at the same location – that is, words were overlaid on faces in the case of composite stimuli. Words and faces are suitable to probe object-based attention because of the well-known, pronounced lateralization of their processing: category-selective neural activity dominantly takes place in the right and left hemisphere in the case of faces and words, respectively [18, 100]. Based on this, we predicted that object-based attention to either category in a compound word-face display will modulate the hemispheric lateralization of visual cortical alpha oscillations. In particular, attending to faces will lead to increased alpha power in the left hemisphere, which is dominantly involved in the processing of word stimuli, whereas attending to words will increase alpha power in the right hemisphere, which is dominant in face processing. We tested these predictions in the case of sustained object-based attentional selection of face or word stimuli, presented sequentially (six stimuli, each presented for 683 ms) within a trial.

## **3.2 Materials and methods**

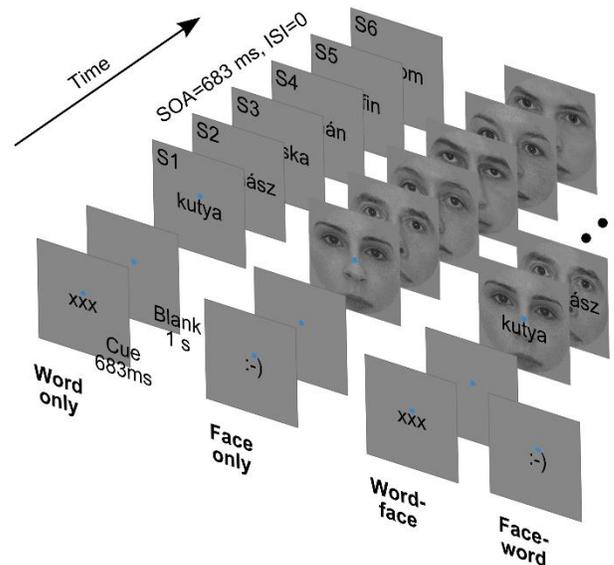
### **3.2.1 Subjects**

Twenty healthy young adults participated in this study. All of them had normal or corrected-to-normal vision; none of them had any history of neurological or psychiatric diseases. All participants gave their informed consent prior to starting the experiment, the procedures of which were approved by the Ethical Committee of the Budapest University of Technology and Economics. The data of three participants was discarded because of excessively noisy EEG recordings (less than 50% of the segments were clean, mean $\pm$ SEM for retained subjects: 77 $\pm$ 3%), and one subject was discarded because of lack of response in more than 15% of the trials (mean $\pm$ SEM for retained subjects: 3 $\pm$ 0.7%). So, the data from 16 subjects was analyzed (9 female, mean $\pm$ SEM age: 21.4 $\pm$ 0.3 years).

### 3.2.2 Stimuli and procedure

In the experiment, participants viewed short sequences of word, face and composite word-face stimuli while performing a one-back task (Fig. 3.1).

Face images were front-view grayscale photographs of 13 male and 13 female faces. The  $2^\circ \times 2^\circ$  square images were cropped with a circular mask with a diameter of  $2^\circ$  to eliminate external facial features and equated for contrast and luminance. Word stimuli were 26 Hungarian nouns (from two semantic categories: 13 fruits and 13 animals) rendered in black using a 12 point Arial font (maximal vertical extent:  $0.4^\circ$ ). Words were 5-7 characters long, corresponding to widths falling between 0.9 to 1.5 degrees of visual angle. From the above, composite stimuli were created by overlaying words centrally on face images (Fig. 3.1, right). All of the stimuli were presented at the center of the screen, slightly ( $0.2^\circ$ ) above which a blue fixation disc with a diameter of  $0.1^\circ$  was always present. The background was mid-grey, matching the mean luminance of face images.



**Figure 3.1 Schematic of the four trial types** corresponding to the four experimental conditions. Each trial consisted of a Cue (at the bottom) and a sequence of six stimuli (top). These trial types followed each other in randomized order during the experiment.

SOA: Stimulus Onset Asynchrony. ISI: Interstimulus Interval.

Trials started with a cue displayed for 683 ms, which was either of the strings 'xxx' or ':-)'' rendered in the format and position described above. The cue was followed by a blank interval of 1 s, when

only the fixation disc was present. Then, six stimuli of one type (word, face or composite) were presented consecutively. Each stimulus was displayed for 683 ms, immediately followed by the next one – there was no interstimulus interval. The intertrial interval, from the offset of the last stimulus to the onset of the next cue, was 2 seconds long.

Subjects had to deploy their attention and perform the task with respect to either words or faces, as indicated by the cue at the beginning of each trial – ‘xxx’ and ‘:-)’ referring to words and faces, respectively. For each subject, 240 attend-word and 240 attend-face trials were presented in randomized order. In both cases, for a 50% random subset of the trials (120 for attend-word and 120 for attend-face), compound stimuli were used, the non-attended stimulus serving as a distractor. In the remaining trials, only the relevant stimulus was displayed. Thus, there were four experimental conditions (Fig. 3.1): attend-word distractor-absent (*word only*), attend-word distractor-present (*word-face*), attend-face distractor-absent (*face only*) and attend-face distractor-present (*face-word*).

In one third of trials, the sub-category (male vs. female faces, animal vs. fruit words) was alternating throughout the stimulus sequence. In the remaining two thirds of trials, one or two one-back repetitions of stimulus sub-category occurred. The task of the participants was to count these one-back events and indicate how much of them they saw with a three-button mouse after each trial, during the intertrial interval. (For example, a ‘male-female-male-female-male-female’ sequence would count as no (zero) one-back repetition, ‘fruit-animal-fruit-fruit-animal-fruit’ would count as one repetition, and so on.) This task was designed to sustain the attentional state of subjects throughout the whole trial as much as possible.

Each subject completed 480 trials in 10 runs, leading to 120 trials per condition. Stimuli were presented on a 26” LG LCD monitor at a refresh rate of 60Hz, viewing distance was 56 cm. Stimulus presentation and subject response registration was implemented in MATLAB 7.1 (The Mathworks Inc., Natick, MA) using PsychToolbox 3 [101, 102].

### **3.2.3 Electrophysiological data acquisition and processing**

EEG was acquired using BrainAmp MR amplifiers and an actiCAP system with 62 active electrodes (Brain Products, Munich, Germany) mounted on an elastic cap according to the 10/10 system. An additional lower vertical EOG electrode was placed below the right eye. All channels were

referenced to the right mastoid (TP10), the ground was at electrode position AFz. Impedances were kept below 20 k $\Omega$ . The sampling rate of EEG was 500 Hz.

Preprocessing and data analysis was done in Brain Vision Analyzer (Brain Products, Munich, Germany) and MATLAB (The Mathworks Inc., Natick, MA) using functions from EEGLAB [103] and custom scripts. The signal was bandpass filtered (Butterworth zero-phase filter in Analyzer, 0.1Hz-70Hz, 24 dB/octave). Trial segments containing artefacts were marked using amplitude ([-100 100]  $\mu$ V), amplitude difference (160  $\mu$ V) and voltage step thresholds (20  $\mu$ V per sample) and by visual inspection; these segments were not used in further analyses. Surface Laplacian approximation of the scalp current density (SCD) was calculated using the CSD Toolbox [71, 72] (spline flexibility  $m=4$ ,  $\lambda=10^{-5}$ ). SCD-transformed data is reference-free, and is less affected by volume conduction [68]. Modulations of alpha oscillations was of particular interest in this study, so whole-trial segments were wavelet transformed using a complex Morlet wavelet (MATLAB `cwt` function, 'cmor1-1' wavelet) with center frequencies 8 to 12 Hz with 0.5 Hz steps. Afterwards, mean log power time series were computed for segments time-locked to each stimulus onset, averaging over trials and frequency bins.

### 3.2.4 Statistical analysis

To investigate the modulation of anticipatory alpha oscillations during the stimulus train, mean prestimulus alpha power was extracted from [-50 -200] ms time windows before each stimulus onset from S2 to S6. This window was chosen to minimize the influence of both the previous and the next evoked response, focusing on induced modulations. The main effects of category (attend word vs. attend face), distractor (absent vs. present) and their interaction were first assessed over the whole scalp using cluster-based permutation tests (cluster-forming threshold  $p=0.05$ , 999 permutations, adjacent stimulus windows and electrodes in less than 5 cm distance were considered neighbors, hypothesis tests were two-tailed) using functions implemented in FieldTrip [74, 75]. For the category  $\times$  distractor interaction, there were no significant clusters (all  $p>0.1$ ), therefore interaction effects between the main effects were not considered in further analyses. To assess anticipatory attentional modulations before S1 a similar permutation test for the category effect involving only the spatial dimension (spanning across recording channels) was performed on alpha power averaged on a longer pre-S1 time window ([-100 -600] ms before S1 onset).

To assess the hemispheric lateralization and temporal dynamics of the two main effects, separate follow-up ANOVAs (one for the category effect, one for the distractor effects) were conducted. In these analyses, the factor ‘sequence’ represented position in the stimulus sequence (time windows from pre-S2 to pre-S6), and ‘hemisphere’ was used to capture lateralization effects. The interactions of these two factors with the current main effect of interest (category or distractor) were also assessed, but not the main effects themselves, as they were already quantified in the whole-scalp statistics stage. The electrode pools of interest for this analysis were defined using the whole-scalp results of the two main effects in the following way. First, electrodes where significant differences were consistently present across the whole temporal extent of the cluster (S2-6 for the category effect, S2-4 for the distractor effect, see Results) were selected. Second, symmetric hemispheric electrode pools were formed, assuring that the pair of each electrode is included in the contralateral pool. (For example, on PO3 the category effect was always sub-threshold, but it was added to the left pool for the category effect as a pair of PO4.) Alpha power averaged within these pools for all the 5 pre-stimulus time windows during the sequence provided the input of the two follow-up ANOVAs. The rationale behind this analysis logic and its validity is detailed in the Methods section of the Introduction chapter (Section 2.4)

Task performance was evaluated by comparing accuracies (percentage of correct responses) in all four conditions in a repeated measures ANOVA with factors ‘category’ and ‘distractor’.

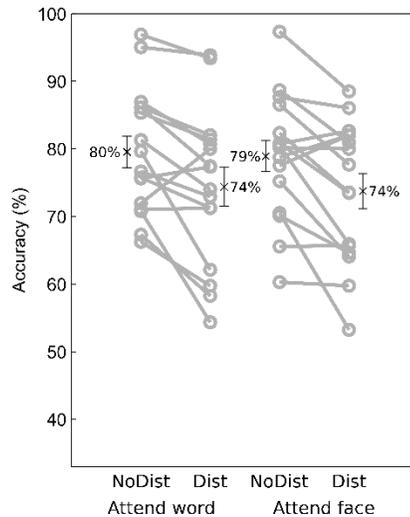
Post-hoc comparisons were conducted using Tukey’s Honestly Significant Differences procedure. The Huynh-Feldt correction for violation of sphericity was applied where necessary (indicated by  $\epsilon_{H-F}$ ; for the F-tests, uncorrected degrees of freedom are reported).

### **3.2.5 Eye tracking data acquisition and analysis**

Eye movements were recorded using IView X Hi-Speed (SensoMotoric Instruments) at a sampling rate of 240 Hz. Data was cleaned of blinks and detrended, then segmented as described in the ERP processing section. To assess fixation stability, the root mean square deviation from the fixation dot across trials was calculated for each time point and then averaged within each [-200 100] ms peristimulus interval for each condition. Then, these RMS fixation stability values were compared in a repeated measures ANOVA with factors ‘category’, ‘distractor’ and ‘sequence’.

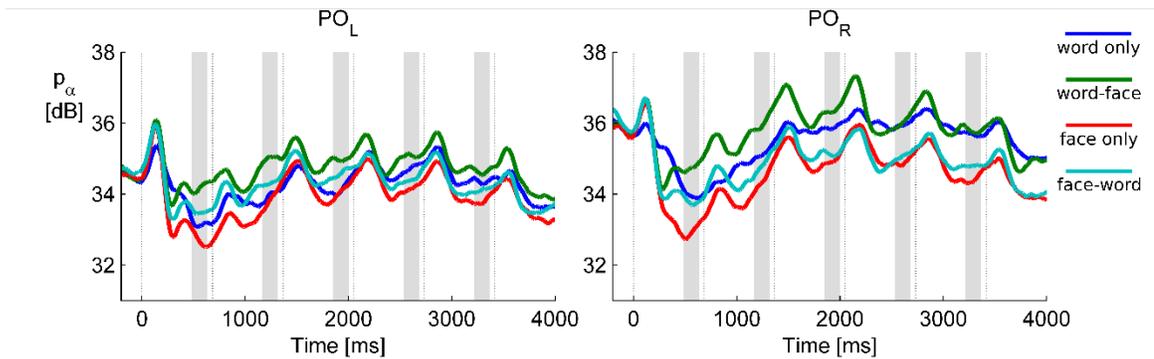
## 3.3 Results

### 3.3.1 Behavior



**Figure 3.2 Behavioral results.** Accuracies in the 4 conditions. Gray circles are individual subjects, crosses and error bars mark condition mean (see also text labels) and SEM, respectively.

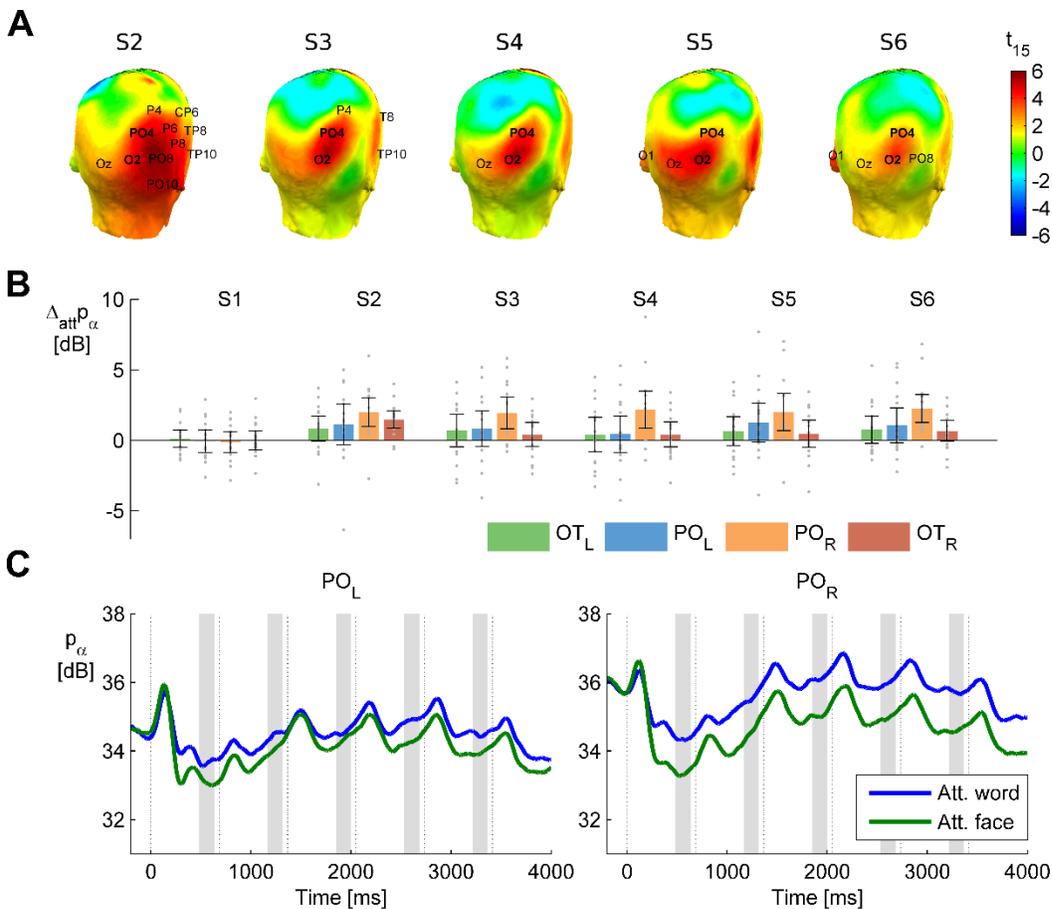
The behavioral results (see also Fig. 3.2) showed that subjects' accuracy was similar in the attend-face ( $76 \pm 2\%$ , mean  $\pm$  SEM) and attend-word ( $77 \pm 2\%$ ) conditions (main effect of category:  $F(1, 15) = 0.11$ ,  $p = 0.74$ ). The presence of distractors had a significant effect on performance both when faces and words were attended (distractor absent:  $79 \pm 2\%$ ; distractor present:  $74 \pm 3\%$ ; main effect of distractor:  $F(1, 15) = 20.43$ ,  $p = 0.00041$ ; category  $\times$  distractor interaction:  $F(1, 15) = 0.00005$ ,  $p = 0.99$ ). These results imply that visual category related attentional effects in the EEG results cannot be accounted for by differences in attentional load or overall task difficulty between the conditions when faces and words were attended.



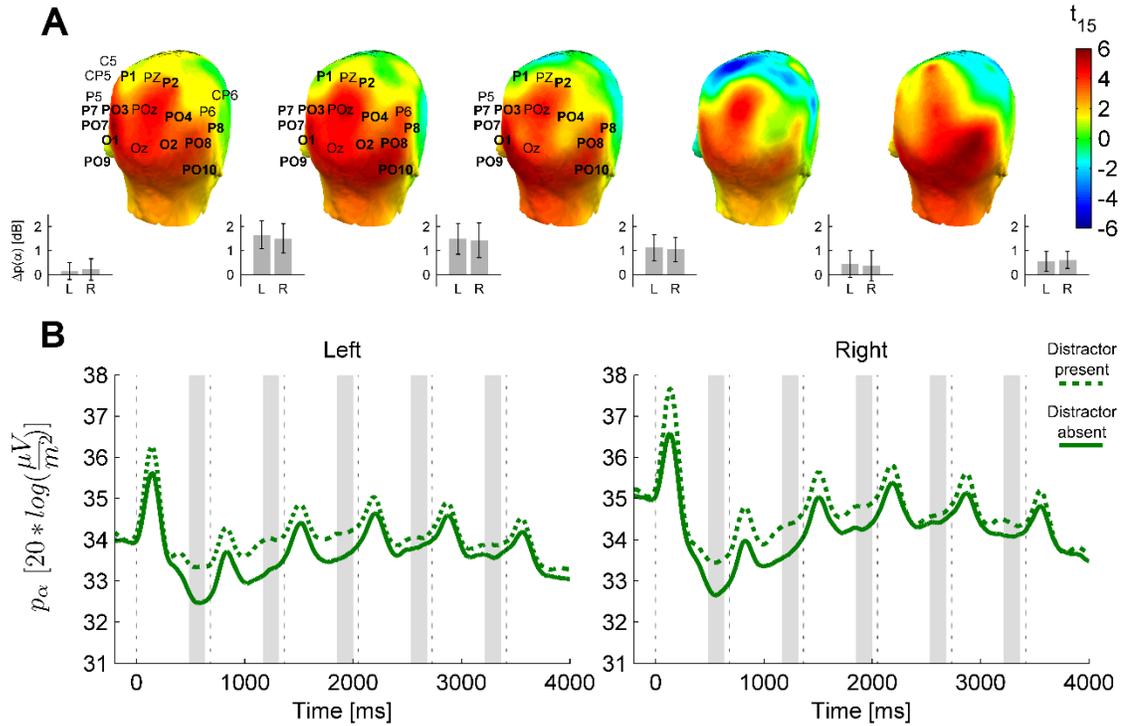
**Figure 3.3. Grand average alpha power over the left (PO<sub>L</sub>: O1 and PO3) and right (PO<sub>R</sub>: O2 and PO3) parieto-occipital cluster.** The temporal evolution of alpha power in all four conditions is shown separately. Thin vertical lines are at the times of stimulus onsets (S1 to S6), shaded areas depict pre-stimulus time windows of interest where anticipatory activity was assessed.

### 3.3.2 Electrophysiology

The results revealed that anticipatory alpha activity measured on parieto-occipital electrodes was modulated depending on whether participants were cued to attend to faces or words, regardless of the presence of distractors (Figs. 3.3, 3.4, 3.5). Alpha power over the parieto-occipital cortex (see topography on Fig 3.4A) was significantly higher when words were attended than when faces were task-relevant (cluster-level  $p=0.02$ ). Importantly, this object category based attentional modulation of alpha power showed a hemispheric lateralization: attending to words as compared to faces led to significantly larger increase in alpha activity over the right than the left hemisphere (category  $\times$  hemisphere interaction  $F(1,15)=6.04$ ;  $p=0.027$ ).



**Figure 3.4. The main effect of attention to object category on alpha power.** T-values (**A**) and raw difference values (**B**) calculated as attend word minus attend face, averaging over distractor absent and distractor present. Positive values indicate larger alpha power to words than faces. Alpha power time series from the PO pools bilaterally for attend-word and attend-face, averaging over distractor conditions are displayed on (**C**) with time windows and stimulus onset marked the same way as on Fig. 3.3. | (**A**) Results of the cluster-based permutation test on the attentional modulation of anticipatory alpha activity in the prestimulus time windows (see shaded areas on panel C) before S2-S6. On the head plots, the color scale shows the results of the parametric t-test. The permutation test yielded a significant spatio-temporal cluster – electrodes that are in this cluster in a given pre-stimulus window are marked on the respective head plots. The names of the two electrodes where the effect was consistently significant across time windows (O2 and PO4) are in bold. These and their contralateral pairs (O1 and PO3) were pooled and used in further analysis. (**B**) Means (bars) and 95% confidence intervals (error bars) of the attentional difference at the electrode pools selected for further analysis (PO<sub>L</sub>: O1, PO3 and PO<sub>R</sub>: O2, PO4) and two more lateral electrode pools (OT<sub>L</sub>: PO7, P7, PO9 and OT<sub>R</sub>: PO8, P8, PO10). Grey dots mark individual difference scores.



**Figure 3.5. The distractor effect on alpha power. (A)** Head plots for t-values of the distractor modulation (distractor present minus absent) of anticipatory alpha activity in prestimulus time windows before S2 to S6. As on Fig. 3.4, electrodes marked are in the cluster of significant difference yielded by the permutation test, and bold electrode names are the ones consistently present in the cluster throughout its temporal extent (pre-S2 to pre-S4), which are used in further analysis. ‘Left’ (L) and ‘Right’ (R) on this figure refer to pools of these electrodes from either hemisphere (Left: P7, PO7, PO9, PO3, O1, P1; Right: P8, PO8, PO10, PO4, O2, P2). Insets on the lower right side of each head plot depict means and 95% confidence intervals of the distractor-related difference in the Left and Right pools; on the left of the figure, this is also shown for the pre-S1 interval. **(B)** Temporal evolution of alpha activity in the presence and absence of distractors in the Left and Right pool selected from the distractor-effect cluster.

The presence of a distractor stimulus also influenced oscillatory power in the alpha band (distractor present > absent, cluster-level  $p=0.002$ , see Fig. 3.5), but this modulation was distinct from the category effect in several ways. First, no interaction was found between category and distractor ( $p>0.1$  for all clusters). Second, the distractor effect had a more widespread topography, covering most of the posterior temporal, centro-parietal and occipital cortex (see Fig 3.5A). Third, the distractor effect, in contrast to the category effect, weakened and disappeared towards the end of the stimulus sequence (distractor  $\times$  sequence interaction:  $F(4,60)=5.89$ ,  $p=0.0028$ ,  $\varepsilon_{H-F}=0.66$ ;  $p_{\text{Tukey}}<0.0005$  for the distractor effect in pre-S2 to pre-S4,  $p_{\text{Tukey}}>0.1$  for pre-S5 and pre-S6).

Alpha power started to grow after the pre-S2 period and levelled off around the time of S3-S4 in all conditions (the trend is visible on Figs. 3.3, 3.4 and 3.5; main effect of sequence:  $F(4,60)=8.17$ ,  $p=0.001$ ,  $\varepsilon_{H-F}=0.53$  for the electrode pools defined by the distractor effect,  $F(4,60)=7.96$ ,  $p=0.0022$ ,  $\varepsilon_{H-F}=0.47$  for the electrode pools defined by the category effect; pre-S2 differing from pre-S3-6  $p_{\text{Tukey}}<0.02$ ,  $p_{\text{Tukey}}>0.5$  for the remaining comparisons), which was due to the fact that alpha desynchronization after S1 was prominent but it gradually became weaker or completely disappeared in the case of subsequent stimuli. This modulation of the strength of alpha desynchronization was more pronounced over the right hemisphere (sequence  $\times$  hemisphere interaction:  $F(4,60)=3.81$ ,  $p=0.036$ ,  $\varepsilon_{H-F}=0.48$  in the distractor-effect electrode pools,  $F(4,60)=2.48$ ,  $p=0.087$ ,  $\varepsilon_{H-F}=0.61$  for the category-effect electrode pools; pre-S3 vs. pre-S4-6  $p_{\text{Tukey}}\geq 0.1$  over the left hemisphere, but  $p_{\text{Tukey}}<0.001$  for pre-S3 vs pre-S4-5 over the right hemisphere).

### 3.3.3 Fixation stability

To assess fixation stability, we measured the subjects' gaze position during the experiment. Most importantly, 77% of the recorded gaze position data was within a circle with a radius of  $0.5^\circ$  – subjects fixated properly at the stimulus. Mean deviation from the fixation dot was  $0.35^\circ$ , and did not differ across conditions or stimuli (for all effects,  $p > 0.05$ ).

## 3.4 Discussion

Our results revealed that during sequential presentation of word and face stimuli, the power of parieto-occipital alpha oscillations increased when attending to words, as compared to when faces were attended. This effect was lateralized to the right hemisphere and persisted throughout the stimulus sequence over the parieto-occipital cortex. The presence of a distractor, as assessed by comparing the compound and single stimulus conditions, also modulated alpha oscillations, but did not interact with the object category-based attentional modulation and had distinct temporal and topographical characteristics.

These results show that visual cortical alpha oscillations are invoked during object-based attentional selection: when words were attended, alpha power increased in the right hemisphere, which is specialized for the processing of task-irrelevant face stimuli [18]. Thus, these results suggest that object-based attentional suppression of task-irrelevant information might involve alpha-based inhibitory processes, analogously to that found in the case of spatial [53–55, 94, 95] and feature-based attention [56]. Although one has to be cautious when interpreting topographic features of EEG results because of the limited spatial resolution of the method [68], it is notable that the topography of the attentional effect in this study, especially after S2, appears to be similar to spatial attentional modulations described in the literature [55, 94, 95]. This might suggest that the object-based attentional modulation of alpha oscillations might originate from earlier visual areas instead of higher-level, object-selective areas of the ventral temporal cortex. This is in line with extensive previous evidence that object-based attentional effects propagate to early visual areas [98, 99, 104]. Furthermore, according to the biased competition theory, the strength of inhibition exerted by attention at a given level of the visual hierarchy should depend on the local degree of competition for representation between the stimuli [14]. In the case of spatially overlapping objects – like the stimuli in our study – competition is expected to be strong in retinotopically organized early visual cortex, which renders it a likely target of attentional inhibition.

Furthermore, previous studies [105, 106] found that in macaques performing an attentional task, alpha activity in the inferior temporal cortex (IT) and early visual cortex have distinct functional and physiological properties. First, alpha activity in the macaque IT, as opposed to V2/V4, has a closed-field laminar source configuration, resulting in a weaker signal on the scalp [105]. Second, also in contrast to V2/V4, increased alpha power in the IT had facilitatory effects both on neural activity (multiunit activity and gamma power) and visual stimulus processing [105, 106]. They also

speculated that the laminar organization and information flow found in the IT might be well-suited for feedback to earlier visual areas [105]. According to these data, it is plausible to assume that the alpha-band effects found in this study indeed reflect top-down modulations in the early visual cortex.

So, our results seem consistent with object-based attention operating early in the visual hierarchy, orchestrated by inhibitory feedback signals originating from higher-level, category-selective areas. The hemispheric asymmetry in the neural processing of words and faces in category-specific temporal areas [18, 107] also affects earlier visual areas, resulting in an inherent category-specific visuo-spatial bias [the right and left visual field advantage for words and faces, respectively; see 108–110] that can possibly be strengthened according to attentional demands. Following this logic, anticipatory alpha power over the left hemisphere might be expected to be larger when attending to faces, as the processing of distractor words in the left hemisphere ought to be inhibited at some level of the visual hierarchy. This analogous modulation would have provided stronger evidence for the hypotheses based on the lateralized processing of word and face stimuli, but our expectations were not met by the results in this respect. The fact that the most stable attentional effect was found to be close to the midline rather than on more temporal aspects of the scalp also makes it less certain that scalp-level laterality actually reflects lateralized source activity. Also, besides results confirming the lateralized processing of faces and words, several studies rather show bilateral activations, point to the dependence of lateralization on other factors, or do not explicitly test for lateralization at all. Thus, while the results provide some support for the lateralization-based interpretation, it is also important not to disregard these ambiguities and consider the facets of the findings that are not dependent on assumed hemispheric dominance patterns. For example, given that faces are known to be intrinsically salient, highly effective distractors that gravitate bottom-up attention [111, 112], they thus might require more top-down inhibition than words, which could manifest as stronger alpha activity. Faces also consist of more complex features and covered a larger area in our stimulus display than words – these could also contribute to the greater demands on inhibitory attentional mechanisms when faces needed to be ignored.

Using stimulus sequences instead of single stimuli we could characterize the effect of sustained object-based attentional selection on anticipatory alpha oscillations. We found no modulation in anticipation of the first stimulus, possibly due to our stimuli being long enough to allow post-onset orienting, exerting no time pressure that would require deployment of attention prior to the first stimulus. After the onset of the stimulus train, the modulation appeared following the early evoked

components, during the alpha event-related desynchronization (ERD), and persisted throughout the whole trial. This result is compatible with an alpha modulation with similar temporal dynamics during sustained spatial attention to rapid serial visual presentation of letter sequences [55]. Interestingly, independently of this persistent attentional difference, alpha power gradually increased during the course of the trial – it started to increase after the ERD for S1, and the subsequent ERDs were smaller and smaller, leading to alpha power levelling off towards the end of the sequence. In terms of the inhibitory account of alpha oscillations [8, 12, 13] – interpreting the ERD as a release from tonic baseline inhibition [9, 50] – this means that less and less excitability is required for processing of stimuli that arrive after others, perhaps up to a certain limit corresponding to the plateau that alpha power reaches during the trial. Interpreted in the predictive coding framework [28, 29], the cortical state established after the first stimulus enables more precise top-down sensory predictions to arise, due to which only the most relevant neuronal subpopulations become activated for subsequent stimuli. Theories about the function of alpha oscillations exactly reflect this kind of inhibition: as alpha amplitude increases, the window of opportunity during which excitatory inputs are effective becomes smaller and smaller, allowing only the neurons with the most strong and most synchronous drive to be active [8].

Interestingly, the attend-word vs. attend-face difference was very similar when distractors were present and when distractors were absent. Although there was a non-significant trend of stronger modulation in the case when the unattended stimulus was also displayed, it appears that the deployment of attention to the attended stimulus is assured independently of the presence of a distractor, but the same process also leads to a potential distractor to be effectively filtered out. Distractors also affected alpha power, but (as the lack of interaction implies) this modulation was additive to the attentional effect, had broader and clearly distinct topography, and disappeared towards the end of the trial. Put differently, towards the end of the trial, alpha amplitudes converge (as the distractor effect disappears) to a level solely determined by the attended stimulus. Although we focused on the – traditionally more dominant – inhibitory facet of oscillatory attentional gating, this result puts the spotlight on the notion that alpha oscillations actively contribute to object representations by facilitating and temporally coordinating the activity of task-relevant neural subpopulations. In this respect, category-dependent alpha power can reflect some intrinsic parameter related to the processing of the stimulus, for example the optimal levels of excitation/inhibition balance which might depend on the attended stimulus.

To conclude, our results provide the first evidence that object-based attention modulates visual cortical alpha oscillations: attending to a word in a compound, foveally displayed word-face image boosted parieto-occipital alpha oscillations over the right hemisphere, consistent with attentional gating in early visual areas.

# 4 Cortical mechanisms of visual expertise in word recognition

## 4.1 Introduction

Reading requires the sophisticated coordination of different perceptual processes with cognitive and motor control. One basic component of reading is the brain's general capability of fast and effective recognition of common visual objects like faces, that through reading acquisition becomes adapted to recognizing printed words. Reading skills develop gradually from childhood to adolescence and acquiring reading expertise has an overall effect on visual information processing [20, 113]. Previous research investigating word reading revealed that neural coding of letters and words is subserved by ventral occipito-temporal visual cortical regions [31, 32, 114], primarily the letter-form and word-form areas, where letter-form and word-form selective neural responses emerge starting from around 150 ms and 220 ms after stimulus presentation, respectively [115]. Furthermore, it was also shown that selectivity of both functional magnetic resonance imaging (fMRI) responses in the visual word-form area [20, 113] and early event-related potential (ERP) components [116–118] to written letter and word stimuli increases in skilled readers as compared to beginners or individuals with reading deficits.

Most previous studies aiming at uncovering the neural substrates of orthographic processing usually took the approach of comparing neural responses to words with those evoked by pseudowords or other objects [31, 32, 114, 115]. The drawback of this approach is that in the results obtained from the comparison of words and non-word stimuli, neural processes subserving skilled orthographic processing would be confounded by the visual cortical effects of overall differences in sensory-cognitive processes and task demands. A possible alternative approach is to manipulate the second-order configural relations [119] within written words by changing spatial distances among the letters. Altering inter-letter spacing is known to affect orthographic processing and reading speed. However, ultimately, after the visual processing stage (the length of which might vary), words in altered formats should trigger the same high-level, lexico-semantic processes as words in usual format [120–122]. Previous research on object vision has shown that perceptual expertise makes visual processing of the highly trained object category more sensitive to its configural information [119, 123–125] and that such expertise-related increase in sensitivity for configural properties was

reflected in the ERP component associated with object-selective visual cortical processing [126–128]. In accordance with this, behavioral studies showed that skilled readers are tuned to the standard spacing [129] and increasing letter spacing to more than 1.5 times the normal spacing leads to reduced reading speed in skilled readers [121, 125, 130]. However, the same manipulation has no effect or even increases reading efficiency in children [131] and dyslexics [130], respectively. Based on this, we hypothesized that the visual components of orthographic processing might be revealed by contrasting EEG activity during reading words with normal letter spacing to that with altered spacing.

Altering letter spacing is expected to affect both the early parallel extraction of letters and computation of bigrams as well as the later stage of word-form processing, and thus could allow us to investigate the neural signatures of these two prominent stages of orthographic processing. In particular, based on previous findings showing that object-selective visual cortical responses are enhanced to objects of expertise [20, 126, 127, 131–134], we predicted that when reading words with altered letter spacing, the neural responses associated with letter- and word-form-related processing will be diminished when compared to those for words with normal letter spacing. To test these assumptions in the current study we recorded EEG in human participants with typical reading skills, and contrasted EEG activity during reading words with normal letter spacing to that with increased and reduced spacing. We will refer to these results as expertise-driven configural effects, since they reflect those neural processes of visual information processing which become selective for normal letter spacing with expertise and will be disturbed independently of whether spacing is increased or decreased, i.e. when configural properties of the written text are modified. In addition, letter spacing also affects the reciprocal interference – crowding – among letters located in close proximity [120, 135]: overall visual perceptual processing load will be increased with enhanced crowding as a result of decreased letter spacing. Therefore, we identified the neural processes that are associated with the modulation of the overall visual processing load and dissociated them from those involved in expert orthographic processing. We will refer to these results as visual processing load effects.

In the research project that this work is part of, we examined the neural correlates of visual expertise during conventional experimental conditions with controlled stimulus presentation and fixation, and also during natural reading [J2]. The latter, novel approach is important because natural reading is essentially an active sensory-motor process [136–138] where visual sampling of the orthographic information is subserved by consecutive saccadic eye movements, but only very few studies

attempted to characterize visual processing under natural viewing conditions, primarily due to the technical and analytical challenges posed by artefacts and the complex dynamics of the signal due to the self-imposed visual sampling [139–141]. The short description of the design and findings of the natural reading experiment can be found in Box 4.1.

The present work focuses on results from the fixed-viewing experiment. First, it will be shown that visual expertise-related modulations induced by the letter spacing manipulation are mirrored in event-related potentials in a manner that is compatible with results observed during natural reading, co-validating the results obtained with the novel methodology. Second, the role of visual cortical alpha oscillations in orthographic expertise will also be investigated. This provides complementary information to fixed-view ERPs and fixation related potentials (also called fixation onset-related EEG activity or FOREA) results, as ERP is only sensitive to activity that is phase-locked to stimulus onset, and analytic methods for oscillatory activity during natural reading are still under development, for which these results can also provide important information.

Alpha oscillations are well-known to reflect changes in neuronal excitability in early visual areas and visuospatial attentional modulations in occipito-parietal cortex [59, 105, 106, 142]. Spatial attentional mechanisms are known to be important in resolving the challenge posed to the visual system by stimuli with altered configuration [39], and measuring alpha desynchronization as an index of visual cortical processing intensity can also inform us about the increased processing demands of words with modified configural properties. More recently, alpha-beta oscillations have also emerged as an important carrier of top-down object knowledge information in the visual hierarchy. Building on this, we hypothesized that parieto-occipital alpha power will be larger for words presented in the usual format as compared to either decreased-spacing and increased-spacing formats, i.e., we will find an expertise-driven configural effect as defined above. Besides this, we expect visual processing load to affect earlier visual alpha responses (potentially including evoked effects) around the occipital pole.

**Box 4.1 – The natural reading experiment**

In the paper entitled 'Visual processing during natural reading' [J2], we studied how early EEG responses were influenced by letter spacing in a traditional, fixed-viewing experiment and also during natural reading. The methods of the two experiments were conceived so that the results would be as comparable as possible. In the dissertation, results from the fixed-viewing experiment are presented, and their relation to the natural viewing results will also be discussed. Here, I shortly describe the natural reading experiment (for all the details, see [J2]) to aid the understanding of these connections.

In the natural reading experiment, 24 undergraduate students (11 female) read – with freely moving eyes – 32 short text excerpts presented line-by-line, centered horizontally on the screen. Switching to the next line was controlled by the participant by button press. Each line was presented with one of the 3 spacing conditions (minimal, normal, double), in random order. After each paragraph a single sentence test statement was presented and participants had to report with a mouse button press whether it was true or false. Other stimulation parameters, recording instrumentation and settings were the same as in the fixed-viewing experiment, except for more frequent recalibration of the eye tracker.

Eye tracking data recorded during the whole experiment was analyzed to compare eye movement parameters across conditions. For EEG analysis, 1 s long artefact-free eye tracking data segments were selected. In these segments, saccades and fixations were detected using an adaptive algorithm, and these data were used in a novel ICA-based procedure for eye-movement artifact elimination from the concurrent EEG segments. Based on the detected fixation onsets, fixation-triggered segments („trials”) were extracted from the artefact free, SCD-transformed data. These segments were used in a single-trial hierarchical linear model that aimed at detecting expertise-driven configural (EDC) and visual processing load (VPL) effects while controlling for potential eye movement-related confounding variables.

Expertise-driven configural effects were present in fixation onset-related activity (FOREA) in three consecutive time windows (120–175 ms, 230–265 ms, 345–380 ms after fixation onset, see Fig 4.2B) and the magnitude of FOREA effects in the two later time intervals showed a

close association with the participants' reading speed: FOREA effects were larger in fast than in slow readers. Furthermore, these expertise-driven configural effects were clearly dissociable from the FOREA signatures of visual perceptual processes engaged to handle the increased crowding (155–220 ms) as a result of decreasing letter spacing: these were reflected in right hemisphere lateralized occipito-temporal and parietal increase of EEG activity between 155–220 ms after fixation onset.

Thus, the results revealed that orthographic processing during natural reading involves sequential stages of information processing with remarkably similar temporal dynamics to those proposed by models of visual word processing with fixed gaze.

## 4.2 Methods

### 4.2.1 Participants

Nineteen healthy right-handed young adults participated in this study. Two of them had insufficient number of artefact-free data segments and accordingly only 17 subjects (11 female; mean±SD age: 24±2.10 years) entered statistical analysis. All of them were native speakers of Hungarian, reported having typical reading skills and had normal or corrected-to-normal vision. None of them had any history of neurological or psychiatric diseases. The experiment was approved by the local ethics committee of the Department of Cognitive Science, Budapest University of Technology and all methods were carried out in accordance with the approved guidelines. Participants gave informed consent before the beginning of the measurements.

### 4.2.2 Visual stimuli and experimental procedure

The stimuli were 4 and 5 letter Hungarian nouns from two semantic categories (living and non-living), presented centrally on a 26" liquid-crystal display using a monospace font (Courier New). Random flanker words were also presented on both sides of the central word, to mimic the visual context during natural reading. Three different levels of letter spacing were used (Fig. 3.1): minimal spacing (MS; 0.707 times the normal spacing); normal spacing (NS; the distance between consecutive characters is 1.16 times the width of the lowercase x); double spacing (DS; 2 times the NS). Normal words subtended approximately 2° in the horizontal dimension. A small blue fixation dot was always present in the center of the screen. The background was white. The subjects were seated in a dimly lit room, their head was supported by a chin rest in a distance of 56 cm from the screen. The experiments were conducted in 6 runs, each lasting cca. 8 minutes, with some minutes of rest in between. Within runs, letter spacing of the words was constant. Condition order was counterbalanced across subjects. In half of the trials, words were presented without flanking words – these trials are not included in this study.

k ö z é r t   f o l t   z a k ó   á l o m   d e l f i n  
 kotta vakond gólya font lepke pajta ganaj épület korcs  
 delfin tojás pata kakadu rend csipa hiúz kakadu koszt gránit katica vipera  
 ▲

**Figure 4.1. Sample stimuli with double (top), normal (middle) and minimal (bottom) letter spacing.** In each trial, one stimulus line was displayed for 800 ms. The words at the position marked with the blue arrow are the target, the category of which (living/non-living) had to be indicated with button press after stimulus offset. The words on the left and right are irrelevant flankers.

In each trial, a word was presented for 800 milliseconds. Subjects were told to respond after stimulus offset with a mouse button press, indicating which category the word (living or non-living) they had seen belonged to. The response interval was maximized in 2 seconds. The length of the inter-trial-interval (ITI, starting from the time of the response or from the end of the response interval) was chosen from a uniform probability distribution between 1250 and 1750 milliseconds. After every third trial an additional 650 ms of pause was added with the fixation dot turning red, and the subjects were asked to try to blink only during this period. The frequency and length of these blink windows were sometimes adjusted to the given subject's propensity to blink. Stimulus presentation and subject response registration was implemented in MATLAB R2008a (The MathWorks Inc., Natick, MA, USA) using PsychToolbox version 3 1–3.

### 4.2.3 Recordings

EEG was acquired using 62 electrodes (Brain Products actiCAP; amplifier: BrainAmp Standard; Brain Products GmbH, Munich, Germany) mounted on an elastic cap according to the 10-10 system. Electrooculogram (EOG) activity was monitored by 3 EEG channels and an additional electrode that was placed below the right eye. The sampling rate was 500 Hz. Eye movements were recorded from participants' left eye using iView X™ Hi-Speed 1250 system (SensoMotoric Instruments GmbH, Teltow, Germany) at a sampling rate of 1250 Hz.

## 4.2.4 Data analysis

Pre-processing of the EEG signal was done in Brain Vision Analyzer (Brain Products GmbH, Munich, Germany). The signal was band-pass filtered (Butterworth zero-phase filter, 0.5-35 Hz, 12 dB/octave) and segmented, with 500 ms preceding and 1200 ms following stimulus onset. Segments containing artefacts were marked using amplitude ( $[-50\ 50]$   $\mu\text{V}$  for EOG,  $[-80\ 80]$   $\mu\text{V}$  for EEG channels), amplitude difference (80  $\mu\text{V}$  for EOG, 120  $\mu\text{V}$  for EEG channels) and voltage step thresholds (10  $\mu\text{V}$  per sample) and by visual inspection; these segments were not used in further analyses. Data were imported to MATLAB, and surface Laplacian approximations of the scalp current density were calculated using the CSD Toolbox [71, 72] (unit sphere radius,  $m=4$ ,  $\lambda=10^{-5}$ , the maximum degree of Legendre polynomials was set to 10).

Analysis of Event-Related Potentials (ERPs) was aimed at testing for effects found in a natural reading experiment (see Box 4.1 and [J2]). Based on group-level results of the natural reading experiment and visual inspection of across-condition aggregated grand average waveform features [80], time ranges of [155 185] ms and [210 270] ms and channels PO9 and PO10 were selected for analysis. First, artefact-free segments were baseline-corrected ( $[-200\ 0]$  ms) and averages for conditions of interest were computed for each subject. EEG amplitudes within the time intervals of interest were averaged and analyzed using repeated measures ANOVA with Tukey's HSD post hoc testing. A two-way ANOVA (factors: spacing with levels MS, NS and DS; electrode with levels PO9 and PO10) was conducted separately for both time windows. Statistical analysis was carried out in STATISTICA (StatSoft Inc., Tulsa, OK, USA). For consistency with the analysis of oscillatory data, planned contrasts for expertise-dependent configural (EDC) and visual processing load (VPL) effects (see below) were tested as well.

Analysis of oscillatory responses to words was aimed at testing for expertise-dependent configural (EDC) and visual processing load (VPL) effects on parieto-occipital alpha power during and following the event-related desynchronization (ERD). For this purpose, single trials were convolved with complex Morlet wavelets at frequencies ranging from 8 to 14 Hz in steps of 1 Hz (MATLAB Wavelet Toolbox, `cwt` function v1.18.4.9, 'cmor' wavelet,  $F_c=1$ ,  $F_b=1$ ). From the complex output ( $c$ ), mean power values ( $p_{s,i}$ ) across trials of each subject and condition ( $s,i$ ) were obtained and converted to decibel scale ( $p_{s,i}=10\cdot\log_{10}(\langle c\cdot c^* \rangle_{s,i})$ ; where  $*$  denotes the complex conjugate and  $\langle \cdot \rangle_{s,i}$  denotes average over trials of condition  $i$  for subject  $s$ ). For statistical analysis, these values were averaged across frequencies (8 to 14 Hz) and electrode pools formed over left and right parieto-

occipital scalp regions (PO<sub>L</sub>: O1, PO3, PO7, P7, P5, P3; PO<sub>R</sub>: O2, PO4, PO8, P8, P6, P4). Baseline power was averaged in the [-150 -400] window and across all conditions and subtracted from the data. To test for lateralization effects, a third derivation channel was formed from the difference of these two pools (PO<sub>R</sub>-PO<sub>L</sub>). To avoid edge artefacts from wavelet convolution, 200 ms from both ends of the time series was discarded. Statistical testing was performed on this three-channel data using the cluster-based permutation method [74] for controlling Type I error rate for multiple comparisons across time and space using the FieldTrip toolbox [75] and custom code. PO<sub>R</sub> and PO<sub>L</sub> were considered to be neighbors during the formation of clusters, while the lateralization channel was considered in isolation. (Note that similar results were obtained using no spatial neighborhood structure during clustering.)

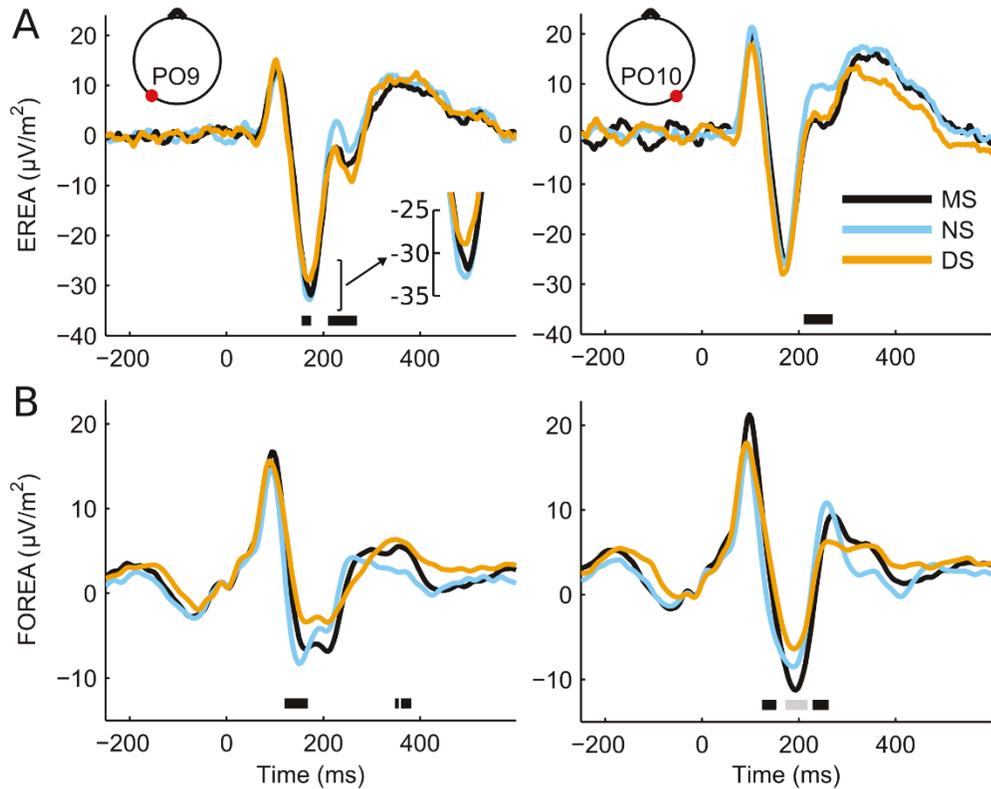
As described in the Introduction section, we were interested in two potential response patterns in the data. First, expertise-driven configural (EDC) effects would appear as the normal-spacing condition differing from both the minimal and double spacing conditions with the same sign, tracking neural processes that are sensitive to departing from the usual format in any direction. Second, visual processing load (VPL) effects reflect neural processes which become more active as spacing decreases/increases, that is, activity depends linearly on spacing. These hypothetical response patterns were transformed to contrast vectors; the null hypothesis that the mean of the linear combination defined by the contrast equals zero (testable with any appropriate one-sample test) is equivalent with the null hypothesis that the given pattern is absent on the group level. The contrast vector for EDC is  $[-0.5 \ 1 \ -0.5] \times [MS \ NS \ DS]$ , and for VPL it is  $[-1 \ 0 \ 1] \times [MS \ NS \ DS]$ . These contrasts tested on the lateralization channel (PO<sub>R</sub>-PO<sub>L</sub>) probe whether the effect is stronger on either hemisphere (EDC  $\times$  hemisphere, VPL  $\times$  hemisphere interactions). The statistic evaluated on each time sample for each channel was a one-sample t-test, clusters were formed with a two-tailed  $\alpha=0.05$  threshold ( $|t(16)|=2.12$ ). The maximum sum cluster statistic was used, the number of permutations was 9999. As the positive and negative effects are compared against separate null distributions, the resulting p-values are multiplied by 2 (`cfg.correcttail='prob'` option in FieldTrip).

## 4.3 Results

### 4.3.1 Event-related potentials

The effects of letter spacing on event-related potentials were investigated bilaterally over the occipito-temporal cortex (on PO9 and PO10) in two time windows ([155 185] ms and [210 270] ms). The results are visualized on Figure 4.2A. In an early time window ranging from 155 ms to 185 ms, we found a significant spacing  $\times$  electrode interaction ( $F(2,32)=7.93$ ,  $p=0.0016$ ). As assessed using Tukey's HSD post hoc tests, this interaction was mainly driven by amplitudes on PO9 in the double spacing condition being less negative than in the normal spacing condition ( $p_{\text{Tukey}}=0.025$ ), with no similar significant difference on PO10 ( $p_{\text{Tukey}}=0.4$ ). In keeping with this, N1 responses were left-lateralized in the normal ( $p_{\text{Tukey}}=0.00014$ ) and minimal spacing ( $p_{\text{Tukey}}=0.00017$ ) conditions, but not in the double-spacing condition ( $p_{\text{Tukey}}=0.8$ ). In terms of planned linear contrasts for EDC and VPL, a marginally significant EDC effect was found on channel PO9 ( $t(16)=-2.14$ ,  $p=0.048$ ), whereas EDC on PO10 and VPL on both electrodes were not significant (all  $p \geq 0.1$ ).

A stronger, significant effect was found in a later 210–270 ms interval: the analysis using a two-way repeated measures ANOVA revealed a significant main effect for letter spacing ( $F(2, 32)=9.29$ ,  $p=0.0006$ ), while the main effect of electrode and the interaction between letter spacing and electrode were not significant ( $F(1, 16)=3.77$ ,  $p=0.07$ ;  $F(2, 32)=1.37$ ,  $p=0.27$ , respectively). This is supported by the results of post hoc testing of letter spacing, showing a significantly higher EEG activity for the NS as compared to MS ( $p_{\text{Tukey}}=0.0025$ ) and DS conditions ( $p_{\text{Tukey}}=0.0019$ ). EEG activity of MS and DS conditions did not differ significantly ( $p_{\text{Tukey}}=0.99$ ). The planned contrast analysis also confirmed the presence of a strong EDC effect ( $t(19)=5.15$ ,  $p=0.00001$ ), while the VPL contrast was, again, non-significant ( $t(19)=-0.087$ ,  $p=0.93$ ).

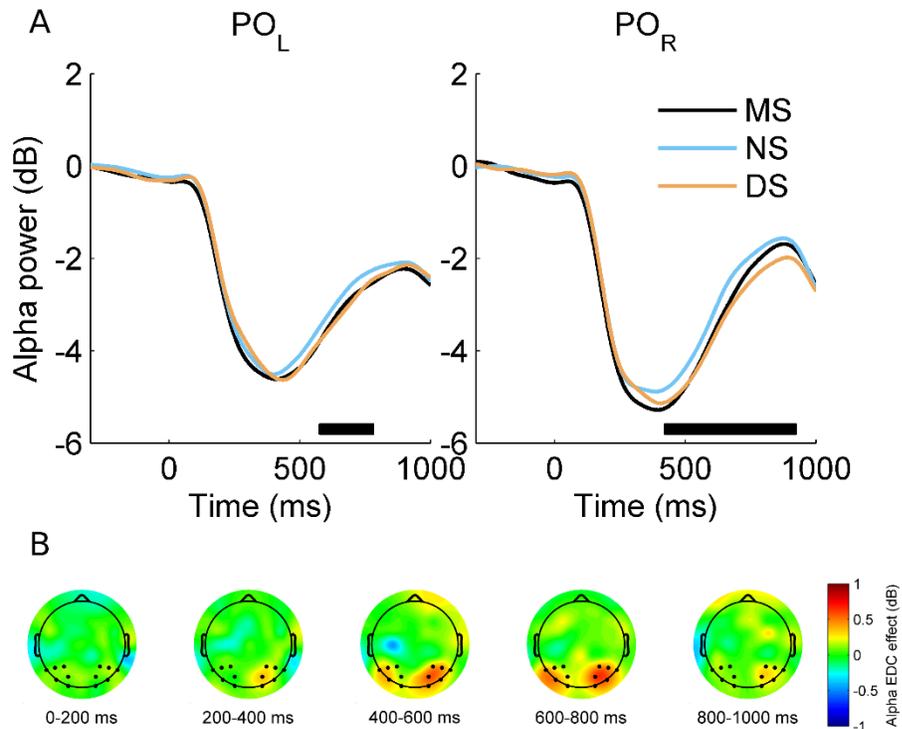


**Figure 4.2. A: The effects of letter spacing on event-related EEG activity (EREA) measured during controlled fixation on electrodes PO9 and PO10 (see insets on top panels). On panel B, fixation onset-related EEG activity (FOREA) results from the natural reading experiment (from [J2], see also Box 4.2) are shown to facilitate comparison. On all panels, black bars denote significant expertise-driven configural effects; the grey bar on the top right panel denotes the visual processing load effect obtained in the natural reading experiment. The inset of the top left panel shows the N1 peak magnified to the same scale at which FOREA is displayed on B. Note that the left N1 modulation is remarkably similar during natural reading and fixed-viewing presentation, despite the gross, condition-independent difference in the amplitude of the component. MS: minimal spacing, NS: normal spacing, DS: double spacing.**

### 4.3.2 Parieto-occipital alpha oscillations

Expertise-driven configural effects of letter spacing on alpha oscillations was found bilaterally on parieto-occipital electrode pools: alpha power was greater for the usual format than either for reduced or increased letter spacing (EDC effect,  $p_{\text{cluster}}=0.02$ ; see Fig. 4.3). The effect appears slightly earlier over the right hemisphere. Although it is not trivial to find the point where alpha power starts to diverge before the difference becoming significant, the difference appears to onset around 250-300 ms and reaching the threshold at 440 ms, then it peaks around 690 ms ( $t_{\text{peak}}=4.26$ ), and finally it falls below threshold at 900 ms. On the left parietal pool, it reaches a lower peak difference ( $t_{\text{peak}}=2.66$  at 675 ms) and is more constrained in time (starting around 400 ms, significant cluster between 600 ms and 760 ms). Despite this apparent pattern of larger effect with an earlier onset over the right hemisphere, the EDC lateralization effect (i.e., EDC  $\times$  hemisphere interaction) did not reach significance ( $t_{\text{peak}}=2$  at 640 ms).

From the VPL contrast, aimed to investigate neural processes that are sensitive to spacing as related to density of visual information and crowding in the stimulus, no significant clusters emerged. A late (non-significant,  $p_{\text{cluster}}=0.1$ ) VPL lateralization (VPL  $\times$  hemisphere interaction) cluster was found starting around 700 ms lasting up to the end of the segment, driven mainly by smaller alpha power over the right parietal cortex for double compared to minimal spacing (visible on Figure 4.3A, right). That is, left parietal alpha power in the MS and DS conditions is similar, and the EDC effect here clearly reflects the NS condition standing out with larger amplitude, while in the right parietal cortex the decreased amplitude in the DS condition might contribute to the expertise effect with larger weight in a late time window.



**Figure 4.3. The effects of letter spacing on alpha oscillations.** (A) Grand average time series of alpha (8-14 Hz) power on the left and right parieto-occipital electrode pools ( $PO_L$ : O1, PO3, PO7, P7, P5, P3;  $PO_R$ : O2, PO4, PO8, P8, P6, P4; see also marked channels on (b)) in the minimal (MS), normal (NS) and double spacing (DS) conditions. Observe that both NS and DS alpha power is lower than NS – the significant difference ( $p=0.02$ , cluster corrected) is marked by black stripes. (B) Grand mean of the expertise-driven configural (EDC) effect on alpha power averaged in five time windows. The EDC contrast is calculated as  $NS - \frac{1}{2}(MS+DS)$ , so positive (red) values indicate NS alpha power being larger MS and DS averaged. Channels of the  $PO_L$  and  $PO_R$  electrode pools are marked with black dots.

## 4.4 Discussion

In this study, our main objective was to examine the neural correlates of expertise-driven configural processing in terms of early event-related potentials and cortical oscillations in the alpha frequency band. Participants categorized simple Hungarian printed words with irrelevant flanking words around them to mimic the visual context of natural reading, and we manipulated the between-letter spacing. As between-letter spacing is known to be an important configural property of printed words that expert visual processing is adapted to, we reasoned that neural processes that are tuned to efficient processing of words with usual spacing would be affected similarly by both decreased and increased spacing (expertise-driven configural effects), as opposed to neural responses modulated simply by the density of visual information (visual processing load effects, captured by comparing the smallest to the largest spacing). We have found a left lateralized expertise effect in the time range of the N1 ERP component, followed by a robust, bilateral expertise effect in a later time window between 210 and 270 ms. Both results are in agreement with corresponding effects we found for fixation-related EEG responses in our experiments during natural reading (see [J2], Figure 4.2B, Box 4.1), and fit well within current models of orthographic visual processing. Importantly, these data corroborate our natural viewing results, and also further validate the letter spacing manipulation as a versatile tool to investigate expert orthographic processing.

Moreover, we provide the first evidence that the adaptation of the visual system to the format of printed text is reflected in the dynamics of post-stimulus visual cortical alpha oscillations. In particular, words in unusual format led to a larger and longer lasting event-related alpha desynchronization, which also led to stronger alpha activity for the normal format as compared to decreased or increased letter spacing in the later phase of the visual cortical alpha response. These results, probably reflecting induced modulations, complement the ERP results, and provide important insight into the neural underpinnings of visual expertise in orthographic processing.

Models of visual word recognition propose hierarchically organized stages of orthographic processing enabling the extraction of increasingly invariant and complex representations of written words [114, 138, 143]. At the low-level orthographic processing stage within the first 200 ms after stimulus onset, letter identity representations are computed, which according to previous EEG studies using masked priming [144–148] are already size-invariant, but still position-sensitive, case-sensitive, and font-sensitive. This is followed by the computation of a more complex orthographic code, involving feature-invariant, abstract letter and word-form representations, taking place in the

200-300 ms time window [115, 144–146, 148]. In agreement with the scheme of visual word processing outlined above, neuroimaging studies [31, 32] showed that word recognition is subserved by the left fusiform gyrus, where orthographic representations are organized in a posterior-to-anterior hierarchy. Letter selective responses were revealed in a posterior part of the fusiform gyrus, a region called visual letter-form area [115]. Word-form selective responses were found in an adjacent, more anterior region of the fusiform gyrus, in the visual word form area [31, 32], which computes a structural representation of the visual word as an ordered sequence of abstract letter identities. Furthermore, a recent study [115] using magnetoencephalography (MEG) and intracranial recordings of local field potentials also provided direct support for the proposed dynamics of orthographic processing by showing that letter processing (identified by contrasting consonant strings vs. false fonts) occurs starting from ~160 ms after stimulus onset, whereas word processing (identified by contrasting real words versus consonant strings) occurs starting from ~225 ms.

Our ERP analysis confirmed that, similarly to during natural reading, visual expertise is reflected in early visual cortical responses obtained under conventional, controlled experimental conditions. We found that over the left hemisphere, the N1 response is smaller in the case of irregular formats, i.e. both for increased and decreased spacing. The N1 component is thought to reflect the first pass of category-specific processing of visual objects, which can be facilitated by visual expertise as evidenced by increased N1 amplitudes. The visual word-evoked N1, also called N150, is linked to sublexical, position-specific letter-level orthographic processing [143, 148, 149], as outlined above. This N1 expertise effect could be related to a similar early visual expertise modulation we also observed during natural reading. The left-lateralization of this response is also in agreement the general finding that the neural systems specialized for the visual processing of words are left-lateralized [31, 113], in connection with the left-lateralized semantic and language systems in the anterior temporal and frontal cortices. A stronger, bilateral expertise ERP effect was found in the time window of the N2/P2 components, between 210 and 270 ms. This time range is linked to the phase when the sublexical orthographic representations are integrated at the whole-word level, which precedes and provides information for the subsequent stages starting at around 300 ms post-stimulus onset when word identification and semantic access occurs [115, 143, 148]. This possibly corresponds to the mid-latency expertise effect we found during natural reading. In accordance with the notion that the formation of abstract whole-word representations is a prerequisite for semantic access, this effect was found to be a strong predictor of reading speed in our natural reading experiment. Thus, altering letter spacing seems to hinder both the parallel extraction of position-

specific letter identity information as well as the subsequent computation of abstract letter combinations, such as bigrams, but in terms of both effect size and behavioral relevance, the influence of visual expertise appears to be stronger in the latter phase. This is in accordance with results from the face processing literature that found effects of second-order configural manipulations in the P2 but not in the N1 time range [150], while the N1 appears to be more sensitive to first-order configuration and a ‘holistic’ mode of expert processing that is argued to be less essential mechanism for expertise in the case of words as compared to faces [151, 152], or might occur at a later stage, as the earliest signs of integration across letter representations usually arises around 200 ms [115, 148].

Two additional effects were found during natural reading that did not show up in the fixed-viewing experiment: an additional expertise effect that predicted reading speed similarly to the N2/P2 effect emerged in the 345-380 ms time window, and a visual processing load effect appeared between 155-220 ms. In the present work, where words were flashed during controlled fixation, we did not find any corresponding pattern of results. This might be due to different signal-to-noise and sensitivity profiles of the methodologies of the two experimental paradigms, but, more importantly, the natural reading experiment was intended exactly to capture the neural processes subserving the active sampling of visual information that might be concealed by the artefactual boundary conditions imposed on participants during conventional, fixed-view experiments. Also, during natural reading, participants read real text, which required them to form fine-grained semantic representations and integrate them into context, which is exactly the process that is thought to take place in the time window of the late expertise effect [143, 148]. In contrast, the fixed-viewing experiment only required a simple binary categorization of the presented words (living vs non-living), which possibly could become relatively automatic and didn’t require deep semantic processing. Therefore, late semantic components are possibly diminished in the fixed-viewing study, while during natural viewing, the increased processing demands could have cascaded into the regime of semantic access and integration, leading to the significant late expertise effect.

Despite these discrepancies, however, the notable correspondence found between the early effects corroborate the validity of both the letter spacing manipulation to tap into expert configural processing of orthographic stimuli, and the experimental and analytic methodology to investigate these processes under natural reading conditions. As a next step, we aimed at characterizing oscillatory expertise effects, focusing on the alpha frequency band. Investigating this under fixed viewing conditions complements the event- and fixation-related potential results, which only reflect

modulations that are phase-locked to stimulus/fixation onset, and can also inform analyses of oscillatory modulations during natural viewing.

Our results clearly show that the visual cortical alpha response is sensitive to configural information in printed words, as indexed by a significant expertise-driven configural effect over bilateral occipito-parietal areas. In particular, the event-related desynchronization response was found to be longer lasting and more deep (i.e., alpha power was lower) for both altered formats as compared to normally spaced words. Although we could not establish that the effect was significantly lateralized, it was more prominent over the right hemisphere. As the scalp current density metric is most sensitive to activity directly below the channel where it is measured [68, 71, 72], the topographic distribution of the effect is compatible with sources in the more occipital aspect of the visual cortex on the right, and lateral, possibly ventral temporal areas in the left hemisphere. This is compatible with the known localization of the different levels of the word processing circuitry in the visual cortex [31, 153]. The lateral occipital cortex [154] could also be considered in the case of the right hemisphere, which has been implicated in ‘on-demand’ reentrant processing during noisy face perception [40, 41].

Despite the fact that in statistical terms, the effect was strongest in a late time window around 600-700 ms, we argue that it is best interpreted in terms of differential visual processing demands. Alpha ERD is often interpreted as disinhibition [50], which is also supported by some neurophysiological evidence [59]. Although the generality of this interpretation is debated [11, 105, 106], currently it appears to hold for sensory and attentional processing in occipito-parietal visual areas [10, 155]. The right occipito-parietal ERD for normal and altered-spacing words was similar up to ~270 ms, whereupon alpha power reached a short negative plateau for the normal condition, but continued to slowly decrease in the altered conditions. The time window of the divergence corresponds to the stage when sublexical orthographic representations are integrated to whole-word representations [143, 148], and we suggest that the continued decrease of alpha power for altered-format words reflects that the default processes of expert orthographic processing should be augmented by additional neural resources when faced with nonstandard input. This is also in accordance with MEG [156] and intracranial [157] studies finding that the integration of letters into a whole-word percept that is accessible to consciousness depends on a late occipito-parietal alpha desynchronization.

Alternatively, it can be conceived that the additional resources required for reading configurally altered text are attentional mechanisms in the dorsal visual stream that can set new sampling strategies to select the features of the object, which in turn provide the input to configural object processing mechanisms. In a previous study that used words with random vertical letter displacement and MEG with source imaging, Pammer and colleagues [158] also found alpha modulations in the right posterior parietal cortex, and fMRI findings also show that several kinds of word stimulus degradation, including letter spacing, reliably recruit parietal areas [39]. It should be noted, however, that unlike the letter spacing and displacement manipulations used in these studies, we show that either increasing or decreasing letter spacing produces similar results, which further confirm that our results do not arise from general visual perceptual load imposed by increased visual information density, but probably reflect the adaptation of the visual system to the habitual format that is subject to visual expertise. It is also interesting to speculate that while considering visual word processing, the N2 component, as also discussed above, is linked to the formation of word-form representations, in the attentional literature the posterior N2 is a prominent correlate of attentional selection [159, 160]. While its most well-known manifestation is lateralized and linked to spatial selection, Loughnane and colleagues [161] have shown that it is generalizable to nonspatial attentional selection that marks the onset and provides input for subsequent stages of perceptual evidence accumulation. Thus, the strong expertise-driven effect in the N2 time window, again, points to the potential role of the dorsal visual areas in selecting relevant features for object processing mechanisms in the ventral stream, especially when expertise-driven processes fail on non-habitual input.

Thus, we argue that the critical perceptual evidence accumulation phase between 200 and 300 ms, leading to the integrated percept of a word, requires more neural resources and gets prolonged for altered-format words, as reflected in the lengthened initial alpha desynchronization over visual areas, and potentially also the N2 ERP modulation. Our experimental design does not permit to characterize how the next, semantic retrieval stage might be affected by this delay, and the alpha power difference that even increases beyond just being carried over to this next phase. This question should be addressed in future experiments, it is nevertheless interesting to speculate on what the present results might imply. Low frequency (alpha and beta) oscillations have also been implicated in forming networks that can coordinate neural activity related to expectation [162, 163], perceptual [164] or working memory representations [165], and also in providing the main channel of high-level object information through feedback connections in the visual cortical hierarchy [65, 67]. So, possibly normal format processing can better exploit prior, ‘predictive’ knowledge about the

structure of the visual stimulus, which can be reflected in the higher alpha power for normally spaced words in the rebound phase of the alpha response.

To sum up, we found that visual expertise for orthography was reflected in the N1 and P2/N2 ERP components, in agreement with our results from natural reading, and also modulated the occipito-parietal event-related alpha response. In line with what we expected, the ERP and oscillatory results provide complementary evidence for our hypothesis that processing text with altered letter spacing requires alternate computational strategies, more neural resources more time, most prominently at the stage where letter-level representations are integrated into whole-word level abstract representations. Considering results from both fixed-viewing and natural-viewing paradigms provides both complementary and confirmatory information, enabling better research in the future by mutually informing experimental design, analysis and interpretation of the results as well.

## 5 Conclusions and future directions

The main aim of this dissertation is to show how alpha oscillations contribute to the visual processing of complex natural objects in the human cortex. EEG alpha oscillations have been known for almost a century [2, 47], and the intensive research focusing on them both in the field of cognitive neuroscience and neurophysiology is continuously converging toward making them one of the first noninvasively measurable EEG markers that can provide information on circuit-level neurobiological processes [60, 65, 67, 166].

Importantly, the stimuli used in the experiments were complex everyday visual objects. Especially in the attention experiment, artificial, controlled stimuli could have allowed for asking more specialized questions, but, due to the role of experience and expertise in the perception of natural objects, it is quite difficult to engage the highest levels of visual processing without using everyday stimuli. Therefore, we decided to use words and faces. Both stimuli have a well-characterized visual cortical circuitry specialized in their processing in all neurotypical and literate humans [18, 31, 32, 41].

In the first part, I showed that alpha oscillations, in accordance with their role already established in the case of spatial [53, 55, 57] and feature-based [56] attention, also contribute to object-based attention. Words and faces were presented foveally, overlapping each other, which precludes the use of coarse spatial selection mechanisms. Also, six consecutive stimuli were presented, which allowed us to investigate how the existing attentional set modulates alpha oscillations in anticipation of more upcoming stimuli. Alpha oscillations with a right hemispheric occipital focus were stronger when words were attended and more desynchronized when faces were attended, and we observed no interaction with whether the other, irrelevant category stimulus was present or not. This modulation was sustained throughout the whole stimulus stream, whereas the presence of distractors only modulated alpha power at the first part of the stimulus sequence, with a broader topography.

In the second part, I characterized cortical processes underlying visual expertise for printed words in terms of alpha oscillations, and also event-related potentials. As the experiment was part of a research agenda aiming at characterizing the same processes during natural reading, I also had the opportunity to consider the results in this context. Both experiments used a novel manipulation, using words with normal, increased and decreased letter spacing. This manipulation was devised so

that it would tap into basic visual processes, while leaving the overall legibility and content of the word stimuli relatively unaffected. First, I showed that the neural correlates of visual expertise in early cortical responses observed during natural reading are manifested in the fixed-view results as well. After pondering on the similarities and discrepancies, I went on to show that the visual cortical alpha response to word stimuli is also sensitive to expertise for print. Particularly, the desynchronization phase was deeper and more prolonged for altered-format stimuli, and this difference was carried over into and even strengthened in the late phase of stimulus processing. These findings – early evoked modulations in fixed-view word recognition and natural reading, augmented by oscillatory modulations presented here – provide converging evidence that the processing phase that visual expertise for print most profoundly influences is that of integrating sublexical representations into abstract whole-word units. Reading words in altered format requires more processing in this phase, which probably also contributes to delay in semantic access and slowing of reading to a considerable degree, as seen in the natural reading data.

In both experiments, the topography of the effects – object attention and object expertise – were nicely constrained to visual areas, assumably mainly from the ventral stream of the visual system. In object-based attention, while the attentional effect was present over a broader part of the cortex in the beginning, the effect remained most stable on electrodes over the early visual cortex. We interpreted this as object-based attentional effects propagating backwards in the visual stream, leading to attentional filtering at the earliest stages. The expertise effect was analyzed using a ROI-based approach, however, observing the topography also implies sources in the ventral visual stream, potentially including the letter-form, word-form areas and earlier, less specific visual areas involved in representing letter features.

Thus, taken together, the results of the two experiments suggest that alpha oscillations in visual cortex play a role during object selection in cluttered environments, and they might also mediate efficient, expert object recognition in the case of printed words. It is clear that further research would be needed to establish what could be the common and disparate neurophysiological network mechanisms behind the alpha-band modulations during attentional selection and expertise in the case of complex, natural objects like words and faces. It is tempting, however, to consider the results in a common framework, as permitted by recent integrative models trying to capture the variability and versatility of attention both in the lab and “in the wild”. These models, instead of dealing with attention as a separate phenomenon, also attempt to integrate it in broader theories of brain function.

The recent work of Buschman and Kastner [167] attempts to integrate several theories that are relevant to discuss the present results, therefore I will use their five-step model of attention to elaborate how the present results could fit in current theories. A central tenet of their model is to explain how broad top-down attentional modulations can give rise to the huge variety of specific and sharp local attentional effects through local interactions in sensory areas. They posit that the pattern-completion nature of the sensory cortex is a key component to achieve this. As detailed in the introduction, the visual system has evolved and developed to represent the environment in a cost efficient way, so it discards any input that is orthogonal to its representational dictionary, while signals that match the representations get boosted. These embedded object representations provide the essence to form the hierarchical network structure of the visual system. They propose that broad top-down influences can act backwards through the same circuitry, allowing the detailed representations that get activated by bottom-up drive to crystallize in a way that is in accordance with current attentional demands. (This occurs early, in Stage 2 of their model, following the initial deployment of attention in Stage 1.) This is captured well, for example, in findings that as soon as one part of an object is selected, attention spreads to the whole object [168]. This is in accordance with the role of alpha oscillations as both reflecting attentional modulations and activity in the feedback circuitry of the visual system that is crucial in the formation of high-level object representations.

Besides the circuits of embedded object representation, Buschman and Kastner [167] (besides, e.g., [21, 22]) also regard normalization as a key local interaction that captures the competition between stimulus representations, and argue that attention can bias competition through modulating these interactions (during the 3<sup>rd</sup> Stage). They argue that lateral inhibition through inhibitory neural populations of the sensory cortex might be the primary mechanism through which this can occur. They mainly emphasize the potential role of higher-frequency oscillations in this and the following 4<sup>th</sup> stage, arguing for the role of rhythmic inhibition and synchrony in organizing population activity during attention. However, there are some implications for the potential role of alpha oscillations in normalization-like phenomena. There is evidence that alpha oscillations in V1 are related to local cortical interactions mediating surround suppression [169, 170]. Also, on the higher level, the antagonistic patterning of alpha ERS/ERD during intersensory and within-modality attention ([50, 56] ,see Introduction) makes it a potential candidate for a mechanism mediating global normalization throughout the brain.

The 5<sup>th</sup> stage of the model concerns the dynamic, rhythmic nature of attention and explores possible connections with lower-frequency oscillations (besides alpha, also involving the theta and beta range). These connections are currently subject to intensive research, and it appears that rhythmicity could be a previously neglected but essential characteristic of attention. A central finding is that attention samples stimuli in a rhythmic fashion. For example, some behavioral [171, 172] and EEG [173] studies found that within-object sampling occurs around 8-10 Hz, i.e. at the lower edge of the alpha band, while between-object switching is dominated by lower rhythms in the theta band. This could be related to the role of alpha oscillations in object-based attention and expert object perception that is the subject of this work. However, another study found that during visual search in macaques, attention sampled stimuli at a rate in the beta frequency range [174]. Also, validly establishing these connections is very challenging in the methodological sense, which make some earlier results in the literature questionable [175]. So, it is clear that still a lot of theoretical and experimental work is needed to reconcile apparent contradictions and fit rhythmic sampling into our current understanding of attention, and discussing these in the context of the present results is beyond the scope of this work.

To sum up, trying to interpret these results in a common framework gives rise to the hypothesis that object-based selection processes both exploit and serve the hierarchical neural system underlying efficient visual object processing, and visual cortical alpha oscillations provide the primary neural communication channel that makes this possible. That is, as described above, visual objects can be selected from cluttered visual scenes by exploiting the high-level knowledge engrained in the ventral visual stream about the structure of these objects (and also how they usually appear in their environment, see ) – this is how visual attention “exploits” the properties of the visual system. But also, perceiving and judging a visual object quickly and effectively also involves selection-like processes (which sometimes appear as complex filter kernels in computational models,) during which the diagnostic parts of the objects are processed more intensively based on contextual and “gist” information from a fast feedforward first processing stage.

A possible good way forward is to test this hypothesis more explicitly and investigate how alpha oscillations contribute to this two facets of visual object processing. This question is also intimately related to how attention and object perception can work so effectively in natural scenes. It would be also intriguing to investigate how the N2pc family of attentional ERP components might be related to neural correlates of detailed object processing in the same latency range (n250r for face individuation, or P2/N2 modulations related to format alteration or noise filtering) – could the latter

be understood as a second-pass selection process aimed at sampling lower-level visual areas for more detailed object information?

An interesting result that warrants further investigation is how in the first experiment alpha power converged according to the attended category towards the end of the trial, independent of whether the other category was present. Although the task-dependence of alpha power is more frequently emphasized than its stimulus-dependence (e.g., [10]), this might suggest that this “steady state” level of alpha power reflects visual processing requirement that is inherent to the given category. That is, to my knowledge, what visual parameters stimulus-related alpha responses are sensitive to is an important basic question that has not been investigated before. For example, computational models (e.g., [176–178]) could yield parameters that I would expect to be related to properties of the alpha response. Alternatively, behavioral markers of visual information load [179] could also be related to alpha responses.

The results on reading have important implications on dyslexia research. It is known that dyslexics are more affected by crowding (they improve if letter spacing is increased [131]), and the neural correlates of this sensitivity could be investigated with similar methods and compared to typical readers. It is possible, for example, that the visual processing load effect (that corresponds to crowding) would be stronger in dyslexics. Besides a larger visual load effect, the expertise effect could be delayed and either smaller – reflecting the impairment itself in this case – or larger – then it would correspond to a compensatory mechanism.

To conclude, I have shown that visual cortical alpha oscillations are modulated during object-based attention and also reflect visual expertise for orthography. These effects have not yet been tested on real-world scenes in natural viewing scenarios, but the results strongly support the prediction that they would also hold in those conditions: for the orthographic expertise effect, it was found that the ERP results are comparable to those acquired during natural reading, and for the object-based attention effect, the experimental design included temporal context and spatial clutter that could be expected in natural viewing. I explored the possibility that the two results on cortical alpha activity might reflect similar neural circuit mechanisms in the visual hierarchy, and put forward a few questions that could be tested experimentally. What the disparate and common underlying neurophysiological patterns might be is not yet clear, but it is certain that alpha oscillations are manifested in multiple facets of object perception.

# 6 Summary of the Theses

## 6.1 Thesis I.

**I provide the first evidence that object-based attentional selection – similarly to spatial and feature-based attention – involves visual cortical alpha oscillations.**

Published in [J1].

Throughout the last two decades, converging evidence from scalp [53, 54, 95, 142] and invasive electrophysiology [59], concurrent imaging methods [180] and neurostimulation [181] has suggested that visual cortical alpha oscillations are involved in attentional gating of the incoming visual information [182]. It is well established that spatial attentional selection results in increased alpha oscillations over the cortical regions representing sensory input originating from the unattended visual field, with concomitant decreases for areas representing relevant parts of the visual field [53]. More recently a similar mechanism was demonstrated for feature-based attention [13]. However, whether attentional gating in the case of object-based selection is also associated with alpha oscillations has not been investigated before.

Here, we measured electroencephalography (EEG) while participants performed an object-based attentional selection task. In each trial, participants were cued to focus attention to sequences of six word and face stimuli, which were foveally presented. The presence of the irrelevant category stimulus was orthogonally manipulated – in half of trials, only the relevant category image was present, in the other half, word stimuli overlaid on faces were displayed. After each sequence of 6 consecutively presented stimuli participants had to indicate how many times (0, 1 or 2) two consecutive stimuli from the same type occurred (faces: male/female, words: fruit/animal). Accuracy on this task was similar for words (77%) and faces (76%), but was reduced by distractors (from 79% to 74%).

*Thesis I/1 – I have shown that object-based attention to foveally presented words versus faces increased right-lateralized anticipatory alpha oscillations over the visual cortex. I have also shown that this effect is remarkably persistent throughout a sequence of stimuli.*

The results revealed that anticipatory alpha activity (8-12 Hz) measured on parieto-occipital electrodes was significantly higher when participants were cued to attend to words (Figure 3.3 ,3.4), as compared to when faces were task-relevant. Importantly, this object category based attentional modulation of alpha power showed a hemispheric lateralization: attending to words as compared to faces led to significantly larger increase in alpha activity over the right than the left hemisphere. The object category-dependent attentional effect on anticipatory alpha activity did not arise before the first stimulus in the sequence, possibly due to our stimuli being long enough to allow post-onset orienting, exerting no time pressure that would require deployment of attention prior to the first stimulus. Before the second stimulus, it had a broader topography extending to right temporal electrodes, but afterwards it was confined to the right parieto-occipital region, where it did not weaken throughout the whole stimulus sequence.

*Thesis I/2 – I have shown that the object-based attentional effect on right parieto-occipital alpha oscillations does not interact with the presence of a strong, overlapping distractor stimulus from the other category. I have also characterized the influence of distractors on visual cortical alpha oscillations, which lacks the temporal persistence and focused topography of the attentional effect, providing further support for their dissociation.*

When stimuli from the unattended category (distractors) were also present at the same foveal location as the attended stimuli, the event-related alpha desynchronization responses were less pronounced, leading to higher alpha power with than without distractors (Figure 3.5). However, this influence of distractors on alpha oscillations was clearly distinct from the category effect in several ways. First, no statistical interaction was found between the two effects. Second, the distractor effect had a more widespread topography, covering most of the posterior temporal, centro-parietal and occipital cortex (see Figure 3.5A). Third, the distractor effect, in contrast to the attentional effect, weakened and almost disappeared towards the end of the stimulus sequence.

Possibly related to this, it was also found that alpha power displayed a saturation pattern during the trial in all conditions, as alpha desynchronization after S1 was prominent but it gradually became weaker or completely disappeared in the case of subsequent stimuli (see e.g. Fig. 3.3). This modulation of the strength of alpha desynchronization was more pronounced over the right

hemisphere. As alpha power is frequently regarded as an index of cortical excitability [183], this could mean that less and less resources were spent on irrelevant stimuli, but it is also possible that the relevant stimuli were processed more efficiently, requiring less resources.

## 6.2 Thesis II.

**I have shown that visual expertise for written words is reflected in early visual cortical evoked and alpha-band oscillatory responses as probed by a novel paradigm using words with altered letter spacing.**

Published in [J2].

In most previous research studying visual word recognition compared neural responses to words with those evoked by pseudowords or other objects [31, 114]. Focusing on visual processing, however, it is a better approach to use subtle manipulations affecting mainly the visual properties of text while leaving its content and overall “legibility” relatively unaffected. With this in mind, we introduced a novel paradigm to study visual processing underlying reading and word recognition: by using words with normal, decreased and increased letter spacing (Figure 4.1) we can probe and dissociate a) visual expertise in word processing by comparing responses for normal and altered spacing regardless of increase or decrease; b) more general visual processing load effects arising from changes in the density of visual information and competitive interactions that depend on the distance between similar visual elements (crowding).

This thesis focuses on results from a traditional experiment with controlled stimulation and fixation, but within the context of results from the natural reading experiment (detailed in [J2]) that was also part of this project. The latter, novel approach can reveal neural processes subserving active sampling of visual information that might remain obscured in conventional experiments, but uncontrolled visual stimulation and ensuing artefacts also impose inherent limitations and technical challenges to solve.

*Thesis II/1 – I have shown that visual expertise for orthography, as measured by altering letter spacing, is reflected in two early visual cortical evoked response components between 150 and 300 ms after stimulus onset, indicating that visual expertise pervades letter-level sublexical to whole-word level prelexical orthographic visual processing in the cortex.*

As between-letter spacing is known to be an important configural property of printed words that expert visual processing is adapted to, we reasoned that neural processes that are tuned to efficient processing of words with usual spacing would be affected similarly by both decreased and increased spacing (expertise-driven configural effects), as opposed to neural responses modulated simply by the density of visual information (as captured by comparing the smallest to the largest spacing, visual processing load effects). We have found a left lateralized expertise effect in the time range of the N1 ERP component, followed by a robust, bilateral expertise effect in a later time window of the P2/N2 components, between 210 and 270 ms (Figure 4b). The left N1 component can be regarded as an index of orthographic processing at the level of single letters [148, 149], while the N2 time range is associated with the integration of these units into abstract, pre-lexical whole-word visual representations [115, 148]. Our results thus indicate that both of these stages rely on expertise-driven configural visual processing mechanisms.

Some minor differences between natural reading and fixed-view results were found (Figure 4.2); a late expertise and an early processing load effect obtained during natural reading did not appear in the fixed-viewing results. Importantly however, the correspondences that do hold corroborate our natural viewing results, and also the letter spacing manipulation as a versatile tool to investigate expert orthographic processing.

*Thesis II/2 – I have shown that the event-related alpha response is sensitive to the configural properties of written words. This provides an index of visual expertise in word recognition that is complementary to the ERP results.*

Our results clearly show that the visual cortical alpha response is sensitive to configural information in printed words, as indexed by a significant expertise-driven configural effect over bilateral occipito-parietal areas (Figure 4.3B). In particular, the event-related desynchronization (ERD) response was found to be longer lasting and more deep (i.e., alpha power was lower) for both altered formats as compared to normally spaced words (Figure 4.3A). Although we could not establish that the effect was significantly lateralized, it was more prominent over the right hemisphere.

Despite the fact that in statistical terms, the effect was strongest in a late time window around 600-700 ms, we argue that it is best interpreted in terms of differential visual processing demands. The right occipito-parietal ERD for normal and altered-spacing words was similar up to ~270 ms, whereupon alpha power reached a short negative plateau for the normal condition, but continued to slowly decrease in the altered conditions. The time window of the divergence corresponds to the stage when sublexical orthographic representations are integrated to whole-word representations [115, 148], and we suggest that the continued decrease of alpha power for altered-format words reflects that the default processes of expert orthographic processing should be augmented by additional neural resources when faced with nonstandard input.

# 7 Bibliography

## 7.1 The author's publications

### 7.1.1 Journal publications

[J1] **B. Knakker**, B. Weiss and Z. Vidnyánszky, Object-based attentional selection modulates anticipatory alpha oscillations. *Front. Hum. Neurosci.* 8:1048., Jan. 2015

[J2] B. Weiss, **B. Knakker** and Z. Vidnyánszky, Visual processing during natural reading. *Scientific Reports* 6, Article number: 26902, May 2016

### 7.1.2 Additional journal publication

[J3] E. Maróti, **B. Knakker**, Z. Vidnyánszky and B. Weiss, The effect of beat frequency on eye movements during free viewing. *Vision Research*, 131: pp. 57-66. Feb. 2017

### 7.1.3 Selected conference publications

[C1] B. Weiss, **B. Knakker**, Z. Vidnyánszky, Electrophysiological Correlates of Letter Spacing in Natural Reading In: IBRO Workshop: International Brain Research Organization Workshop, Debrecen , Hungary, Paper P199; Jan. 2014

[C2] **B. Knakker**, B. Weiss, I. Kóbor, P. Hermann, Z. Vidnyánszky, Electrophysiological correlates of the different hierarchical levels of visual word processing, In: IBRO International Workshop, Szeged, Hungary, *Ideggyógyászati Szemle/Clinical Neuroscience*; p. 35. S1; Jan. 2012

[C3] **B. Knakker**, P. Hermann, I. Kóbor, ÉM. Bankó, Weiss B, V. Gál, Z. Vidnyánszky (2011). Habituation of face specific visual cortical responses are modulated by attention. *Front. Neurosci.* Conference Abstract: 13th Conference of the Hungarian Neuroscience Society (MITT).

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