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Neural entrainment to musical rhythms in dyslexia DIPLOMA THESIS

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Annotation:	Previous researce domain. Particul information abo seems that dysle be caused by the in speech as well new intervention	ch suggests that j arly, there is a det ut prosody and rh ctics have probled dysfunction of bi l as in music. Res n and prevention	primary deficit in dyslexia is in the auditory eficit in perception of acoustic features carrying hythmic characteristics of speech. Moreover, it ems with musical rhythm perception, what may orain regions responsible for rhythm perception esearch in this area may lead to development of a methods in the future.
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- Názov:
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 Synchronizácia mozgu s hudobnými rytmami pri dyslexii
- Ciel': Naštudujte si literatúru v oblasti moderných teórií dyslexie, so zameraním na vnímanie rytmu. Navrhnite experiment s použitím metódy EEG a s dôrazom na neurálne spracovanie hudobného rytmu v populácii dospelých dyslektikov. Uskutočnite navrhnutý experiment, spracujte a vyhodnoť te dáta.

Literatúra: Goswami, U. (2011). A temporal sampling framework for developmental dyslexia. Trends in Cognitive Sciences, 15(1), 3–10. http://doi.org/10.1016/j.tics.2010.10.001
 Nozaradan, S. (2014). Exploring how musical rhythm entrains brain activity with electroencephalogram frequency-tagging. Philosophical Transactions of the Royal Society B: Biological Sciences, 369(1658), http://doi.org/10.1098/rstb.2013.0393

Anotácia: Predchádzajúce výskumy na dyslektickej populácii naznačujú, že primárny deficit u týchto jedincov má sluchový charakter. Ide o problémy s vnímaním akustických vlastností rečového signálu, ktoré poskytujú informácie o prozódii a rytmických charakteristikách reči. Taktiež sa ukazuje, že dyslektici majú problém s vnímaním hudobného rytmu, čoho príčinou môže byť dysfunkcia oblastí mozgu zodpovedných za vnímanie rytmu tak v reči ako aj v hudbe. Výskum v tejto oblasti môže v budúcnosti prispieť k vývoju nových intervenčných a prevenčných metód.

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I hereby declare that the work presented in this thesis is original and the result of my own investigations. Formulations and ideas taken from other sources are cited as such.

Abstract

Across languages, dyslectic individuals have problems with the accurate neural representation of phonological aspects of speech. Recently proposed "temporal sampling framework" (TSF) suggests that this phonological deficit may arise from the reduced sensitivity to speech prosody and syllable structure. State of the art neural models of speech perception suggest that auditory system "samples" continuous speech by entraining (phase-locking) endogenous oscillatory activity to its spectro-temporal modulation patterns at different timescales. TSF proposes that dyslectics may exhibit atypical entrainment at slow frequencies (<10 Hz), corresponding to syllable and prosodic structure of speech. This would explain the observed difficulties in perceiving speech rhythm and its acoustic correlates.

Given the fact that speech and music both exhibit rhythmic metrical structure and neural oscillations seem to play an important role in processing of this structure, TSF predicts deficits also in tasks involving musical rhythm. Dyslectics indeed show difficulties in behavioral tasks requiring musical rhythm perception, sensorimotor synchronization, and also impaired neural entrainment to simple rhythmic stimuli. However, no study has investigated neural correlates of complex rhythm perception, which gives rise to representation of a metrical structure.

This thesis attempts to build upon the suggestion of TSF that dyslectics are "in tune but out of time". An overview of recent literature is provided with the focus on the role of oscillatory entrainment in processing of speech and music, and in particular rhythmic aspects of both domains. Empirical evidence supporting the hypothesis that dyslectics have difficulties with processing rhythmic aspects of speech and music is reviewed. Results of studies suggesting that these difficulties stem from a deficit in neural entrainment are presented.

A small-sample experiment was carried out to examine neural entrainment to musical meter in adult dyslectics and control participants. While EEG was recorded, subjects listened to either metrically simple of complex rhythm. It was hypothesized that the overall magnitude of neural entrainment at meter related frequencies will be lower in dyslectics. This effect should be particularly manifested in the complex rhythm, as it places higher demands on the brain networks that are supposed to process temporal structure in sound.

However, no supportive evidence was found for either hypothesis. The results are discussed with respect to recent neuroscientific theories of dyslexia and musical rhythm processing.

Abstrakt

Naprieč rôznymi jazykmi, ľudia trpiaci dyslexiou vykazujú problémy s detailnou reprezentáciou fonologických aspektov reči. Nedávno navrhnutá "teória časového vzorkovania" (TSF, z angl. "temporal sampling framework") tvrdí, že tento fonologický deficit môže byť zapríčinený zníženou citlivosťou vo vnímaní prozodických vlastností reči a štruktúry slabík. Moderné neurálne modely percepcie reči naznačujú, že sluchový systém "vzorkuje" spojitú reč pomocou synchronizácie fázy endogénnych oscilácií mozgu s jej spektro-temporálnou štruktúrou v rôznych časových intervaloch súčasne. TSF tvrdí, že dyslektici vykazujú netypickú synchronizáciou v nízkych frekvenciách (<10 Hz), ktoré zodpovedajú slabikovej a prozodickej štruktúre reči. Tento deficit by mohol vysvetliť ťažkosti s percepciou rytmických vlastností reči a ich akustických korelátov, ktoré boli pozorované u ľudí s dyslexiou.

Na základe toho, že aj reč aj hudba vykazujú rytmickú a metrickú štruktúru a neurálne oscilácie hrajú dôležitú rolu pri percepčnom spracovaní tejto štruktúry, TSF predpokladá u dyslektikov deficity taktiež v kognitívnom spracovaní hudobného rytmu. Dyslektici naozaj vykazujú ťažkosti pri úlohách zahŕňajúcich vnímanie hudobného rytmu, senzo-motorickú synchronizáciu a tiež je u nich narušená mozgová synchronizácia s jednoduchými rytmickými podnetmi. Avšak žiadna štúdia doteraz neskúmala neurálne koreláty percepcie komplexných rytmov, ktoré navodzujú reprezentáciu metrickej štruktúry.

Táto diplomová práca sa pokúša stavať na výroku, že dyslektici sú "naladení, ale mimo rytmu". Je v nej ponúknutý prehľad literatúry, zaoberajúcej sa úlohou synchronizácie oscilácií v spracovaní reči a hudby, obzvlášť ich rhytmických aspektov. Práca taktiež poskytuje prehľad empirických dôkazov v prospech hypotézy, že dyslektici majú problémy so spracovaním rytmických apektov ako reči, tak hudby a tieto ťažkosti pramenia z deficitu v mozgovej synchronizácii.

V rámci tejto práce bola tiež vykonaná štúdia na malej vzorke dospelých dyslektikov a kontrolných participantov. Participanti počúvali metricky jednoduchý alebo komplexný rytmus, a súčasne im bolo snímané EEG. Predpokladalo sa, že celková magnitúda mozgovej synchronizácie s frekvenciami súvisiacími s metrom daného rytmu bude u dyslektikov nižšia. Tento efekt by sa mal prejaviť silnejšie v metricky komplexnom rytme, keď že tento kladie vyššie nároky na siete mozgu, ktoré sa podieľajú na spracovaní temporálnej štruktúry zvuku.

Napriek očakávaniam sa hypotézy nepotvrdili a tento výsledok je diskutovaný vzhľadom na súčasné neurovedecké teórie dyslexie a percepcie hudobného rytmu.

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Abbreviations

AC	auditory cortex
AM	amplitude modulation
AST	asymmetric sampling in time hypothesis
BG	basal ganglia
CSD	current source density
DAT	dynamic attending theory
EEG	electroencephalography
ENV	amplitude envelope
ERP	event-related potentials
FFT	Fast Fourier transform
FM	frequency modulation
IOI	inter-onset interval
ITC	inter-trial coherence
ITI	inter-tap interval
LFP	local field potentials
mCBGT	motor cortico-basal-ganglia-thalamo-cortical circuit
MEG	magnetoencephalography
MMN	mismatch negativity
MTRM	multi-time resolution model
MUA	multi-unit activity
PA	phonological awareness
PMC	premotor cortex
preSMA	presupplementary motor area
RAN	rapid automatized naming
S-AMPH	spectral-amplitude modulation phase hierarchies
SS-EP	steady state-evoked potentials
TFS	temporal fine structure
TMS	transcranial magnetic stimulation
TSF	temporal sampling framework
VLPFC	ventrolateral prefrontal cortex
VSTM	verbal short-term memory

1 Introduction

Developmental dyslexia is a common learning disorder that is characterized by severe difficulties in reading and spelling despite normal intelligence, adequate opportunities to learn and no overt neural or sensory deficit. In the modern world where the ability to read is a crucial skill this disorder represents a major problem. This calls for a development of efficient therapeutic interventions that would ameliorate the difficulties of people who suffer from dyslexia. However until now, the underlying cause of dyslexia remains unknown. Scientific investigation led to proposals of multiple theories that suggest quite heterogenous range of underlying deficits. For instance, Ramus and Ahissar (2012) reported 12 competing theories of developmental dyslexia. However the aim of this thesis is not to provide an extensive critical review of all theories that have been proposed to explain the reading deficits in dyslexia. Rather this work focuses on one particular theory that has been recently proposed and tries to formulate and test hypotheses based on this theory.

It is widely accepted that dyslectics have problems with representing and processing phonological aspects of speech. "Temporal sampling framework" (TSF) belongs to a category of theories which attempt to explain this phonological deficit by an underlying subtle low-level sensory deficit. TSF proposes that this deficit involves perception of prosodic aspects of speech and its neurological basis may be in atypical neural oscillatory activity.

Recent research into the function of neural oscillations suggests that precise alignment of the oscillatory phase with the temporal structure of the stimulus is an important mechanism in speech processing, but also in processing of musical rhythms. This thesis aims to show that impairments in oscillatory entrainment could account for the pattern of difficulties that can be observed in dyslexia, namely processing of rhythmic structure of speech and music.

The present thesis can be considered to consist of basically three parts. The first two are dedicated to speech and music respectively. The aim is to provide an overview of recent findings regarding the role of neural oscillatory entrainment in both domains, particularly concerning the processing of temporal structure. A review of empirical evidence suggesting that dyslectics have difficulties in processing that temporal structure is presented and possible links with atypical neural oscillations are highlighted. Throughout the thesis, the role of motor system is emphasized with regard to temporal structure processing and possible links with low-frequency oscillatory entrainment suggested by recent findings are outlined. In the third part, based on the previously reviewed literature, two hypotheses are set and tested in an experiment and the results are discussed.

2 Neural oscillations

From vibrating bridges to circadian rhythms, walking and music, periodic oscillations are ubiquitous phenomenon in the nature. Oscillations are present in the brain on multiple levels. Single neurons demonstrate sub-threshold oscillations of membrane potential which reflect states of depolarization and hyperpolarization. The current state of the membrane affects the probability of firing. Different neurons can have different natural resonant frequencies to which they selectively respond (Wang, 2010). Similarly as in single neurons, at the level of neuronal populations, oscillatory activity can be recorded, again not reflecting action potentials directly, but rather sub-threshold changes in the probability of firing in the neuronal ensemble, i.e. local neuronal excitability (Young & Eggermont, 2009). When recording electric potential changes from brain tissue, transmembrane currents from adjacent neurons (but also glia) are summed and contribute to the extracellular field changes. The most prominent contribution rises from slow synaptic transmembrane currents (excitatory or inhibitory) that create electrical dipoles which are slow enough to be temporally summed (in contrast to action potentials). Spatial summation of multiple dipoles is possible in cortical pyramidal neurons due to the fact that they are aligned in columns (when not spatially aligned, individual dipoles cancel out) and therefore it is possible to record field potentials from the cortex. However, the origin of field potentials is rather complex and currently there are many different sources suggested to contribute to the recorded signal (Buzsáki, Anastassiou, & Koch, 2012)

Field potentials can be recorded with electrodes placed directly on the brain surface or penetrating brain tissue (local field potentials, LFP) or from scalp surface (scalp electroencephalography, scalp EEG). Magnetic fields that arise from electrical brain activity can be measured with magnetoencephalography (MEG). Closer to a particular source of electrical activity the recording site is, more contribution from this source is recorded. Once moving further away from a particular source, its contribution to the signal diminishes substantially and contributions from larger pool of neurons are intermixed in the signal. Additionally, especially in scalp EEG the signal is spatially smeared by different conductivities of the tissues separating brain and electrode. From here, we will refer to the periodic fluctuations in this meso- or macroscopic field potentials as brain oscillations (or neural oscillations).

Brain rhythms were the first characteristic brain activity that was observed at the very beginning of electroencephalography research. Hans Berger in 1920s was the first who observed a prominent periodic oscillations of the electrical brain activity that he called alpha rhythm (Stone & Hughes, 2013). Later on, oscillations were observed at multiple frequencies ranging from 0.05 to 500 Hz. Researchers (based on experimental observations) subsequently divided this interval into several bands with center frequencies separated by identical linear distances on a natural logarithmic scale and

dubbed them with greek letters (delta, theta, alpha, beta, gamma) (Buzsaki & Draguhn, 2004). Although activity at different frequency bands has been linked with different brain states (e.g. deep sleep with delta activity), it was mainly associated with brain idling (the state when brain is not "working"). With rapid development of event-related potentials (ERP) research, it was assumed that the brain is a purely "reactive device" where all background activity (including intrinsic oscillations) was considered noise which needed to be eliminated by averaging techniques. Only at the beginning of a new century an interest in brain oscillatory activity has been restored and important role of oscillations in cognition has been more and more recognized.

Neural oscillations have multiple functional roles in brain information processing. One of the most important ones is a functional binding of neuronal assemblies. Neuronal populations that take part in a particular computation may be spatially separated which causes time delays in action potentials transmission. Synchronizing both populations at the same oscillatory frequency is an efficient way to achieve sensitivity of an upstream network to projections from a downstream assemblies by providing longer integration times. This linking of neuronal ensembles can take part in a small local networks when simple computations are carried out. At the small scale, high frequency oscillations are employed in neuronal binding (such as gamma). On the other hand, when large populations separated by long distances need to be coupled, low frequency bands are used (such as delta or theta) (Buzsáki, 2006).

As noted before, techniques like LFP, scalp EEG and MEG measure changes in electric potentials generated mainly by slow transmembrane currents that occur simultaneously in large populations of neurons, although they differ in spatial resolution (and therefore the relative size of neuronal population that needs to be temporally synchronized in order to be measurable by a particular technique). Oscillations in brain electric potentials can be observed in cortical layers measured with LFP. When this data are transformed into current source density (CSD) (second spatial derivate of LFP, which eliminates volume conduction effects) oscillations can be seen as an inward and outward current flow through the membranes (current sinks and sources). It has been shown that these current fluctuations affect multiunit activity (MUA) which represents neuronal population firing, such that the firing is increased at sinks and decreased at sources (Buzsaki & Draguhn, 2004). Hence similarly to the probability of firing of individual neuron depending on its current state (i.e. depolarized or hyperpolarized), at the neural assembly level this probability depends on the oscillatory phase the network is in. This rhythmic fluctuations of excitability entail the fact that the probability of processing the input to the network is higher at a particular phase of the oscillatory cycle (this is called preferred phase), while it is considerably low at the opposite phase.

2.1 Neural entrainment

Although oscillatory activity is an intrinsic property of brain networks (i.e. it is self-sustained even without any external input) it can be influenced by the environment by changing the frequency, phase or amplitude of ongoing oscillations. Moreover, when an input from the environment is itself rhythmic, intrinsic brain oscillations adjust their phases (phase-lock) with the temporal structure of this stimulus (Galambos, Makeig, & Talmachoff, 1981). This is called neural entrainment and it has been a widely studied phenomenon in cognitive neuroscience in recent years.

In the context of rhythmically structured stimulus, the brain seems to take advantage of the stimulus temporal structure by resetting the phases of endogenous oscillations (especially low frequency oscillators) in sensory cortices, in order to align the high excitability phase with the time when the input of interest is expected to occur (Besle et al., 2011; Morillon & Schroeder, 2015; Schroeder & Lakatos, 2009). Modulatory effect of the momentary oscillatory phase on neuronal activity has been shown for oscillations in multiple frequency bands, including slow delta, theta and fast gamma rhythms. Moreover there is a notable relationship between oscillations at different frequencies called cross-frequency coupling (see Figure 1), where the phase of slower oscillation modulates the amplitude of faster oscillation (Lakatos, 2005). Hence a hierarchy of oscillations emerges where changes in slow frequency phase cause changes throughout the whole system (e.g. gamma amplitude is modulated by theta phase and theta amplitude is modulated by delta phase).

Aligning high excitability phases with expected rhythmic stimulus occurrence can be used for attentional streaming in complex environments. Lakatos et al. (2013) presented monkeys with two concurrent streams of repetitive tones. Each stream contained tones of different spectral properties (5.7 vs. 16 kHz) presented at different rate (1.6 vs. 1.8 Hz). When monkeys attended to one stream, slow neural oscillations in their auditory cortex entrained to the rate of this particular stream. Moreover, as auditory cortex is tonotopically organized, the narrow region tuned to the task-relevant spectral content and remaining neuronal population (not tuned to the relevant stimulus features) were entrained in opposite phases (see also O'Connell, Barczak, Schroeder, & Lakatos, 2014). This means that neural oscillations may promote attentional streaming by rhythmically enhancing excitability of regions representing expected stimulus properties, while at the same time suppressing excitability in the irrelevant regions. Thus neuronal oscillations in sensory cortices can create a precise spectro-temporal filter that sharpens selectivity of sensory brain networks to the task-relevant stimuli.

These findings lend support to an attentional theory (postulated 40 years ago) which proposes that attention is not a continuous process, but exhibits periodic fluctuations. Dynamic attending theory (DAT) suggested that endogenous attentional oscillators (as an abstract entity) can be synchronized with temporally structured stimulus, thus allocating attentional resources (and enhancing stimulus processing) toward expected points in time (Large & Jones, 1999). DAT has been supported by many

studies showing enhanced processing of perceptual events that can be temporally predicted in a rhythmic context (e.g. Lawrance, Harper, Cooke, & Schnupp, 2014). Recent evidence indicates that after presenting a rhythmic auditory stimulus, the ability to detect a near-threshold auditory target is modulated at the rate of the stimulation for some time even after the rhythmic stimulus itself has ceased (Gregory Hickok, Farahbod, & Saberi, 2015) which points towards entrainment of oscillators that exhibit self-sustained properties such as brain oscillations. Indeed DAT has been lately explicitly linked with brain oscillatory activity (Herrmann & Henry, 2014; Large, Herrera, & Velasco, 2015). Importantly, DAT has been also used for describing musical meter processing (Large, 2008) (see Section 4.2).

Schroeder and Lakatos (2009) proposed that attention can operate in two modes, a "continuous mode" and a "rhythmic mode". Whether a system operates in a particular mode depends on task demands. Whenever it is possible to extract temporal regularities in the attended stimulus stream, the system operates in efficient "rhythmic mode" where high excitability phases of slow frequency delta oscillations are aligned with expected stimulus occurences. By cross-frequency coupling, gamma amplitude is modulated by delta phase, and therefore firing probability of a neuronal ensemble is enhanced at the predicted times of relevant stimulus occurrence. However when there is no temporal structure in a to-be-attended stimulus (i.e. classical vigilance paradigm), and therefore no possibility to entrain slow frequency oscillators, the system switches to "continuous mode" where slow frequency oscillations amplitude is suppressed and gamma amplitude is tonically enhanced instead (i.e. continuous high excitability state is maintained).



Figure 1: Idealized hierarchy of neural oscillations where the phase of the slower oscillation modulates the amplitude of the faster oscillation (cross-frequency coupling) in a hierarchical fashion. The top trace represents an EEG signal that would be recorded as a sum of the underlying oscillations at different frequencies. Adapted from Calderone, Lakatos, Butler, and Castellanos, 2014.

Most of the studies investigating neural oscillatory entrainment and its effect on excitability or attention has been done with intracranial electrodes, i.e. with very good spatial resolution, targeting carefully defined neural assemblies. The question is whether such entrainment can be observed at the level of scalp, i.e. measured by scalp EEG (or MEG). In order to be detectable at the scalp, a large neuronal population must be synchronized. In EEG research there is a well known phenomenon called steady state-evoked potentials (SS-EP). This is observed in paradigms where rhythmic stimulation (auditory, visual or tactile) causes synchronization of the recorded brain activity at the frequency of the stimulation. In auditory modality, SS-EP around 40 Hz have been widely studied (Galambos et al., 1981), but recently also slow rates have been shown to cause synchronization in large brain networks (Will & Berg, 2007). But is the phase of synchronized oscillations recorded from the scalp linked with the quality of stimulus processing in a systematic fashion?

The ongoing phase of cortical oscillations has been shown to influence auditory (Kruglikov & Schiff, 2003) and visual (Jansen & Brandt, 1991) evoked potentials. Stefanics et al. (2010) used EEG to investigate the processing of isochronous streams of tones where targets could be predicted from the pitch of preceding tones in the stream with varying probability for different pitch cues (higher pitch of the preceding tone – higher probability of the next event to be target). They found that the phase of delta oscillations at the target onset predicted reaction time. The phase consistency was strongest at the targets predicted with high confidence (based on the pitch of previous tones). These results indicate that low-frequency synchronization of large neural populations (engaged in sensory and response processing) guides efficient communication between brain networks and facilitates fast response by setting high excitability phase at the target stimulus onset (employing temporal predictions) when the target is expected to occur with high probability. Another study employed a task with detection of short gaps that were radomly distributed in frequency-modulated (3 Hz) continuous tone (Henry & Obleser, 2012). Although there were no sharp acoustic edges or amplitude modulations in the stimulus, it reliably entrained slow frequency brain activity. Importantly, instantaneous phase of this entrained brain oscillation predicted gap detection performance better than the phase of stimulus frequency modulation. Furthermore, Henry, Herrmann and Oblesser (2014) demonstrated that near-threshold gap detection performance was determined by an interaction between phases of brain oscillations entrained to multiple different frequency bands simultaneously (3.1 and 5.075 Hz). Performance was highest when the gap coincided with the preferred phase in both neural oscillatory frequencies.

Arnal and Giraud (2012) proposed a theoretical framework, linking brain oscillations and sensory predictions. According to them, low frequency oscillations (delta and theta) entrain their high excitability phases to the temporal structure of the stimulus, thus providing "when" prediction by suppressing sensory processing of irrelevant stimuli that come at unexpected time-points. On the other hand, beta and gamma activity is employed in "what" prediction, providing information about

predictions and prediction errors respectively (see also Section 4.2). Beta provides predictions by presynchronizing neuronal population that represents expected stimulus features. When these predictions are not fulfilled, gamma carries prediction error to higher levels for prediction updating.

2.2 The role of motor system in predictive timing

Mounting evidence provides support to the involvement of motor system in predictive timing and interactions between sensory and motor system seem to provide a substrate for extraction of temporal regularities from a stimulus and exploitation of these regularities to guide further sensory processing via oscillatory activity (Arnal, 2012). Morillon and colleagues (2015) proposed that motor system is a crucial part of an active sensing framework, where it shapes perception in two ways. First it guides sensing organs toward relevant stimuli, and second it supports active sampling of information by sending so called "corollary discharges" or "efferent copies" to the relevant sensory areas. These corollary discharges contain information about motor plans and guide attentional mechanisms in sensory systems, so the sensory input is sampled at the time when it is most efficient with respect to motor sequences. Hence motor system helps to allocate attention to the right moments in time. Notably, sensing is often performed in a rhythmic manner, e.g. sniffing, whisking or eye movements. Although there is no movement related to auditory perception (in comparison to other modalities), auditory perception demonstrates the best temporal precision and in humans it is explicitly linked with movement e.g. in dancing. Hence, Morillon and colleagues propose that when an auditory stimulus exhibits a temporal structure that allows temporal predictions to be made, motor system provides predictions about anticipated stimulus timing to the sensory cortices. This is done by means of modulating hierarchy of nested oscillations in auditory networks in a way that high-excitability phases align with expected stimulus occurrences (Morillon & Schroeder, 2015). Evidence for this account has been provided in a recent study where participants needed to attend to a rhythmically presented stream of target tones that were intermixed with distractor tones of similar physical properties, but not temporally related to the target stream (Morillon, Schroeder, & Wyart, 2014). The ability to attend selectively to the target stream was significantly enhanced when participants were allowed to move their body in synchrony with the target tone stream. This provides direct evidence that motor system can influence temporal selection of auditory information in a top-down manner. A structural substrate for such a top-down projections has been proposed by Nelson et al. (2013) who showed that motor system can inhibit auditory cortex response via direct projections in mice, what may primarily serve for suppressing perception of sounds produced by self-generated movements. Recently Arnal, Doelling and Poeppel (2014) found that coupled delta phase and beta power influenced timing judgements of participants. The judgements were most precise when preferred delta phase was aligned to the target stimulus expected onset, and power of beta was strongest in this interval. Furthermore, stronger the

phase-amplitude delta-beta coupling, better the performance on time judgement. As this effect was observed at auditory and motor sensors of the recorded MEG, the authors suggested that "predictive timing mechanisms are controlled through sensorimotor synchronization with the beat" (p. 7) (note that sensorimotor here refers to brain networks and not overt movement synchronization).

Interactions of motor system and auditory sensory system are a ubiquitous motif that repeats throughout the topics reviewed in this thesis and it has potential to link recent theories of speech and music perception with deficits observed in developmental dyslexia.

To summarize, recent research in neuroscience, particularly auditory neuroscience indicates that 1. neural oscillations rhythmically modify neural excitability, 2. oscillations can be entrained by a temporally structured stimulus, thus becoming a substrate of temporal prediction, 3. motor system may play an important role in top-down modulation of oscillatory activity in rhythmic context. Many naturally occurring stimuli exhibit temporal rhythmic structure. Even though perfect periodicity is not present in all natural phenomena, it might not be necessary and only certain amount of statistical regularities in the stimulus temporal structure should be sufficient for oscillatory entrainment and temporal prediction formation (Kraus & Slater, 2015; Zoefel & VanRullen, 2015). In particular, two domains that are relevant for this thesis have been extensively studied with regard to neural oscillatory entrainment. The first one is human speech that is discussed in Section 2 and the second one is music, discussed in Section 4.

3 Neural oscillations in speech processing

3.1 Amplitude envelope and speech perception

As suggested in the previous section, neural oscillations entrain to a temporally structured stimulus in such a way that the high excitability phases coincide with the expected time-points of relevant stimulus occurrence. Many naturally occurring stimuli demonstrate some degree of temporal structure. One of them is human speech.

Complex speech signal can be decomposed (by Hilbert transform) into two components: fast varying temporal fine structure (TFS) and slowly varying temporal envelope (ENV). From signal processing perspective these can be thought of as carrier and modulation signal respectively. Acoustic signal can be first filtered into a number of narrow frequency bands (or channels), which is exactly what happens in the cochlea). In case of processing speech, filtering into more bands provides better information about the spectral structure of a stimulus. TFS can be characterized as rapid oscillations of constant amplitude near the center frequency of the band and provides cues about pitch and formant transitions in speech. It is also important for perception of melody (Moon & Hong, 2014). ENV represents slower amplitude modulations of TSF and is important for speech rhythm and segmental

information perception (Leong, Stone, Turner, & Goswami, 2014). Original signal can be recovered as a product of TFS and ENV for each frequency band and summation over bands. Changes in ENV correspond to amplitude modulations (AM) and changes in TFS on the other hand to frequency modulations (FM).

In speech perception, both components are important and provide complementary information about the signal. However for speech intelligibility, ENV is considered to be more important and speech remains intelligible even after spectral information is degraded and fine structure is replaced by noise of the same bandwidth (only three broadband channels are sufficient for successful speech recognition) using a technique called noise-vocoding (Shannon, Zeng, Kamath, Wygonski, & Ekelid, 1995). Drullman and colleagues (1994) showed that only AMs up to 16 Hz contribute significantly to speech intelligibility, while higher modulation frequencies do no significantly enhance speech understanding. When speech chimeras are constructed by combining ENV from one spoken sentence and TFS from a different one, resulting signal is recognized by human listener as the sentence from which ENV was used in the chimera (Smith, Delgutte, & Oxenham, 2002). Further support for superiority of ENV cues in speech perception is provided by cochlear implant users who are capable of understanding speech correctly with mainly ENV information in restricted number (15-20) of frequency channels that replace 3000 hair cells (Nie, Barco, & Zeng, 2006). It has been suggested recently that fluctuations in speech envelope at multiple timescales convey essential information for detection of different phonological units within the speech stream (Leong et al., 2014). Spectral Amplitude Modulation Phase Hierarchy (S-AMPH) model has been proposed based on AM statistics of acoustic structure of a speech corpus (data-driven) to show how human listeners might use AM in speech signal to derive different phonological units such as stress, syllable and onset-rime units (Leong, 2013). Leong used principal component analysis (PCA) to find non-redundant spectral and AM rates in speech resulting in five spectral and three AM rates. The AM rates were associated with the timescales of different linguistic units, 0.9 – 2.5 Hz for prosodic stress, 2.5 – 12 Hz for syllable and 12 – 40 Hz for phoneme. These bands have been suggested to entrain neural oscillatory networks in auditory cortex with similar frequency properties (delta, theta and gamma).

3.2 Multi-time resolution models

Human speech is a quasiperiodic highly complex spectro-temporally modulated signal that contains relevant information at multiple timescales. Temporal modulations are ubiquitous in continuous speech and as mentioned above, AMs (particularly at slow rates) have been linked with speech intelligibility. Speech is a "multiplexed" signal, which means that it carries nonidentical information at several timescales and different rates of modulation in speech are related with different linguistic units such as phonemes, syllables, stressed syllables, words, phrases etc. (see Leong, 2013). Most prominent (and most widely studied) timescales have been identified at the mean rate of phonemes (25-80 ms) and syllables (150 – 300 ms), that is ~40 and ~4 Hz respectively (although also syllable stress occurring at approximately 2 Hz has been emphasized by many researchers) (Ghitza, 2011; Hickok & Poeppel, 2007). In order to successfully match acoustic speech input to discrete representations of linguistic units, continuous stream has to be parsed and chunked into smaller units that allow for integration and analysis of differently sized features. Poeppel and colleagues (Giraud & Poeppel, 2012; Hickok & Poeppel, 2015) suggested that brain analyzes speech signal in two differently sized temporal integration windows at the same time, corresponding to syllabic (and prosodic) and phonemic rate, and that information extracted from both timescales interacts. This can be compared to analysis of visual stimulus, where different information is conveyed at low versus high spatial frequencies, corresponding to global and local levels of analysis respectively. The idea is that an auditory input can be concurrently analyzed at fast and slow time-scales, that provide distinct information about the input (Poeppel & Monahan, 2008). For instance it has been shown that when speech with band-pass filtered amplitude modulation spectrum preserving either slow (~4 Hz) or fast (~33 Hz) rates is presented dichotically (slow to one and fast to the other ear), resulting speech intelligibility is enhanced much more then linear summation would predict (i.e. intelligibility score from combined presentation is higher then the sum of scores when presented with fast or slow condition in isolation) (Chait, Greenberg, Arai, Simon, & Poeppel, 2015). Further, intelligibility is not significantly diminished when temporal asynchronies between fast and slow signals are introduced up to ~45 ms. This supports the hypothesis that information at the two timescales is simultaneously extracted by independent mechanisms and subsequently combined.

In a recent theoretical accounts of speech perception (multi-time resolution models), brain oscillatory mechanisms are considered to be exploited to sample acoustic information concurrently at time-windows of different sizes. Oscillations in gamma band have been linked to phonemic sampling (segmental information), while slower delta and theta band have been proposed to track prosodic and syllabic (supra-segmental) structure. Furthermore, it has been proposed that there might be hemispheric differences in slow versus fast timescale analysis. Tracking of slow modulations was proposed to be lateralized in the right hemisphere, while rapid timescales might be analyzed in the left hemisphere or bilaterally (Giraud & Poeppel, 2012; Poeppel, 2003; Zatorre, Belin, & Penhune, 2002). However, these hypotheses are still discussed.

Temporal clustering of spiking activity to a specific phase of the oscillatory cycle enables neuronal population to integrate input over a period of time and subsequently propagate the input to higher level networks. Gamma rate oscillations may provide discrete sampling of small speech segments, which has been supported by modelling work. Shamir et al. (2009) reported that their neural network successfully decoded artificial signals (with similar properties as speech segments) based on three

gamma-cycle samples (differently tuned neurons fired at the high-excitability phase of each cycle). It has been proposed that this mechanism could be implemented in speech gamma sampling, reliably encoding different diphones in the signal. However, the amount of useful information is continuous speech varies, as periods of high energy (syllables) alternate with periods of relative silence (between syllables). Therefore it is advantageous for the brain to align high-excitability phases of neuronal oscillations with these most informative parts of the signal. In the model of Shamir and his colleagues this was done by phase-resetting cue that preceded the stimulus. In more recent models (Ghitza, 2011; Hyafil, Fontolan, Kabdebon, Gutkin, & Giraud, 2015) employed a theta oscillation ("theta master") that entrains to the slow speech amplitude envelope and by cross-frequency coupling mechanisms modulates gamma in a way that it coincides with the most informative parts of the signal. This is in accordance with the findings that entrainment of neural oscillations guides the high excitability phases toward time-points where high amount of useful information is expected.

3.3 Entrainment of low-frequency oscillations to speech envelope

Oscillatory entrainment at delta and theta modulation rates in speech perception has been widely studied over the past years. Zoefel and VanRullen (2015) suggest that if oscillatory alignment of "good" and "bad" phase to a stimulus should provide all the processing benefits (filtering out distracting stimuli that do not coincide with the preferred phase, and at the same time parsing the attended stimulus into chunks), the signal of interest has to have three properties. It has to by rhythmic (or quasi-rhythmic, i.e. temporally predicable), the rhythmic properties should comprise relatively stable frequency the brain can entrain to and finally, there must be alterations between parts with relatively high vs. low information content. According to Zoefel and VanRullen, speech possesses all of these characteristics and therefore it represents a perfect signal to which oscillatory entrainment can be applied. Even though speech is not strictly periodic (unless employed e.g. in singing) it is also not random (regarding temporal structure). It is rather considered a quasi-periodic signal that exhibits enough temporal regularities to enable prediction formation and entrainment of neuronal oscillators. Therefore the term "rhythm" is widely used among speech scientists to refer to the speech temporal structure (Peelle & Davis, 2012). Quasi-rhythmic jaw openings and increases in amplitude ("energy arc") associated with syllable nucleus produce dominant peak in the speech modulation spectrum approximately at 4 Hz for syllables and 2 Hz for stress patterns. Converging evidence suggests that modulations at this rate are necessary for speech intelligibility (although not sufficient, as some amount of spectral information is needed to achieve comprehensible speech) (for a review, see Peele & Davis, 2012). Indeed, mounting evidence indicates that slow oscillations in auditory cortices phase-lock to speech envelope modulations (i.e. there is a consistent relationship between phase of the oscillation and the stimulus amplitude structure) and this envelope tracking is related to speech comprehension.

Luo and Poeppel (2007) showed that theta (4-8 Hz) phase, but not amplitude, could reliably discriminate between different sentences and the reliability of this discrimination was related to speech intelligibility. For noise-vocoded sentences with lower number of frequency channels (more difficult to comprehend) the phase did not provide as reliable discrimination information as for vocoded sentences with more channels or the original sentences. Similar results were reported by Ding and Simon (2013), who additionally tested whether phase entrainment in low frequencies is robust when speech is presented in background noise. They reported that tracking at syllable rate (4-8 Hz) is disrupted with increasing amount of noise, but oscillations at the rate of prosody (stressed syllables) (<4 Hz) remain robustly entrained to the speech. Precision of the synchronization at the individual level was strongly correlated with the ability to understand speech in noise. Enhanced theta tracking of syllable structure when speech is intelligible has been supported by other studies (e.g. Peelle, Gross, & Davis, 2013), but there is still an ongoing debate about whether and how cortical tracking is related to speech intelligibility (Ding & Simon, 2014; Millman, Johnson, & Prendergast, 2015).

In an influential study, Gross and colleagues (2013) used MEG to measure mutual information between the phase of speech envelope modulations and the phase of neural oscillatory activity between 1 and 60 Hz. Their results revealed two distinct bands at delta (1-3 Hz) and theta (3-7 Hz) frequency which were entrained (phase-locked) to the corresponding speech modulations that the authors interpreted as prosodic and syllabic rate respectively. Interestingly, gamma (35-45 Hz) amplitude was also modulated by speech envelope and detailed analysis showed that there were phase-amplitude coupling relationships between both, delta and theta and theta and gamma rates. Thus successful alignment of slowest oscillations would also influence high frequency sampling, resulting in coordinated speech analysis across multiple relevant timescales.

Furthermore, recent evidence indicates that neural entrainment to speech rhythmic modulations is not just a purely reactive process driven by stimulus acoustics, but can be modulated by top-down mechanisms (for an excelent review, see Zoefel & VanRullen, 2015). For instance, visual information (watching the face of the talker) can phase-reset ongoing phase of oscillations in auditory areas in a way that high excitability phases are predictively aligned with highly informative parts of speech (for a recent review, see Peelle & Sommers, 2015; Schroeder, Lakatos, Kajikawa, Partan, & Puce, 2008). Additionally, there is evidence that high-level attentional processes influence entrainment to speech in lower areas. When selectively attending to one particular speaker in a cocktail party (multi-speaker) enviroment, the phase of low frequency delta and theta oscillations follows the speech signal of the attended speaker much more than the not-attended speaker (Horton, D'Zmura, & Srinivasan, 2013; Kerlin, Shahin, & Miller, 2010; Zion Golumbic et al., 2013). Recent studies further employed complex mathematical techniques (that can reveal direction of information flow in the brain) to provide evidence for modulation of entrainment to speech by higher cortical areas. Fontolan et al. (2014) recorded intracranial signal from human primary auditory cortex and higher level auditory association cortices in response to speech stimuli. Analysis of the data employing Granger causality revealed information flow in distinct frequency channels representing top-down (1-40 Hz) and bottom up (>40 Hz) signals. While gamma activity reflected bottom-up information flow from lower to higher level cortices, delta-beta activity in the opposite way modulated this gamma response (by phase-amplitude cross-frequency coupling). Notably, Park and colleagues (2015) reported top-down effects (measured by transfer entropy from MEG data) of frontal and motor areas on auditory networks. The top-down modulatory signals were observed in delta (1-3 Hz) and theta (4-8 Hz) frequency bands, but delta oscillatory activity (related with suprasegmental speech units) was strongest. Involvement of motor cortices converges with previous findings and theoretical predictions about the role of motor system in active sensing and rhythmic signal processing (Morillon et al., 2015).

As speech is not strictly periodic (in comparison to e.g. music), its quasiperiodic structure requires theta oscillators to constantly adjust the phase (but also the frequency to a certain amount) in order to track speech fluctuations. One possible mechanism to achieve this is that acoustic edges in the signal (caused by fast changes of amplitude linked with syllable nuclei) phase-reset theta oscillators. Indeed, after removing amplitude modulations at 2-9 Hz (theta range) the speech intelligibility decreases severely. However, adding brief uniform noise bursts at the time points where the maximal energy was prior to the amplitude degradation (time of syllable nucleus, carrying information about speech rhythm) significantly restores comprehension (Ghitza, 2012). Later study showed that indeed neural theta-tracking is substantially increased as a result of adding these cues about speech rhythm (called also "acoustic landmarks") to speech stimulus with no theta rate amplitude modulations (Doelling, Arnal, Ghitza, & Poeppel, 2014). At the neural level it has been shown that sharp edges in continuous speech (sharp increases in amplitude) caused phase-reset of theta brain oscillations and this was linked with increased cross-frequency coupling across the whole oscillatory hierarchy, thus contributing to realignment of internal reference frame with the speech temporal structure (Gross et al., 2013).

In line with these findings, impairments in neural tracking of speech temporal structure via delta and theta oscillations would result in inefficient parsing of speech signal at multiple timescales, as the brain would sample the signal at less informative time-points. Recently, clinical research has started to recognize the importance of neural entrainment and its potential to explain symptoms observed in multiple disorders. Disrupted entrainment of neural oscillations has been proposed schizophrenia, ADHD and dyslexia (for a review, see Calderone, Lakatos, Butler, & Castellanos, 2014). The next section focuses on one particular theory that proposes a link between deficits in low-frequency oscillatory entrainment and poor reading skills.

4 Developmental dyslexia

Developmental dyslexia is a specific learning disability that can be characterized as an "unexpected difficulty in reading in children and adults who otherwise posses the intelligence and motivation considered necessary for accurate and fluent reading" (Shaywitz & Shaywitz, 2005, p. 1301). Prevalence of dyslexia is approximately 3-20% depending on the language and diagnostic criteria (Elliott & Grigorenko, 2014). Developmental dyslexia occurs across different languages and orthographies (Ziegler, Perry, Ma-Wyatt, Ladner, & Schulte-Körne, 2003) and problems with reading skills remain also in adults that have been diagnosed as dyslectic in childhood (Shaywitz et al., 1999). Despite the fact that more than a century has passed since the first reported case of dyslexia, there is still no universally accepted theory that would explain underlying causes of this disorder (for a recent review, see Elliott & Grigorenko, 2014).

4.1 Phonological deficit

One of the most widely acknowledged theory of dyslexia over past decades has been phonological deficit theory (Vellutino, Fletcher, Snowling, & Scanlon, 2004) which proposes that the underlying impairment in dyslectic individuals has phonological character (phonological core deficit), i.e. concerns speech sounds (Goswami, 2000; Ramus, 2003). According to this perspective, dyslectics have degraded phonological representations (mental representations of spoken language) which are poorly specified, fuzzy, noisy or simply different than in intact individuals (Goswami, 2011, 2015).

In reading the primary process is phonological recoding, i.e. mapping speech sounds (phonology) onto visual symbols (orthography). When phonological representations are corrupted this mapping becomes problematic and manifests itself in a disrupted reading ability. Problems with phonological recoding in dyslexia are present across different orthographies with different levels of transparency ((Moll et al., 2014; Ziegler & Goswami, 2005). Ramus et al. (2003) reported phonological deficit in 100% of their dyslectic sample in contrast to lower occurrence of magnocellular or cerebellar deficits (proposed by other theories). Therefore they proposed that phonological deficit is sufficient to be a source of reading problems in dyslexia.

Poor readers are consistently found to be impaired in three types of tasks that are supposed to involve phonological representations of spoken word forms: phonological awareness (PA), verbal short-term memory (VSTM) and retrieval of lexical information from long-term memory (e.g. rapid automatized naming, RAN). PA can be described as the ability to reflect and manipulate (e.g. add, delete, substitute, separate etc.) component sounds of speech (Tunmer & Rohl, 2012). It involves different grain sizes of spoken language including syllables, syllable onsets, rimes and also individual phonemes. RAN requires fast access to the stored phonological representations in order to rapidly name presented objects (e.g. colors). A large number of studies have shown that the performance on

these tasks is a reliable predictor of later reading skills (e.g. Bradley & Bryant, 1983; Melby-Lervåg, Lyster, & Hulme, 2012; Vaessen & Blomert, 2010) Causal role of phonological skills in literacy development has been further supported by longitudinal studies in Finnish (Lyytinen et al., 2006) and Dutch (Boets et al., 2010).

However the relationship between phonological measures and reading is still not completely understood. It has been pointed out that reading instruction improves PA (especially regarding phoneme grain size) so the influence may be in both directions, i.e. better PA promotes reading development and reading development enhances PA. PA appears to be the best predictor in early years of reading development while RAN better predicts reading abilities after a few years of reading experience (Boets et al., 2010; Vaessen & Blomert, 2010). Some researchers even consider two independent deficits, one manifested in impaired RAN and associated with reading difficulties in transparent orthographies and deficit in PA more predictive in less transparent orthographies (Wolf & Bowers, 1999). However conclusive evidence has not been provided (for a discussion see Elliot & Grigorenko, 2014). There is an extensive debate about the nature of phonological deficit in recent years. Ramus and Szenkovits (2008) argued against the hypothesis of degraded phonological representations in dyslexia. They suggested that the phonological deficit may not stem from corrupted representations per se, but rather from impaired access to (otherwise intact) representations. In their review they have shown that poor performance in tasks investigating phonological skills can be explained by other variables such as task requirements, short-term memory and time constraints. Phonological deficit theory has been also criticized for other theoretical issues, e.g. the fact that it predicts poor performance on wide range of tasks where dyslectics appear to perform normally (Ramus & Ahissar, 2012). Despite these potential difficulties, phonological deficit remains widely accepted core deficit underlying developmental dyslexia.

When searching for the origin of atypical phonological representations of speech sounds in dyslectic individuals, some researchers have suggested that more basic difficulties might prevent dyslectics from establishing well specified phonological representations. There are multiple theoretical frameworks proposing impairments in auditory processing to be such a cause. However, the exact nature of such auditory deficit is still hotly debated.

4.2 Temporal sampling framework

In order to explain difficulties in phonological processing that characterize dyslectic individuals, a "temporal sampling framework" (TSF) was proposed by Goswami (2011). TSF emphasizes the role of phonological representations at coarser grain-sizes than phoneme, especially syllabic and prosodic levels. This is based on observations that phonological awareness exhibits typical developmental trajectory from word to syllable to onset-rime. Importantly, awareness of phonemes does not develop

naturally, but is a result of learning to read alphabetic scripts. For instance illiterate people, or people using non-alphabetic scripts never develop phonemic awareness (Ziegler & Goswami, 2005). Focusing on the level of syllable stems from the fact that syllable has been suggested as the primary processing unit in all languages. Syllabic structure is important also because the phonetic realization of segmental information depends on whether the syllable is stressed or not (Greenberg, Carvey, Hitchcock, & Chang, 2003). Impaired perception of supra-segmental information would lead to cascaded effects causing atypical development of the whole phonological system. Accurate perception of prosodic aspects of language (prosody in linguistic theory refers to aspects of grouping, rhythm and prominence) is important for language processing from early life. It has been argued that prosodic sensitivity is crucial for speech stream segmentation by infants and that mental representations of spoken language involve also information about prosodic properties of words (Pierrehumbert, 2003). Difficulties with perception of syllable and prosodic structure of speech might have cascading effects on the development of well-specified phonological representations that follows a typical developmental sequence from syllable to phoneme (Goswami, 2011).

4.2.1 Processing of speech rhythm in dyslexia

Because slowly varying amplitude modulations of speech signal provide cues about speech rhythm and prosody (Greenberg, 2006), TSF proposed that perception of these sound features may be impaired in dyslectic individuals. One important AM cue is amplitude rise time, which is the time from the physical onset of a stimulus to the time point where it reaches maximum amplitude (also can be understood as a rate of change of the increasing amplitude). For instance in speech, rise time is longer for sonorants (e.g. /ma/) than for stop consonants (e.g. /ba/) hence it can provide cues about phoneme identity (Goswami, Fosker, Huss, Mead, & Szűcs, 2011). Most importantly, it is critical for segmenting syllables from speech stream and perception of syllable stress (Goswami, Gerson, & Astruc, 2010; Scott, 1998). Rise times play role in detecting perceptual centres of events (P-centres) which represent subjective moment of occurrence (for a review, see Villing, 2010). For instance in music, different instruments have distinct rise times ("attack times"), which entails different positions of the P-center relative to the onset of the sound (e.g. slow sound onset of bowed violin vs. sharp piano sound). When musicians are playing together and they need to align sounds of their specific instruments in a common timing, violinist needs to start little bit earlier relative to the pianist in order to sound "in time". The same holds for speech rhythm. When asked to align their speech with a pacing isochronous metronome, people tend to to align their syllables according to P-centres and not the physical onsets of syllables (Morton, Marcus, & Frankish, 1976). P-centre is further associated with the beginning of vowel nucleus within a syllable which may be used to onset-rime division (Greenberg, 2006). For instance in Slovak in order to speak rhythmically with the metronome one would start the monosyllabic word "ZVAŤ" little bit earlier than the word "ZAŤ" because of aligning the nuclei of the syllable rime (same in both syllables "-AŤ").

According to TSF, particularly perception of longer rise times (mathematically corresponding to slow AM) is disrupted in dyslexia (Richardson, Thomson, Scott, & Goswami, 2004; Gabor Stefanics et al., 2011). This would lead to lesser precision in discrimination between different rise times, hence affecting the ability to successfully parse syllables from the speech stream, use rise time cues for segmental identification and also a range of prosodic and rhythmic skills (Goswami, 2011; Goswami & Leong, 2013). Rise time sensitivity impairment has been consistently reported in dyslectic children as a cross-sectional and longitudinal predictor of reading and phonological skills (Goswami et al., 2002; Goswami, Huss, Mead, Fosker, & Verney, 2013; Huss, Verney, Fosker, Mead, & Goswami, 2011). Similar profile has been observed in adults (Pasquini, Corriveau, & Goswami, 2007) and rise time perception difficulties have been reported across languages and orthographies such as English, French, Hungarian, Spanish, Finnish and Chinese (Goswami, Wang, et al., 2011; Muneaux, Ziegler, Truc, Thomson, & Goswami, 2004; Richardson et al., 2004; Surányi et al., 2009). In a review of studies investigating auditory processing in dyslexia Hämäläinen et al. (2012) reported that only rise time perception deficit (compared to other sound properties, e.g. pitch) was reported in 100% of reviewed behavioral and ERP studies (with average effect size 0.8).

Besides focusing on rise times as simple acoustic edges (which was criticized e.g. by Scott and McGettigan, 2012), recent advances in theoretical models of speech AM structure allowed to further explore perceptual deficits in dyslexia proposed by TSF. According to the S-AMPH model of Leong (see Section 2.1), slow AMs in speech carry information about speech rhythm (pattern of strong and weak syllables). Whether particular syllable is stressed can be determined by looking at the phase of "Stress" (~2 Hz) and "Syllable" (~5 Hz) amplitude modulations. When peak in the Syllable cycle coincides with a peak in Stress cycle, the ongoing syllable is considered "strong". It has been shown experimentally that artificially shifting the relative phase between these two AM bands reversed the perceived metrical pattern (from trochaic to iambic patterning) in tone-vocoded nursery rhymes (Leong et al., 2014). TSF suggests that it is indeed impaired processing of these slow timescales that may cause prosodic perception deficits.

There is mounting evidence available suggesting that consistently with TSF predictions, reading skills and perception (but also production) of speech prosody are related. In a classic study, Wood and Terrel (1998) showed that poor readers were significantly worse than good readers in matching low-pass filtered sentence (so only prosodic, but no phonetic information was available) with other sentence based on the rhythmical properties. Another study reported that Dutch children aged only 3 years that were at risk of dyslexia had more problems in repeating nonwords that contained irregular or forbidden stress patterns compared to non-risk children (de Bree, Wijnen, & Zonneveld, 2006). When

asked to repeat sequences consisting of single syllable repeated multiple times (2,3 or 4) while stressing one particular syllable in the string, dyslectic students demonstrated considerable difficulties when repeating 3 and 4-syllable patterns. Particularly they showed greater variability in inter-syllable intervals and made more mistakes in stress assignment than controls (Wolff, 2002).

In general population, prosodic and literacy skills were correlated after controlling for age, IQ and vocabulary in the study of Wood (2006), who used a "mispronunciation task". Children had to identify the right object in the picture when the name of this object was pronounced with wrong stress pattern or with other control mispronunciations, e.g. changed vowel. Children with worse reading skills showed poorer performance selectively at identifying mis-stressed words. These results were replicated in additional studies (Holliman, Wood, & Sheehy, 2008, 2010). Kitzen (2001) developed a task where each syllable in the stimulus phrase is substituted for a syllable "dee". According to the stress pattern of the original phrase, these nonsense syllables are either stressed or not which creates "DEEdee" phrases that can be matched with the originals only by using prosodic similarity. In her study, adults with history of dyslexia performed significantly worse on this matching task than controls. Subsequently, "DEEdee" task was adopted by other researchers and used with school-aged children who were asked to identify pictures of famous people and movie characters whose names were converted into DEEdee phrases (e.g. "Harry Potter" became "DEEdeeDEEdee"). Two different versions were used, one where human speaker recorded the stimuli and the other where "DEEdees" were synthesized, thus no other cues than syllable stress were retained). Similarly to adults in the study of Kitzen, dyslectic children performed worse than age-matched controls in both conditions and this was predicted by auditory rise time discrimination skills (Goswami et al., 2010). Further evidence for lower sensitivity to syllable stress in adults with dyslexia has been provided by Leong and colleagues (2011) who showed that these individuals were impaired on judging whether pairs of four-syllable words had the same stress pattern (e.g. "maTERnity" - "boTAnical"). This deficit was significant even when the same word was used for the comparison (e.g. "MAternity" - "maTERnity"). A longitudinal study measured prosodic stress sensitivity in 9-year-old children with "DEEdee" task and after four years the same children were tested with direct stress perception task described above (Goswami et al., 2013). Although the first measurement revealed significant impairment of dyslectic children compared to both age- and reading-level matched controls, this was true only in comparison to age-matched controls after four years. The authors argued that dyslectic children eventually develop prosodic sensitivity but later than their peers and the developmental trajectory into adulthood is influenced by reading experience. Importantly auditory measures of rise time, duration and frequency sensitivity, development of phonological processing at prosodic and sub-lexical levels and reading skills were all related in a longitudinal fashion. Prosodic processing has been shown to be impaired also in consistent orthographies such as Spanish. Children with dyslexia had problems with discrimination of minimal

pairs created by stress difference (in Spanish, syllable stress can distinguish words with different meanings) (Gutiérrez-Palma & Palma Reyes, 2007) and with explicitly detecting which syllable was stressed in words and pseudo-words (Jiménez-Fernández, Gutiérrez-Palma, & Defior, 2015).

Recently, studies were designed to directly test predictions derived from S-AMPH model and investigate speech perception and production in dyslectic individuals at multiple timescales. Leong and Goswami (2014a) asked adult participants to tap along to the beat of rhythmically spoken (syllable rate 4 Hz, stressed syllables at 2 Hz) nursery rhymes with different metrical foot patterns (trochaic and iambic). Analyzing the instantaneous phase of AM at all three relevant timescales (Stress, 0.9-2.5 Hz, Syllable, 2.5 - 12Hz and Phoneme, 12 – 40 Hz) revealed that dyslectic adults tapped significantly earlier with respect to the Syllable rate phase than controls. In the same study participants also produced nursery rhymes in time with a metronome. Dyslectics showed larger problems with synchronizing at the target rate when the metrical complexity of the nursery rhyme increased (iambic patterns considered more complex than trochaic). Furthermore, when analyzing the produced speech (using S-AMPH) at different AM rates, the phase relationships between syllable and phoneme timescales were different (i.e. aligned under different phase angle) between groups, suggesting that coordination of phonemes and syllables (mainly vowel nuclei) was different in produced speech of dyslectics compared to controls. The same participants took part in another study (Leong & Goswami, 2014b) where the same nursery rhymes as before were used and their amplitude modulations were extracted at timescales of Stress, Syllable and Sub-beat (instead of Phoneme, this corresponded to < 20Hz modulations of reduced syllables in the nursery rhymes). These extracted amplitudes were used to modulate sinusoid carrier which led to unintelligible stimulus that contained only particular amplitude modulations of the original sentences. Different timescales were used alone (Stress, Syllable and Subbeat) or in combination of Syllable and either Stress or Sub-beat. Trying to identify the original nursery rhyme after listening to the "sine-wave version", dyslectics performed poorer when a combination of timescales was used. Notably, individual performance on this task correlated with tapping phase (with respect to Syllable rate) from the previous experiment. According to the authors these studies provided evidence that syllables and integration between syllables and other timescales might be processed differently in dyslectics. When different syllable processing is present, the whole phonological system at all grain sizes might be affected (e.g. by misalignments between representations of syllables and phonemes). Deficits in concurrent encoding and subsequent integration of all timescales into a highdimensional phonological representations might result into atypical lexicon of spoken word-forms that is observed in dyslexia (Goswami & Leong, 2013).

To summarize, processing of prosody, speech rhythm and its acoustic correlates has been consistently linked to reading skills in many studies. Thus previous extensive focus on the level of phoneme and phonemic awareness might be worth reconsidering and the role of supra-segmental features should be taken into account in theories of reading development in normal population and developmental dyslexia (Goswami & Leong, 2013). Notably, there is also other work besides TSF that aims to theoretically link perception of speech rhythm, phonological awareness and reading. For instance Wood, Wade-Wolley and Holliman (2008) proposed four different possible theoretical models of how speech rhythm perception could affect literacy. Despite the fact that further research is required in order to specify how exactly speech rhythm processing may underpin reading development, the studies reviewed above provide converging evidence that these two cognitive skills are related in general population across languages and orthographies and they are both disrupted in dyslectic individuals.

4.2.2 Neural oscillations in dyslexia

In order to explain difficulties with speech envelope perception in dyslexia, TSF adapts the multitime resolution model of speech perception and AST hypothesis (Gregory Hickok & Poeppel, 2007) and proposes that these deficits can be explained by impairments in neural oscillatory sampling of slow modulations in speech. Particularly phase-locking of right lateralized delta and theta oscillations to slow modulations might be atypical in dyslexia, and this inefficient envelope tracking would account for observed deficits in rise time discrimination and processing of rhythmic aspects of speech. Such impairments would in turn lead to differently specified system of spoken word representations, resulting in phonological deficit observed in dyslexia (Goswami, 2011). Indeed, increasing amount of studies points towards deviant brain oscillatory activity in dyslectic individuals.

4.2.2.1 Differences in lateralization

Inter-trial phase coherence or ITC (measure of how "similar" are the phases of brain response in particular frequency band between trials) indicates how reliably the brain follows modulations in the same stimulus repeated over trials. If the response would be exactly the same every time the stimulus is presented, ITC would have value 1. However if the tracking is not robust (there is variability in phase over trials), the value is lower. Hämäläinen et al. (2012)reported lower ITC in the right hemisphere of dyslectic adults when listening to amplitude modulated noise at 2 Hz. This is in line with TSF proposal (based on multi-time resolution models and AST hypothesis) that right lateralized network which parses speech at delta and theta rates is impaired in dyslexia. Deficits in right-lateralized network were also observed in response to speech stimuli. Degree of right-asymmetric processing of speech envelope accounted for up to 41% of variance in reading performance and poor readers showed less right-lateralized processing (measured by cross-correlation of brain response and stimulus envelope, and root mean square of the evoked activity) (Abrams, Nicol, Zecker, & Kraus, 2009). Missing lateralization for theta (4 Hz) entrainment to amplitude modulated noise has been reported also in

Spanish dyslectic participants including children and adults, which may point to the higher importance of syllable than stress (compared to English) in Spanish (Lizarazu et al., 2015).

However, as noted before, AST hypothesis is still not fully resolved and is hotly debated (Hickok & Poeppel, 2015). Some studies (contrary to the hypothesis) point towards the role of left hemisphere in slow amplitude modulations processing. For instance better rise time (but not simple intensity) discrimination has been linked with lower activation in left posterior STG (Ugolini et al., 2016). It has been proposed that left hemisphere might show delayed response to slow modulations, maybe receiving input from the right hemisphere and performing more complex operations on the input, possibly integration with faster timescales (see also Kovelman et al., 2015). This result also converges with recent findings that top-down modulations from frontal regions via slow oscillatory frequencies are more prominent in the left hemisphere (Park et al., 2015). Furthermore, developmental changes in lateralization might also play a role (Lizarazu et al., 2015). Therefore establishing an exact pattern of how exactly different integration timescales are processed in left and right hemisphere requires further investigation. This makes the observed differences between good and poor readers hard to interpret, besides the obvious conclusion that can be drawn from such observations – dyslectic brain processes speech (and slow AM) differently.

4.2.2.2 Phase of low-frequency oscillations

Power and colleagues (2012) used a paradigm where syllable /da/ was isochronously presented at 2 Hz rate. Children from general population listened to the stream and detected small deviances in timing (some syllables were temporally misaligned). Slow neural oscillations entrained to the stimulus at the frequency of delta (2 Hz, same as stimulus presentation rate) and theta (4 Hz). ITC of 4 Hz activity correlated with reading measures. However this result might be misleading as there was no 4 Hz modulation in the stimulus and thus the measured synchronization in this band may be just a harmonic of the 2 Hz component. When employing the same paradigm with a group of dyslectic and control children (Power, Mead, Barnes, & Goswami, 2013), there were no differences in power of the entrained activity of ITC. However, the phase of delta (2 Hz) oscillation (relative to the stimulus) was significantly different in dyslectics (converted from angle to milliseconds the difference was ~12.8 ms). This points to suboptimal phase of oscillatory sampling which may lead to inefficient alignment of gamma oscillations via cross-frequency couping in the oscillatory hierarchy, thus resulting in different representations of segmental content of syllables. Soltézs et al. (2013) used classic paradigm investigating anticipatory processing by presenting isochronous tone sequences (rate 1.5 and 2 Hz) while the task was to identify when a tone was occasionally replaced by white noise. As reviewed in Section 1.1, the phase of the entrained slow frequency activity predicts performance on tasks where rhythmic mode of attention can be employed. This was indeed true in control group, as their reaction

times to the target noise sounds were reliably predicted by the instantaneous phase of delta at the target onset. However, there was no such relationship in the group of dyslectic adults, who additionally showed lower ITC of 2 Hz activity and reduced contingent negative variation (CNV) ERP component which is related to temporal expectancy. These data were interpreted in a way that rhythmic attending is deficient in dyslectics, thus they have problems with exploiting stimulus regularities for anticipatory attention allocation to particular time-points via oscillatory entrainment. In the context of speech, this would mean system-wide effects originating from inability to predict when stressed syllables might occur and inefficient alignment of oscillatory sampling at all timescales with respect to the relevant moments in the speech stream (see also Greenberg, 2006). According to TSF, dyslectic brain may compensate for the impaired low-frequency entrainment by gamma "oversampling" (see also below) which would result in over-specified representations of spoken word-forms at the segmental level.

4.2.2.3 Fast timescales and "oversampling"

Different (but not necessarily incompatible) perspective was proposed by other researchers. Although also building on multi-time resolution models of speech perception, their findings point toward deficits at faster timescales (in gamma range) and not low frequency oscillations. For instance, Poelmans et al. (2012) reported lower strength of entrainment to 20 Hz, but not 4 Hz AM noise. Measuring SS-EP response (assessing the magnitude of brain oscillatory entrainment to a periodic stimulus) to amplitude modulated noise. Lehongre and colleagues (2011) showed that dyslectics had less left lateralized response in the range of 25-35 Hz. Disrupted sampling at ~30 Hz was also observed in left auditory cortex of dyslectics when measured by combined EEG and fMRI (correlating hemodynamic response and EEG power in particular frequency bands over time) during naturalistic speech stimulus presentation (Lehongre, Morillon, Giraud, & Ramus, 2013). The authors argued that this decreased left-hemisphere bias in dyslectics might cause problems with phonemic sampling, particularly when fast modulations need to be analyzed in the left lateralized language network. Atypical lateralization patterns might cause deficits in the system of oscillations that has been proposed by AST (left hemisphere specialization for fast timescales and right hemisphere for slow timescales). Furthermore, Lehongre et al (2011) reported superior entrainment to fast (50-70 Hz) modulations in dyslectic individuals. This was interpreted as "oversampling" which means that phonetic information is sampled with unnecessarily high rate, resulting in over-specified phonological representations which are hard to store and manipulate. Such view is supported by studies suggesting that dyslectics may be more sensitive to allophonic variations than normal population (Bogliotti, Serniclaes, Messaoud-Galusi, & Sprenger-Charolles, 2008; Serniclaes, Heghe, Mousty, Carré, & Sprenger-Charolles, 2004). "Oversampling" as a potential compensatory strategy has been proposed also by TSF (Goswami, 2011). Because of inefficient low frequency sampling, dyslectics might rely more on information in

high frequency modulatory bands (i.e. gamma) which would result in different phonological representations.

However, these studies analyzed oscillatory power and not phase (although efficient phase-locking is necessary in order to establish steady-state response). Notably, slow frequency ranges were not investigated in the study of Lehongre et al. (2011) at all (only AM from 10 to 80 Hz were used as a stimulus), and although the other two studies included also slower oscillations, they were not analyzing phase properties of the recorded brain activity. Therefore these results may be complementary to the studies reporting slow oscillatory phase deficits, pointing to a system-wide atypical temporal sampling in reading impaired individuals. It has been hypothesized that genetic anomalies typically associated with dyslexia might disturb neuronal migration in auditory cortices and contribute to different microcircuit architecture which would impact oscillatory activity (in delta, theta and gamma frequencies) and auditory functions (Giraud & Ramus, 2013).

4.2.2.4 In tune but out of time

Difficulties with perceiving temporal aspects of sound in dyslexia led to suggestion that not only speech might be affected, but also other auditory domains that require processing of temporal rhythmic structure. Of particular importance for this thesis is the hypothesis proposed by TSF that processing of musical rhythm and meter might be impaired in dyslexia (Goswami, 2011). Dyslectics have been described as being "in tune but out of time", which is a reference to individuals with amusia (tone deafness) that have been identified as "out of tune but in time" (Hyde & Peretz, 2004). Dyslexia and amusia might represent impairments in perception of two independent sound features – timing and pitch.

In speech, a rhythm is created by alternating "strong" (stressed) and "weak" (unstressed) units at multiple levels (syllable, foot etc.) which are hierarchically nested. Leong and Goswami (2014a) provide an example of the word "mississippi" where strong and weak syllables alternate ("MI-ssi-SSI-ppi"). Syllables are further grouped into metrical feet (in this case "strong-weak" foot) which also differ in relative prominence hence resulting in "strong-weak-STRONG-WEAK" pattern of lexical stress in this particular word. Similar hierarchically nested levels of prominence can be observed in musical meter (see Section 4.1). Indeed, grids and tree structures used by metrical phonology to describe prosodic prominence in language are very similar to the ones used by music theorists to represent metrical structure of musical rhythm (Dilley, McAuley & Dilley, 2011). The question whether rhythmic aspects of human language and music are similar (therefore possibly processed by similar brain networks) has been hotly debated in recent years. Patel (2008) noted that the biggest difference between language and music regarding rhythmic properties is periodicity. Albeit there have been attempts to show periodicities in spoken language (Dauer, 1983), according to Patel this approach

needs to be abandoned and non-periodic rhythmic properties of language must be compared to music if similarities are to be shown. Rhythm in language "does not involve the periodic recurrence of stress, syllables, or any other linguistic unit" (p. 159), rather it comprises "systematic temporal, accentual and grouping patterns of sound" (p. 150). However the need for strict periodicity in an auditory stimulus in order to be perceived as temporally regular has been questioned. Notably, live performed music often exhibit substantial tempo fluctuations and deviations from precise timing are used for expressing emotions (Honing, 2013). Still, human listeners are capable of perceiving stable periodicities in live music (Kraus & Slater, 2015). Hence it may be that only some amount of statistical temporal regularity in the stimulus is sufficient for human auditory system to perceive the stimulus as periodic (maybe even more periodic than it objectively is).

Nevertheless, metrical rhythmic structure in both music and language provides temporal "map" or framework that can be exploited to organize the input, predict (anticipate) the timing of future events and interpret incoming input according to the prior experience (Kraus & Slater, 2015). Additionally, one interesting phenomenon that points to similar mechanisms of processing time in speech and music is motor synchronization. Synchronization of body movements with the rhythm of music is a universal phenomenon in humans. Similarily synchronization can be found in speaking when employing speech in musical activities (singing). Moreover, speakers seem to use rhythmical aspects of speech when they synchronize with each other in praying or chanting even without musical context (Cummins, 2009).

Not only synchronization of movements, but also entrainment of neural oscillations has been recently proposed as a fundamental aspect of processing in both domains (Giraud & Poeppel, 2012; Large et al., 2015). It is therefore possible that the same cortical and subcortical networks that take part in temporal processing and prediction generation are involved in perception of linguistic and musical rhythm (Kotz & Schwartze, 2010; H. Merchant, Grahn, Trainor, Rohrmeier, & Fitch, 2015). This may provide interesting possibilities for using musical training in treatment of disorders that include deficits in speech rhythm processing, particularly developmental dyslexia (see Section 6).

5 Neuroscience of musical beat and meter perception

5.1 Theoretical background

In the context of music, rhythm is defined as a "pattern of time intervals demarcating a sequence of stimulus events" (Leow & Grahn, 2014, p. 326). This pattern is defined by onsets of individual events and time intervals between these onsets (inter-onset interval; IOI). The most contrasting characteristic of musical rhythm compared to speech is that it gives rise to a perception of a periodic pulse (or beat). In everyday speech there is no such rhythmic feature present unless the speech is employed in a musical context such as a song or rap. The beat consists of an isochronous series of regularly recurring

salient psychological moment in time and is a mental construct actively created by the listener (Cooper & Meyer, 1963), i.e. it is not a physical feature of the stimulus. Beat is the pulse humans synchronize movements to when tapping a foot, clapping or dancing to music. In the literature, there is a dissociation between duration-based (or absolute) timing where temporal patterns are encoded as absolute durations, and beat-based (or relative) timing where temporal patterns are represented relative to a reference provided by a periodic beat interval (Teki, Grube, & Griffiths, 2012).

There are multiple aspects of rhythm that give raise to the perception of beat. One of the necessary conditions is that IOIs of individual events in the rhythm must be related by small integer ratios (e.g. 1:2:4). Interval lengths of non-integer ratios (e.g. 1:3.1:4.5) would not give rise to beat perception because of no underlying temporal regularity. Additionally, there is a preferred rate of beat around 300-900 ms IOI between individual pulses (Fraisse, 1963). The beat percept is guided by an accent structure of the rhythm. Accent is a feature of a particular event (sound) in music and the level of accentuation defines a relative salience of the event (making it more or less "important" for the listener). There are many ways to accent an event in music. Most common accent types are temporal (how events are organized in time, e.g. in a group of two events the second one is perceived as more salient), intensity, duration, melodic, harmonic and timbral (changing the "color" of the sound) (Lerdahl & Jackendoff, 1983). Hence, first the beat must be extracted from an accent structure of the rhythm by the listener and then used to set an "internal clock" in his mind. Once set, all following events are interpreted relatively to this clock (Povel & Essens, 1985).

Moreover in music there can be multiple levels of the beat consisting of subdivisions (i.e. harmonics, e.g. 2:1, 3:1) and strong-weak grouping (i.e. subharmonics, e.g. 1:2, 1:3) of the main pulse. These different levels form a metrical structure (or hierarchy) of beats sometimes just simply called "meter" (see Figure 2) where faster beats are nested within the slower beats. If we follow the clock analogy, we can (for the sake of an example) choose the level of seconds as our main beat level. Then we get a nested hierarchy of subdivisions of this "beat" by milliseconds (subdivision by 10^3) and microseconds (by 10^6) and at the same time higher levels contain minutes (grouping by 60), hours (60^2) etc. However, in music the grouping and subdivisions are usually by factor of 2 or 3 therefore much smaller numbers than in the clock example. For instance basic waltz meter contains two levels of beats, where the slower beat coincides with every third faster beat (thus we are counting "ONE – two – three – ONE – two – three...").

In a metrical hierarchy some beat levels are perceptually more salient (important) than others. Time points where pulses of more levels of the metrical grid coincide (e.g. the "ONE" in the waltz example) are more important (salient) for the listener, therefore complete metrical grid creates a structure of alternating strong and weak beats. The amount of salience imposed on a particular time point guides anticipation of the listener - "something important is probably going to happen at this moment" (London, 2012). Predictive nature of the beat representation can be observed in tapping paradigms where human subjects are required to tap the pulse of a rhythm (actually, this can be observed also when tapping to an isochronous metronome). If the beat is successfully extracted people tend to place their taps a few tens of milliseconds before the beat which is a sign that they anticipate rather than react to the pacing rhythm (Repp & Su, 2013). In perception, these predictions decrease uncertainty and enhance effectivity of processing. Indeed there is a vast amount of evidence showing improved accuracy of time perception in rhythms where the beat and meter can be easily perceived (e.g. Grube & Griffiths, 2009). Enhanced processing of events coinciding with strong metrical positions has been shown in studies of event-related potentials. For instance MMN component which is an automatic brain response to violations of sound sequence regularities has greater magnitude when violations are made at metrically strong positions (Ladinig, Honing, Háden, & Winkler, 2009; Winkler, Háden, Ladinig, Sziller, & Honing, 2009). Tierney and Kraus (2013b) reported increased P1 amplitude to a sound when it coincided with the beat, in comparison to when it was shifted away from the beat of simultaneously presented music. This indicates better early sensory processing of the on-beat stimulus.



Figure 2: Example of musical rhythm and its plausible metrical interpretation. Top row represents how the rhythm is notated in a musical score. Second row depicts the same rhythm decomposed into individual events (line stands for a tone and dot stands for a silence). Pulses of the main beat are represented as dots in the third row. At the bottom is the whole metrical hierarchy with 4 beat levels. More dots superimposed over a particular event, more salient that position is for the listener. Note that one such salient position coincides with silence (marked by grey rectangle), which is a phenomenon called "loud rest". Adapted from Honing, Bouwer, and Háden, (2014).

Similarly to a simple beat, meter is a cognitive phenomenon that is not a physical attribute of the rhythm. Thus according to Honing (2013) meter perception can be seen as "an interaction between the music - the sounding rhythm - and the listener - who projects a certain meter onto it" (p. 381). The process of extracting beat (and meter) from a temporal pattern of musical rhythm is called beat or meter induction. Meter induction can be quite straightforward particularly when the structure of accents provides unambiguous cues about the location and rate strong beats. Usually people try to interpret the rhythm with a metrical hierarchy where the highest number of accented events coincides

with most salient beats in the hierarchy. However some rhythms employ accent structure that is ambiguous and there is not one simple "solution" how to metrically interpret the rhythm (Leow & Grahn, 2014). For instance modern jazz music often contains such rhythms. In this case some weak beats in the meter will coincide with strongly accented events and some strong beats will coincide with weakly accented events or even silences (see Figure 2). This means that the mental representation of the meter in the mind of the listener is not supported by the musical rhythm. In music theory this kind of misalignment between metrical and accent structure is referred to as syncopation. Syncopation makes the metrical interpretation unstable and creates feeling of "tension" which is used by music composers to evoke certain feelings in the audience. However, in this thesis, the term "rhythm complexity" will be used as a synonym to syncopation, as this term is widely used in the psychological and neuroscience literature (e.g. Chapin et al., 2010; Kung, Chen, Zatorre, & Penhune, 2013). In highly complex rhythms, it is much more difficult for the listener to find and keep the representation of a metrical hierarchy (Honing, 2013). There have been attempts to find a way how to quantitatively evaluate the complexity of a particular rhythm. Different researchers proposed different heuristics to do that. For instance Povel and Essens (1985) suggested that rhythmic complexity can be calculated by counting how many events fall on strong relative to weak beats in the imposed metrical hierarchy.

5.2 Neural processing of musical meter

Despite the fact that how does the brain extracts meter from the rhythm is still not completely understood, there have been multiple models of this process proposed, which used algorithmic approach to meter extraction (e.g. Lerdahl & Jackendoff, 1983). However more recent theories emerging from the dynamical systems branch of cognitive science have been shown to explain some empirical phenomena that the old theories could not account for. For instance there is a phenomenon of "missing pulse" where the frequency of the beat is missing from the stimulus (rhythm) envelope modulation spectrum, i.e. there is zero energy present at the frequency of the beat. Nevertheless, people are able to extract and entrain their tapping to the correct beat (Large et al., 2015).

Currently most widely accepted is the model designed by Edward Large (resonance theory), which is based on DAT (see Section 1.1). This model suggests that neural oscillations are the main substrate of processing musical meter. Entrainment of slow-frequency oscillations (i.e. rhythmic excitability changes in the neuronal population) at multiple frequencies representing individual beats in the metrical hierarchy could explain why the processing of a stimulus that coincides with strong beat is enhanced. Furthermore, when considering neural oscillations that can entrain to a complex rhythmic stimulus, one can abandon abstract representations and computations described by early models. Meter induction becomes a dynamical phenomenon that is natural for the neural architecture in a similar way that resonance to certain frequencies is natural for other physical systems (Large & Snyder, 2009).
The model is based on nonlinear oscillators, representing neuronal populations where oscillations arise from excitatory – inhibitory interactions (similarily as in the cortex). Each oscillator has its own resonance region which represents frequency band where it is able to phase-lock to the input. Additionally it may exhibit self-sustained oscillations (which are important for retaining the oscillation despite perturbances in the input, such as syncopation). Networks of these oscillators are created with resonance frequencies sorted on a gradient covering logarithmically spaced frequencies from 0.25 to 16 Hz (i.e. the whole range of human beat perception). There are two such networks in the model, representing auditory and motor brain areas with plastic connections within and between these networks, enabling for reciprocal coupling. When stimulated with a complex rhythm both networks synchronize their output oscillations with the input. However, while the sensory network closely reproduces the input, the motor network is capable of introducing pulses that are not present in the stimulus. This process depends on interactions between both networks and is supposed to predict dynamics of SS-EP in EEG response to complex rhythms (see below). Because of strong nonlinearities, the model is able to produce frequencies that have zero energy in the stimulus but carry the beat of the rhythm (Velasco & Large, 2011).

Large et al. (2015) suggest that their model simulates brain networks where entrainment of slow delta oscillators to the beat within auditory and motor networks enables coordination of perception and rhythmic movement with a musical rhythm. Interactions between sensory and motor cortices may also fit the data from functional imagining where increasing rhythm complexity was related to increase in auditory-motor functional connectivity (Kung et al., 2013). Further, albeit more speculative, increased interactions between sensory and motor networks may be required for more syncopated rhythms which would explain why these are related to increased musical groove (desire to move to music) (Witek, Clarke, Wallentin, Kringelbach, & Vuust, 2014).

Recent research indeed points toward interactions of auditory and motor systems in beat perception. For instance a metrical interpretation of ambiguous rhythms (with accent structure that allows for multiple metrical interpretations) can be influenced by previous motor experiences (Phillips-Silver & Trainor, 2007) or even without overt movements using direct stimulation of the vestibular system (Trainor, Gao, Lei, Lehtovaara, & Harris, 2009). At the neural level interval-based and beat-based timing have been dissociated and related to different structures. Interval-based timing has been linked to cerebellum, as damaged cerebellum (or disrupted by TMS) leads to impaired processing of absolute timing but intact beat perception (Grube, Cooper, Chinnery, & Griffiths, 2010; Grube, Lee, Griffiths, Barker, & Woodruff, 2010). On the other hand beat-based timing has been associated with motor cortico-basal-ganglia-thalamo-cortical (mCBGT) circuit including BG, SMA, preSMA, PMC, AC and VLPFC (for a review, see Merchant et al., 2015). Patients with Parkinson's disease (where BG are mainly damaged) have severe difficulties in perception of simple metric rhythms but their performance

is at the level of intact population when temporal patterns with no underlying beat structure are used (i.e. when absolute timing is required) (Grahn & Brett, 2009). Particularly, greater activation of putamen and SMA was reported when participants listened or synchronized their movements to metrical rhythms (Grahn, 2009; Kung et al., 2013; Teki et al., 2012) even without attention focused on the rhythm (Bengtsson et al., 2009). However, attention seems necessary for beat induction in more complex rhythms (Chapin et al., 2010). Furthermore, greater functional connectivity between auditory and premotor cortices has been correlated with increasing complexity of the rhythm (Chen, Penhune, & Zatorre, 2008).

Studies of electromagnetic brain dynamics provide support for Large's model. Moreover, they indicate that similarly to speech (see Section 2.3), entrainment of endogenous neural oscillations is present in perception of beat and meter. Interestingly, preferred beat interval in music is similar to the mean rate of stressed syllables in language (Fraisse, 1963; Leong et al., 2014), therefore neural oscillations mainly at delta frequencies are phase-locked to the musical beat. Particularly, the work of Sylvie Nozaradan and colleagues (for a review, see Nozaradan, 2014) suggests that slow neural oscillations (measured by SS-EP method) entrain to multiple beat frequencies in the input (which was proposed by Large). Moreover brain entrainment at some metrical frequencies can be elicited (or modulated) by top-down imagination or by motor activity. SS-EPs can be influenced by imagining binary or ternary meter over an isochronous stimulus (isochronously amplitude modulated pure tone) at 2.4 Hz rate (Nozaradan, Peretz, Missal, & Mouraux, 2011). While imagination of the binary meter (grouping by two) was associated with emergence of additional frequency component at 1.2 Hz, ternary meter (grouping by three) imagination elicited 0.4 Hz periodic component in the EEG spectrum. These frequencies corresponded to the rate of the imagined higher pulse level in the metrical hierarchy and importantly, neither 1.2 nor 0.4 Hz frequency was physically present in the stimulus envelope. In another study (Nozaradan, Zerouali, Peretz, & Mouraux, 2015) the same stimulus stream was used but subjects tapped their hand on every second event, thus imposing a binary meter. This resulted in two SS-EP components, one at 2.4 Hz related to the sensory input (as it was the original rate of the stimulus) and second component at the rate of the motor entrainment (1.2 Hz; no energy at this frequency was in the stimulus). Interestingly the SS-EP component related to the stimulus was significantly enhanced when subjects were tapping in comparison to listening only. Furthermore its relative phase was modulated by the tapping performance when analyzed in the time domain. If the particular single tap was earlier, also the peak of 2.4 Hz component was earlier relative to the stimulus onset. These results suggest a compelling interplay between sensory and motor systems in beat perception.

Further support for the role of motor system in neural entrainment to musical meter is provided by the finding that previous motor experiences can bias brain response to a metrically ambiguous complex rhythm which can be interpreted by both, binary or ternary meter. SS-EPs at the frequencies related to either binary or ternary meter were enhanced after participants moved their body (prior to EEG recording) in a way that corresponded to that particular metrical interpretation (Chemin, Mouraux, & Nozaradan, 2014). This converges with studies of Trainor and colleagues (e.g. 2007; 2009) who reported similar results but they measured only behavioral output and not neural entrainment. Finally and most importantly, synchronization of slow brain oscillations at metrical frequencies has been reported in highly complex rhythms where the acoustic energy at these frequencies is not predominant in the stimulus amplitude envelope. However, those AM frequencies in the stimulus that were related to the perceived meter were selectively enhanced in the brain response in contrast to meter-unrelated ("distractor") frequencies which were suppressed (Nozaradan, Peretz, & Mouraux, 2012). Moreover this selective frequency enhancement reflected natural range of beat perception. When the same rhythm was presented at a four times faster rate, the beat previously placed on every fourth event was not in the natural range of beat perception anymore. As the result, SS-EP at the frequency related to grouping by twelve (but not four) events was enhanced instead.

Altogether, these results suggest that neural populations in human brain do not simply follow the amplitude envelope of the stimulus, but selectively reflect metrical interpretation of musical rhythms, carrying predictions about temporal structure of the stimulus. This is in line with studies of speech perception reviewed in Section 2.3 that reported top-down modulations of slow brain rhythms entrained to speech envelope fluctuations. Nozaradan et al. (2014) suggest that the observed synchronized brain activity probably contains envelope following response of neurons from auditory cortex, but this response is modulated by higher level processing (in accordance with DAT). The neural generators in auditory cortex have been supported by intracranial recordings (Nozaradan, Jonas, Vignal, Maillard, & Mouraux, 2014).

Neural entrainment has been observed also in the context of ecologically valid music, which is an important finding considering the fact that real music is much more complex than artificial rhythmic stimuli used in previously reviewed studies. Moreover, as previously noted, performed music is not strictly periodic, i.e. there are tempo fluctuations and expressive timing which may make tracking of the beat more challenging. Tierney and Kraus (2014b) presented a short auditory stimulus together with a pop song. When this stimulus was aligned with the beat of the song, cortical entrainment was observed at the frequency of the beat and its subdivision (i.e. two levels of the metrical hierarchy). However when the stimulus was shifted away from the beat, SS-EP was not observed at the second hierarchical level (the subdivision) anymore. This indicates that neural tracking of metrical structure on multiple timescales can be disrupted by presenting incongruous cues that do not support induced metrical interpretation of a musical piece.

To summarize, processing of rhythmic structure of music is tightly linked with entrainment of low-

frequency oscillations. This is similar to the entrainment to speech temporal structure. In both domains a hierarchy of oscillations could be employed to track the complex structure and carry anticipations about the future events, thus promoting efficient attention allocation to the relevant time-points in accordance with active sensing framework and DAT. Possibly, in both domains the role of interactions between auditory system and motor system might play a role during the temporal structure processing. As reviewed in the next section, performance of individuals with developmental dyslexia is inferior to normal readers in a wide range of tasks that require processing of musical (periodic) rhythm. This is predicted by TSF and as suggested, deficits in neural entrainment to the stimulus temporal structure might underlie the poor performance of dyslectics on tasks involving speech as well as non-speech rhythm.

6 Impaired rhythmic abilities in dyslexia

6.1 Tapping

Large number of studies has pointed out the link between motor timing and literacy. Mostly they employed tapping task either requiring synchronization with a pacing stimulus (e.g. isochronous metronome) or continuation of tapping without external pacing in different tempos. Early studies found deficits in bimanual tapping (alternating hands) in dyslectic boys and interpreted these results as an impaired hemispheric communication in children with reading difficulties (Badian & Wolff, 1977; Klicpera, Wolff, & Drake, 1981; Wolff, Cohen, & Drake, 1984). However, subsequent studies have failed to replicate this findings (e.g. Wolff, 2002; Wolff, Michel, Ovrut, & Drake, 1990). Wolff et al. (1990) reported greater tapping variability (i.e. larger deviation of inter-tap intervals, suggesting less consistent response) in dyslectic students when compared to controls or even to controls with other learning disabilities (but normal reading performance). Dyslectics demonstrated greater variability across different tempi regardless of whether they tapped with both hands in unison or with alternating hands. Similar results were obtained from family members of dyslectic children, if they were also affected by dyslexia (Wolff, Melngailis, Obregon, & Bedrosian, 1995, Wolff, Melngailis, & Kotwica, 1996)). However, only half of the dyslectic children (and only their affected relatives) demonstrated rhythmic difficulties. The authors suggested that temporal resolution deficits are part of vertically transmitted behavioral phenotype at least in some dyslexia subtypes. Wolff (2002) reported that students with dyslexia exhibited significant deficits in multiple motor rhythmic tasks including tapping to isochronous pacing stimulus, adjusting their tapping rate to changing tempo and rhythmic pattern reproduction. Anticipation of the stimulus while tapping to isochronous metronome (negative mean asynchrony) was significantly greater in dyslectics (130 ms and 41 ms respectively). They further needed longer time to recalibrate their tapping when the pacing stimulus rate has changed. Finally,

dyslectics had difficulties with simple rhythmic pattern reproduction and this deficit has been even more pronounced when they were asked to tap out the pattern to a pacing metronome beat.

Thomson and colleagues in series of two studies investigated externally paced and self-paced tapping (at rates of 1.5 – 2.5. Hz) in groups of dyslectics and control subjects consisting of university students (Thomson, Fryer, Maltby, & Goswami, 2006) or 10-year-old children (Thomson & Goswami, 2008). Results revealed significantly greater ITI variability in the dyslectic groups, but excluded general motor difficulties (i.e. without rhythmic component). Children and adults with larger ITI variability were significantly worse in reading and phonology skills after controlling for IQ and these effects were most prominent at slower tempi. Both studies failed to replicate increased negative mean asynchrony in dyslectics reported by Wolff (2002), however the authors suggested possible methodological differences as an underlying cause of this discrepancy. Interestingly, in children the relation between rhythm and reading was significant only for paced condition while adult dyslectics were significantly worse at both paced and unpaced tapping. This was mainly due to the large ITI variability in both, dyslectic and control children. Hence it may be that typically-developing children get better in internal generation of steady pulse with increasing age, whereas dyslectic children struggle also in adulthood (which would point toward impaired development of slow brain oscillations).

Birkett (2014) provided strong evidence for the relation between ITI variability and phonology skills. After controlling for age, IQ and correcting for multiple comparisons (which has not been treated in previous studies) tapping variability at 2.5 Hz still predicted 30% of unique variance in spelling, RAN and VSTM in dyslectic children. She further used statistical techniques for time series analysis (Wing-Kristofferson model) in order to differentiate between two subcomponents of rhythmic tapping performance: timekeeping and implementation system. Timekeeping system is (metaphorically) considered a clock-like mechanism that generates stable pulses at the target rate and implementation system provides motor execution of the taps according to the timekeeper pulses. Variance produced by either system can be mathematically extracted from the tapping performance. Birkett argued that literacy difficulties are linked to larger variance in the timekeeping system in contrast to ADHD where implementation system might by impaired. This is in accordance with Thompson and Goswami (2008) and other authors (Ramus, Pidgeon, & Frith, 2003; van Daal & van der Leij, 1999; Wimmer, Mayringer, & Raberger, 1999) who also excluded general motor deficit in dyslexia.

Although the precise pattern of difficulties might vary throughout the development as indicated by Thompson et al. (2008) and possibly compensatory strategies might play a role in adult dyslectics, these studies altogether provide support for temporal deficit in dyslexia. The data might be partially explained by auditory difficulties proposed by TSF. Impaired perception of amplitude rise times which carry information about P-centres may cause diminished ability to precisely represent sound onsets and

thus place individual taps when synchronizing to the metronome. Nevertheless, atypical entrainment of neural oscillations at the rate of tapping could provide even better explanation for both paced and unpaced tapping deficits. Deviant entrainment would result in worse predictions about the location of next tap. Furthermore, as interactions between sensory and motor networks have been proposed in beat-based timing, inefficient predictive coupling of these networks by low frequency oscillations might lead to decreased ability to use auditory input to correct subtle deviations of tapping to a pacing stimulus. There have been proposals that the ability to use sensory feedback to guide motor timing might account for poor paced tapping in dyslexia (see Section 6).

Indeed, recent evidence suggests that there is a close relationship between ability of individual to consistently tap and measures of how well his brain can represent the beat or meter. For instance Tierney and Kraus (2013b) employed a paradigm (described in Section 4.2) where short sound was repeatedly presented simultaneously with a pop song. When this sound coincided with the beat of the song, early auditory ERP obligatory component P1 showed larger amplitude than when the sound was shifted away from the beat. Notably, this P1 enhancement varied between subjects and was significantly correlated with their tapping skills. Larger difference between brain response to on-beat and off-beat sound related to less variable paced tapping. Tierney and Kraus suggested that cortical tracking of the beat in music might share neural resources with tapping to the beat. Especially connectivity between auditory and motor areas could represent this underlying relationship. Importantly the authors proposed that measuring neural responses to the beat might help to disentangle neural and motor components which are necessarily mixed in tapping performance. Therefore such a measurement would be a convenient way to test whether there is indeed a deficit in neural processing of musical rhythm in developmental dyslexia as suggested by TSF and not simply difficulties with motor implementation. Moreover, relationships between tapping performance and neural entrainment to complex rhythms have been recently reported (Nozaradan, Peretz, & Keller, 2016). Two rhythms (syncopated and unsyncopated) of were used and neural entrainment to the stimulus envelope was measured by assessing SS-EPs at the frequencies related and unrelated to the meter. Participants who had larger amplitude of the SS-EP related to the main beat and greater suppression of meter-unrelated SS-EPs tapped (to the beat of the same rhythms) with smaller negative mean asynchrony, i.e. they placed the taps closer to the corresponding beat. Additionally, the ability to robustly entrain to the beat despite conflicting information in the high complex rhythm was correlated with the ability to predict tempo changes in tapping to a pacing stimulus that continuously changed rate. These results suggest that deficits in neural tracking of the stimulus metrical structure might underlie impaired tapping performance observed in dyslectic individuals. However, up to date no studies have directly aimed to test such prediction (see Section 8).

6.2 Music and musical rhythm

Besides sensorimotor synchronization with rhythmic stimulus, TSF proposes general difficulties in perception and processing of temporal structure in music. Indeed, converging evidence indicates that dyslectic individuals show severe difficulties when it comes to rhythmic skills.

7-11 year old children with dyslexia scored significantly lower on tasks involving musical rhythms. The ability to tap out the rhythm of a song has been related to spelling and dyslectics had enormous problems with tapping out the rhythm while singing (reciting) the lyrics (e.g. "Happy birthday"). Therefore it seems that dyslectics have problems especially when they need to explicitly connect rhythmic aspects of speech and music. Interestingly, they were better than controls in tasks involving pitch processing which provides support for selective impairment of temporal abilities and not general cognitive abilities (e.g. attention) Overy, Nicolson, Fawcett and Clarke (2003).

Furthermore, relationship between musical rhythmic skills and reading abilities (or skills predicting reading development such as PA) has been reported in typically-developing population. This is important, because dyslectics may only represent the lower end of the distribution. Thus showing that temporal abilities are linked with reading also in general population provides further support for the hypothesis that these skills might be particularly diminished in dyslectic individuals. In an early study Douglas and Willatts (1994) reported that rhythmic musical ability in 8-year-old children correlated with reading and spelling. In another study with more than 1000 French children, reproduction of 21 simple rhythmic patterns (tapped by the experimenter) at the age 5-6 years explained 26% of variance in reading performance in the second grade. Strong linear relationship between these two variables was observed even after controlling for socioeconomic factors, attentional, visuospatial skills and verbal repetition (Dellatolas, Watier, Le Normand, Lubart, & Chevrie-Muller, 2009). Finally, longitudinal study of typically-developing children during the first five years of school education showed that performance on rhythmic tasks (tapping and marching to the beat of musical recordings) in grade 1 correlated with predictors of reading (PA and RAN) and also reading abilities during the whole observed period (up to grade 5). After partialling out PA, rhythm abilities still predicted unique variance in reading of pseudo-words in grade 5 and when controlling for RAN it predicted word reading in grades 2 3 and 5 (David, Wade-Woolley, Kirby, & Smithrim, 2007). These results suggested that rhythm may be more important for older readers when requirements for reading move beyond the level of simple monosyllabic word decoding towards more complex polysyllabic words where prosodic stress patterns play a stronger role.

Influential insights into possible developmental trajectories in dyslectics regarding rhythm perception have been provided by two studies of Goswami and colleagues who investigated a same sample of children first when they were 10 years old and subsequently one year later (Goswami et al., 2013; Huss et al., 2011). The main task of interest (perception of musical beat distribution) consisted of

short rhythmic patterns made up of accented and unaccented tones (volume accents) with underlying pulse of 2 Hz. Children had to detect small deviances in the accented tone when it was prolonged by 100 or 166 ms (which disturbed the regular temporal structure of the pattern). Scores in this task predicted 60% of variance in single word reading after controlling for age and IQ in the first study, which was more than rhyme awareness (traditional PA measure and good predictor of literacy) that explained only 33%. In the second study it was possible to examine also longitudinal variance i.e. how well can literacy development be predicted by scores on other tasks from a year before. Reading scores and reading comprehension were both predicted by the beat perception (15% and 18% of unique variance respectively) even after partialling out PA skills. Notably, concurrent performance on the beat perception in both studies was not predicted by simple duration discrimination skills, despite the nature of violations in the beat task was indeed durational (the accented tone was prolonged). As the change in duration also disrupted rhythmic aspects of the pattern, impaired processing of higher temporal features of the pattern in dyslectic participants could be a better interpretation. Rise time discrimination seemed to be the only auditory task that predicted both beat perception, PA and reading skills providing further evidence for perception of AM being a unique associate of rhythmic skills in music and language (as proposed by TSF). The first study reported differences between dyslectic and agematched group but not reading level-matched group, while a year later dyslectics were significantly worse than both control groups in musical beat and rise time perception. This suggests that dyslectics have severe impairments in sensory processing and these are becoming more pronounced with age as typically-developing children improve (possibly because of reading experience) their performance but dyslectics do not.

Multiple rhythmic skills were assessed in a sample of Italian dyslectic children selected by very strict criteria (controlling for comorbidities etc.) (Flaugnacco et al., 2014). Zero-order correlations revealed strongest relationships between reading, PA and complex temporal tasks especially rhythmical pattern reproduction and metronome-paced tapping variability. Secondly logistic regression showed that the only significant predictors for reading after controlling for age, sex, IQ etc. were again more complex temporal tasks, namely rhythm reproduction and perception of musical meter (the same task as in Goswami et al., 2013). Notably, neither PA, nor attention or memory predicted reading performance in this sample of dyslectics. Factor analysis revealed high loadings of the same factor in phonological and rhythmic skills, which supports the link between these abilities. Interestingly, rise time discrimination was the only skill that was present in the same factor with all reading measures. This suggests that perception of rise time and complex temporal tasks may not be driven by same cognitive resources as suggested by TSF. Although both seem to influence reading, it may be that more complex rhythmic tasks require additional processes for global representation of the stimulus structure whereas rise time discrimination depends on purely perceptual skills. Altogether, the authors concluded

that temporal processing in dyslexia may be impaired at multiple timescales, however they emphasize more global level of temporal processing such as grouping events into chunks and building the representation of metrical hierarchy. Other studies also highlighted the importance of global temporal representations and sequence analysis rather than simple, local temporal relations between events. Grube, Cooper and Griffiths (2013) reported that literacy skills in typically-developing adults were correlated with detection of temporal regularity of sound sequences and discrimination of metrical rhythmic patterns, but not single time interval judgement or perception of tempo changes. The authors argued that the ability to process temporal regularities related to regular or quasi-regular beat might be important for language skills and they propose a link between beat-based timing, oscillatory brain entrainment in music and language, and reading. Weaker pre-attentive response to deviations in temporal rhythmic pattern (inter-onset intervals 200-150-50 ms in standard and 200-50-150 in deviant) measured with mismatch negativity ERP component in dyslectics lends further support for deviant processing of higher temporal organization of auditory stimulus (Kujala et al., 2000).

To summarize, large number of studies reported difficulties with rhythmic processing in dyslexia and showed that this processing is also related to reading in normal population. Notably, there is a huge diversity of employed measures between different studies. While some involved only perceptual tasks such as judging similarity of two patterns or detecting rhythmic deviations, others included also production tasks such as rhythm copying or tapping with a pacing stimulus. Also different types of rhythmic stimuli were used ranging from simple isochronous metronome to ecologically valid musical tunes. Despite this apparent methodological differences the deficit in temporal tasks is consistently reported in dyslectic individuals. Difficulties with extraction and precise representation of beat and meter might represent an underlying deficit that could account for the observed poor processing of musical rhythms. Beat-based timing is critical for good perception and production of musical rhythms, because it enables coding of individual intervals in the rhythm according to the internal representation of an underlying beat at multiple levels (organized in metrical hierarchy). If mental representation of the stimulus metrical structure would not be precise, this could lead to inefficient coding of rhythms that would result in difficulties in rhythm discrimination and reproduction, and accurate detection of subtle deviances in the temporal structure of the rhythm. Considering the proposal of TSF that neural oscillatory activity might be atypical in dyslectics at the timescales that in speech coincide with syllable and syllable stress rate, while in music the same timescales characterize beat perception, it could be that same atypical oscillatory mechanisms underlying deficits in representing quasi-rhythmic prosodic structure of speech and metrical beat structure of musical rhythms in dyslectic individuals.

6.2.1 Relations to subcortical sound processing

Interesting results regarding tapping and neural processing of sound in poor readers have been

reported by Nina Kraus and her colleagues. Although their approach focuses on subcortical processing of sound at short timescales it may be consistent with TSF, particularly when considering auditory system as distributed (i.e. there are separate relay stations that are specialized for particular functions) but integrated circuit where "although each structure is specialized to perform a specific function, this specialization has evolved in the context of the entire circuit" (Kraus & White-Schwoch, 2015, p. 643). This means that the auditory pathway is highly interconnected and information is not passed only in a bottom-up direction but there is a tremendous amount of efferent (top-down) projections (Bajo & King, 2013). Thus changes in one part of the system can influence other parts and modification at one level affects the whole system.

EEG can be used to record responses from early stages of the auditory pathway, where the neural response very closely represents stimulus physical features (note that as moving up along the auditory pathway, representations become more and more "abstract"). Interestingly, when using simple syllable as a stimulus, poor readers consistently demonstrate delayed (Banai et al., 2009), more variable (Hornickel & Kraus, 2013), less discriminative (White-Schwoch & Kraus, 2013), and less robust to noise (Chandrasekaran, Hornickel, Skoe, Nicol, & Kraus, 2009) brainstem representations of important features such as onsets, formant transitions, and harmonic structure of speech sounds. Even though detailed description of the approach of Kraus et al. is beyond the scope of this thesis, particularly interesting are the studies investigating rhythmic tapping. It has been shown that consistency tapping performance (ITI variability) and precise speech sound representations at the level of brainstem are related in highschool students (Tierney & Kraus, 2013c) and pre-school children aged 3-4 years (Woodruff Carr, Tierney, White-Schwoch, & Kraus, 2016). High ITC of brainstem responses to single syllable stimulus was further related to better ability to adapt the tapping when perturbations were introduced in the pacing stimulus. Interestingly, there was no such relationship for slow cortical entrainment (5-10 Hz) to the stimulus (Tierney & Kraus, 2016). Moreover, tapping variability and consistent brainstem response were associated with reading performance in normal population of high school students (Tierney & Kraus, 2013d). This relationship was more prominent for 2 Hz (compared to 1.5 Hz) tapping tempo and paced (compared to unpaced) tapping. Pre-reading children with low scores in traditional tasks that predict future literacy skills (PA, RAN and VSTM) showed less precise encoding of syllable amplitude envelope at the brainstem level and worse music perception, especially when judging rhythmic aspects of music (Woodruff Carr, White-Schwoch, Tierney, Strait, & Kraus, 2014). This results suggest that diminished tracking of slow modulations of amplitude may stem from early levels of auditory pathway and not be solely a problem of cortical phase-locking as suggested by TSF. Additionally structural equation modelling (which evaluates the fit of priori hypothesized model) revealed that music aptitude (but only rhythm aptitude and not tonal skills) in children predicted 38% of variance in reading ability and this is mainly by its impact on subcortical processing of speech

regularities (brainstem response enhancement in repetitive context) and auditory working memory/attention (as a single latent variable) (Strait, Hornickel, & Kraus, 2011).

Can these findings be successfully interpreted within TSF? White-Schwoch and Kraus (2013) suggest that this is indeed feasible despite the fact that TSF proposes primary deficit in phase-locking of slow cortical oscillations. As auditory system can be considered an "integrated circuit that interacts dynamically with cognitive, reward, and other sensory systems" (White-Schwoch & Kraus, 2013, p. 6) it is possible that neural tracking at slow and fast rates is interconnected. For example Wible (2004) reported significant relationship between subcortical and cortical response to syllable /da/ and Abrams, Nicol, Zecker, & Kraus (2006) showed that response timing in brainstem correlates with hemispheric asymmetry of cortical response to the same syllable. Further, abnormal subcortical responses are related to weak cortical sensitivity to acoustic change (MMN) (Banai, 2005). Synchrony of firing at higher cortical areas may depend on the fidelity of input from subcortical structures and on the other hand development of precise subcortical tracking may be influenced by efferent projections from the cortex (Kraus & White-Schwoch, 2015). It may be that inefficient tracking of slow modulations at higher levels in the pathway (i.e. rhythmic structure) and thus decreased ability to form temporal predictions results into inefficient focusing of attentional resources to the important portions of the signal (Large & Jones, 1999) and accordingly, into disability to tune lower level sensory responses by providing top-down predictions about future events. This may play a role also in the experiments from Kraus lab where they consistently use stimulus presentation rate of 4.35 Hz which is exactly the syllable-rate where dyslectics should be impaired according to TSF. An overarching framework should therefore include rapid phase locking at the subcortical level and slow oscillatory envelope tracking at the cortical level as dynamically interacting components within a broad network of auditory system (Goswami, Power, Lallier, & Facoetti, 2014). Possibly, the core deficit in reading impairment may be broader than just isolated impairment in slow phase-locking and affect the whole system. The idea of reduced firing synchrony at multiple timescales throughout the auditory system would account also for other sensory theories of dyslexia such as rapid auditory processing hypothesis (Tallal, 1980) which proposes impairments in auditory processing at fast timescales, but likewise it may explain attentional deficits in reading impaired individuals (Strait et al., 2011; Tierney & Kraus, 2013a). Hence such perspective provides means for merging multiple theories of dyslexia (see also Goswami, 2015).

7 Interventions

Considering insights of the studies suggesting auditory system dysfunction in dyslexia one might ask whether there is a possibility of intervention that would contribute to improvement in these brain networks. Indeed, recent work on brain plasticity provides promising results. It has been suggested that auditory system can change significantly with experience (experience-dependent plasticity) and these changes can be observed throughout all levels from high cortical to low brainstem networks (Kraus & White-Schwoch, 2015). Kraus and White-Schwoch (2015) suggest that there must be more cognitive systems engaged for plasticity to occur, especially attention, working memory, sensorimotor and reward systems. Based on several assumptions regarding language and music processing in the brain Patel proposed an OPERA hypothesis which suggests that musical training may improve language skills (Patel, 2011, 2014). He claimed that speech processing might benefit from musical activities if five conditions are met. First there must be a common sensory or cognitive process which is used by both speech and music and this process has to be underpinned by overlapping (O) brain networks. Next, higher precision (P) must be required to employ the particular process in music than in speech. Musical training has to be linked with positive emotion (E), the particular cognitive process must be repeated (R) frequently, and focused attention (A) should be necessary in order to successfully engage in the musical activity.

As a response to OPERA hypothesis, Tierney and Kraus (2014a) proposed PATH hypothesis (Precise Auditory Timing Hypothesis) which applies OPERA concept to one particular aspect of language and music: reading ability and auditory-motor synchronization. This synchronization could be defined as a "process of moving to a repeated auditory signal such that there is a consistent relationship between the timing of one's movements and the timing of sound onsets" (Tiernev & Kraus, 2014a, p. 1). Tierney and Kraus suggest that precise auditory timing is the underlying factor contributing to both skills (reading and auditory-motor synchronization) and it satisfies all requirements of OPERA hypothesis for succesful transfer from music to language, and thus provides a potential for interventions in children with dyslexia (or at risk of dyslexia) based on musical rhythmic training. As reviewed in Section 5, there is currently a fair amount of evidence suggesting disrupted rhythmic skills in dyslectic children, and showing that these abilities (particularly tapping skills) relate to the precision of brain synchronization with auditory stimuli. Especially tasks that require precise analysis of the stimulus and utilization of temporal features of the stimulus for succesful performance seem to make problems to reading-disabled individuals. The best example is paced tapping where careful monitoring of the pacing stimulus is required in order to correct small errors in tapping. This auditory-motor monitoring can be considered a third component besides timekeeper and implementation in the Wing-Kristofferson model used by Birkett (2014) to analyze tapping in dyslexia. If neural representation of the sound structure is less precise it will result in larger tolerance to error in timing and consequently greater ITI variability which is exactly what has been reported in dyslexia (Thomson et al., 2006; Thomson & Goswami, 2008; Tierney & Kraus, 2013a). Accurate temporal representation of sound temporal features is an essential ability necessary for developing well defined phonological representations as proposed by auditory theories of dyslexia. Tierney and Kraus (2014a) suggest that neural substrates of processing timing in speech consist of inferior colliculus, cerebellum

but also other structures involved in motor processing (Kotz & Schwartze, 2010) and are overlapping with the networks involved in processing of musical timing (Leow & Grahn, 2014).

Although the PATH hypothesis has been based on the research of subcortical sound representations in dyslectic individuals, precise temporal processing of slower timescales at the cortical level is also important for auditory-motor synchronization. Therefore the OPERA hypothesis might be also applied on processing of slow amplitude modulations and higher temporal structure of the stimulus as suggested by TSF. In line with this, Goswami (2011, 2012) proposed that musical training might be beneficial for dyslectics, particularly if rhythmic aspects of music are emphasized. She suggested that rhythm and meter are more overt in music in comparison to language, thus linking prosodic rhythm of speech with musical rhythms may be particularly helpful. For instance singing nursery rhymes, moving in time to music and playing instruments might be beneficial for children with reading difficulties. All activities that require entrainment of slow brain oscillations (delta and theta) might be possibly profitable for dyslectics because engagement of networks that might be impaired in dyslexia should promote neuro-plasticity.

If the hypotheses of OPERA, PATH and TSF are correct there should be an observable transfer from music to reading. Such a transfer could be exploited in therapy of dyslectic children or even children that have been identified at risk of developing reading difficulties. Early interventions are crucial because brain plasticity is highest in early development. Indeed, musical training might be used as a complementary training besides traditional interventions especially in the subset of dyslectics who exhibit auditory difficulties (Ramus et al., 2003). A reasonable question is why to use music to improve reading and phonological skills when these can be trained directly? According to Patel (2014), music places higher demands on precision than speech in many domains of auditory perception. In case of rhythmic timing this is obvious as musical timing requires very fine performance (even more difficult when playing live with other musicians). Furthermore, as speech is a highly redundant signal, Patel suggests that some acoustic cues in speech might be less used by certain individuals because other features might provide means for compensation without significant decrease in performance. This might be indeed the case in older dyslectics (Goswami et al., 2011). Furthermore, musical activities can be carried out in groups of children thus exploiting social dynamics to promote attention, motivation and overall involvement in the training. Playing an instrument can be also considered less boring than explicit training to read and music can evoke strong emotions (Koelsch, 2014) which may be linked to reward (Blood & Zatorre, 2001). Employment of reward circuits and executive networks has been proposed drive neural plasticity during auditory learning (Kraus & White-Schwoch, 2015).

7.1 Effects of musical training on reading skills

7.1.1 Comparisons of musicians and non-musicians

If musical training has any effects on literacy, comparing musically trained and untrained individuals should reveal superior performance of musicians on measures associated with reading development (reading, PA, and auditory skills based on the auditory theories of dyslexia). Indeed there is mounting evidence that indicates superior rhythmic, prosodic and auditory skills in musically trained subjects.

For instance, French musicians showed better performance on linguistic stress perception than control participants even though French speakers are "stress-deaf" because stress cues are irrelevant in their native language (Kolinsky, Cuvelier, Goetry, Peretz, & Morais, 2009). Further, behavioral and neural (ERP) measures indicated enhanced perception of a metric structure of words but not semantic structure in musicians (Marie, Magne, & Besson, 2011). More years of musical training were associated with superior perception of amplitude rise time in syllables (Zuk et al., 2013). Additionally, highly trained musicians have significantly better performance (lower ITI variability) in tapping synchronization tasks (Repp, 2010) than non-musicians which can be interpreted in concordance with PATH hypothesis and serve as another piece of evidence pointing toward relation between musical training and reading related skills. These findings indicate that those skills that were in many studies correlated with reading performance and suggested as impaired in dyslectic population by TSF are enhanced in musically trained individuals.

Empirical research into the low-frequency oscillatory entrainment in musicians is currently missing. However, there is mounting evidence supporting superior subcortical sound representations (see Section 6.2.1) as a result of musical training (for a recent review, see Tierney & Kraus, 2013a). People that play music seem to have much more precise responses to speech sounds at the brainstem level than the rest of the population (e.g. Parbery-Clark, Strait, & Kraus, 2011; Skoe & Kraus, 2013; White-Schwoch, Carr, Anderson, Strait, & Kraus, 2013), which is behaviorally manifested in better perception of speech in noise (Strait & Kraus, 2011). Auditory processing of speech in noise has been proposed as a hallmark of dyslexia (Travis White-Schwoch et al., 2015), as it requires precise representation of speech throughout the auditory system (see also Ziegler, Pech-Georgel, George, & Lorenzi, 2009). Perception of speech in noise has been linked with rhythm abilities in musicians playing different instruments. Percussionists showed better speech-in-noise perception compared to vocalists (Slater & Kraus, 2016). The effect of rhythm competence was present in perception of sentences in noise but not words in noise suggesting that perception of a rhythmic pattern of a particular sentence provided cues about possible content and musicians with better rhythmic skills were able to use these cues more than others. Although these results do not directly support TSF (because mostly dealing with different timescales), it is notable that musical training is linked with remarkably better processing of sound features in the auditory system. Despite most of the work on musicians has focused on subcortical processing, it may be presumed that neural plasticity that takes place in brainstem and midbrain nuclei might shape also higher processing areas in cortex. Further investigation of superior auditory skills of musically trained individuals with regard to cortical oscillatory processing is desirable and direct links with reading should be also assessed.

However there is also evidence speaking against the direct influence of musical training on reading performance. The main reason of such a doubt might be studies of dyslectic musicians. Although hitherto there are only few investigations of this sort, they consistently report enhanced auditory perceptual skills in dyslectic musicians, but it seems that these auditory skills do not contribute to increased reading abilities in these individuals. Weiss, Granot and Ahissar (2014) observed superior performance of dyslectic musicians compared to typically-reading non-musicians in frequency and temporal interval discrimination, speech in noise perception and tapping to a metronome. However the reading impairment was still quite severe in dyslectic musicians and thus did not correlate with their auditory skills. Similarly, Bishop-Lieber et al. (2014) reported comparable auditory perception of rise time and other features, as well as rhythmic skills in conservatory students with and without dyslexia, but concluded no automatic transfer from rhythmic processing to PA and reading. The authors suggested that maybe explicit instruction about relations between speech and language rhythmic characteristics (e.g. speaking word syllables to the musical rhythm) is required in order to achieve transfer from auditory skills to reading. In any case further research in this area is needed and investigation of dyslectic musicians can be a promising source of data about the relations between musical training, auditory skills and dyslexia.

7.1.2 Longitudinal studies of musical training

Nevertheless, there may be many factors in play when interpreting the results of such crosssectional studies. It is always possible that there is some uncontrolled underlying factor that influences both variables. Maybe people with some genetic predisposition for better auditory skills are more successful in their musical training and consequently they have higher motivation to play the instrument in contrast to people with genetically conditioned worse auditory skills. One possible solution are randomized longitudinal trials where musical training is randomly assigned to one subset of participants while some other control training is provided for the rest. Comparing enhancement of the dependent variable after such intervention between these two groups provides stronger evidence for an effect of musical training on literacy-related skills.

Effects of musical training on reading and related skills have been investigated in a number of

longitudinal studies employing test-intervention-retest paradigm (for a review, see Tierney & Kraus, 2013a) but it must be noted that the exact nature of such training varies extensively between different studies. Some researchers provided children with a broad training of musical abilities like melody, timbre, rhythm etc. (e.g. Flaugnacco et al., 2015), while others constructed specialized training programmes based on particular theory (TSF) and focused on specific aspects of music such as rhythm (e.g. Thomson, Leong, & Goswami, 2013). Another aspect is the type of activity (if any) that control group was engaged in. If the control group does not take part in any additional activity (but experimental does) any improvements may be just a result of increased interest from the researcher. Unfortunately this was the case in multiple otherwise promising intervention studies (e.g. Cogo-Moreira, de Ávila, Ploubidis, & Mari, 2013; Taub & Lazarus, 2012).

7.1.2.1 Effects on typically-reading individuals

As reviewed at the beginning of this section the PATH emphasizes the role of tapping and synchronization to the external pacemaker as a process that could serve to enhance reading.

Training sensorimotor synchronization to an isochronous metronome at multiple rates has been linked to improved reading in students. The training involved paced tapping while feedback about tapping timing error has been provided to participants. The control group took part in regular classroom activities. After four weeks there was a significantly greater improvement in reading in the experimental group, however the effect sizes were small (Taub & Lazarus, 2012; Taub, McGrew, & Keith, 2007).

Twelve months of musical (but not painting) training have been associated with enhanced preattentive discrimination of syllable duration and VOT (measured as amplitude of mismatch negativity ERP component) (Chobert, Francois, Velay, & Besson, 2014). Interestingly no effect has been observed for frequency discrimination. This could provide support for effects of musical training on reading being mediated by enhanced perception of supra-segmental temporal cues as proposed by TSF. Importantly the effects were observable 12 months after the training itself ended which lends support to long lasting changes promoted by musical training. Another study compared children attending kindergartens that employed more versus less frequent music classes. Greater enhancement in PA at the level of rhyme (large effect size) was observed after 6 months in the children that had more frequent music education (Moritz, Yampolsky, Papadelis, Thomson, & Wolf, 2013). Moreover children with better rhythmic skills in kindergarten had superior non-word reading scores in the second grade of elementary school.

Although results described above were assessed with children speaking English, effects of musical training have been reported in multiple languages that differ in orthographic depth and rhythmic properties. Rautenberg (2015) provided 159 German primary school students with 9 months of training

in music or painting (random assignment). At the second measurement (after the training) rhythmic but not tonal abilities correlated with reading accuracy. The same was true about reading prosody scores (how well children produced prosody when reading, e.g. stress, reduction of unstressed syllables). After controlling for IQ and socioeconomic status there was a significantly greater improvement in reading accuracy and prosody in the group that received musical but not painting instruction. Another study on German preschoolers reported comparable improvements in PA in groups that received training in phonology or music but not in the group that trained sports (random assignment) (Degé & Schwarzer, 2011). Training lasted 10 minutes per day for 20 weeks. Interestingly the observed enhancement of PA was only in the tests that employed phonological units of large grain size (syllables and rhymes) but not small grain size (phonemes). This provides evidence for TSF, which proposes relations between rhythm in speech and music mainly at the level of syllable and stress. Similarily, Moreno et al., (2009) reported improvements in reading (word reading) after 9 months of musical instruction in children speaking Portuguese but not after painting classes. Furthermore there have been enhanced ERP responses to pitch incongruities in speech in the first group.

7.1.2.2 Effects on dyslectics

Cogo-Moreira et al., (2013) observed enhanced PA and reading speed in children from Brazil with reading difficulties that were randomly chosen to participate in additional music classes compared to control group that did not receive any treatment (N = 114 and 121 respectively). However the effects, despite significant, were radher small. In their carefully designed study Flaugnacco et al., (2015) selected Italian dyslectic children and randomly assigned them to music or painting group where training was provided for 7 months. Musical training included a lot of elements concerning rhythmic skills (using percussions, rhythmic syllables, body synchronization etc.). Difference in improvement between groups with medium effect size has been reported for reading accuracy measures (largest for pseudo-word reading) but not speed. Additionally, auditory attention and working memory have been enhanced in the musical training group with small to medium effect sizes. Notably, the best predictor of PA (and improvement in PA) was not WM or attention but rhythmic reproduction (improvement in rhythm reproduction). French dyslectic children have been recently investigated by Habib et al. (2016). Specially developed, theory based intervention that included rhythmical tasks requiring body entrainment and conversion between modalities was provided with careful control for confounds. All dependent variables were assessed four times (separated by 6 weeks), but the training was employed only between the second and third assessment. Therefore although no control group was used it was possible to control for enhancements not related to training, and also to see whether the effects persist 6 weeks after the end of the intervention. Indeed there were significant improvements in auditory skills (categorical perception based on VOT, syllable duration discrimination) and particularly large (almost one SD) improvement in reading relative to norms received from age and reading level matched controls.

In order to show that musical training can contribute to phonological and reading skills in a similar way as direct training of phonological skills group around Goswami carried out two studies with dyslectic children utilizing predictions of TSF and focusing on basic rhythmic skills that have been proposed to play role in successful reading development (and dyslectic individuals perform poorly on them). Control group always received intervention directly targeting phonology. In the study of Bhide, Power and Goswami (2013) GraphoGame Rime intervention was used in the control group, focusing on training PA of rime units. Experimental group received training in tapping to metronome, tempo and rhythm judgement, rhythm repetition, rise time discrimination, DeeDee task (see Section 3.2.1) and clapping and marching to the beat of a song. Results revealed comparable effect sizes for overall reading score improvement in both groups (combining reading, PA, RAN, VSTM and amplitude rise time measures). Likewise, Thomson et al. (2013) compared similar 6 weeks long intervention (additionally drumming to syllables) with commercially available training of phoneme discrimination. Additionally they employed a third group which received no treatment. While both musical- and phoneme-focused intervention groups showed comparable gains in PA (medium to large effect sizes in individual subtests) the group with no treatment demonstrated significantly smaller improvements.

In summary, mounting evidence supports the hypothesis that musical, particularly rhythmic training might promote enhancement of reading and related skills. Studies reviewed in this section suggest that musical training may be beneficial for reading impaired children, but also contribute to enhancement of reading skills in typically-developing individuals. However, when mata-analyzing 17 intervention studies (selected from 178 candidate papers) that employed musical training in order to enhance reading or reading-related abilities, Gordon, Fehd and McCandliss (2015) concluded rather mixed results. On average these studies reported modest effect sizes (d = 0.2) when improvement between experimental and control group has been compared. The authors suggested that it may be the length of musical instruction which promotes better results because they observed an effect of number of training hours on PA. Indeed, recent evidence indicates that changes in the brain due to the neural plasticity take place only after the child is exposed to a musical training for a longer time. Kraus et al. (2014) reported significant enhancements of subcortical mechanisms associated with reading abilities in a randomized controled study where children at risk of learning and social problems received free musical education for two years. Although no benefits of musical training were observable after one year, after two years there have been significant differences in subcortical syllable processing. The number of hours of instrumental training was linked with the magnitude of enhancement in neural precision (r = 0.48). Similarly, robustness of neural representation of speech in noise has been considerably enhanced after two years of musical training (but less after only one year) in children

aged 3-5 (Strait, Parbery-Clark, O'Connell, & Kraus, 2013).

Thus further research with longer training periods and carefully controlled experimental manipulations is required in order to reliably establish the role of musical training in reading development. Particularly, narrowly aimed studies should be carried out in order to find out which specific aspects of music are those that drive reading enhancements. Yet, recent results provide support for an importance of rhythmic training, which is in line with TSF.

8 Experiment

8.1 Overview and research questions

To summarize the theoretical part of this thesis, entrainment of neural oscillations plays an important role in cognition. Recent work suggests that synchronizing the phase of slow brain rhythms to a temporal structure of a stimulus is important in speech perception as well as in musical rhythm perception. This entrainment with the rhythmic (or quasi-rhythmic) structure provides predictive attention allocation to the time-points where highly informative parts of the signal are expected (based in the temporal regularities), and orchestrates the activity over the whole oscillatory hierarchy, thereby enabling for efficient sampling of the signal over multiple timescales.

Although whether rhythm in speech and music can be considered equivalent is a hotly debated question (Goswami & Leong, 2013; Kraus & Slater, 2015; Patel, 2006), and a further research is needed to resolve some discrepancies, we assume that the basic oscillatory mechanisms for processing temporal (or metrical) structure in music and speech might be similar. The fact that processing of rhythmical structure in both, speech and music seems to be impaired in poor readers lends further support for shared cognitive mechanisms. Temporal sampling framework proposes that oscillatory mechanisms might be disrupted in developmental dyslexia which would result in problems with perceiving prosodic aspects of speech that are important for developing well specified phonological representations. The suggestion that there is a general rhythmic deficit in dyslexia is supported by following findings of multiple studies showing that:

1. Dyslectics demonstrate atypical neural entrainment to simple rhythmic stimuli.

- 2. They show deficits in processing of rhythmical structure of speech.
- 3. They have difficulties in tasks requiring perception or production of musical rhythms.

4. Addressing rhythmic processing in therapeutic interventions improves reading skills in typicallydeveloping and reading impaired individuals.

Although impaired processing (perception and production) of musical rhythm has been shown behaviorally, to the best of our knowledge no empirical research exists addressing neural correlates of this processing in dyslectic population. Previous studies investigating neural entrainment in dyslexia employed rather simple rhythmical stimuli, for instance amplitude modulated noise (e.g. Hämäläinen, et al., 2012), isochronous tones (Soltész et al., 2013), or single isochronously presented syllable (Power et al., 2013). Thus no study explored neural entrainment to a stimulus that would exhibit multiple metrical levels (even though ecologically-valid music and speech indeed demonstrate such structure). Forasmuch as the processing of metrical structure (i.e. analyzing stimulus at multiple nested timescales) might be disrupted in dyslexia (Goswami & Leong, 2013), and it has been shown at the behavioral level in music and language (Flaugnacco et al., 2014; Goswami, Huss, et al., 2013; Leong & Goswami, 2014a), investigating neural processing of musical meter in dyslectic individuals would contribute to the currently available evidence in favor of the hypothesis that the underlying deficit in dyslexia lies in impaired processing of higher temporal structure of the stimulus and stems from an atypical oscillatory entrainment. Therefore the current study aims to seek for impaired representation of musical beat and meter in a sample of dyslectic adults.

Ability of individuals to track the temporal structure of a stimulus has been related to the tapping performance which suggests domain-general mechanisms (Schwartze & Kotz, 2015). As tapping and perceiving a regular structure is disrupted in dyslexia, it could be that deficits in such a general temporal-predictive system may explain all four points presented above. In both speech and music, the motor system contributes significantly to the predictive processing of temporal structure (Grahn & Brett, 2007; Kotz & Schmidt-Kassow, 2015). Top-down modulatory influences of motor cortices on sensory areas has been connected with slow oscillatory activity in active sensing (Morillon et al., 2015) and recently also speech perception (Morillon et al., 2010; Park et al., 2015). In music, it seems that motor system is involved to a greater extent when highly complex rhythms are employed (Kung et al., 2013; Large et al., 2015). Therefore by manipulating the rhythm complexity, it may be possible to test whether problems with processing the temporal structure of speech and music might be mediated by dysfunction in the motor system network or perhaps in atypical connectivity between sensory and motor systems (Yeatman et al., 2011). Hence the secondary aim of the current study is to test, whether dyslectics will show worse neural entrainment to the metrical hierarchy of a highly complex rhythm, in contrast to a less complex rhythm.

The experiment described below adapted a paradigm that has been previously used to study beat and meter perception in typically-developing individuals. Brain representations of the metrical structure are captured by measuring steady state-evoked potentials (SS-EP) in scalp EEG. In contrast to transient responses that are traditionally measured in the research of event-related potentials, SS-EPs are elicited when stimulus-stream is presented in a way that the brain response to the previous stimulus does not subside to baseline before the next stimulus is presented (Galambos et al., 1981). Thus SS-EPs are periodic, that means they can be analyzed in the frequency domain as well as in the time domain, although generally frequency-domain analysis is preformed because it better captures the characteristics of this type of response (Plourde, Stapells, & Picton, 1991). In the frequency domain, neural tracking of a particular frequency can be evaluated as an amplitude of this frequency in the EEG signal.

As reviewed in Section 4.2, when presenting participants with a musical rhythm, entrained brain oscillations at the frequencies contained in the amplitude envelope of this rhythm can be observed from the electrical brain activity. Some of these frequencies correspond to the frequencies of beat pulses at multiple levels in the metrical hierarchy or the particular rhythm. However, rhythm envelope contains also frequencies that are not related to the meter and can be considered "distractor" frequencies. Human brain seems to selectively enhance the entrainment to meter-related frequencies and suppress entrainment to meter-unrelated frequencies (Nozaradan et al., 2012). In the envelope of highly complex rhythms, meter-related frequencies are not predominant when compared with meter-unrelated frequencies and therefore it is more difficult to selectively entrain to them (Large et al. 2015). The magnitude of entrainment differs between individuals and recently has been linked with behavioral performance in tapping (Nozaradan et al., 2016), which is in line with studies suggesting shared underlying mechanisms in perception and production of temporal structure (Schwartze & Kotz, 2015).

Amplitude of the SS-EP at the frequency of the main beat in the metrical hierarchy correlated with the mean asynchrony of tapping (see Section 4.2). Dyslectics have been shown to tap with larger asynchronies to the pacing metronome (Wolff, 2002) and to rhythmic speech (Leong & Goswami, 2014a). Further, differences in the entrainment to complex and simple rhythm (see Methods) have been linked with temporal prediction abilities (in tapping to a tempo-changing stimulus). Such predictions may be important for assessing the rhythmic structure of natural speech which is not strictly periodic and includes tempo fluctuations (such as slowing down at the end of a sentence). Thus this ability may contribute to the deficits in perceiving prosodic rhythm in speech observed in dyslexia (Leong & Goswami, 2014b). Directly measuring how dyslectic brain processes metrical structure of a rhythm provides advantage over studies employing various behavioral tasks, where multiple confounds might underlie the poor performance of dyslectics (for a discussion, see Ramus & Szenkovits, 2008).

Hence the experiment described here has a potential to provide further evidence in favor of the suggestion that individuals with dyslexia are "in tune, but out of time".

In the experiment described below, neural entrainment to two rhythmic patterns with low and high level of metrical complexity was measured in a group of dyslectic and control adults. It was hypothesized that:

1. Dyslectics will show weaker neural entrainment to the meter-related frequencies (which correspond to delta and theta rates) regardless of the metrical complexity.

2. This deficit will be more prominent in the highly complex rhythm because of higher demands on the top-down processes in the predictive system (possibly involving motor areas).

8.2 Methods

8.2.1 Participants

Seven adult participants (2 females, mean age 20.3) that received diagnosis of developmental dyslexia from a certified speech and language therapist at the POLIN laboratory (University of Zagreb) were recruited to take part in this study. No comorbidities such as lower IQ or attentional deficits were found in dyslectic participants. Dyslectics were taking part in another study that was carried out at POLIN and they agreed to take part also in the current experiment. Additionally, 11 control subjects (8 females, mean age 22.8) with normal reading skills (confirmed by speech therapist after a diagnostic session) were recruited. All participants spoke Croatian as their first language and had no history of neurological, psychiatric or hearing disorders.

8.2.2 Auditory stimuli

The auditory stimuli were created in Matlab 8.5.0.197613 (The MathWorks, Inc., Natick, MA, USA). Two different rhythmic patterns adapted from the study of Nozaradan et al. (2012) were synthetized. The choise to use these two particular patterns was motivated by the fact that they have been previously used in normal population and reliable neural entrainment to metrical frequencies was reported in both rhythms (Nozaradan et al., 2012). Furthermore, these patterns differ in their metrical complexity and thus differences in entrainment to metrically simple versus complex rhythm can be compared.

Each pattern consisted of 12 events with duration of 200 ms (Figure 3). There were two types of events, either a white noise sound (10 ms rise and fall time) or a silence. Rhythms were established by alternating noise sounds and silences in a particular pattern. Nozaradan et al. (2012) designed the patterns based on previous theoretical work on music cognition (Essens & Povel, 1985) with the aim to induce perception of the main beat pulse by promoting preferential grouping of 4 events (corresponding to 1.25 Hz). Additional beat levels were established by considering subdivisions of the main beat by 2 (thus 2.5 Hz) and 4 (equal with the rate of individual events, 5 Hz). Another metrical level was constituted by grouping the main beat by 3 (resulting in the period of the whole pattern, 0.417 Hz). One pattern was considered metrically simple (or unsyncopated), i.e. it was assumed that the perception of beat (and meter) is straightforward for this rhythm, because each individual beat pulse coincided with sound. On the other hand the second pattern was considered metrically complex (or syncopated), because some pulses coincided with silence (see Section 4.1 for further description of metrical complexity/syncopation). Thus beat perception was assumed more difficult in this second pattern.

Analysis of the amplitude envelope of the stimuli further supported the differences in metrical

complexity between the two rhythmic patterns. Hilbert transformation was applied using Matlab buildin function "hilbert". This provides a complex analytical signal from which amplitude envelope can be extracted by taking the absolute value of the complex-valued signal. Subsequently, fast Fourier transformation (FFT) was performed and peaks extracted (using "fft" and "findpeaks" functions). This revealed 12 distinct frequencies that were present in the pattern envelope (Figure 4) ranging from the slowest pulse in the hierarchy (0.417 Hz) to the fastest pulse in the hierarchy (5 Hz). Frequencies above 5 Hz were not analyzed. From 12 frequencies that constituted the pattern, 0.417 Hz, 1.25 Hz, 2.5 Hz and 5 Hz were considered meter-related frequencies, because they corresponded with the expected rates of the levels in the metrical hierarchy. Other frequencies were considered meter-unrelated. For each frequency in the pattern envelope, z-score of the magnitude was calculated using the formula $z=(x-\mu)/\sigma$, where x is the magnitude at the particular frequency, μ is the mean magnitude over all 12 frequencies in the particular pattern and σ is standard deviation. This transformation was necessary in order to allow for comparing how different frequencies were predominant in the pattern relatively to each other (without considering their absolute magnitude). Similar procedure was used later on the EEG data.

Higher metrical complexity of Pattern 2 is noticable from the relative magnitude at the main beat frequency (1.25 Hz) when comparing it to the magnitudes of other frequencies. While in the metrically simple pattern this frequency stands out relatively to the other frequencies, this is not the case in the metrically complex pattern. Z-scores for 1.25 Hz frequency were 2.76 in the simple and 1.4 in the complex pattern.



Figure 3: Design of the rhythmic patterns used for the experiment. Noise sounds are plotted as "X" and silences as "." (both have duration 200 ms). The positions of the hypothesized main beat in the metrical hierarchy are marked by red arrows above the events that coincide with the beat. The whole expected metrical hierarchy induced by the rhythms is displayed under each pattern as a metrical grid. More asterisks under an event indicate that it coincides with more salient (or "important") position in the hierarchy. Higher saliency means that the listener expects a sound (generally an "accent") to appear at this position. Note that in the metrically complex pattern only one out of three beat positions coincide with sound which causes syncopation and therefore it is more difficult to find and keep the beat in this pattern. (Left) Frequencies of the metrical levels.



Figure 4: Amplitude envelope spectrum of the experimental stimuli. Amplitude fluctuations of both patterns contain 12 distinct frequency peaks. Meter-related frequencies are marked by arrows above the particular peak. Magnitude is normalized to 1. Note that in the metrically simple pattern (Top), the main beat frequency (marked by red asterisk) is predominant relatively to the other frequencies, whereas in the metrically complex pattern (Bottom) also meter-unrelated frequencies have comparable magnitude.

8.2.3 Procedure

The auditory stimuli were presented running Matlab and using Cogent 2000 library (developed by the Cogent 2000 team at the FIL and the ICN and Cogent Graphics developed by John Romaya at the LON at the Wellcome Department of Imaging Neuroscience, University College London). Participants were seated in a chair in front of a computer screen and instructed to relax, avoid unnecessary movements and to keep their eyes fixed on a cross displayed on the screen during each trial. Participants were allowed to move between individual trials or between experimental blocks.

Experimental procedure included two blocks, each consisting of 10 trials. Individual trials were made up of the particular pattern looped continuously over 33 s. All trials in one block consisted of the same pattern (either simple or complex) and the order of the blocks was counterbalanced across participants. Two random trials in each block, contained one noise sound event (at random position) that was prolonged by 30% (thus instead of 200 ms it lasted 230 ms). Participants were asked to listen carefully and search for these prolonged sounds. After each trial they reported whether the prolonged sound was present or not. The purpose of this task was to ensure that participants attended to the stimulus and the nature of the task (searching for prolonged sounds) was supposed to make them focus on temporal aspects of the sound. EEG data from the trials that contained prolonged sound were

discarded. 3 additional trials were introduced at the end of each block. Participants were asked to tap along the beat of the rhythm as they were spontaneously tapping their foot or clapping to music at a concert. The experimenter provided a short demonstration and if participants did not understand the task, further explanation was given. Tapping was performed on a computer mouse. However, data were not further analyzed due to inability of most of the participants (in both, experimental and control group) to perform the task (see Discussion).

8.2.4 EEG recording and preprocessing

EEG data were recorded using QuickAmp amplifier (BrainProducts GmbH, Munich, Germany). 32 active Ag/AgCl electrodes (ActiCap, BrainProducts GmbH, Munich, Germany) were placed at positions Fp1, Fp2, Fz, F3, F4, F7, F8, FC1, FC2, FC5, FC6, Cz, C3, C4, T7, T8, TP9, TP10, CP1, CP2, CP5, CP6, Pz, P3, P4, P7, P8, Oz, O1, O2, PO9 and PO10 according to the international 10/20 system. Ground and reference electrode were integrated in the EEG-cap. Horizontal and vertical eye movements were monitored with 4 additional electrodes. All signals were low-pass filtered online at 250 Hz and digitized at 1000Hz and referenced to the common average.

All the processing steps were performed using BrainVision Analyzer 2.0.4.386 software (BrainProducts GmbH, Munich, Germany). Data was filtered offline between 0.1 and 70 Hz and rereferenced to average mastoids (Tp9 and Tp10). Eye blinks and eye movement artifacts were removed using independent component analysis as implemented in Analyzer. Subsequently, data was segmented into 32 s epochs ranging from +1 to +33 s relative to the onset of each trial. The first second after the stimulus onset on each trial was discarded because sharp stimulus onset evokes a transient response, and to provide time for brain to synchronize with the rhythm. Data was then visually inspected and epochs containing artifacts were rejected from further analysis. Finally, epochs were averaged in the time-domain across trials for each pattern in order to improve signal-to-noise ratio (by attenuating the activity that was not time-locked to the stimulus).

Consecutive processing was performed in Matlab using custom-written scripts. Topographic maps were created with the help of EEGlab topoplot function. Time-domain averaged data for each participant and pattern type were transformed into frequency domain using FFT, yielding a spectrum ranging from 0 to 500 Hz with a resolution of 0.03 Hz. This allowed for assessing the amplitude at each frequency of interest in the EEG signal. Acquired frequency spectrum was further processed by applying a denoising procedure that has been widely used in studies using similar paradigm (e.g. Nozaradan et al., 2016; Tierney & Kraus, 2014b). For each frequency bin, mean amplitude of third and fourth neighboring bins from each side was subtracted (with the current resolution of FFT this was approximately -0.12, -0.09, +0.09 and +0.12 Hz). This procedure is based on the assumption that the recorded signal is a sum of entrained activity and task-unrelated background noise which is broadly

distributed over frequencies, whereas entrained activity comprises a peak that is concentrated in a narrow band. If no SS-EP would be elicited, amplitude at a single frequency bin should not be significantly different from the mean amplitude at neighboring bins. This denoising makes it possible to compare SS-EPs at different frequencies, as EEG noise exhibits 1/f power spectrum (He, 2014). Finally, data from all electrodes were averaged in the frequency domain in order to avoid any electrode-selection bias.

8.2.5 Statistical analysis

For statistical analysis, magnitude of the response at each target (meter-related or meter-unrelated) frequency was defined as the mean amplitude at two frequency bins closest to this target frequency. In order to test whether neural oscillations were entrained at the meter-related frequencies, noise-subtracted amplitude at each meter-related frequency was compared with 8 neighboring bins from each side using paired-samples t test.

The magnitude of entrainment at the meter-related frequencies was compared between groups and patterns by conducting Two Way mixed design ANOVA with a between-subject factor of Group (Dyslectic vs. Control) and a within-subject factor of Complexity (metrically simple vs. metrically complex) separately for each meter-related frequency. The dependent variable was the noise-subtracted amplitude of SS-EP at the particular frequency.

To assess the selective enhancement of meter-related frequencies and suppression of meterunrelated frequencies, z-scores were calculated from the amplitude values at each target frequency by a similar procedure as described for the sound pattern analysis. Averaging z-scores over meter-related and meter-unrelated frequencies allowed for comparing how these frequencies were represented in the signal relatively to each other. This is different from the absolute measure of amplitude that does not take into consideration amplitudes at other frequencies. Z-scores at meter related frequencies can be considered a measure of how well the metrical structure is represented by the brain as a whole. Calculated z-scores were entered into Three-Way mixed design ANOVA with Group as a betweensubject factor and Meter-Relatedness (meter-related vs. -unrelated) and Complexity as within-subject factors.

To assess the relative strength of the ability to endogenously create and maintain the beat despite the counter-evidence due to syncopation, index of neural entrainment to an endogenous beat at the main beat frequency was calculated, in line with previous studies (Nozaradan et al., 2016). This procedure assumes that in the metrically simple pattern, brain entrainment to the beat is mainly driven be stimulus physical properties (note that all 3 beat pulses in this rhythm coincide with a noise sound, and the main beat frequency stands out relatively to other frequencies in the pattern envelope spectra), whereas in metrically complex pattern, top-down modulations (or endogenous processes) are required

in order to follow the beat despite syncopation (only 1 out of 3 beat pulses is supported by a noise sound while other 2 instances coincide with silence, and beat frequency is not predominant in the envelope spectrum). Thus subtracting the amplitude of the SS-EP at 1.25 Hz (main beat in the metrical hierarchy) in the metrically simple rhythm from the amplitude of the same SS-EP in the metrically complex rhythm gives an estimate of the ability to endogenously maintain the beat even if it is not strongly present in the rhythm envelope structure. To assess whether there were differences between dyslectic and control participants in the ability to employ top-down processing of temporal structure (possibly related to motor system), the index of neural entrainment to an endogenous beat was compared between groups using two-sample t test. Statistical analyses were conducted in SPSS 22.0 and Matlab. Significance level threshold was set to 0.05 in all statistical tests.

8.3 Results

Significant entrainment was observed in both groups at almost all expected meter-related frequencies (Figure 5). Exact values of one-sample t tests for each elicited SS-EP, pattern and group are reported in Table 1.

Contrary to the predictions, none of four ANOVAs separately carried out for each meter-related SS-EP revealed a statistically significant main effect of Group (for 0.417 Hz [$F_{(1,16)} = 1.36$, p = 0.26], for 1.25 Hz [$F_{(1,16)} = 0.1$, p = 0.76], for 2.5 Hz [$F_{(1,16)} = 0.56$, p = 0.47] and for 5 Hz [$F_{(1,16)} = 0.78$, p = 0.39]). This results suggest no differences in the magnitude of entrainment to any of the meter-related frequencies between dyslectic and control participants, when not taking into consideration metrical complexity of the pattern. Similarly, contrary to the hypothesis there was no interaction between the groups, even when considering two levels of metrical complexity (for 0.417 Hz [$F_{(1,16)} = 0.05$, p = 0.83], for 1.25 Hz [$F_{(1,16)} = 0.04$, p = 0.84], for 2.5 Hz [$F_{(1,16)} = 0.09$, p = 0.77] and for 5 Hz [$F_{(1,16)} = 1.74$, p = 0.2]). The only statistically significant effect was revealed by the ANOVA conducted for 1.25 Hz SS-EP. There was a significant main effect of Complexity [$F_{(1,16)} = 26.44$, p < 0.001, $\eta_p^2 = 0.62$]. This indicates that regardless of group, the magnitude of entrainment at the main beat frequency was higher in the metrically-simple, compared to metrically-complex pattern. Mean amplitudes of SS-EPs at each meter-related frequency for the two groups and patterns are shown in Table 1.

The three-way ANOVA carried out on the standardized magnitudes (z-scores) revealed a main effect of Relatedness [$F_{(1,16)} = 242.3$, p < 0.001, $\eta_p^2 = 0.94$] which suggests that in both groups the meter-related frequencies were on average more strongly represented by the brain than meter-unrelated frequencies. There was also a significant Complexity x Relatedness interaction [$F_{(1,16)} = 27.19$, p < 0.001, $\eta_p^2 = 0.63$], which indicates that there were larger differences in the relative representation of the meter-related and -unrelated frequencies in metrically simple compared to complex pattern. This is to

be expected, as meter-related frequencies in the complex pattern were less predominant in the envelope spectrum. However, again no differences between Dyslectic and Control group were observed $[F_{(1,16)} = 0.4, p = 0.4]$. Mean values of the z-scores for meter-related and -unrelated SS-EPs are reported in Table 2.



Figure 5: Frequency spectrum of the EEG data obtained from participants when they listened to the rhythmic patterns. Data are plotted in red for the dyslectic group and in blue for the control group. Light-colored lines represent the data from individual participants, while dark-colored lines correspond to group averages. Vertical dashed lines depict the expected frequency of SS-EP at each beat level in the metrical hierarchy. Asterisks mark significantly different amplitude compared to 8 neighboring frequencies from each side (*p<0.05, **p<0.01, ***p<0.001).

Finally, two-sample t test revealed no differences in the index of entrainment to an endogenous beat between dyslectics (M = -0.19 ± 0.15) and controls (M = -0.17 ± 0.14); t₍₁₆₎ = -0.21, p = 0.84.

Visual inspection of the obtained data indicated that there could be a difference between the groups in one particular peak at 0.833 Hz. This frequency was considered meter-unrelated and therefore it was not analyzed separately but only grouped with the z-scores of other meter-unrelated frequencies. Based on this observation, one more ANOVA was conducted for this SS-EP. It revealed that there was a significant effect of Complexity $[F_{(1,16)} = 6.3, p = 0.02, \eta_p^2 = 0.28]$ that was driven by a higher

amplitude in the metrically complex rhythm. Furthermore, significant difference between groups was observed [$F_{(1,16)} = 5.94$, p = 0.03, $\eta_p^2 = 0.27$] with the Control group showing higher amplitude than Dyslectic group. An attempt to interpret this unexpected finding can be found in the Discussion section.

Pattern	Group	0.417 Hz	1.25 Hz	2.5 Hz	5 Hz
metrically simple	Dyslectics	0.12 ± 0.07 μV t ₆ = 0.23	0.39 ± 0.13 μV t ₆ = 7.38 ***	0.08 ± 0.05 μV t ₆ = 2.54 *	0.08 ± 0.02 μV t ₆ = 6.43 ***
	Controls	$0.17 \pm 0.08 \ \mu V$ $t_{10} = 2.63 \ *$	0.37 ± 0.13 μV t ₁₀ = 8.45 ***	$0.09 \pm 0.05 \ \mu V$ $t_{10} = 4.18 \ **$	0.08 ± 0.05 μV t ₁₀ = 4.48 **
metrically complex	Dyslectics	$0.14 \pm 0.12 \ \mu V$ $t_6 = 0.2$	0.21 ± 0.11 μV t ₆ = 3.75 **	0.07 ± 0.04 μV t ₆ = 2.73 *	0.07 ± 0.09 μV t ₆ = 3.2 *
	Controls	0.18 ± 0.07 μV t ₁₀ = 3.22 **	$0.2 \pm 0.08 \pm \mu V$ $t_{10} = 6 ***$	0.08 ± 0.03 µV t ₁₀ = 4.9 ***	0.11 ± 0.07 μV t ₁₀ = 3.88 **

Table 1. Amplitudes (mean \pm standard deviation) of SS-EPs at the meter-related frequencies in μ V. Results of comparing the amplitue at each frequency with 8 neighboring bins from each side using one-sample t test.

*p<0.05, **p<0.01, ***p<0.001

Table 2. Mean ± standard deviation of z-scores for meter-related and meter-unrelated SS-EPs. Meter-related frequencies consist of 0.417 Hz, 1.25 Hz, 2.5 Hz and 5 Hz SS-EP, while meter-unrelated frequencies represent other 8 peaks estimated from the amplitude envelope spectrum of the pattern.

Pattern	Group	meter-related	meter-unrelated
metrically	Dyslectics	0.69 ± 0.15	-0.35 ± 0.07
simple	Controls	0.7 ± 0.12	-0.35 ± 0.06
metrically	Dyslectics	0.44 ± 0.3	-0.22 ± 0.14
complex	Controls	0.34 ±.19	-0.17 ± 0.09

8.4 Discussion

The present study examined the neural processing of musical meter in adults with and without diagnosis of dyslexia. Based on the temporal sampling framework (Goswami, 2011) and previous research on temporal structure processing in dyslexia it was predicted that dyslectic individuals should exhibit weaker neural entrainment to the metrical structure of music. Additionally, it was hypothesized that this deficit in entrainment should be more pronounced in rhythms where top-down processing and involvement of frontal and motor areas is needed to robustly represent the metrical structure.



Figure 6: Overlaid EEG frequency spectra for Dyslectic and Control group. Notice that there are no pronounced differences in entrainment between the two groups (neither in metrically simple, nor complex pattern)

The data recorded from both, typical and impaired readers is consistent with previous studies employing similar paradigm (e.g. Nozaradan et al., 2012), showing significant entrainment to almost all frequencies related to the metrical structure of the rhythm in both, metrically simple and metrically complex rhythm (Figure 5; Table 1). Although entrainment to the slowest frequency corresponding to whole pattern period (0.416 Hz) did not reach significance when tested against neighboring frequency bins in the dyslectic group, this might be due to the lower number of participants and thus lower statistical power. Both groups showed similar topographical distributions of the response at the main beat frequency, which was symmetrically distributed over frontocentral electrodes (Figure 7). This is in accordance with previous studies investigating neural entrainment to beat and meter (e.g. Tierney & Kraus, 2014b; Nozaradan, 2012) These results lend further support for the neural resonance theory which proposes that metrical structure of music entrains brain oscillations at the beat frequencies in the particular hierarchy (Large et al., 2015).



Figure 7: Topographic distributions of the SS-EP at the frequency of the main beat in the metrical hierarchy (1.25 Hz) averaged over metrically simple and complex pattern. Responses exhibit typical frontocentral distribution in both groups.

Inconsistent with the hypothesis, no differences between groups in the magnitude of entrainment were found at any of the four meter-related frequencies ranging from slow delta to theta timescales. Neither considering how strongly the meter was represented relatively to the meter-unrelated frequencies (comparing z-scores) did revealed any differences. This is in contrast with the suggestions of TSF, that processing of slow amplitude fluctuations should be disrupted in dyslexia and neural oscillatory tracking of stimulus temporal structure should be atypical. One possible explanation of the current data is the nature of accents that were used to create the meter. The present study relied exclusively on temporal accents, where the only cue to the metrical structure is the alignment of events in time (here, simple noise sounds alternated with silences and created rhythmic patterns). In speech however, the meter is created by alternating the relative prominence of syllables. For instance, in their task involving musical meter perception Huss et al. (2011) employed rhythms where the metrical structure was created by volume accents (besides the temporal pattern of events and silences), which better resembles speech prosody. Therefore it is possible that using volume accents to create the metrical structure of the rhythm would result in more pronounced differences between dyslectics and controls. However, despite this possible methodological issue, neural entrainment should still be expected to be impaired in dyslectics when considering proposed deficits in slow brain oscillatory activity suggested by TSF.

Furthermore, the data from the present study did not support the second hypothesis. Dyslectics showed similar differences in entrainment between simple and complex rhythm as controls. This was true when the absolute magnitude of entrainment at each frequency was analyzed and also when standardized scores of meter-related and -unrelated frequencies were considered. In accordance with these findings, the index of entrainment to an endogenous beat was not different between groups, which suggests that both dyslectics and controls demonstrated similar ability to employ top-down

processing in order to maintain the beat representation despite syncopation. These results indicate that the top-down processing of temporal structure might be unimpaired in poor readers. Indeed, auditory theories of dyslexia mostly propose deficits in early sensory processing, possibly caused by impaired bottom-up information stream. The prediction that disrupted interaction between auditory and motor cortices could explain rhythmic deficits in dyslexia was mainly based on the findings that motor system might play a role in temporal processing. However, TSF does not explicitly involve such prediction. Therefore the finding that dyslectics show similar top-down processing of temporal regularities as normal readers does not provide direct evidence against TSF.

The observed significant difference between groups at the 0.833 Hz frequency was unexpected. The interpretation of the effect of rhythm complexity is quite straightforward, forasmuch as this frequency was more pronounced in the metrically complex pattern. However, it was considered meter-unrelated and therefore it should have been selectively suppressed in the brain oscillatory activity. From the current pattern of results it seems that dyslectics were more successful in this suppression than controls which would be the exact opposite of the hypothesis that they have deficits in the meter representation.

In case of the rhythmic patterns used here, this specific frequency corresponds to grouping by 6 smallest events and in fact, it is a plausible metrical interpretation of the rhythms (resulting in nested grouping by 2, 3, and 2, starting from smallest events). Using this metrical interpretation in the metrically complex pattern could actually result in all main-beat pulses coinciding with sounds (therefore there would be less syncopation). However, it is difficult to assess the plausibility of this meter without possessing an implementation (and parameters) of the original algorithm used for the stimulus construction that would compute this expected perceptual plausibility (Povel & Essens, 1985). It should be considered a limitation of the present experiment as it simply adopted already designed stimuli from previous studies (Nozaradan et al., 2012) together with the predictions about the most probable metrical interpretation without investigating in detail perceptual plausibility of various meters using different computational models of meter perception (e.g. Povel & Essens, 1985; Large et al. 2015). In the future, more attention should be paid to the careful construction of the rhythmic stimuli and detailed reports of how the rhythms were constructed, why the particular design method was used and its possible pitfalls. Inability to control for the metrical interpretation used by participants is indeed a serious problem of studies investigating beat or meter perception using brain imaging or other techniques where no overt response is produced (in contrast to e.g. studies of tapping). In case where subjects are only passively listening to the rhythm, the experimenter has no available information about the metrical grid participants use and how exactly they align this grid over the rhythm (i.e. where they feel the "ONE"). However, these factors are important because they modulate the EEG response (see e.g. Nozaradan et al. 2011; Iversen, Repp & Patel, 2009).

A speculative interpretation of the observed difference at 0.833 Hz might be that controls could

sometimes use this (2-3-2) metrical interpretation and keep it stable for the whole trial what would be observable from their EEG. However, dyslectics were unable to employ and reliably keep this particular meter. This would mean that originally hypothesized top-down neural mechanisms are indeed stronger in controls. However, all these previous comments must be taken with caution because of the small sample used in this experiment.

8.4.1 Power versus phase and whole brain versus asymmetry

The lack of differences in observed power of neural entrainment can be explained with regard to some previous studies which employed simple isochronous stimuli. Many researchers reported no differences in oscillatory power, but significant differences in the phase properties of the entrained activity. For instance Soltézs et al. (2013) reported lower ITC of phase at 2 Hz. This means that the phase angle between the oscillation and the stimulus was more variable in adult dyslectics (across trials). Theoretically speaking, large variability of the phase (lower phase-locking to the stimulus) should result into lower amplitude when time-domain averaging is performed over trials. This was indeed observed by Soltézs et al. (2013) who reported lower CNV component (slow frequency oscillations were proposed to underlie this component) in dyslectics and showed that its amplitude correlated with the ITC of slow frequency activity. In the present study, time-domain averaging was also employed, but only 8 segments were averaged for each condition and participant. Thus even if there was small phase variability between trials, this may not result in decreased power and a higher number of averaged segments would be required in order to observe an effect. Moreover, employing children participants, Power et al. (2013) found similar ITC in dyslectics and controls and the only significant difference was in the preferred phase angle of delta oscillation. This means that dyslectics consistently entrained to the stimulus rate, but with different angle. These examples suggest that the neural deficit in dyslexia might be related to phase rather than power of the oscillations and the exact nature of such deficit (whether it is larger variability or just different preferred angle) is still not clearly established. The importance of the phase of rhythmic entrainment at multiple timescales has been further emphasized behaviorally, showing different preferred phase of tapping to a rhythmic speech in dyslectic adults (Leong & Goswami, 2014a). Indeed, according to the multi-time resolution models of speech perception (Giraud & Poeppel, 2012; Ghitza, 2011), it is the phase of slow oscillations (and not amplitude) that is crucial for successful sampling of speech stream. Therefore atypical phase of neural oscillations might be the only neural deficit in dyslexia. The fact that phase and power of brain oscillatory activity (at the same frequency) are (in principle) independent could explain the current failure to show differences in the amplitude of entrained activity between groups. However, the asynchrony of tapping to a pacing metronome has been previously linked with the same measures of entrainment to a musical beat employed here, i.e. the amplitude of SS-EPs (Nozaradan et al., 2016). As

dyslectics have been shown to tap with larger mean asynchrony (Wolff, 2002), it could be still expected that they will demonstrate lower amplitude of the SS-EPs. Therefore, further basic research is required to explain the relationships between meter perception, sensory-motor synchronization and amplitude vs. phase of the neural entrainment in normal and clinical populations.

Some studies report even more complicated pattern of results, where only differences in lateralization of the slow oscillatory activity are considered relevant for reading skills. Thus without considering differences between hemispheres, dyslectics might show similar entrainment as normal readers. For instance Abrams et al. (2009) reported link between the degree of rightward asymmetry in speech-envelope tracking and reading. Similarily, Hämäläinen et al. (2012) observed the only difference between dyslectic and control adults in lower ITC at 2 Hz in the right hemisphere (but not left). The interpretation of these results is based on the asymmetric sampling in time hypothesis (AST), which proposes rightward lateralization of slow sampling, whereas leftward (or bilateral) lateralization of fast sampling (Hickok & Poeppel, 2007). However, there are no clear predictions about how should different (atypical) lateralization pattern influence speech perception. Thus, a lot of research in the area of neural speech processing needs to be done before precise explanation of the perceptual deficits in dyslexia can be provided in terms of atypical lateralization.

8.4.2 Rhythm in speech and music

Another issue that may explain the current results is the possibility that meter in speech and music is processed differently in the brain. Particularly, many researchers criticized the view that beat-based timing might be employed in speech, as speech exhibits no periodicity (Cummins, 2012; Patel, 2008, Turk & Shattuck-Hufnagel, 2013). Thus it is possible that even though slow oscillatory mechanisms have been suggested in processing of temporal structure in both domains, there are different networks dealing with quasi-periodic syllable structure of speech and periodic structure of music, and only the latter employs beat-based timing that is required to perceive meter in music. Yet, processing of both, speech rhythm and musical rhythm is disrupted in dyslexia, which suggests that there should be at least some common neural processing of these two domains. Possibly though, there might be some other process impaired in dyslexia, that is crucial for good behavioral performance on tasks involving rhythmical structure processing in speech and music, which would cause the observed deficits, but spare the processing of beat-based metrical structure in music. This calls for further investigation of temporal structure processing in speech and music, especially regarding neural underpinnings of processing the meter in both domains.

8.4.3 Different timescales

Moreover, there is still an ongoing debate about the relevant processing timescales that might be

impaired in developmental dyslexia. While TSF suggests slow timescales and focuses on the level of syllable and stress (Goswami, 2011; Goswami, 2014; Leong & Goswami, 2013), others emphasize the role of fast phonemic sampling in gamma range (Lehongre et al., 2011), or even processing at the brainstem level, which involves rates that are two orders of magnitude faster than those proposed by TSF (White-Schwoch et al., 2015). As all of these theoretical accounts received some empirical support, it is difficult to determine which one should be considered the right approach. A great deal of research is yet to be done on this issue if the true nature of auditory deficit in dyslexia is to be determined. It may be that all these accounts are not mutually exclusive, as the auditory system is an integrated circuit, where changes one part result in the whole system being affected (Kraus & White-Schwoch, 2015).

Another issue might stem from the fact that not all dyslectic individuals demonstrate auditory difficulties (Ramus et al., 2003). Boets et al. (2011) suggest that even though dyslectics might show similar phonological difficulties, they may differ in an underlying cause of such difficulties. Hence, perceptual deficit might be present only in a subgroup of individuals demonstrating poor phonological and reading skills. Therefore it is possible that the specific sample recruited to participate in the present study did not contain individuals with the proposed deficits, but employing a larger sample would elevate the probability of finding dyslectics with the hypothesized difficulties.

Additionally it is worth considering the age of participants. Despite adult dyslectics have still difficulties in tasks involving reading, spelling and phonological awareness, they may develop successful strategies to (at least partially) compensate for their deficits. How such compensation strategies in the domain of rhythm perception would affect involved neural networks throughout the lifetime remains an open question. Although rhythmic processing seems to remain affected in the adulthood, some reports suggest differences in the specific pattern of difficulties depending on age (e.g. Goswami et al., 2013; Thomson & Goswami, 2008). However, studies of neural entrainment in dyslectic adults indicate that even if behavioral performance in some tasks might be at the level of typically-developing controls, neural processing is still atypical (Soltész et al., 2013). More longitudinal research is therefore desirable to explore the developmental trajectories of specific impairments suggested in dyslexia.

8.4.4 Tapping task

As stated in the Methods section, besides analyzing the brain entrainment, the current experiment was originally designed to investigate also tapping to the beat. However, most of the participants in both groups were unable to tap the beat despite an extensive effort of the experimenter to explain and demonstrate the task. Most probably, longer training would result in a successful performance, but this was not possible due to time constraints, because the dyslectic participants were taking part also in one

other study and they were undergoing experimental procedures for approximately 3 hours. Thus employing a protracted training of tapping was not appropriate. Extensive training was not provided also because of the fact that beat perception was proposed to be spontaneous in general population. Hence the ability to perceive and synchronize to the beat should be natural to humans even in highly complex rhythms (Large et al., 2015). In contrast with the difficulties observed here, previous studies that employed the same rhythms as used in the present experiment reported that their participants naturally synchronized their tapping with the beat without previous training (Nozaradan et al., 2012; Nozaradan et al., 2016). This raises a question about the distribution of rhythmic timing abilities in general population which (to our knowledge) has never been systematically investigated. The problems with experimental procedure observed here highlight the important role of pilot experiments in similar task-domains which was not exploited in the current study due to the lack of time resources. Nevertheless, the present experiment can be considered a pilot study per se, forasmuch as only 7 dyslectics subjects were successfully recruited.

8.4.5 Limitations

The results of this study must be taken with caution due to the multiple limitations. First and most important is the small sample size of the dyslectic group. Previous studies investigating entrainment to a musical beat using SS-EPs reported significant results when employing 10-20 participants (e.g. Chemin et al. 2014; Nozaradan et al., 2011; 2012; 2015; 2016). In order to assess potential differences between dyslectics and controls, similar number of participants would be probably required in each group. Although the expected effect size could not be estimated due to the fact that no previous studies employed the current paradigm to compare two groups of individuals, investigations of neural oscillations in dyslexia yielded significant results when employing 10 to 20 participants in each group (e.g. Hämäläinen et al., 2012; Lehongre et al., 2011; Soltész et al., 2013). Therefore it might be that doubling the sample size would lead to different results. However, there were no observable trends in the current data which indicates that even with larger sample size, there might be no statistically significant effects.

The design used here did not allow to control for strategies participants used to perform the detection task (detecting the prolonged tones). It may be that they employed a motor imagination, which could bias the recorded brain signals. Particularly, carrying out the tapping task after the first block might lead to an imagination of movements during the second block (because the participants knew now that they are going to tap also after the second block, so they might covertly "practice" in mind). Despite the fact that the order of blocks was counterbalanced, it might be better to isolate the tapping to both rhythms in a completely separate block after the listening.

Additionally, the present experiment utilized only one tempo of the rhythmic patterns (the main beat
in the metrical hierarchy was 1.25 Hz). This tempo was used mainly due to the fact that the individual beat levels in the hierarchy corresponded to the natural rates in speech (single event period was 200 ms which coincides with the mean syllable rate). It would be interesting though to use different conditions with additional distinct tempos (for instance main beat at 2 Hz and 0.6 Hz). Wider range of rates could provide means to explore the rhythmic deficit in more detail, as some studies reported slightly different rates that were impaired in dyslectic individuals (e.g. Lizarazu et al., 2015; Thomson & Goswami, 2008).

Finally, there is still an ongoing debate about the nature of periodic EEG activity in response to rhythmic stimuli. It could be that the observed periodic component is a result of entrained endogenous neural oscillators or it might consist of summed transient responses elicited by individual auditory events in the stimulus. However these two interpretations might not be mutually exclusive (Tierney & Kraus, 2014b).

8.4.6 Future directions

As suggested above, analyzing the phase of the entrained oscillations could show significant differences between the groups in the present study. Accordingly, future analysis will aim to investigate the phase properties of the data. In line with the previous studies (Power et al., 2013; Soltész et al., 2013), such analysis might reveal either lower ITC in dyslectic individuals, or different preferred phase of synchronization with the rhythm, which would point towards inefficient attention allocation via oscillatory alignment, that would have implications for speech processing in these individuals.

Summary and conclusion

There is an extensive debate about the nature of an underlying deficit in dyslexia. A large number of competing theories that suggest deficits in visual, attentional, memory, or phonological processes are currently aiming to explain this specific learning difficulty. However, up to date there is still no unifying framework that could account for the deficits observed in dyslectic individuals.

Considering recent neuroscientific findings on the role of neural oscillations in perception and attention, focusing on brain rhythms in the search for an underlying deficit might be a good path to follow in the future research. Entrainment of neural oscillations is crucial for perception and attention across modalities, dynamically binding distant brain areas in a predictive manner and contributing to effective processing of the sensory input. Particularly speech and music seem to be two domains where alignment of oscillatory phase with the temporal structure of the stimulus can be an essential processing mechanism. Temporal sampling framework suggests that in dyslexia, deficits in entrainment of slow frequency oscillations in auditory cortical areas with the temporal structure of speech stream could result in subtle perceptual difficulties that would lead to differently developed phonological representations. This would eventually result in phonological and reading difficulties as they are observed in dyslexia.

Moreover, as proposed by Goswami (2015), considering pan-sensory global oscillatory entrainment deficit could explain many other difficulties in the visual domain and also in attention. Thus general oscillatory deficit might be considered the unifying framework that has been sought for so long in the research of developmental dyslexia (Goswami et al., 2014). Besides that, impaired oscillatory entrainment has been proposed also in other clinical conditions such as schizophrenia and ADHD (Calderone et al., 2014). This suggests that studying brain rhythms might be the future of clinical neuroscientific research.

Although there are still many open questions regarding the role of oscillatory entrainment in cognitive processing, systematic basic research in multiple fields of cognitive neuroscience should promote our understanding of how impaired oscillatory system of the brain could contribute to the specific deficits that have been observed in dyslexia.

As TSF is very recent, only upcoming empirical verification of hypotheses drawn from this theory will show whether it has an explanatory power. In this thesis I attempted to combine the recent neuroscientific findings about speech processing, musical rhythm processing and developmental dyslexia. Based on the TSF and the available literature literature on the role of brain oscillations in speech and music, I tried to set and test hypotheses about the neural processing of musical meter in dyslexia. Despite the fact that the experimental findings presented in this thesis failed to support the hypotheses, investigating possible links between reading, music and the brain remains an interesting

area of research. Not only it can lead to important discoveries that would contribute to our understanding of human cognition, but also could provide effective and evidence-based tools for education and early diagnostics of children that have problems with reading.

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