# UNIVERSITY OF SZEGED FACULTY OF ARTS DOCTORAL SCHOOL OF EDUCATION DOCTOR OF PSYCHOLOGY PROGRAM

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# THE INVESTIGATION OF THE NEURAL BASIS OF VISUAL CATEGORIZATION IN TIPICAL DEVELOPING CHILDREN AGED 7-15 YEARS, IN ADULT AND IN DEVELOPMENTAL DYSLEXIA

Summary of PhD Thesis

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#### The theoretical background and the structure of the dissertation

The aim of dissertation was to investigate the neural basis of visual categorization and the processing of low and high spatial frequencies information in adults, in children aged 7-15, and in developmental dyslexia.

Traditionally, theories assume a hierarchical architecture behind human object recognition, in which feed-forward activation spreads from lower-level, posterior regions to higher-level, anterior cortical areas (Grill-Spector & Malach, 2004; Logothetis & Sheinberg, 1996). However, evidence also suggests that object recognition is influenced by top-down modulation of lower-level visual representations (Gilbert & Li, 2013), and prefrontal areas also play an active role in it (Bar, 2003, 2004). Several studies of top-down modulations focus on the role of the magnocellular (M) and parvocellular (P) pathways that are respectively sensitive to low (LSF) and high spatial frequencies (HSF), and propose a spatial frequencybased coarse-to-fine processing model of visual object recognition (Bar, 2003; Bullier, 2001). Whereas global characteristics of the visual input such as image layout and object shapes are primarily linked to low spatial frequency information and activity in the magnocellular system, HSF-sensitive P-neurons convey information about local stimulus details and fine texture. According to a very influential model of visual processing, coarse, LSF representation of the object is conveyed rapidly to the prefrontal cortex where representations of the most possible objects are activated, triggering predictions about object identity that are projected back to posterior, occipital areas in a top-down manner (Bar, 2003; Kveraga et al., 2007). These low spatial frequency-based predictions are verified or rejected based on the (slow) high spatial frequency information conveyed by parvocellular channel (Bar, 2003, 2004).

Despite the fact that there are several studies dealing with the effect of spatial frequencies on event-related potentials (ERPs) (mainly regarding early components over occipital regions: C1, P1, N1) (Ellemberg, Hammarrenger, Lepore, Roy, & Guillemot, 2001; Foxe et al., 2008; Hansen, Jacques, Johnson, & Ellemberg, 2011), and that in his model Bar (2003, 2004) emphasizes the role of spatial frequencies and top-down effects in visual stimulus processing, we have not found an EEG study that linked the two, or was able to confirm or disprove Bar's theory by analyzing ERPs over the entire scalp and during the first 600 ms of information processing.

Despite the fundamental nature of categorization, this cognitive process and the underlying neural mechanism appears to continue maturing after early childhood, even during

adolescence (Batty & Taylor, 2002). In addition, previous behavioral and electrophysiological studies using artificial stimuli suggest that the M- and P-channels also undergo development after early childhood (Adams & Courage, 2002; Benedek et al., 2010; Mahajan & McArthur, 2012; van den Boomen, Jonkman, Jaspers-Vlamings, Cousijn, & Kemner, 2015). However, neither behavioral, nor EEG results are clear: several experiments support the late maturation of the M-pathway and low spatial frequency processing (Adams & Courage, 2002; Benedek et al., 2010), whereas other studies argue for prolonged development of the parvocellular channel and analyzing of high spatial frequency information (Gordon & McCulloch, 1999; van den Boomen et al., 2015; van den Boomen & Peters, 2017). For these reasons, our second study focuses on examining the visual categorization processes, and how LSF and HSF information affect natural image categorization at both behavioral and electrophysiological levels in children aged 7-15 years and adults.

The damaged and weaker function of the magnocellular/dorsal (M/D) system has been verified in several developmental disorders however, in our third experiment and I the dissertation we focus on developmental dyslexia. Our goal is to emphasize the complexity of dyslexia which is proven (beside the multiplicity of symptoms) by the fact that despite the numerous examinations and approaches, it is still not clear what causes its emergence. Among the several approaches in literature, in the dissertation we focus on the theories and studies assuming a visual deficit, and within that, the deficit of magnocellular/dorsal system. There is a marked diversity in the results concerning the visual processing of dyslexics: while some of them suppose the deficit of the M/D system (Demb, Boynton, & Heeger, 1998; Eden, VanMeter, Rumsey, & Maisog, 1996; Gori, Seitz, Ronconi, Franceschini, & Facoetti, 2016; Hansen, Stein, Orde, Winter, & Talcott 2001; Lehmkuhle, Garzia, Turner, Hash, & Baro, 1993; Livingston, Rosen, Drislane, & Galaburda, 1991; Talcott et al., 1998), there are results according to which the function of both pathways is weaker (Séra et al., 2010). Morever, we may even find such study that refers to the damage of the parvocellular pathway (Farrag, Khedr, & Abel-Naser, 2002); others, however, have not verified any differences (Johannes et al., 1996; Tsermentseli et al., 2008). In these studies, artificial stimuli were used to investigate the role and function of the two channels, thus, due to our complex natural images, we attempt to solve this controversy.

In the dissertation, we take steps to draw near cognitive neuroscience, cognitive psychology, and educational science, even if these prove to be small steps, since electroencephalogram (EEG) was used to examine the age-related changes of neural processes

during visual categorization, in typically developing children aged 7-15 years and developmental dyslexics.

In the dissertation, we offer insight into the literature about the theoretical background and the electrophysiological correlates of visual categorization, and about the role of M- and P-channels. Then, we attempt to map the age-related changes of these processes and we discuss the main theoretical approaches of developmental dyslexia, especially theories assuming M/D system involvement. We present one behavioral and three electrophysiological experiments. The aim of behavioral pilot study was to test the experimental methods, procedure, stimuli and spatial frequency filtering, and to define the presentation time of images before the electrophysiological experiments. In the first EEG study we investigate the neural basis of visual categorization, and the role of low and high spatial frequency information. In the second study age-related changes of visual categorization and processing of low and high spatial frequency were examined in children aged 7-15 years and adults; and finally we investigated the visual categorization processes and functioning of the M-and P-channels in developmental dyslexia.

# Aims and hypothesis of electrophysiological experiments

# Experiment I.:

The aim of first study was to investigate how low and high spatial frequency filtering of complex natural images modifies neural activity over occipital, frontocentral and parietal regions. Traditionally, object recognition was associated with posterior regions, but recent theories suggest that frontal areas also play an active role in it (Bar, 2003, 2004; Bar et al., 2006). Therefore we investigated the role of LSF and HSF information in top-down facilitation of object categorization using natural images containing animal or vehicle. Based on previous studies using artificial stimuli (Ellemberg et al., 2001; Foxe et al., 2008; Hansen et al., 2011) we hypothesized that the C1 amplitude would be greater for stimuli containing high spatial frequencies. In case of P1 component, our hypotheses were less unambiguous, since previous study using artificial stimuli found larger P1 amplitude for low spatial frequency stimuli (Ellemberg et al., 2001; Foxe et al., 2008; Hansen et al., 2011), but Craddock et al. (2013, 2015) found a reverse pattern presenting isolated living and non-living objects on a homogeneous background. Given that the stimuli and the task in our experiments

(and dissertation) corresponded better to those reported by Craddock, Martinovic and Müller (2013, 2015), we predicted that the P1 and the subsequent N1 components would be enhanced in amplitude for stimuli containing high spatial frequencies (intact and HSF pictures). Additionally, we hypothesized that top-down effects, manifested by ERP amplitude changes spreading to anterior areas and shortening of the posterior N1 latency would also be detected in the 140–200 ms time interval. Given the two-state interactive model of visual object recognition suggests that the N350 and the LPC ("late positive complex") index post-sensory processes (Schendan & Kutas, 2007; Schendan & Lucia, 2010), we expected the amplitudes and latencies of these two components primarily to correspond to classification performance (accuracy, reaction times) (Craddock et al., 2013).

#### Experiment II.:

The aim of second study was to investigate how low and high spatial frequency information modulates behavioral data and neural activity in children aged 7-15 years during complex natural image categorization. We analyzed the classification accuracy, reaction times and modulations of amplitude and latency of the visual P1 and N1 at occipital electrodes. Based on previous study results, we hypothesized that sensitivity to LSF and HSF information continues to develop in school-aged children, but at a different speed and pattern, with slower maturation of the magnocellular pathway (Adams & Courage, 2002; Benedek et al., 2010). We predicted that this effect would be observable both on the behavioral data and by electrophysiological correlates when subjects are asked to categorize natural images, a task that heavily relies on processing low spatial frequency image properties. These results would support the different developmental speed of magnocellular and parvocellular pathway. In literature, there are few studies which focus on electrophysiological correlates of processing visual stimuli optimized for the M- and P-channels and there are some contradictions. Therefore, by studying the electrophysiological correlates and developmental patterns of LSF vs. HSF processing with complex images, we can get closer to understanding the neural basis of this process and the role of low and high spatial frequency information conveyed by Mand P-channels in natural image categorization during school-age.

## Experiment III.:

In the third EEG study we investigate the modulatory effect of low and high spatial frequency filtering on accuracy, reaction time and on the amplitude and latency of early

event-related potentials (visual P1 and N1) above the occipital regions in typical developing and dyslexic children. We are seeking the answer for the question, whether there is a difference between the two groups, and if so, in which frequency range. Several studies demonstrated the deficit of the M/D system in developmental dyslexia (Demb et al., 1998; Eden et al., 1996; Gori et al., 2016; Hansen et al., 2001; Livingstone et al., 1991). However, the results are not clear, since we can also read studies which disprove the selective deficit of the M-channel (Amitay, Ben-Yehudah, Banai, & Ahissar, 2002; Farrag et al., 2002; Johannes, Kussmaul, Münte, & Mangun, 1996; Tsermentseli, O'Brien, & Spencer, 2008). In the current study, we also attempt to map the plausible deficits in the visual processing, since using our complex modified images we may find the answer to the question, whether the selective damage of the M/D system characterizes dyslexics; or much rather, there is a general deficit affecting both channels. We hypothesized that dyslexic children will categorize images containing low spatial frequencies worse, which will manifest mainly in more inaccurate categorization. Furthermore, we predicted, that in the case of EEG correlates the immaturity of the M-pathway will manifest in the changes of the P1 component. To our knowledge, no study has used similar complex natural stimuli focusing on magnocellular deficit in dyslexia, so our experiment can by all means produce interesting and important results.

#### **Participants**

Experiment I.: twenty-one healthy adults (mean age: 23.9, SD: 3.48, 13 females) participated in an animal vs. vehicle categorization task. Experiment II.: ninety six participants aged between 7-30 years were clustered into five age groups: 7–8 (N=19, mean age: 7.74, SD: 0.45, 10 female), 9–10 (N=20, mean age: 9.45, SD: 0.51, 12 female), 11–12 (N=20, mean age: 11.4, SD: 0.50, 8 female), 13–15 year-old children (N=16, mean age: 13.75, SD: 0.77, 11 female), and adults (N= 21, mean age: 23.90, SD: 3.48, 13 female). Experiment III.: fifteen developmental dyslexic (mean age: 12, SD: 1.732) and age, gender and class matched typically developing children (mean age: 11.67, SD: 1.49) from Experiment II.

#### Stimuli, methods and procedure

Images containing either an animal or a vehicle were selected from a commercially available collection (Corel Photo Library). All pictures had a resolution of 75 pixels/in., and size of 256 × 256 pixels. Three stimulus types were used: intact grayscale stimuli and their low spatial frequency or high spatial frequency modified versions. Color extraction and spatial frequency filtering were done with Adobe Photoshop CS5 (Adobe Systems Inc., San Jose, USA) to match images used in a previous study (Bar et al., 2006). Low-pass filtering was carried out with a Gaussian blur filter (6.1 pixel kernel), whereas high-pass filtering was performed with a radius of 0.3 pixels.

The stimulus battery included 1080 images, 180–180 stimuli containing either an animal or a vehicle, in intact, low or high spatial frequency modified versions. Each participant viewed 360 pictures in a randomized order (120 per stimulus type, 50% of them containing animals and 50% vehicles). Each pictures was presented only once to a given subject (either in its intact, LSF or HSF version), counterbalanced across participants.

Participants were seated in a dark and sound-proof room, 110 cm from screen to perform animal vs. vehicle categorization task. The E-Prime software (Psychology Software Tools, Inc., Sharpsburg, USA) was used for stimulus presentation. A forced-choice animal vs. vehicle categorization task was used. Participants were instructed to press one of the two response buttons with their left or right index finger. Response buttons for two categories were counterbalanced across subjects. Pictures were presented for 2000 ms, but participants were asked to press the correct button as fast as they could. Inter-stimulus interval was randomized between 1000 and 1500 ms. Behavioral data (accuracy and reaction time) and electrophysiological correlates were analyzed during natural image categorization. We used a 32-channel BioSemi ActiveTwo DC Amplifier (BioSemi B. V., Amsterdam, Netherlands) for EEG recordings. We performed different types of ERP data analyses. In the first study three types of analyses were used to investigate how low and high spatial frequencies influence neural activity during animal vs. vehicle categorization task: (1) the point-by-point permutation analysis was used for the pairwise comparison of two ERP waveforms (Intact vs. LSF, Intact vs. HSF or LSF vs. HSF); (2) the scalp-wide analysis was performed in time intervals of posterior C1, P1, N1, and frontocentral N350 components (80–110 ms, 120–160 ms, 170-210 ms, 300-400 ms); (3) and finally we examined latencies of posterior C1, P1 and N1, frontocentral N350, and centroparietal LPC components. Experiment II. and III.: amplitude and latency of visual P1 and N1 components were analyzed at occipital regions.

# Results of the Experiment I.

In the first study we investigated the role of low and high spatial frequency information in top-down facilitation of object categorization using intact complex natural images and their LSF and HSF modified versions, containing animals or vehicles. We examined the modulatory effect of spatial frequencies on behavioral data (classification accuracy, reaction times) ERP amplitudes/latencies measured above occipital, frontocentral and parietal regions and scalp maps were compared among the three stimulus conditions to understand the dynamics of neural activity.

When examining the effect of stimulus type on accuracy and reaction times obtained during an animal vs. vehicle classification task, we observed that participants were significantly less accurate and slower for pictures containing low spatial frequencies only.

The C1 amplitude was larger for high spatial frequency images, which is in line with results reported in the literature (Ellemberg et al., 2001; Foxe et al., 2008; Hansen et al., 2011). When analyzing the P1 component, an opposite pattern was observed over the occipital midline region and at the left and right parietal sites (P7 and P8 electrodes). P1 amplitude was greater for low spatial frequency stimuli at the occipital electrodes which is in accordance with results of previous studies using artificial stimuli (Ellemberg et al., 2001; Hansen et al., 2011) and LSF and HSF modified faces (Nakashima et al., 2008). We found reverse pattern at the electrodes above the left and right parietal sites (P7, P8 electrodes), with larger P1 amplitude for high spatial frequency pictures. Craddock and colleagues (2013, 2015) found similar effect laterally at occipitotemporal scalp sites using similar task condition and isolated object as stimuli.

With regard to the posterior N1, amplitudes for high spatial frequency stimuli were more negative than in the other two image conditions, and intact stimuli containing high spatial frequencies evoked larger N1 amplitudes than low spatial frequency pictures. This finding is also in line with the results of Craddock, Martinovic and Müller (2013, 2015) pointing towards the posterior N1 component indexing fine-grained discrimination processes (Vogel & Luck, 2000).

Over frontal areas, the modulatory effect of spatial frequency filtering could be observed from approximately 180 ms (in time interval of posterior N1 component), both by the scalp-wide and by the point-by-point permutation analysis. In accordance with findings of Bar et al. (2006) using MEG and fMRI, neural activity evoked by high spatial frequency stimuli differed from intact and low spatial frequency stimulus conditions, indicating differential involvement of frontal areas in the processing of LSF information conveyed by the M-pathway. In addition to the spread of spatial frequency-based amplitude modulations to frontal regions, the longer latencies to high spatial frequency stimuli at posterior electrodes around the time rage of the posterior N1 are also indicative of top-down modulation of visual processing (Pollux, Hall, Roebuck, & Guo, 2011). A plausible explanation for the longer N1 latencies to high spatial frequencies images might be the faster information processing of the M-channel (Craddock et al., 2015), but the absence of such latency differences for the preceding C1 and P1 components contradicts this idea, and support the hypothesis that top-down processes in this time interval also affect the processing of visual categorization.

When examining electrophysiological results at anterior sites, ERPs did not show significant differences until ~320 ms between images containing LSF information (intact vs. LSF). Results observed in time range of frontocentral N350 amplitudes for LSF and HSF images are in line with previous results (Craddock et al., 2013). At this point it is not clear why this waveform was larger in amplitude for intact images than for the two modified stimulus conditions. These results suggest that the object model selection is determined to a great extent by the complexity of stimuli and the depth of analysis, to which all the spatial frequencies must be present.

Among the components analyzed in Experiment I., the amplitude and latency of the LPC registered above centroparietal regions were the only indicators that reflected the behavioral data, since significantly smaller amplitudes and longer latencies were detected for low spatial frequency stimuli, which were categorized with the worst accuracy and longest reaction times. Thus, the effect of spatial frequency extraction influenced the late time interval of visual processing, ERPs for intact and HSF images were markedly different from those recorded for low spatial frequency stimuli. The moderate positive correlations between LPC latencies and reaction times in the intact and high spatial frequency stimulus types strengthen the notion that this component represents the end of the stimulus processing (Falkenstein, Hohnsbein, & Hoormann, 1994).

In the first experiment, we have presented that even the scalp map analysis and the assessment of ERP amplitude and latency changes might be sensitive enough to find evidence for Bar's model (2003) assuming the involvement of low spatial frequency information conveyed by M-channel in the generation of top-down predictions. Moreover, our results indicate that the low or high spatial frequency filtering also affects later ERP waveforms indexing object model selection (N350) and secondary categorization processes (LPC) (Schendan & Kutas, 2007; Schendan & Maher, 2009), with only the latter reflecting the behavioral performance of the subjects directly.

# Results of the Experiment II.

The aim of Experiment II. was to investigate how low and high spatial frequencies affect behavioral data and early visual components (P1 and N1) registered over the occipital region in children aged 7-15 years and adults during an animal vs. vehicle categorization task.

We found robust age-related changes in classification accuracy and reaction times with the age increasing, both with behavioral correlates indicating better performance in older participants. While reaction times were gradually reducing with age, a relatively abrupt improvement of accuracy was observed after the age of 7-8 years. Although age-related modulations of accuracy were detected for each stimulus type, greater accuracy improvements were present between 7-12 years of age for LSF stimuli. The results can be interpreted as evidence for the prolonged development of the magnocellular pathway (Adams & Courage, 2002; Benedek et al., 2010).

Nonetheless, we think that categorization accuracy should be interpreted with caution because it does not exclusively reflect activity of the magnocellular or parvocellular channels, and the processing of low or high spatial frequencies. In this respect, it is important that categorization of natural images was shown to rely on non-visual areas as well, such as the prefrontal cortex (Freedman, Riesenhuber, Poggio, & Miller, 2001; Ganis, Schendan, & Kosslyn, 2007; Thorpe & Fabre-Thorpe, 2001). According to an influential model of visual object recognition, the prefrontal cortex receives coarse, LSF information from early visual areas, and triggers predictions about object identity that are projected back to posterior regions in a top-down manner (Bar, 2003). Therefore, any age-related changes in accuracy of low spatial frequency pictures can as easily be attributed to the suboptimal functioning of the

magnocellular channel, as to the decreased sensitivity of cortical neurons to LSF information, to the relative immaturity of the frontal lobe, or to weak top-down effects.

We observed age-related changes both for P1 and N1 components with increasing age, a result that is in accordance with literature data for intact images (Batty & Taylor, 2002; Itier & Taylor; 2004; Mahajan & McArthur, 2012; Peters, Vlamings, & Kemner, 2013; van den Boomen et al., 2015; van den Boomen & Peters, 2017). By analyzing parameters of the early visual components in five age groups, we found that the sensitivity of the P1 and N1 amplitudes to spatial frequencies in 7-8-year-olds is the reverse of what is observed in adults in Experiment I. and what is found in literature (Craddock et al., 2013; Ellemberg et al., 2001; Hansen et al., 2011). A similar revers pattern was reported for P1 earlier by Boeschoten and colleagues (2007), but that study involved only children between 9-10 years. To our knowledge, this work is the first to report reverse patterns of spatial frequency sensitivity of the P1 and N1 components in early school-age relative to adulthood with the involvement of several age groups.

In adults, visual P1 component traditionally is associated to the processing of LSF information (e.g. Hansen et al., 2011), however our findings suggest that in contrast to adults, in early school-age P1 is more sensitive to the local image properties, to the details of stimulus, and with age this component becomes increasingly sensitive to low spatial frequency, global information. These results indicate a gradual shift from high spatial frequencies to low spatial frequency information, and similarly to accuracy suggest the prolonged maturation of LSF processing.

Similarly to P1 amplitude, opposite pattern of spatial frequency-sensitivity of the N1 was found in early school-age relative to adulthood, since in childhood larger N1 amplitude was observed for LSF images. In literature, previous studies involving adults have linked the N1 component not only to the processing of high spatial frequency and local stimulus details, and fine-grained discrimination processes (Craddock et al., 2013, 2015; Vogel & Luck, 2000), but also to top-down effects that facilitate object recognition (Hopf et al., 2002; Melloni, Schwiedrzik, Müller, Rodriguez, & Singer, 2011; Schendan & Lucia, 2010). As mentioned earlier, it was suggested that the rapid transmission of LSF information to prefrontal regions triggers feedback projections that affect the analysis of high spatial frequency inputs (Bar, 2003). In this regard, age-related changes in N1 in our study possibly reflect the maturation of LSF-based top-down processes as well. Developmental changes of this LSF-based top-down effect were principally supported by age-related changes of peak-to-peak latency of the LSF-

evoked N1 which gradually reduced with age. This effect cannot be explained by the myelination of the magnocellular channel, since similar latency reductions were not found in the time interval of P1. Given that shorter N1 latencies evoked by coarse, gist-like LSF information have been associated with top-down effects in adults (Experiment I.), age-related N1 latency reductions for low spatial frequency images can be interpreted as signatures of the maturation of the cortical feedback system (Giedd et al., 1999; Nagy, Westerberg, & Klingberg, 2004).

In Experiment II., we present electrophysiological evidence for the ongoing maturation of cortical processing of both low and high spatial frequencies in late childhood and adolescence. By analyzing the early visual components associated with the categorization of natural complex images, we found that the sensitivity of the P1 and N1 amplitudes to spatial frequencies in 7-8-year-olds is the reverse of what is observed in adults. However, based on literature about the neural mechanisms of image categorization and brain development, together with developmental and spatial frequency-related changes in early visual components, we came to the conclusion that neither behavioral nor ERP parameters reflect exclusively the maturation of the magnocellular and parvocellular channels, so we think that developmental effect of LSF and HSF processing should be interpreted with caution. Based on behavioral an EEG data we suggest that in early school-age cortical processing of both low and high spatial frequencies develop and are influenced by a number of factors including (but not limited to) maturation of subcortical channels and processing of visual inputs in occipitotemporal regions. We argue that greater improvement observed in accuracy for LSF stimuli could has been due to the development of LSF information processing, as well as the maturation of top-down effects, which idea is confirmed by age-related changes of N1 peakto-peak latencies evoked by LSF pictures. Our main result is the shifting sensitivity of the P1 and N1 components to low and high spatial frequency information with increasing age. We used complex images with objects embedded in natural and man-made scenes, which is in contrast to previous studies presenting abstract, artificial stimuli or isolated objects on a homogeneous background. This difference could explain why no such pattern has ever been shown in the early visual eletrophysiological correlates, which further support our theory about the complexity of this process.

## **Results of the Experiment III.**

The aim of the third EEG study was to map the modulatory effect of spatial frequency extracting on behavioral data and on parameters of early visual components (P1 and N1) above the occipital regions during animal vs. vehicle categorization task in typical developing and dyslexic children. We examine whether there is a difference between the two groups and if so, in what frequency range.

According to the accuracy, dyslexics in the case of LSF images were less accurate, however such differences were not found for intact and high spatial frequency stimulus types. This pattern may indicate the weaker function of the magnocellular channel and the suboptimal processing of the LSF information in developmental dyslexia. The results are in accordance with those of previous behavioral studies, which also call attention to the weaker function of the M-pathway in dyslexia (Gori et al., 2016; Hansen et al., 2001; Talcott et al., 1998).

Although the result of the accuracy data indicate the reduced function of the M-channel and the selective deficit of the processing of low spatial frequencies, the electrophysiological correlates suggest a much more complex pattern, since in case of EEG data we did not find such changes that would verify exclusively the deficit of the magnocellular pathway. Although in the case of the P1 amplitude (similarly to the accuracy) for LSF stimuli a greater difference was observed between the two groups, still, a statistically significant difference was not verified. It is important to note that according to our analysis that aimed at the normalization of the differences among participants, tendentious difference was found between the typical developing and dyslexic groups in the relation of the intact and the LSF pictures: in the case of dyslexics, the intact/LSF relation is larger than in the control group. This pattern and effects suggest that the magnocellular pathway and the processing of low spatial frequencies are less mature in developmental dyslexia.

A similar effect was observed for N1 latency. Where the ANOVA did not show significant difference, observed effect was confirmed by our analysis aimed at the normalization of the differences among subjects, since tendentious differences were found. Namely, the relations of LSF/HSF images latencies differ between two groups. This effect is mainly due to the fact that in the case of typical developing control group, the low spatial frequency stimuli evoke shorter N1 latency than HSF images; however, in dyslexic children,

the pattern is the reverse. Since in adults the shorter N1 latency evoked by coarse, low spatial frequency information seems to reflect top-down effects (Experiment I.), and the results of Experiment II. seem to confirm it, the age-related N1 latency shortening for low spatial frequency stimuli may be interpreted as the development of the cortical "feedback system", in this way. Thus in the case of dyslexic children, the longer N1 latency for low spatial frequencies may suggest weaker top-down processes. These results are in accordance with the recent theories, which emphasize the role of top-down effects and predictions from higher associational regions in reading (Price & Devlin, 2011).

These results also draw attention to that fact that accuracy data should be interpreted more carefully. The result that significant difference for LSF images was found in case of accuracy only suggest that, in the background of the effect manifested in behavioral data there may be something else beside the reduced function of the M-pathway. As mentioned earlier, it seems that the categorization of natural complex images was shown to rely on other, non-visual areas, such as the prefrontal cortical regions (Bar, 2003; Freedman et al., 2001; Ganis et al., 2007). Accordingly, it is possible that the immature magnocellular channel and the weak top-down effects together result in the less accurate categorization for the LSF images in dyslexic group. Our results of analysis aimed at the normalization of the differences among subjects also support this idea, with tendentious effects for the P1 amplitude and the N1 latency.

In sum, apart from the analysis to the normalization of the differences among participants, in case of the EEG data we did not observe such statistical differences between the two groups that would unambiguously confirm the deficit of the magnocellular pathway, however, our results are in accordance with those of Livingstone et al. (1991) and Lehmkuhle et al. (1993), since the accuracy and the pattern of the P1 amplitudes and the N1 latencies suggest the damage of the M-channels, which seems to be confirmed by the analysis for the relation between the image types. Based on these results we do not assume that the deficit of the M-cells/pathway is exclusive in the background of developmental dyslexia; rather we think that there are several factors behind dyslexia, as the weaker function of the M-system does not alone explains our accuracy results. It seems that the magnocellular deficit does not alone explain developmental dyslexia, but it may be much rather an important part of a complex pattern. These results confirm the view that dyslexia is a multifactorial disorder, characterized by a number of deficits which together result in a reading disorder (Menghini et al., 2010).

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# Studies forming the basis of and related to the thesis

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