The Diverse Role of Alpha Oscillations in Visual Object Processing

Theses of the *Ph.D.* dissertation

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Budapest, 2016

Introduction

The research of alpha oscillations has a long history. Based on early observations [1, 2] that alpha has large amplitude in the eyes-closed state and disappearing upon the opening of the eyes, it was considered a sign of idling for a long time. Later on, its power drop related to sensory and motor events, termed event-related desynchronization (ERD) has been shown to be related to intensive local cortical computations [3], while its counterpart, event-related synchronization was still interpreted as idling. Based on a body of accumulated research, the theory of relating large alpha power with inhibition or suppression was born [4, 5], which has proven to be particularly fruitful in the field of attention research [6]. A key element in attentional selection is the suppression of irrelevant stimuli that compete for representation to free up resources for important ones [7], and this function has become a flagship of the inhibitory theory of alpha oscillations.

From a neurophyisological perspective, alpha oscillations and low-frequency oscillations in general has profound effect on neural activity. In particular, neural spiking, and also high frequency oscillations are observed to be often coupled with the phase of alpha oscillations [8], preferentially occurring at favorable phase intervals, and getting inhibited in the rest of the time. While inhibition has a role in this account as well, the more dominant aspect here is that alpha oscillations provide channels for cortical communication, through which local and brainwide neural ensembles can engage in coordinated computations [9, 10]. More recently, alpha oscillations have been shown to be the main carriers of feedback information in the visual cortical hierarchy [11, 12], which connections have important theoretical role in the predictive coding account of visual function [13].

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 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 also 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.

1. Methods

The theses described herein are the result of 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.

For the experiments, all participants had reported to have normal or corrected vision and no neurological disorders, and signed informed consent. EEG and EOG was recorded using BrainAmp amplifiers (BrainAmp MR and Standard, Brain Product GmbH, Munchen, Germany) and a 64-channel active electrode system (ActiCAP from Brain Products) mounted on an elastic cap (Easycap GmbH, Herrsching-Breitbrunn, Germany). Fixation was monitored online and measured using IViewX Hi-Speed (SensoMotoric Instruments GmbH, Teltow, Germany) tower mounted eye trackers. Stimulation and response collection was controlled using MATLAB and PsychToolbox 3 [14, 15].

For EEG preprocessing and analysis, I used Brain Vision Analyzer 1.05 (Brain Products) and MATLAB, also using EEGLAB toolbox [16]. ERP preprocessing involved standard methods for filtering, segmentation and artefact rejection [17]. The Surface Laplacian approximation of the scalp current density (SCD) was calculated using the CSD Toolbox [18, 19]. SCD-transformed data is reference-free, and is less affected by volume conduction [20]. Time-frequency representations were obtained using wavelet convolution with complex Morlet wavelets [21] as implemented in the MATLAB Wavelet Toolbox. Statistical analysis was done in STATISTICA (StatSoft, Tulsa, OK, USA) and MATLAB. Mass univariate statistics were conducted using FieldTrip [22], using cluster-based permutation statistics for type I error control [23].

2. New scientific results

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 [24–27] and invasive electrophysiology [8], concurrent imaging methods [28] and neurostimulation [29] has suggested that visual cortical alpha oscillations are involved in attentional gating of the incoming visual information [5]. 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 [24]. More recently a similar mechanism was demonstrated for feature-based attention [6]. 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 attenional 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%).

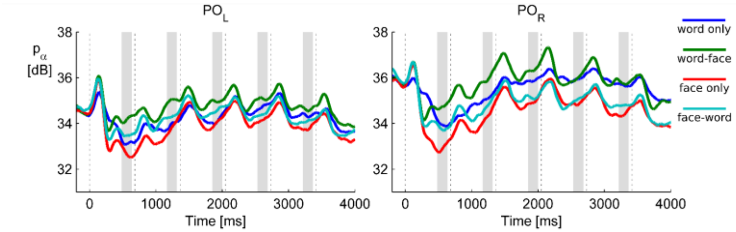

Figure 1. Grand average alpha power over the parieto-occipital cortex during the stimulus sequence in the four conditions. See the following figures for the details on the effect of attention and distractor.

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 1,2), 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.

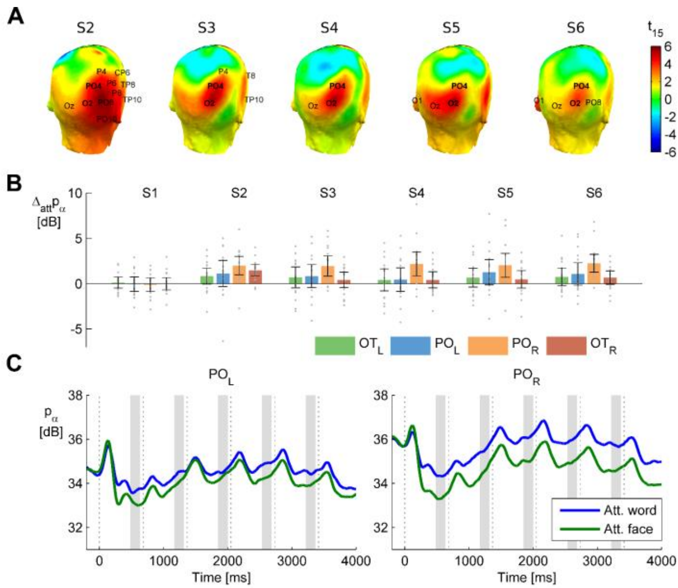

Figure 2. Object-based attentional selection modulates alpha oscillations. Persistently throughout the six-stimulus sequence, anticipatory alpha power over the right parieto-occipital cortex was higher when words were attended to (positive values on *A* and *B*), as compared to when faces were task-relevant. Depicted are T-values (color on *A*), individual (grey dots on *B*) and average (bars with 95% CIs on *B*) difference values from the periods of interest (marked with grey on *C*) before each stimulus onset (dashed lines on *C*). On *A*, electrodes where the effect is significant in the current time window are marked on each headplot, and the labels where the effect was consistently present throughout the sequence (O2 and PO4) are emboldened. On *C*, group-level average alpha power time courses are plotted for the two categories, averaged across distractor conditions. Electrode pools: PO_L: O1, PO3; PO_R: O2, PO4; OT_L: PO7, P7, PO9 and OT_R: PO8, P8, PO10.

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 3B). 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 3A). 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 Fig. 1). 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 [3], 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.

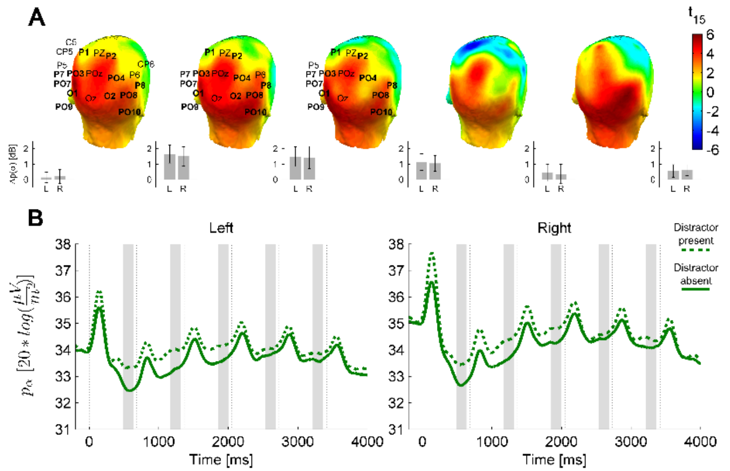

Figure 3. The presence of a stimulus from the unattended category weakened the alpha desynchronization response, but it had less and less influence towards the end of the stimulus sequence. (A) Head plots for *t*-values of the distractor modulation (distractor present minus absent) of anticipatory alpha activity in prestimulus time windows before S2–S6. As on Figure 2, electrodes marked are in the cluster of significant difference and bold electrode names are the ones consistently significant from pre-S2 to pre-S4. 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 electrode 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. Electrode pools: Left or L: P7, PO7, PO9, PO3, O1, P1; Right or R: P8, PO8, PO10, PO4, O2, P2.

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 [30, 31]. 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) 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, EDC), 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, VPL). 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 5A). The left N1 component can be regarded as an index of orthographic processing at the level of single letters [32, 33], while the N2 time range is associated with the integration of these units into abstract, pre-lexical whole-word visual representations [32, 34]. 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 5B); a late expertise and an early processing load effect obtained during natural reading [J2] 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.

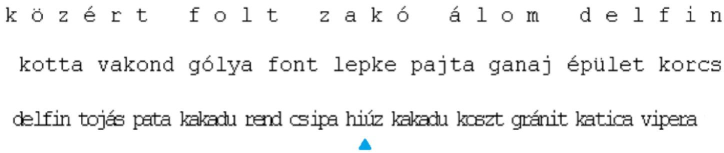

Figure 4. Sample stimuli with double (top), normal (middle) and minimal (bottom) letter spacing. The blue arrow marks the task-relevant word at the center of the screen, surrounded by irrelevant flanker words.

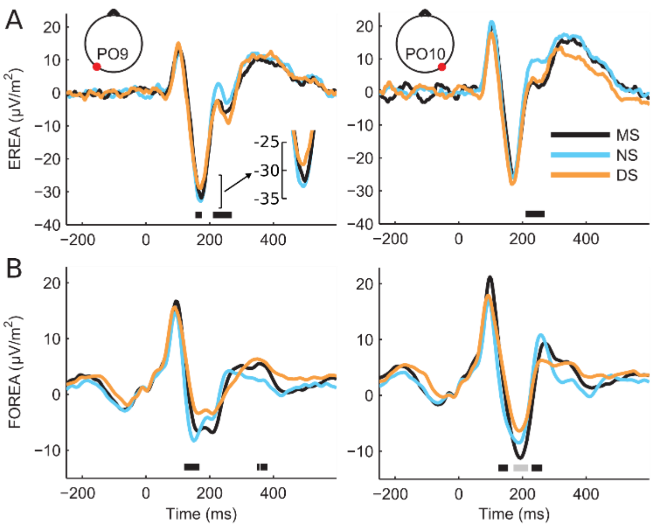

Figure 5.A: The effects of letter spacing on EEG activity during viewing words with controlled fixation measured on electrodes PO9 and PO10 (see insets). On panel B, fixation onset-related EEG activity (FOREA) results from the natural reading experiment (from [J2]) are shown to facilitate comparison. On the left panel of A, the N1 effect is magnified in an inset so that the scale matches that of panel B. Black bars denote significant EDC effects; the grey bar on the top right panel denotes the VPL effect obtained in the natural reading experiment. MS: minimal spacing, NS: normal spacing, DS: double spacing.

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 6B). 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 6A). 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 [32, 34], 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.

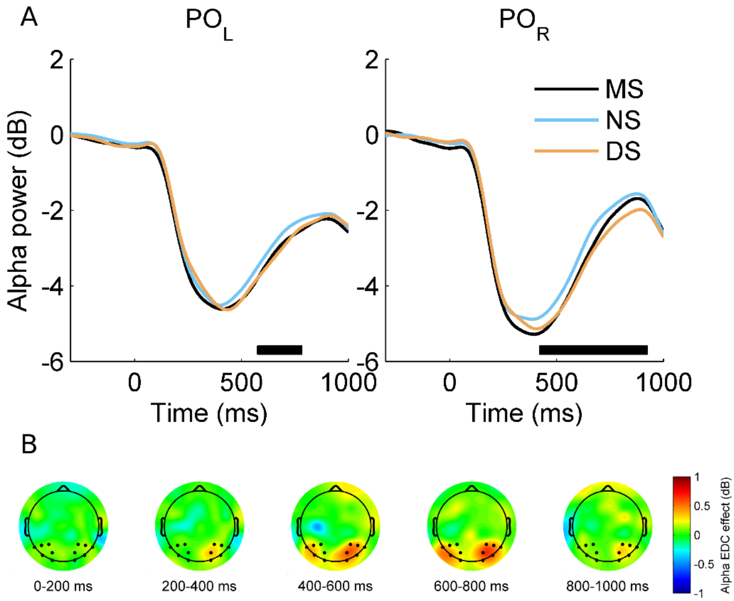

Figure 6. The effects of letter spacing on alpha oscillations. (A) Grand average time series of alpha (8-14 Hz) power on the left and right parieto-occipital clusters (PO_L: O1, PO3, PO7, P7, P5, P3; PO_R: O2, PO4, PO8, P8, P6, P4; see also marked channels on *(b)*) in the minimal (MS), normal (NS) and 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 topographies of the expertise-driven configural (EDC) effect on alpha power averaged in five time windows. The EDC contrast is calculated as NS-½(MS+DS), so positive (red) values indicate NS alpha power being larger MS and DS averaged.

Conclusions and possible applications

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 [1, 2], 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 [11, 12, 35, 36].

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 [31, 37–39].

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 cortical stream, potentially including the letter-form, word-form areas and earlier, less specific visual areas involved in representing letter features.

Besides the first experiment yielding results that are in keeping with the role of alpha oscillations in attention, both results are compatible with the proposed role of alpha oscillations as the main carrier of high-level object information through feedback connections from cortical areas down the ventral stream [12, 40]. Some newer theories of attention, instead of dealing with it as a separate phenomenon, attempt integrating it in broader theories of brain function. The model of Buschman and Kastner [41], for example, makes extensive use of the assumption that attention has a broad modulatory effect, and its specific local visual cortical effects are achieved by propagating through feedback connections to lower levels of the cortical hierarchy. Importantly, they emphasise that this probably does not occur through channels dedicated separately to attentional modulatory signals, but they posit that this is possible because the adaptive, sparse representations that become embedded into the structure of the visual hierarchy through experience [13]. Interpreting our results in this framework suggests that both during object-based attention and expert object recognition, alpha oscillations realize the high-level object knowledge originating from category specific areas through modulating lower-level areas via feedback connections.

Understanding the visual cortical processes underlying reading and word recognition in neurotypical subjects can also provide a deeper understanding of reading disorders like dyslexia. The experimental paradigm based on letter spacing could potentially be used to probe visual representations in dyslexia, or the markers uncovered in this study and the concomitant natural viewing study [J2] could be tested in a neurofeedback protocol aimed at inducing perceptual learning in subjects to acquire more effective orthographic representations.

3. Acknowledgements

First and foremost, I would like to express my gratitude towards my supervisor, Prof. Zoltán Vidnyánszky. Without his continued support, guidance and patience, this work would not have been possible. I would also like to thank Béla Weiss, for mentoring me on the complex methods of electrophysiology, for the numerous discussions. Their guidance and support has been invaluable for me both personally and professionally.

I am indebted to the Doctoral School, with special regard to Prof. Péter Szolgay and Prof. Tamás Roska, for providing the opportunity to pursue a PhD in a multidisciplinary environment.

I am utterly grateful to Petra Hermann, for her friendship and support, and for introducing me to the subtleties of techno music. I am also thankful to my close colleagues and collaborators in the research group, Pál Vakli, Petra Kovács, Éva Bankó, Emese Maróti, Viktor Gál, István Kóbor, Vanda Nemes, Gergely Drótos, Regina Meszlényi, Ádám Kettinger, Dávid Farkas, Annamária Manga, Máté Kiss, Krisztián Buza for the opportunity to work together with them, their help, fruitful and inspiring discussions, and for enduring all the puns I told throughout the years. I also owe thanks to the Department of Cognitive Science at BME, Márta Zimmer, Kornél Németh, Ágnes Szőllősi, Bertalan Polner and Péter Pajkossy, for the help, inspiring discussions and fun we had together.

I also acknowledge the help of the administrative personnel, especially Katinka Tivadarné Vida for her supportive kindness, and I also owe thanks Anna Torma, Ágnes Bereczki and Mónika Herege.

Last but not least, I am most grateful to my Mother and Father, Zsófi, my sister and my grandparents for the love, support, and also for the roots of all the inspiration that ultimately brought me here. I am also thankful to my family and friends for keeping my chin up in hard times, and all the good times we had together. Thank you!

4. Publications

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

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

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 , Magyarország, 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, Magyarország,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).

5. References

[1] H. Berger, “Über das Elektrenkephalogramm des Menschen,” *Arch. Für Psychiatr. Nervenkrankh.*, vol. 87, no. 1, pp. 527–570, Dec. 1929.

[2] E. D. Adrian and B. H. C. Matthews, “The interpretation of potential waves in the cortex,” *J. Physiol.*, vol. 81, no. 4, pp. 440–471, Jul. 1934.

[3] G. Pfurtscheller, “Functional brain imaging based on ERD/ERS,” *Vision Res.*, vol. 41, no. 10–11, pp. 1257–1260, Május 2001.

[4] W. Klimesch, “EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis,” *Brain Res. Rev.*, vol. 29, no. 2–3, pp. 169–195, Apr. 1999.

[5] W. Klimesch, P. Sauseng, and S. Hanslmayr, “EEG alpha oscillations: The inhibition–timing hypothesis,” *Brain Res. Rev.*, vol. 53, no. 1, pp. 63–88, Jan. 2007.

[6] J. J. Foxe and A. C. Snyder, “The Role of Alpha-Band Brain Oscillations as a Sensory Suppression Mechanism during Selective Attention,” *Front. Psychol.*, vol. 2, 2011.

[7] R. Desimone and J. Duncan, “Neural mechanisms of selective visual attention,” *Annu. Rev. Neurosci.*, vol. 18, pp. 193–222, 1995.

[8] S. Haegens, V. Nácher, R. Luna, R. Romo, and O. Jensen, “α-Oscillations in the monkey sensorimotor network influence discrimination performance by rhythmical inhibition of neuronal spiking,” *Proc. Natl. Acad. Sci.*, vol. 108, no. 48, pp. 19377–19382, Nov. 2011.

[9] P. Fries, “Rhythms for Cognition: Communication through Coherence,” *Neuron*, vol. 88, no. 1, pp. 220–235, Oct. 2015.

[10] S. Palva and J. M. Palva, “New vistas for α-frequency band oscillations,” *Trends Neurosci.*, vol. 30, no. 4, pp. 150–158, prilis 2007.

[11] A. M. Bastos, J. Vezoli, C. A. Bosman, J.-M. Schoffelen, R. Oostenveld, J. R. Dowdall, P. De Weerd, H. Kennedy, and P. Fries, “Visual Areas Exert Feedforward and Feedback Influences through Distinct Frequency Channels,” *Neuron*, vol. 85, no. 2, pp. 390–401, Jan. 2015.

[12] G. Michalareas, J. Vezoli, S. van Pelt, J.-M. Schoffelen, H. Kennedy, and P. Fries, “Alpha-Beta and Gamma Rhythms Subserve Feedback and Feedforward Influences among Human Visual Cortical Areas,” *Neuron*, vol. 89, no. 2, pp. 384–397, Jan. 2016.
[13] K. J. Friston and C. J. Price, “Generative models, brain function and neuroimaging,” *Scand. J. Psychol.*, vol. 42, no. 3, pp. 167–177, Jul. 2001.
[14] D. H. Brainard, “The Psychophysics Toolbox,” *Spat. Vis.*, vol. 10, no. 4, pp. 433–436, Jan. 1997.
[15] D. G. Pelli, “The VideoToolbox software for visual psychophysics: transforming numbers into movies,” *Spat. Vis.*, vol. 10, no. 4, pp. 437–442, Jan. 1997.
[16] A. Delorme and S. Makeig, “EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis,” *J. Neurosci. Methods*, vol. 134, no. 1, pp. 9–21, Mar. 2004.
[17] T. C. Handy, *Event-related potentials: a methods handbook*. Camridge, Mass.: MIT Press, 2005.
[18] J. Kayser and C. E. Tenke, “Principal components analysis of Laplacian waveforms as a generic method for identifying ERP generator patterns: I. Evaluation with auditory oddball tasks,” *Clin. Neurophysiol.*, vol. 117, no. 2, pp. 348–368, Feb. 2006.
[19] F. Perrin, J. Pernier, O. Bertrand, and J. F. Echallier, “Spherical splines for scalp potential and current density mapping,” *Electroencephalogr. Clin. Neurophysiol.*, vol. 72, no. 2, pp. 184–187, Feb. 1989.
[20] P. L. Nunez and R. Srinivasan, *Electric Fields of the Brain: The Neurophysics of EEG*. Oxford University Press, 2006.
[21] M. X. Cohen, *Analyzing Neural Time Series Data: Theory and Practice*. MIT Press, 2014.
[22] R. Oostenveld, P. Fries, E. Maris, and J.-M. Schoffelen, “FieldTrip: Open Source Software for Advanced Analysis of MEG, EEG, and Invasive Electrophysiological Data,” *Comput. Intell. Neurosci.*, vol. 2011, p. e156869, Dec. 2010.
[23] E. Maris and R. Oostenveld, “Nonparametric statistical testing of EEG- and MEG-data,” *J. Neurosci. Methods*, vol. 164, no. 1, pp. 177–190, Aug. 2007.

[24] M. S. Worden, J. J. Foxe, N. Wang, and G. V. Simpson, “Anticipatory Biasing of Visuospatial Attention Indexed by Retinotopically Specific Alpha-Band Electroencephalography Increases over Occipital Cortex,” *J. Neurosci.*, vol. 20, no. 6, pp. RC63-RC63, Mar. 2000.
[25] G. Thut, A. Nietzel, S. A. Brandt, and A. Pascual-Leone, “α-Band Electroencephalographic Activity over Occipital Cortex Indexes Visuospatial Attention Bias and Predicts Visual Target Detection,” *J. Neurosci.*, vol. 26, no. 37, pp. 9494–9502, Sep. 2006.
[26] T. A. Rihs, C. M. Michel, and G. Thut, “Mechanisms of selective inhibition in visual spatial attention are indexed by α-band EEG synchronization,” *Eur. J. Neurosci.*, vol. 25, no. 2, pp. 603–610, 2007.
[27] A. Capilla, J.-M. Schoffelen, G. Paterson, G. Thut, and J. Gross, “Dissociated α-Band Modulations in the Dorsal and Ventral Visual Pathways in Visuospatial Attention and Perception,” *Cereb. Cortex N. Y. N 1991*, Oct. 2012.
[28] J. M. Zumer, R. Scheeringa, J.-M. Schoffelen, D. G. Norris, and O. Jensen, “Occipital Alpha Activity during Stimulus Processing Gates the Information Flow to Object-Selective Cortex,” *PLoS Biol*, vol. 12, no. 10, p. e1001965, Október 2014.
[29] P. Capotosto, C. Babiloni, G. L. Romani, and M. Corbetta, “Frontoparietal Cortex Controls Spatial Attention through Modulation of Anticipatory Alpha Rhythms,” *J. Neurosci.*, vol. 29, no. 18, pp. 5863–5872, Jun. 2009.
[30] S. Dehaene, L. Cohen, M. Sigman, and F. Vinckier, “The neural code for written words: a proposal,” *Trends Cogn. Sci.*, vol. 9, no. 7, pp. 335–341, Jul. 2005.
[31] S. Dehaene and L. Cohen, “The unique role of the visual word form area in reading,” *Trends Cogn. Sci.*, vol. 15, no. 6, pp. 254–262, Június 2011.
[32] S. Laszlo and K. D. Federmeier, “Never seem to find the time: evaluating the physiological time course of visual word recognition with regression analysis of single-item event-related potentials,” *Lang. Cogn. Neurosci.*, vol. 29, no. 5, pp. 642–661, May 2014.
[33] J. Grainger, “Cracking the orthographic code: An introduction,” *Lang. Cogn. Process.*, vol. 23, no. 1, pp. 1–35, 2008.

[34] T. Thesen, C. R. McDonald, C. Carlson, W. Doyle, S. Cash, J. Sherfey, O. Felsovalyi, H. Girard, W. Barr, O. Devinsky, R. Kuzniecky, and E. Halgren, “Sequential then interactive processing of letters and words in the left fusiform gyrus,” *Nat. Commun.*, vol. 3, p. 1284, 2012.
[35] M. X. Cohen, “Where Does EEG Come From and What Does It Mean?,” *Trends Neurosci.*, 2017.
[36] A. de Pesters, W. G. Coon, P. Brunner, A. Gunduz, A. L. Ritaccio, N. M. Brunet, P. de Weerd, M. J. Roberts, R. Oostenveld, P. Fries, and G. Schalk, “Alpha power indexes task-related networks on large and small scales: A multimodal ECoG study in humans and a non-human primate,” *NeuroImage*, vol. 134, pp. 122–131, Jul. 2016.
[37] N. Kanwisher, J. McDermott, and M. M. Chun, “The Fusiform Face Area: A Module in Human Extrastriate Cortex Specialized for Face Perception,” *J. Neurosci.*, vol. 17, no. 11, pp. 4302–4311, Jun. 1997.
[38] P. Hermann, É. M. Bankó, V. Gál, and Z. Vidnyánszky, “Neural Basis of Identity Information Extraction from Noisy Face Images,” *J. Neurosci.*, vol. 35, no. 18, pp. 7165–7173, May 2015.
[39] C. J. Price and J. T. Devlin, “The interactive account of ventral occipitotemporal contributions to reading,” *Trends Cogn. Sci.*, vol. 15, no. 6, pp. 246–253, Jun. 2011.
[40] A. Brodski-Guerniero, G.-F. Paasch, P. Wollstadt, I. Oezdemir, J. T. Lizier, and M. Wibral, “Activating task relevant prior knowledge increases active information storage in content specific brain areas,” *bioRxiv*, p. 089300, Nov. 2016.
[41] T. J. Buschman and S. Kastner, “From Behavior to Neural Dynamics: An Integrated Theory of Attention,” *Neuron*, vol. 88, no. 1, pp. 127–144, Oct. 2015.