Impact des statistiques temporelles sur le traitement des stimuli auditifs

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IMPACT OF TEMPORAL STATISTICS ON SOUND PROCESSING
/
IMPACT DES STATISTIQUES TEMPORELLES SUR LE TRAITEMENT DES SONS

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ABSTRACT

The temporal regularities in the sensory context are known to affect the perception of an upcoming sensory event. For instance, when listening to a metronome, we can readily predict when the next sound will occur, which enhances our ability to detect subtle acoustic changes due to this anticipation. However, how the temporal variability can impact temporal prediction mechanisms remain poorly understood. This question is crucial because, from a naturalistic point of view, in music and speech in particular, sensory events rather follow patterns of temporal regularity and thus may also occur with a certain amount of temporal variability. In this thesis, we investigated how temporal variability of sound sequences impacts auditory perception, associated neural responses, and their potential impact on language processing. In a first behavioral study, we used an auditory oddball experiment in which participants listened to different sound sequences where the temporal interval between each sound was drawn from gaussian distributions with distinct standard deviations. We established that temporal predictions in probabilistic contexts are still possible and progressively declined as the temporal variability in the context increase. In a second EEG study, we show that temporal variability in context influences the evoked response to sounds as more regular sound sequence showed stronger ramping activity post-target onset, higher N2-P2 amplitude and increased P300 response. The results further support current theories linking observed neural entrainment dynamics to temporal predictions mechanisms: periods where neural entrainment was high was associated with faster target sounds discrimination. Finally, in the third part of this thesis we showed a deficit in temporal prediction mechanisms in dyslexia. Using the same paradigm as in the first experimental chapter, dyslexic participants had significantly more difficulty discriminating sounds in regular temporal sequences than matched controls. Overall, this thesis provides insights into temporal predictions mechanisms in probabilistic contexts and discusses their potential impact in auditory language processing.

RÉSUMÉ

Les régularités temporelles du contexte sont connues pour affecter la perception d'un prochain événement sensoriel. Par exemple, lorsque nous écoutons un métronome, nous pouvons facilement anticiper quand le prochain son se produira, ce qui améliore notre capacité à détecter des changements acoustiques subtils. Cependant, l'impact de la variabilité temporelle sur les mécanismes de prédiction reste mal compris. Cette question est cruciale car, d'un point de vue écologique, dans la musique et la parole en particulier, les événements sensoriels suivent plutôt des motifs réguliers mais dans lesquels peuvent également se produire une certaine variabilité temporelle. Dans cette thèse, nous avons étudié l'impact de la variabilité temporelle des séquences sonores sur la perception auditive, les réponses neuronales associées et leur impact potentiel sur le traitement du langage. Dans une première étude comportementale, nous avons réalisé une expérience dans laquelle les volontaires ont écouté différentes séquences sonores où l'intervalle temporel entre chaque son était tiré de distributions gaussiennes avec des écarts-types distincts. Nous avons établi que les prédictions temporelles dans des contextes probabilistes sont possibles et qu'elles diminuent progressivement à mesure que la variabilité temporelle du contexte augmente. Dans une seconde étude EEG, nous montrons que la variabilité temporelle du contexte influence la réponse évoquée aux sons. En effet, dans des séquences sonores plus régulières, la réponse aux sons cible présente une activité évoquée précoce, une amplitude N2-P2 plus élevée, et une réponse P300 plus importante. Les résultats supportent les théories actuelles liant la dynamique d'entraînement neuronal aux mécanismes de prédiction temporelle : les périodes où l'entraînement neuronal était élevé étaient associées à une discrimination plus rapide des sons cibles. Enfin, dans la troisième partie de cette thèse, nous avons montré un déficit des mécanismes de prédiction temporelle dans la dyslexie. En utilisant le même paradigme que dans le premier chapitre expérimental, nous avons montré que les volontaires dyslexiques ont significativement plus de difficultés que des volontaires témoins appariés à discriminer des sons dans des séquences temporelles régulières. Dans l'ensemble, cette thèse fournit des informations sur les mécanismes de prédiction temporelle dans des contextes probabilistes et discute de leur impact potentiel sur le traitement du langage.

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CONTENTS

Chapter 1:
INTRODUCTION

1.1 What is a rhythm?

"Rhythm is to time what symmetry is to space." **Eugène d'Eichthal**

1.1.1 Notion of rhythm

"Music is also, for harmony and rhythm, a science of amorous movements." **Plato, The Banquet**

The word rhythm comes from the Greek "rhythmos" which in Plato's time meant "the order of movement". Rhythm is a fundamental and universal concept that can be broadly defined as the characteristic pattern that emerges from the perception of a repeating structure. This repetition, whether in human production or present in nature, creates a sense of form and "movement" that profoundly influences our perception and understanding of the world around us. At its core, rhythm is the organizing principle of time, much like how symmetry organizes space. We recognize the same rhythm in phenomena of varying cadence and periodicity when the order of succession and the ratio of duration between moments of tension and release are identical (Cooper et al., 1963). These moments, often described as rise (arsis) and fall (thesis), are the fundamental building blocks of rhythm. The cyclical nature of arsis and thesis creates a dynamic interplay between expectation and resolution, driving the perception of rhythm as a coherent and structured experience (Nowell Smith, 2020). Due to the variability in terminology used to

articulate the critical elements of rhythm and timing, this thesis will begin by delineating the specific definitions and applications of these terms as they are employed here. We define rhythm as the structured arrangement of temporal intervals within a given stimulus sequence. The rhythmic structure is generally indicated by the onset of a stimulus (such as an auditory tone, click or other sound), and the duration between onsets (stimulus onset asynchrony SOA), which delimit the temporal lengths between successive stimulus onsets.

In the natural world, rhythms are evident in the cycle of the seasons, which dictates the timing of plant growth, animal migration, and the blooming of flowers. The alternation of day and night governs our periods of wakefulness and rest (Cajochen, 2007), while the lunar cycles exert a powerful influence over ocean tides. In humans, they are fundamental to existence, starting with our heartbeat and breathing (Muehsam & Ventura, 2014; Parviainen et al., 2022; Prokhorov et al., 2003; Schäfer et al., 1998). These rhythms affect sleep patterns, birth and death timings, and even medical treatment efficacy (Foster & Kreitzman, 2014). Of interest to this thesis, are rhythmic patterns occurring to the hundreds of milliseconds to seconds' scale, such as movement patterns and speech cadence, which are distinctive and can be used for individua identification (Gkalelis et al., 2009; Hoitz et al., 2021). Theses rhythms are pervasive across various human behavior (walking, repetitive movement, speech). Interestingly, there are also present in various art forms, including music, dance, and poetry (Brown, 2018; Lamkin, 1934; Martinec, 2000). Every culture throughout history has recognized and celebrated the power of rhythm, from the ancient drum circles to the structured verses of classical poetry. The pleasure experienced by listening to the rhythms present in music is a universal characteristic of humanity (Levitin et al., 2018; Ravignani et al., 2016; Salimpoor et al., 2009; Savage et al., 2015; Witek et al., 2014) as evidenced by its presence across diverse cultures (Jacoby et al., 2019; Mehr et al., 2019; Ravignani et al., 2016; Savage et al., 2015).

In his musical sense, rhythm can be defined by the organization of time often through hierarchical structures as the beat (i.e., the basic unit of time that give rise to a pulse), the tempo (i.e., the speed of these beats, measured in beats per minute: bpm), and the meter (i.e., the grouping of beats into recurring patterns, usually with strong or weak beats). It also involves rhythmic patterns (i.e., specific sequences of durations and accents) in which beats occurs at different nested tempos and syncopation (i.e., the emphasis on off-beats or weaker beats), creating the flow and movement that characterize a piece of music (Cooper et al., 1963; Kotz et al., 2018; Large, 2008; Patel, 2008) (**Figure 1.1**).

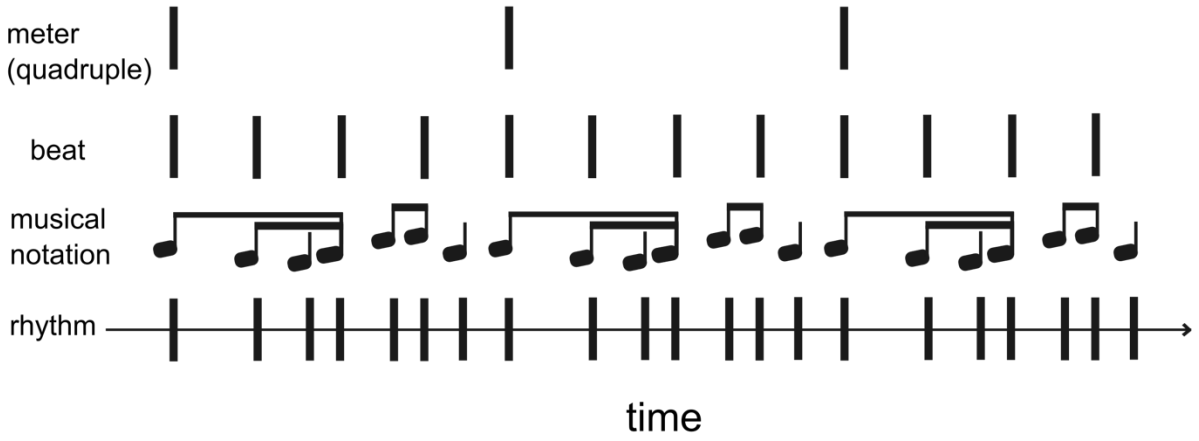

Figure 1.1: What is a rhythm? The concept of rhythm is composed of hierarchical structures organized in time. A series of regular beats marked by stronger or weaker accents, creating rhythmic cycles at different levels. The notes and subdivisions shown indicate that musical rhythm is made up of repeating patterns in which some beats are more accentuated than others, forming a temporal base that can be subdivided into smaller units. Adapted from (Cameron & Grahn, 2014).

In the case of speech, rhythm occur at the level of temporal intervals between the different units constituting the language (**Figure 1.2**). For instance: the inter-onset intervals of syllables occur with a certain amount of temporal regularity, so that we observe an average syllabic rate of 4-5 Hz across languages (Zhang, Zou, et al., 2023a, 2023b). As in music, there are nested hierarchical beat levels, corresponding to phoneme, syllable, word, and phrase structures (Ding et al., 2017; Keitel et al., 2018). Across the different languages, speech envelop dynamics, and speech rates are known to variate reflecting prosodic and rhythmic differences although the same information rate is kept constant (Coupé et al., 2019; Frota et al., 2022; Inbar et al., 2020; Tilsen & Arvaniti, 2013). Spoken languages have been categorized by linguists based on their rhythmic characteristics, distinguishing between 'syllable-timed' and 'stress-timed' languages, though this categorization is more and more debated (Tilsen & Arvaniti, 2013). This classification is contingent upon whether the linguistic rhythm is governed by the isochrony of syllables or the isochrony of interstress intervals, applicable to all languages throughout the world (Abercrombie, 1967; Bertinetto, 1989; Ladefoged, 1975; Pike, 1945; Port et al., 1987; Ramus et al., 1999; Rubach & Booij, 1985; Steever, 1987).

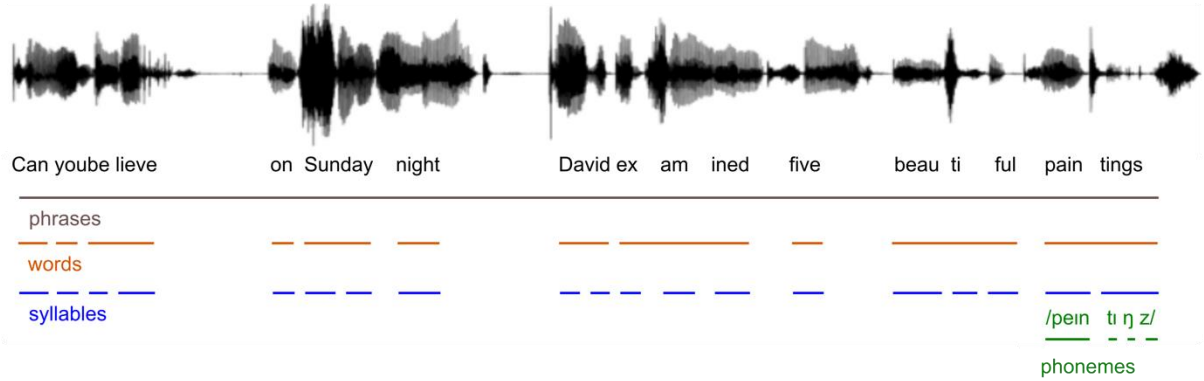

Figure 1.2: Rhythmicity in speech. Temporal intervals between phonemes, syllables and words form structured patterns. As with music, speech has nested hierarchical levels contributing to the perceived rhythm of language. Adapted from (Keitel et al., 2018).

1.1.2 Rhythm perception

This ability to produce and perceive rhythmic patterns is nearly ubiquitous among animal species, for instance birdsong and human language share remarkable parallels. Structurally, birdsong and language are hierarchically organized with syntactic constraints which follow sequential structures (Sainburg et al., 2019), though birdsong is best characterized as 'phonological syntax' without semantics or words (Berwick et al., 2011). Birds produce songs through a unique vocal organ called the syrinx, which has similarities to the human larynx in sound generation mechanisms (Mindlin & Laje, 2005; Riede & Goller, 2010; Trevisan & Mindlin, 2009). Both species involve vocal learning (Berwick et al., 2011; Hyland Bruno et al., 2021; Y. Zhang, Zhou, et al., 2023) and birds as human, can perceive regularities in structured auditory patterns (ten Cate et al., 2016; ten Cate & Spierings, 2019), that are crucial capacities for speech acquisition and communication. Consequently, the perception of these rhythmic events, such as sound, may have played a crucial role in evolutionary processes. In the case of vocalization, the rhythmic motions associated with facial displays (e.g., lip-smacking) observed in certain non-human primates align with the frequency range of syllables in human speech as well as musical beats (Ghazanfar et al., 2013; Morrill et al., 2012). This observation suggests that these facial displays may represent an evolutionary precursor to speech production (Bergman, 2013; Ghazanfar & Logothetis, 2003; Ghazanfar & Takahashi, 2014a, 2014b).

Research on rhythmic abilities has been conducted in both animals and humans. The specific rhythmic behaviors demonstrated by various species can differ significantly, ranging from

humans dancing to a consistent musical beat, to the rhythmic birdsongs that feature precisely timed rhythmic patterns. It have been suggested that rhythmic abilities may differ between species (Bouwer et al., 2021), humans could share interval-based timing with other primates whereas only partially share the ability of rhythmic entrainment (i.e., beat-based timing) (Merchant & Honing, 2014). The resulting mechanisms to build expectations based on timing intervals may thus differ between non-human primates and humans (Bianco et al., 2024). Moreover, the ability to perceive hierarchical rhythmical structure could also variate within species, animal entrainment clearly demonstrates the capacity to extract the pulse from rhythmic music, and to entrain periodic movements to this pulse (Fitch, 2013). While rhythmic abilities vary across species, with humans demonstrating complex beat-based timing, rhythmic perception is present even at early stages of human development.

Human perception of rhythms starts early in the lifespan. Even before birth, the premature neonate brain is already able to code both simple beat and beat grouping (i.e., hierarchical meter) regularities of auditory sequences (Edalati et al., 2023). Moreover, neural evidence suggests that late premature newborns are already sensitive to rhythmic temporal patterns (Edalati et al., 2022, 2023; Háden et al., 2015; Ortiz Barajas et al., 2021; Winkler, Háden, et al., 2009). Babies are able to use rhythms to distinguish languages categories suggesting that newborns could have poor skills of speech segmentation (Nazzi et al., 1998; Nazzi & Ramus, 2003; Ramus, 2002; Ramus et al., 1999; Sansavini et al., 1997). The auditory cortex in 3 months and 9-month-old infants begins to show adult-like processing of naturalistic sounds (Wild et al., 2017) and then gradually mature up to 11-12 years of age (Moore, 2002; Moore & Guan, 2001; Moore & Linthicum, 2007). During this age of 3-9 months, infants perceive rhythmic patterns with duple meter more readily than those with triple meter (Bergeson & Trehub, 2006) and were able to categorize auditory sequences based on rhythm and tempo (Trehub & Thorpe, 1989). Altogether, these results supporting the idea that early in the human development stages, there is a crucial need to be able to process rhythms before the complete maturation of the auditory cortex.

Central to the ability to perceive rhythms is our innate sense of time, a psychological construct that not only enables us to perceive rhythms but also to anticipate and organize auditory patterns. This mental framework, crucial for interpreting rhythm, allows us to make sense of temporal sequences in music and our everyday experiences.

Indeed, to be able to perceive a pattern of repeated elements in an auditory stream we need to make an intern representation of time. But what is time, and how do we experience it? Time, in a psychological sense, is more than just the ticking of a clock or the movement of the sun across the sky. It is a construct that our brains create, allowing us to organize experiences into a coherent sequence (Michon, 2001). When we perceive a rhythm, our brains do not simply register a sequence of beats or pulses; they actively construct a mental representation of the temporal pattern (McAuley, 2010; Povel & Essens, 1985; Povel & Okkerman, 1981; van Wassenhove, 2016). This involves predicting the timing of future events based on past experiences, a process known as temporal prediction. This temporal framework enables us to perceive rhythms, anticipate future events, and make sense of the world (Nobre et al., 2007).

In the context of music, meter is a fundamental element that contributes to the percept of a rhythm over time. The metrical structure of a musical composition enables us to perceive the beat, synchronize our movements with it, anticipate its progression, and retain it in our memory. Our perception of meter in music reflects a wider biological ability to recognize temporal patterns in the acoustic environment (Grahn, 2012; Large, 2009; Large & Kolen, 1994; Nozaradan et al., 2012; Palmer & Krumhansl, 1990; Vuust & Witek, 2014). The perception of meter, or the awareness of a rhythmic beat, is produced by the presence of regularly spaced accents that align at multiple coordinated levels of temporal periodicity in the rhythm, i.e., the succession of note onsets over time (Fitch, 2013; Geiser et al., 2010; Large, 2009; Longuet-Higgins & Lee, 1984; Palmer & Krumhansl, 1990; Parncutt, 1994; Povel & Essens, 1985). Regular accents are a consistent characteristic found in the music of diverse ages and cultures (Ravignani et al., 2016; Savage et al., 2015; Wallin et al., 2000). The metrical structure of Western music is generally organized into several hierarchical levels of periodicity (Hannon & Trehub, 2005; Large & Kolen, 1994), the perceptual tracking of these structures has been confirmed by tone weight judgments, sensorimotor synchronization and evoked potentials (Palmer & Krumhansl, 1990; Repp, 2008). It has been demonstrated that when the sensory context contained strong meter, the precision of temporal encoding was significantly enhanced compared to contexts with weaker meters. Additionally, the subjective perception of rhythm in the sequences is also known to improves with the presence of a strong meter (Grube & Griffiths, 2009). While rhythm is a universal concept, its perception and interpretation are uniquely personal experiences. Each individual's perception of rhythm is shaped by a complex interplay of cognitive, sensory, and cultural factors, making the inner representation of rhythm a deeply subjective phenomenon (Fiveash et al., 2022; Geiser et al., 2009; Krause et al., 2010; Repp,

2010; Roerdink et al., 2011). For instance, someone with musical training may perceive and analyze complex rhythms in ways that others might not, detecting nuances and variations that go unnoticed by a less trained ear (Bigand, 1997a, 1997b; Fiveash et al., 2022; Neuhaus et al., 2006). Moreover, the subjective experience of time itself can vary. When engaged in an enjoyable activity, time may seem to fly by, while in stressful situations, it may drag on. This subjective perception of time alters how we experience rhythm, with fast-paced rhythms feeling even more intense during moments of excitement and slow rhythms feeling more languid during periods of calm (Droit-Volet & Meck, 2007; Gérard et al., 1993). Thus, the inner structure of music through time can affect how the rhythm will be perceived, this perception can vary significantly among individuals, as the experience of listening to music is inherently subjective.

"I've always felt music is the only way to give an instantaneous moment the feel of slow motion." **Taylor Swift**

1.1.3 Rhythms influence perception by better predicting when an event will occur

This inherent perception of rhythmic components naturally present in these environmental rhythms is extremely helpful to predict the time of new sensory events. For instance, consistent patterns in sensory input, such as the rhythm of a metronome or the trajectory of a baseball, can lead to expectations regarding the timing of events. Targets that emerge at intervals anticipated by temporally regular auditory (Barnes & Jones, 2000) or visual (Correa & Nobre, 2008) contexts are processed with greater speed and accuracy compared to targets that appear out of the expected time. Literature separates the timings that are implicit, based on the extraction of temporal contingencies between perceived events resulting in behavior facilitation, and timings that are explicit, defined as the deliberate engagement in timing, resulting in overt temporal estimates (Herbst, Obleser, et al., 2022). In our previous example the trajectory of the baseball is based on implicit timing, whereas if you are instructed to estimate the time elapsed between the last tone of the metronome and a future target, this relies on an explicit timing situation. Empirical findings provide evidence for at least, some shared mechanisms between these two strategies that the brain might use to encode time.

When judging time intervals, the scalar expectancy theory (SET, (Gibbon, 1977)) is commonly used to assess how humans or animals perceive and estimate time (Malapani & Fairhurst, 2002). This law explains that the variability in timing judgments increases proportionally with the

length of the time interval being judged. In other words, the larger the interval to be timed, the greater the expected error or variability in estimating it, and this relationship is linear. In the case of explicit or implicit timing, it was shown that both implicit and explicit timing are influenced by the SET (Piras & Coull, 2011), however, another study proposed that it could be more complicated and depend on the task used (i.e., perceptual vs oculomotor task) (Ameqrane et al., 2014). Additionally, behavioral measures of implicit and explicit timing when temporal intervals are long, show partial correlations among participants (Coull et al., 2013). Several studies have also identified distinct response patterns in implicit versus explicit timing tasks (Droit-Volet et al., 2019; Droit-Volet & Coull, 2016; Los & Horoufchin, 2011; Mioni et al., 2018) although a recent study compared neural dynamics in an explicit and implicit task, and found no distinction between brain neural dynamics in these conditions (Herbst, Obleser, et al., 2022). These findings suggest that timing mechanisms are at least partially task-specific, but further investigation is needed to clarify the cognitive and neural processes underlying these divergences.

More than only influencing the explicit and implicit perception of timing, environmental rhythms are also known to have a profound impact on the content of perception. Rhythmic patterns create temporal expectations about when the next event will occur, making it easier to focus on specific details at the right time therefore enhancing behavior performance (Nobre, 2001). Thus, one of the main effects of the rhythms on behavior is conducted through timing prediction. Be able to predict "when" a new event will occur is very helpful to better allocate cognitive resources in time (Jones & Boltz, 1989; Large & Jones, 1999; Nobre et al., 1999) and temporal predictions are thought to play a prominent part in the processing of sensory information (Arnal & Giraud, 2012; Jones, 1976; Nobre et al., 2012; Schroeder & Lakatos, 2009). Therefore, rhythmic stimulation generates temporal prediction of incoming sensory events and this improves sensory perception (Jazayeri & Shadlen, 2010; Jones, 1976; Taatgen et al., 2007). For instance, periodic visual stimulation facilitates the prediction of future events and the discrimination of visual gratings' orientation (Baker et al., 2014; Samaha et al., 2015). The enhancement of visual discrimination is demonstrated in various tasks using regular visual cues (Correa & Nobre, 2008; Griffin et al., 2002; Kimura, 2023; Miniussi et al., 1999) or visual flicker stimuli (Ahrens & Sahani, 2011; Cravo et al., 2013; Echeverria-Altuna et al., 2024; Pariyadath & Eagleman, 2007; Recanzone, 2003; Thomaschke & Dreisbach, 2013). Furthermore, temporal predictability effects are also observed in other sensory modalities, particularly within the auditory domain. For instance, periodic auditory sequences influence

rhythmically the perception of ongoing auditory events (Arnal et al., 2015; Jaramillo & Zador, 2010; Lawrance et al., 2014; Morillon et al., 2016; Rimmele et al., 2011). Interestingly, temporal expectations about upcoming auditory events through rhythmic activity also modulate activity in visual cortex, even for stimuli not presented visually (Bueti et al., 2010). This suggests a cross-coupling between sensory modalities, and several studies have reported temporal predictability effects using audio-visual stimulation (Bahrick & Lickliter, 2000; Bolger et al., 2013; Jones, 2015; Kösem & Van Wassenhove, 2012; Morillon et al., 2016; ten Oever et al., 2014).

Speech is a complex naturalistic stimulation that presents regularities at the acoustic level, the signal envelope in particular presents a rhythmicity around 5 Hz, representative of the syllabic rhythm (Ding et al., 2017). Theoretically, these rhythmic regularities play a crucial role in speech processing: they provide temporal cues to listeners that can help predict in time the arrival of the next word in a sentence (Kösem & van Wassenhove, 2017), enabling them to segment speech into syllables and words as well as to predict key moments within a sentence (Arnal & Giraud, 2012). Rhythm is one of the first cues used by infants to discriminate syllables (Goswami et al., 2002). Later in adulthood, rhythmicity in speech enables better comprehension and more effective interpretation of spoken discourse. For instance, speech rhythm plays a crucial role in conveying information and facilitating comprehension. In a noisy environment such as at a dinner it can be very difficult to hold a conversation. Speaking rhythmically improves speech recognition in the presence of competing talkers, likely through temporal prediction of target words (Wang et al., 2018). Moreover, in noise-masked speech it was shown that listeners can perceive speech rhythm and use durational cues to locate word boundaries (Smith et al., 1989). The use of rhythmic cues in speech makes it temporally predictive: a change in speech rate during sentence processing leads to a change in temporal prediction, leading to a change in perception of words and word boundaries. For instance, altering the speech rate context by slowing talkers' speech rate around a target word induced a misperception of the target and accelerating the speech rate between two matched words could led to a perception of a new word (that was never spoken) (Dilley & Pitt, 2010). This distal speech rate effect is assumed to modulates the interpretation of durational cues during word recognition by evaluating upcoming phonetic information continuously during prelexical speech processing (Reinisch et al., 2011). Additionally, speech rate was shown to modulates the speech intelligibility and to modify brain activity (Kösem et al., 2018; van Bree et al., 2021) supporting the idea of the crucial significance of temporal cues for language comprehension.

Therefore, the rhythm in speech provides cues to predict the time of arrival of subsequent critical bits of information and hence, enhance speech comprehension (Giraud & Poeppel, 2012).

Temporal regularities in a sequence of event give to the brain a prior knowledge about the structure of the world and enhance perception and decision making. In this view, humans can be seen as anticipatory systems who construct predictive models about themselves and the environment (Clark, 2013; Rosen, 2012). One theoretical framework, the dynamic attending theory (DAT) examines how attention fluctuates over time (Jones, 1976, 2004; Jones & Boltz, 1989; Large & Jones, 1999). Its central insight is that attention varies, rather than remains constant, with temporal changes. The model conceptualizes these attentional fluctuations as a dynamic system with a limit-cycle attractor (Large & Jones, 1999), characterized by time-varying oscillatory phases and periods. Key properties of internal attentional oscillations include: (1) the system oscillates at its intrinsic period in the absence of stimulation; (2) attention can synchronize with rhythmic environmental stimuli through entrainment; and (3) the oscillation is self-sustaining, reverting to endogenous dynamics when external stimulation ceases. A key component to consider is the attentional pulse, representing concentrated attentional energy within each oscillation cycle and modeled as a periodic probability density function (Large & Jones, 1999). Perception is most effective for stimuli that align with the peak of the attentional pulse, while it is less effective for those that do not. The DAT model predicts that the quality of perception and behavioral performance fluctuates in accordance with the attentional phase. Importantly, attentional fluctuations can synchronize to rhythms through entrainment, where phase and period adjustments reduce asynchrony between external stimuli and the internal oscillation. This phenomenon allows perceivers to anticipate the nature and timing of future events, maintaining temporal expectations even in the absence of stimulation due to the self-sustaining oscillation. The width of an attentional pulse varies with the stimulation's temporal regularity. High regularity fosters concentrated attentional pulses and tight phase coupling, while high entropy produces diffuse pulses and loose coupling. The attentional pulse, modeled as a probability density function, links width and height, so greater regularity results in more attentional energy at expected future stimulus times.

Building on the idea that rhythms enable precise timing predictions and the allocation of cognitive resources, we can further examine how these predictive mechanisms operate across various contexts. Rhythmic structures offer a temporal framework that aids the brain in

anticipating forthcoming events, but this raises important questions about the nature of rhythm itself. While rhythmicity supports temporal orientation and improves perception within predictable sequences, the human brain also encounters more ambiguous and complex temporal patterns within natural environments. Gaining an understanding of how the brain differentiates between rhythmic and non-rhythmic sequences, as well as its processing of less regular or more complex rhythms, is essential for a more comprehensive understanding of the mechanisms underlying temporal prediction.

1.1.4 When does it cease to be a rhythm?

The term of "rhythm" by itself is ambiguous and there is still no clear, unified definition of rhythm across all fields of research. For example, in the field of music cognition, they use the term "rhythm" to describe the temporal pattern of amplitude modulation of the acoustic waveform, which usually consists of varying inter-trial intervals between adjacent tones in music, and "beat" refers to the invariant isochronous unit of time underlying the amplitude modulation rhythm (Kotz et al., 2018; Patel, 2008). Under this definition, beat is the level at which temporal prediction occurs. However, in the field of predictive timing research, the term "rhythm" is commonly used to refer to isochronous sequences (Nobre & van Ede, 2018), as the majority of research in this field primarily employs periodic stimuli as sensory inputs. In this context, "rhythm" and "beat" are equivalent terms, and temporal prediction mechanisms are applicable at this level. However, it may not always be true, especially when dealing with more naturalistic stimulation.

Feeling a sensory context as a 'rhythm' is not trivial. What factors contribute to the creation of rhythm beyond the complexity of sound? Many types of sequences may be perceived as rhythmic, despite being notably aperiodic and exhibiting a significant variance in the intervals that constitute the rhythm. For instance, metrical musical rhythms that consist of intervals of differing lengths (such as quarter notes, half notes, and dotted half notes) can evoke a sense of regularity at a level that is not directly represented by any of the individual intervals within the sequence (Desain & Honing, 2003; Motz et al., 2013). The complexity of rhythm arises from how different types of accents, such as intensity (i.e., loudness) and temporal accents, influence beat perception. Accents typically align with the beat, making it easier to detect; however, when accents are missing or occur off-beat, it becomes harder to find the beat. It was shown that

musical experts are better at detecting beats, particularly when accents occur on-beat, and that temporal accents are more influential than intensity accents in beat detection (Bouwer et al., 2018). Moreover, more than the intrinsic complexity of rhythm, the timing between events composing the stream is also a crucial factor for the perception of the rhythmic structure. Successive discrete sensory events in a stream can be perceived either as distinct events or an unique stream of events depending on their stimulus onset asynchrony (Huggins, 1975). To perceive sensory information as a continuous sensory streams or a succession of discrete events in time, the brain is thought to employ cognitive hierarchical generative models that predict upcoming events and detect temporal boundaries (Kuperberg, 2021). This process would involve monitoring predictability structure via statistical learning to be able to learn and integrate the temporal regularities of the environment (Baldwin & Kosie, 2021; Conway, 2020; Turk-Browne et al., 2009). Furthermore, even if the stream is perceived as a rhythmic sequence, the perceived temporal structure can be distorted. Human perception is tolerant to asynchrony: two visual elements may be perceived as flashed synchronously while they are actually delayed in time (Blake & Lee, 2005; Chakravarthi & Cavanagh, 2007; Fahle & Koch, 1995; Verstraten et al., 2000). In the same manner delayed auditory and visual information may be perceived synchronous (Benjamins et al., 2008; Fujisaki & Nishida, 2005, 2010; Keetels & Vroomen, 2012; van Wassenhove et al., 2007; Vroomen & Keetels, 2010; Zampini et al., 2005). Therefore, if our perception can be tolerant to asynchrony by perceiving sensory stimuli delayed in time as synchronous, we could wonder until which temporal variability between the events composing a complex stream no longer give rise to a perception of rhythmicity. What is not a rhythm? Stochastic streams of events such as noise of a cascade or the crackle of a radio are clearly not rhythmic streams but the boundary between rhythmic and no rhythmic stimulations is not trivial. To what extent must a sequence of events vary before our brains no longer recognize it as rhythmic?

While temporal regularity is a fundamental aspect found throughout the natural world, the irregularities and variability of temporal intervals is an equally crucial component playing a key role on temporal predictability. However, very little is known on the effect of temporal variability on temporal predictive mechanisms for perception. Previous studies rather opposed regular versus irregular contexts to argue for the advantages of temporal regularity on perception (e.g., Geiser et al., 2012), and define "rhythm" in terms of isochrony. Literature on temporal predictions induced by rhythmic contexts mainly focused on streams containing determinist streams as when auditory stimulation is periodic (Cravo et al., 2013; Jaramillo &

Zador, 2010; Lawrance et al., 2014; Morillon et al., 2016; Rimmele et al., 2011). However, temporal prediction effects on auditory perception are also observable in sensory contexts that are not periodic but where the temporal intervals between sounds are fully predictable. For instance, when temporal intervals are repeated (Breska & Deouell, 2017), or when the temporal intervals are slowing down decreasing or increasing at a predictable pace (Cope et al., 2012; Morillon et al., 2016). Furthermore, from a naturalistic point of view, temporal contexts are rarely fully isochronous. Speech acoustic signals in particular presents complex statistical temporal regularities (Cummins, 2012; Singh & Theunissen, 2003; Varnet et al., 2017) (**Figure 1.3**) that are supposedly used to form temporal expectations and influence language comprehension (Aubanel & Schwartz, 2020; Jadoul et al., 2016; Kösem et al., 2018; Kösem & van Wassenhove, 2017; Tillman, 2012; Zellner, 1996). The role of temporal predictions in non-fully predictable temporal contexts like speech and music and their impact on auditory perception is debated (Herbst & Obleser, 2017; Jadoul et al., 2016; Zoefel & Kösem, 2024). In particular, temporal prediction mechanisms are believed useful for acoustic segmentation and processing relevant auditory information during speech perception (Giraud & Poeppel, 2012; Meyer et al., 2020; Peelle & Davis, 2012; Zoefel & Kösem, 2024). Temporal predictability based on rhythmic cues present in the signal, specifically on the average speech rate, is known to influences speech perception (Dilley & Pitt, 2010; Kösem et al., 2018; Reinisch et al., 2011; van Bree et al., 2021). Yet, speech processing must consider natural probabilistic variations in syllable and word durations (Jadoul et al., 2016; Ten Oever & Martin, 2021; Varnet et al., 2017). However, it is unclear to what extent probabilistic temporal predictions influence the discrimination of sounds per se.

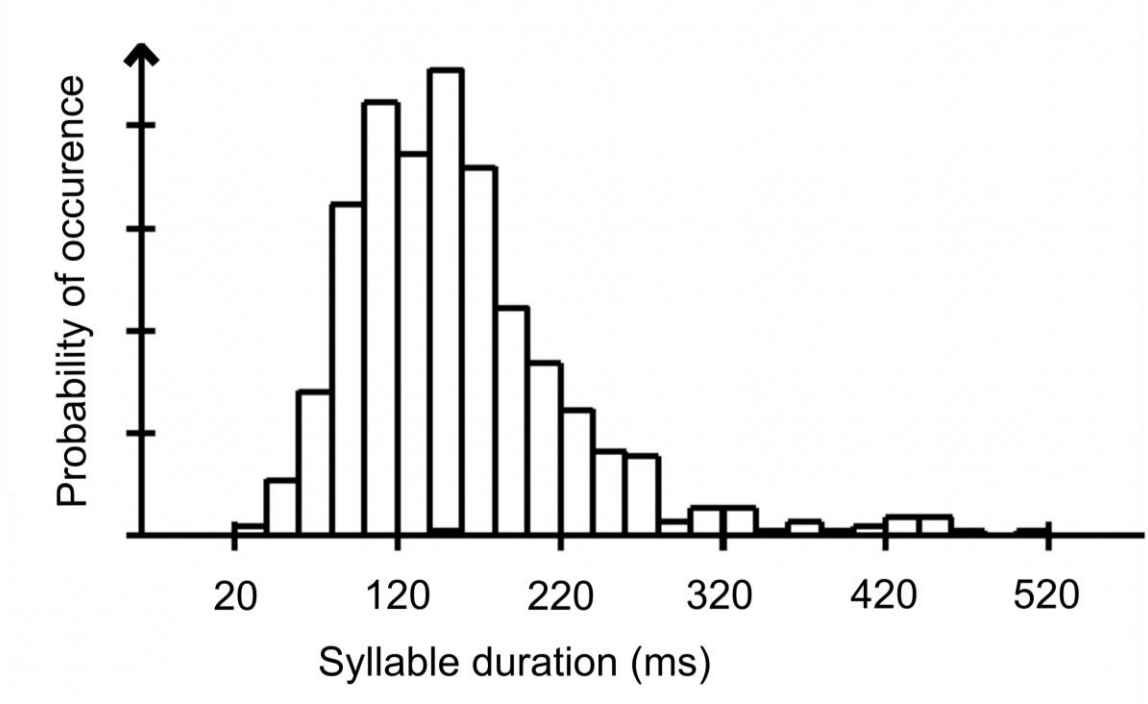

Figure 1.3: In French, the average syllable durations follow probabilistic rules. Around 80% of the syllable's duration are between 80 and 180 ms, making it possible to build expectations on when a new syllable is likely to occur in the continuation of a sentence. Adapted from (Zellner, 1996).

1.2 Rhythms in the brain – What is a rhythm for the brain?

1.2.1 Rhythmicity is also present in the brain – the history of neural oscillations

The brain is a complex machinery who is not foreign to rhythms neither. The first mention of rhythms in the brain comes from Edgar Douglas Adrian, a British electrophysiologist, when he accidentally discovered the presence of electricity in nerve cells (1928).

"I had placed electrodes on the optic nerve of a toad as part of retinal experiments. The room was almost dark, and I was intrigued by repeated noises in the loudspeaker connected to the amplifier, indicating intense impulse activity on the nerve. It was only when I compared these noises with my own movements that I realized that, being in the toad's field of vision, these noises signaled what I was doing." **Edgar Douglas Adrian**

Meanwhile, during the period of 1924-1929 Hans Berger, a German neurologist, undertook his journey of inventing the first method able to record brain activity. He needed five years to create the first electroencephalogram in history, it was a genuine technical achievement for its time. Indeed, it was not trivial to build a tool capable of finding potential differences of the order of a few tens of millionths of a volt with the poor galvanometers available at the time, and without the slightest electronic amplification equipment. After these five years of effort, he was finally convinced that he was indeed recording bioelectrical activity of cortical origin, and not artifacts caused by pulsating vessels, muscle contractions, eye movements or head tremors. Hans Berger documented the first neural oscillations in history (Karbowski, 1990; Stone & Hughes, 2013), he published his first paper in which he described the famous alpha rhythm, consisting of sinusoidal waves repeated ten times per second, occurring when relaxed with eyes closed and which disappear to give way to a much faster and less ample rhythm, the beta rhythm, when the subject's attention is required.

A neural oscillation can be described by his frequency (e.g., alpha rhythm), his amplitude and his phase at a given time (**Figure 1.4**). First, frequency is the number of cycles per second and is expressed in Hertz (Hz). Literature have provided different frequencies range to describe and categorize neural oscillations: e.g., delta (0.5 – 4 Hz), theta (4 – 7 Hz), alpha (7 – 13 Hz), beta (15 – 30 Hz), and gamma (> 30 Hz). The amplitude of neural oscillations represents the magnitude of change of an oscillation and represents the distance between the centerline and the peak or trough. By squaring the amplitude, we can determine the power of the oscillation, which indicates the energy within the corresponding frequency band. Additionally, phase refers to the position of the oscillation along the sine wave (or the cosine wave, which is 90 degrees out of phase with the sine wave) at any specific moment, and it is measured in radians or degrees.

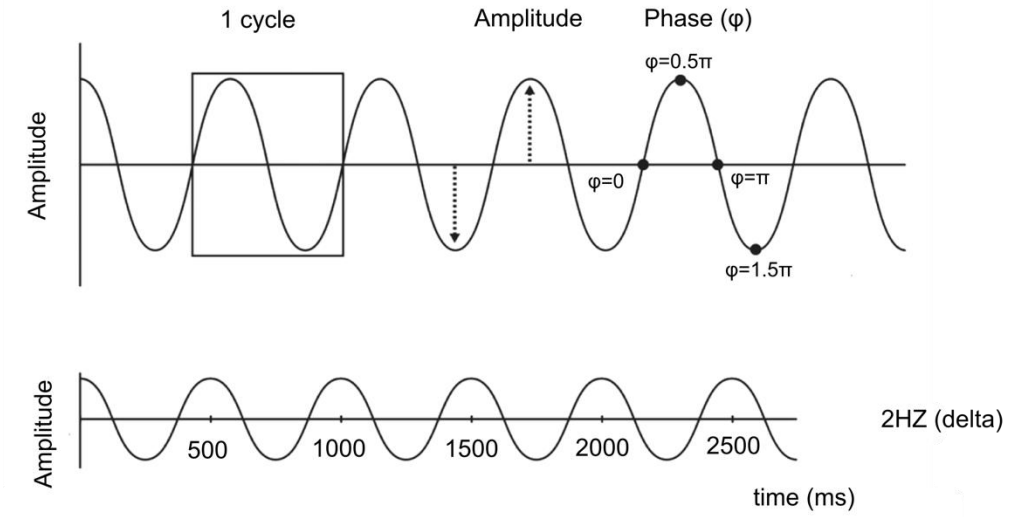

Figure 1.4: Features to describe a brain oscillation. The phase refers to the specific position of the oscillation at a given moment. A full cycle of a neural oscillation corresponds to the time required for the oscillation to return to its initial phase. Frequency is typically quantified by the number of cycles occurring per second. Additionally, the amplitude serves as an indicator of the 'strength' of the oscillating component. Altogether these features are very useful to describe oscillatory patterns in the brain.

"Time is neuronal space" **Buzsáki**

Therefore, rhythmicity is also present in the brain through neural oscillations. Brain oscillations fluctuate rhythmically through the brain and have been hypothesized as instrumental for transferring information necessary for cognition (Buzsáki, 2006; Buzsáki & Draguhn, 2004). It has been postulated 75 years ago by the Hebbian theory that neuronal activity could be the substrate through which various sensory regions communicate with each other. The Hebbian theory proposes that the encoding of the sensory information in the brain could be done through cell assemblies of neurons firing together (Hebb, 1949), with certain populations of neurons being specifically activated by certain types of stimuli, and the sum of discharge rates indicating whether or not a stimulus will be perceived. According to this idea, a neuron could participate in several assemblies (i.e., neurons population firing together), and the identification of all the assemblies would enable the complete representation of a complex stimulus to be assembled (with, for example, different assemblies coding for different features of a visual scene), making assembly coding an extremely flexible phenomenon, as an infinite number of patterns could be created to represent different external stimuli. The problem with this proposal is the ambiguity

of the representation when different complex stimuli occur over time, and the processing speed of such complex stimuli could be slow to integrate all the activity of all neural assemblies at each time. One solution that has been proposed to solve this binding problem (i.e., how to bind together all the features of an external complex stimulation) is the adding of time in the model (Gray et al., 1989; Guo et al., 2007; Wallis, 1998). With the consideration of both space and time (spatio-temporal coding), the firing rate of neurons assemblies over time, when these neurons are synchronized (i.e., the coincidence of neuronal action potentials), gives rise to a neuronal oscillation. At the local level in a neuron population, the firing rate and degree of synchronization of these neurons define the parameters of such oscillation (e.g., amplitude and frequency).

Time, when several action potentials arrive together on a dendrite of a receiving neuron, can be considered as the neuronal space that will define whether or not an action potential can be generated on this neuron (Buzsáki & Vöröslakos, 2023), and whether the signal can be transmitted to other networks. The exact mechanisms by which neural oscillations are produced in the brain have yet to be elucidated and depend mostly on the functions involved, however some studies suggest for instance that gamma rhythms could occur when individual interneurons fire periodically at the same frequency and transmit signals to downstream neurons (Buzsáki & Wang, 2012; Whittington et al., 2011) whereas the delta rhythm could be generated by a slow intrinsic oscillation of thalamic neurons that is modulated by cortical inputs and brainstem cholinergic suppression (Dossi et al., 1992; Steriade et al., 1991). Through this view a complex stimulation would give rise to synchronize neuronal action potential in specific brain areas sensible to distinct features (e.g., motion, shading, …) and then neural oscillations will be generated and propagates to more advanced sensory areas in the hierarchy of sensory processing to at the end give rise to the representation of the external stimulus. Therefore, time through the dynamic of the neural oscillations is crucial for the encoding of the external world.

In mammals this phenomenon of rhythmicity in the brain through neural oscillations is widely distributed across various brain regions (Hari & Salmelin, 1997; Kahana, 2006). Neural oscillations in non-human primates are known to play a role in memory formation and retrieval (Jutras & Buffalo, 2014), sensory motor system (Haegens, Nácher, et al., 2011) or beat perception (Merchant et al., 2015). Many studies in animals and humans have revealed the existence of several types of oscillatory activity across the cortex and, although still poorly understood, are believed to play an important function in both the normal physiology and pathophysiology of this system (Başar, 2012; Buzsáki & Silva, 2012; Hutchison et al., 2004).

It is noteworthy that the frequency of certain neuronal oscillations has remained consistent throughout evolution, even with changes in brain size (Buzsáki et al., 2013), suggesting a significant functional relevance for specific timescales in the brain. Overall, the convergence of recent evidence suggests that brain oscillations are generated in almost every part of the brain and then spreads throughout the whole brain to play a wide range of functions in both human and animal cognition.

1.2.2 Brain oscillations shapes behavior in Human

Ongoing fluctuations of neuronal activity have long been considered intrinsic noise that introduces unavoidable and unwanted variability into neuronal processing, which the brain eliminates by averaging across population activity (Georgopoulos et al., 1986; Lee et al., 1988; Maynard et al., 1999; Shadlen & Newsome, 1994). It is now well understood that the seemingly random fluctuations of cortical activity form rather highly structured activity patterns, including oscillations at various frequencies, that can shape the neural response to sensory events (Arieli, 1996; Greicius, 2004; He, 2013; Lakatos et al., 2005; Marguet & Harris, 2011; Poulet & Petersen, 2008) and affect perceptual performance (Boly, 2007; Buzsáki, 2006; Linkenkaer-Hansen, 2004; Palva et al., 2013; Sadaghiani et al., 2009; Vinnik, 2012). Interestingly, recent studies demonstrated how in specific models of spiking networks, oscillatory dynamics can emerge even from an asynchronous initial state (di Volo et al., 2022; di Volo & Torcini, 2018) suggesting that even 'noisy' brain fluctuations could let emerge oscillations to convey information through the brain.

Over 90 years ago, Bishop raised the fundamental proposition that brain oscillations could reflect rhythmic fluctuations of neuronal assemblies between high and low excitability states (Bishop, 1932). A recent framework went further by proposing that neuronal oscillations could serve as an instrument to brain operations (Buzsáki, 2010; Schroeder & Lakatos, 2009; Wang, 2010) in which oscillations in the brain reflect the modulation of neural excitability (Buzsáki & Draguhn, 2004; Lakatos et al., 2005) and can constrain perceptual excitability with periods of high and low excitability. A cerebral oscillation is characterized by this alternation between phases of high excitability and phases of low excitability, so that the amplitude of the phase at a given time defines the excitability of the network (Henry & Obleser, 2012) resulting in

moments of better probability to perceive a sensory event and others with more probability to miss it (Schroeder & Lakatos, 2009; VanRullen & Koch, 2003).

Theorical work and experimental findings support the idea that neural oscillations shape perceptual processing across multiple modalities (Helfrich et al., 2017; Henry & Obleser, 2012; Herbst & Landau, 2016; Jensen et al., 2012; Schalk et al., 2017; Schroeder et al., 2008; Schroeder & Lakatos, 2009; Thut et al., 2011; VanRullen, 2016). In vision, the phase of prestimulus oscillations in the alpha and theta frequency bands can predict visual detection performance (Busch et al., 2009; Dijk et al., 2008; Hanslmayr et al., 2007) and visual awareness (Linkenkaer-Hansen, 2004; Mathewson et al., 2009). When the strength of excitability fluctuations increases (i.e., when alpha/beta amplitude is high), neural populations exhibit longer periods of low excitability and thus inhibition, resulting in overall decreased performance compared to when alpha/beta amplitude is low (Bonnefond & Jensen, 2012; Capilla et al., 2014; Ede et al., 2011; Haegens, Händel, et al., 2011). Artificially manipulating the phase with tCDS affected the detection threshold in a discrimination task highlighting that brain oscillations have a causal influence on perception (Neuling et al., 2012). The phase and the power of neural oscillations can affect tactile perception (Ai & Ro, 2014; Baumgarten et al., 2016) and audiovisual detection (Besle et al., 2011; Grabot et al., 2017). More specifically in audition, rhythmic contexts influence auditory perception and this is associated with changes in neural oscillations in auditory cortices (Henry & Obleser, 2012). In addition, the oscillatory phase can shapes syllable perception by biasing perception of near-boundary sounds, improving perceptual discrimination (Ten Oever et al., 2020; ten Oever & Sack, 2015). Altogether, there is a growing consensus on the idea that neuronal oscillations play a significant role in brain operations, suggesting that a thorough understanding of these oscillation 'rhythms' is essential for comprehending overall brain function (Buzsáki, 2006, 2007; Buzsáki & Draguhn, 2004).

Thus, through this view, brain rhythms could serve as effective mechanisms for sensory selection, for instance: if the high-excitability phase of these oscillations is aligned with the presence of task-relevant sensory input, that input would be processed most effectively (Schroeder & Lakatos, 2009). Such a mechanism would be extremely helpful to advance the understanding of how the brain can predict the “when”, anticipating when an upcoming sensory event and to focus attention and cognitive resources accordingly (Nobre et al., 2007). Oscillatory brain dynamics could play a role in activating and modulating sensory and motor networks (Engel et al., 2001; Jensen & Mazaheri, 2010), enhancing the processing and the

anticipation of a new rhythmic stimulus which leads to behavioral benefits (e.g., Correa & Nobre, 2008; Large & Jones, 1999; Rohenkohl et al., 2012).

1.2.3 Interaction between external and brain rhythms

Neural oscillations are shown to be sensitive to biological rhythms, such as breathing or heartbeats. Breathing contributes, via multiple sensory pathways, to a rhythmic component that modulates ongoing cortical activity that influences cognitive and emotional processes (Heck et al., 2016, 2017; Tort et al., 2018; Varga & Heck, 2017). Heartbeats influence spontaneous neural fluctuations which can affect sensory processing (Park et al., 2014; Park & Blanke, 2019) and may also during resting state provides specific information on conscious states (Babo-Rebelo et al., 2016, 2019; Candia-Rivera et al., 2021). Circadian rhythms can also modulate neural circuits and brain functions including mood, memory, pain, sleep, and circadian rhythms (Huang et al., 2024; Zomorrodi et al., 2019).

Of interest to this thesis, brain rhythms also interact with external sensory rhythms. One mechanism has been proposed to link the apparent correlation between the rhythmic structure of external stimuli and the rhythmic patterns observed in brain oscillations. The "neural entrainment" theory (Lakatos et al., 2008; Schroeder & Lakatos, 2009) suggests that intrinsic brain oscillations can be entrained (i.e., through period correction and phase alignment) by rhythmic sensory stimuli, aligning the temporal dynamics of neural processing to the external patterns (Calderone et al., 2014; Helfrich et al., 2019; Lakatos et al., 2019; Obleser & Kayser, 2019). Entrainment could thus facilitate the temporal alignment of neural excitability with anticipated stimuli (Arnal & Giraud, 2012; Haegens & Zion Golumbic, 2018; Lakatos et al., 2013; Obleser & Kayser, 2019) (**Figure 1.5**). In this interaction, the influence is unidirectional; the external rhythm impacts the neural oscillating system, while the system does not affect the external rhythm. As a result, the brain oscillating system adjusts to the rhythm of the driving force, leading to an effective coupling between the two rhythms (Lakatos et al., 2019).

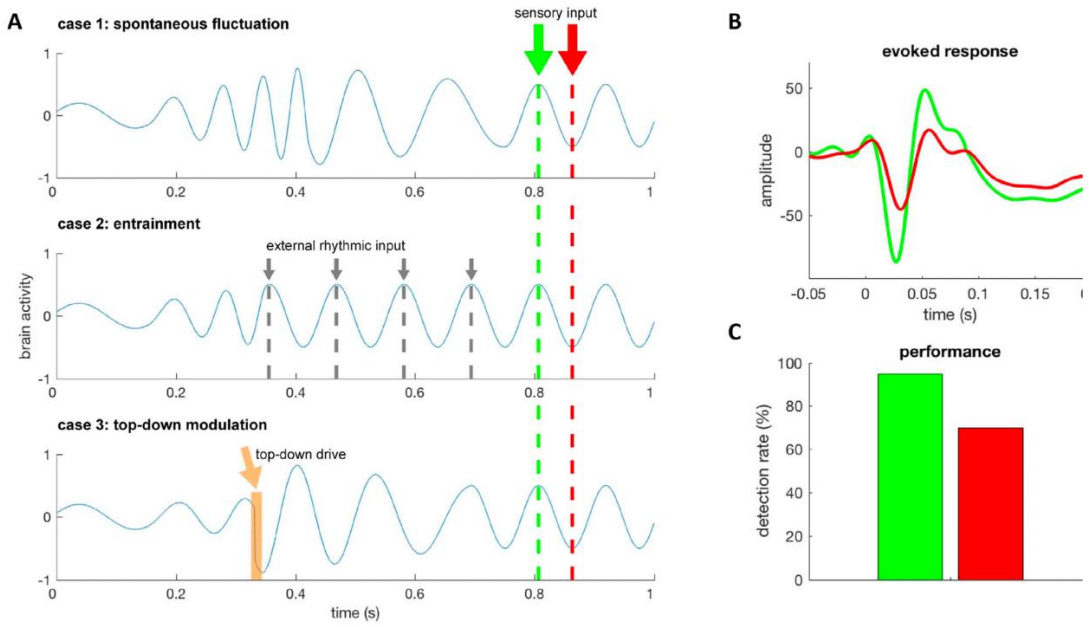

Figure 1.5: Schematic description of rhythmic facilitation. (A) Case 1: spontaneous fluctuations of ongoing intrinsic oscillations. Case 2: entrainment to external rhythmic input. Case 3: phase modulations by a top-down drive from higher-order areas. (B) Sensory input at peak (green) generates a stronger response than at trough (red). (C) Input at peak (green) has a higher detection probability than at trough (red). Adapted from (Haegens & Zion Golumbic, 2018).

This neural mechanism could reflect the formation of temporal predictions in periodic sensory contexts (Henry & Herrmann, 2014; Large, 2008; Schroeder & Lakatos, 2009). Indeed, auditory discrimination performances are correlated to the strength of neural entrainment to the periodic stimuli (Cravo et al., 2013; Jaramillo & Zador, 2010; Lawrance et al., 2014; Morillon et al., 2016; Rimmele et al., 2011). Moreover, the neural amplitude of the delta-band also modulates temporal expectations with better probability to detect a stimulus if occurring synchronously in the phase of low frequency oscillation during a state of high amplitude (**Figure 1.6**) (Herbst, Stefanics, et al., 2022; Herrmann et al., 2016; Stefanics et al., 2010).

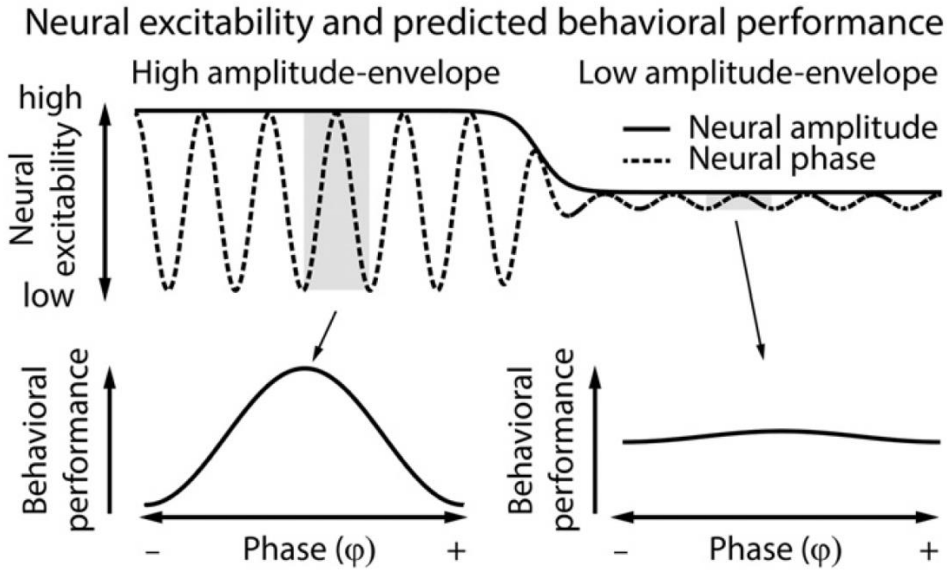

Figure 1.6: Neural excitability shapes behavioral performance. The fluctuations of neural excitability, (i.e., amplitude envelope changes), predict perceptual performance based on high and low neural amplitudes in relation to phase/temporal expectation. Adapted from (Herrmann et al., 2016).

1.2.4 Temporal constraints in neural entrainment

According to this framework of neural entrainment, oscillators in the brain could synchronize together and enhance the behavior. In this perspective, oscillators are viewed as populations of neurons within the brain, governed by specific physical constraints (Doelling et al., 2022). Therefore, a key parameter known to play a crucial role on temporal predictability is the tempo at which the external rhythm is presented. Time judgments are influenced by the rate of an induction sequence with best performance occurring when the standard time interval ended as expected, given the context rate (Barnes & Jones, 2000). Although individuals were shown to have multiple, harmonically related preferred rates (Kaya & Henry, 2022), the sampling capacities of temporal attention have been investigated in vision and reported a preferred rate at ~0.7 Hz whereas in audition the preferred tempo was 1.4 Hz (Zalta et al., 2020, 2024). Other studies reported a better neural entrainment to modulation rates in audition at 2-3 Hz (Farahbod et al., 2020) and strongest neural synchronization in response for tempi between 1 and 2 Hz (Weineck et al., 2022) but also in higher frequencies with strongest entrainment echoes after 6-Hz and 8-Hz stimulation (L'Hermite & Zoefel, 2022). Interestingly, this preference rate for low frequencies tempi seems to coincide with the natural musical beat frequency at 2 Hz.

Spontaneous motor rhythmic behaviors such as finger tapping also operate at a preferred tempo of ~1.5–2 Hz and motor tapping has an optimal temporal precision within the range of 0.8–2.5 Hz (McAuley et al., 2006; Moelants, 2002; Repp & Su, 2013). Additionally, delta (0.5–4 Hz) neural oscillations are also known to shape the dynamics of motor behavior and motor neural processes (Morillon et al., 2019). Thus, this 2 Hz preferred rate could be seen in the dynamic attending theory and neural entrainment framework as a physiological constrained by neural oscillators.

Furthermore, there is a seeming match between the rhythmic structures of many natural, behaviorally relevant events, such as speech (Zion Golumbic et al., 2013), and those of brain oscillations (Zoefel & Kösem, 2024). This analogy between the brain's syntax and the replicative characteristics of human language may extend beyond mere metaphor. The coevolution of the brain and body could have influenced the relationship between brain rhythms and their regulation of the motor system in sound production (Buzsáki & Vöröslakos, 2023). In particular, throughout the development of human speech, the articulatory motor system has likely adapted its output to align with the rhythms that the auditory system is best able to perceive (Heimbauer et al., 2011), and thus could explain the remarkable stability of temporal structures in speech across different languages (Poeppel & Assaneo, 2020). In a similar manner, the auditory system has presumably adjusted to the complex acoustic signals generated by the rhythmic movements of the jaw and articulators (Liberman & Mattingly, 1985). Additionally, both the auditory and motor systems must consider the biophysical constraints inherent to the neuronal infrastructure. This suggests that brain activity may have adapted through evolution to correspond to the temporal constraints of environmental stimulation (Zoefel & Kösem, 2024). Acoustic, neurophysiological, and psycholinguistic analyses of speech indicate that there are organizational principles and perceptual units of analysis that operate across varying time scales (Poeppel, 2003), in a hierarchical framework (Ghitza, 2011; Giraud & Poeppel, 2012; Lakatos et al., 2005; Schroeder et al., 2008). Gamma oscillations correlate with attributes at the phonemic scale such as formant transitions (for example, /ba/ versus /da/), the coding of voicing (for example, /ba/ versus /pa/), and other features whereas the acoustic envelope of naturalistic speech closely correlates with syllabic rate (i.e., theta frequency band) and the build-up of signal input into lexical and phrasal units—perceptual groupings that, for instance, convey the intonation contour of an utterance—occurs at a lower modulation rate, approximately 1–2 Hz (i.e., delta). In this way, the nesting of delta, theta and gamma oscillations is useful to covey the information of speech (Giraud & Poeppel, 2012) and in the chunking in parallel of the different

levels of language (phonemes, syllables and words) to help language comprehension (Ghitza, 2011).

1.2.5 Is neural entrainment theory restricted to isochronous sequences?

What happens when the sensory context is not fully isochronous? Is neural entrainment theory still applicable? Empirically, neural entrainment is observable for stimuli that are not fully isochronous (Breska & Deouell, 2017; Calderone et al., 2014; Herrmann et al., 2016; Kösem et al., 2018; Lakatos et al., 2008). Yet, it is still unclear what exact degree of temporal variability entrainment mechanisms can handle. Neural tracking of the external stimulation mean rate by brain activity have been reported in numerous studies, for example musical rhythms can entrain neural oscillations to follow the beat of the music (Nozaradan, 2014; Nozaradan et al., 2011, 2012; Tal et al., 2017; Tierney & Kraus, 2015; Trost et al., 2014) and the level of neural tracking can predict speech perception (Ding & Simon, 2014; Kösem et al., 2018; Obleser & Kayser, 2019; Riecke et al., 2018; Vanthornhout et al., 2018). However, whether these results could be attributed to enhancement of processing of the target stimulus or to neural tracking of the beat of the music remains uncertain. When dealing with neural entrainment, one caution is the distinction between neural entrainment in the narrow sense supposing one or more self-sustained oscillating processes that can adjust their rhythm of oscillators (i.e., synchronization) induced by an external source of energy (Obleser & Kayser, 2019), thus this definition of entrainment need endogenous brain oscillations to synchronize with the external rhythm. On the contrary, entrainment in the broad sense includes neural tracking of the stimulation rate but do not require an active process of synchronization. It is often not trivial to disentangle whether we talk about entrainment in his narrow sense or not. Very few studies have demonstrated that external rhythms can induces narrow entrainment that subsist more than a few cycles after the end of the stimulation (e.g., Kösem et al., 2018; Zoefel et al., 2024)).

Previous works on temporal prediction has shown a similar level of temporal predictability effects to those caused by a periodic context when the time intervals between stimuli were repeated over time (memory based predictions) (Breska & Deouell, 2017) or when the temporal intervals were slowing decreasing or increasing at a predictable pace (Cope et al., 2012; Morillon et al., 2016). In particular, Breska & Deouell paper showed that periodic sequences uniquely result in obligatory depression of preparation-related premotor brain activity when an

on-beat event is omitted, suggesting a distinction between periodic and memory-based neural mechanisms. However, they also found that both: periodic and memory-based contexts lead to greater phase concentration at the arrival of the expected target and higher contingency-negativity variation (CNV) compared to a random context. These results question the theory of neural entrainment in non-periodic contexts and identify both overlapping and distinct neural mechanisms for periodic or memory based contexts (Breska & Deouell, 2017). Using non-periodic stimulation, other reports have shown increased delta phase concentration and neural delta-band amplitude when the target was cued in time (Herbst, Stefanics, et al., 2022; Stefanics et al., 2010) and showing a direct correlation between delta phase/amplitude and behavioral measures (Cravo et al., 2013; Henry & Obleser, 2012; Herrmann et al., 2016). These phase effects are also correlated with evoked potentials such as the CNV that is a potential peaking at on-beat times and resolve immediately after (Breska & Deouell, 2016; Praamstra et al., 2006; Walter et al., 1964). This early negative shift is a component present in tasks involving stimulus timing and can be interpreted as an index of expectancy for an upcoming stimulus (Breska & Deouell, 2017a; Miniussi et al., 1999). Post-stimulus evoked activity is also influenced by temporal expectations, the mismatch negativity (MMN) a component related to the prediction error commonly measured in oddball paradigms with a peak at 150-250ms from change onset (Näätänen et al., 2007) showed higher amplitude MMN responses when deviance occurred on the expected beat but was weaker when the deviance occurred off-beat (Bouwer et al., 2014). Moreover, the P300 component, a well know ERP (Polich, 2007) dominated by the delta-band component (Bernat et al., 2007; Ergen et al., 2008; Ishii et al., 2009; Schürmann et al., 2001) show greater amplitude when the target events are cued and can be predicted (Miniussi et al., 1999; Stefanics et al., 2010).

Another study specifically investigated the persistence of neural entrainment mechanisms in temporally variable sensory contexts (Herrmann et al., 2016). In this MEG study, participants listened to an auditory stimulation at a 2Hz rate with a temporal jitter of 0.14 Hz and showed an alignment of neural oscillations at the expected rate of the stimulation. Additionally, this study demonstrated that that auditory detection was influenced by the pre-target neural amplitude, specifically the phase of 2Hz amplitude at the arrival of the target was a good predictor of behavioral performance (Herrmann et al., 2016).

Overall, these findings indicate that both low-frequency dynamics and evoked activity may reflect temporal prediction mechanisms that are involved in the processing of non-isochronous

sequences. However, it remains uncertain to what extent neural oscillatory and evoked responses interact, as well as the impact of contextual temporal variability on these responses.

1.3 Rhythms in Pathology

1.3.1 Rhythm perception and production is affected in certain pathologies

Temporal processing impairments are observed across various neurological and psychiatric conditions (Hinault et al., 2023), as for instance, in the Autism Spectrum Disorder (ASD) (Foss-Feig et al., 2017), in the Attention Deficit and Hyperactivity Disorder (ADHD) and in Parkinson's disease (PD) (Allman & Meck, 2012; Noreika et al., 2013; Rammsayer & Classen, 1997; Smith et al., 2002; Toplak et al., 2003). In the context of PD in particular, rhythmic auditory stimulation has emerged as a potentially effective therapeutic approach, even in light of the temporal processing challenges faced by patients (Dalla Bella, 2020; Ghai et al., 2018; Hove & Keller, 2015; Koshimori & Thaut, 2018; Wang, 2010; Ye et al., 2022). Motor symptoms in PD, specifically gait dysfunctions, can be alleviated by presenting patients with rhythmic cues. When a rhythmic cue is present, patients typically show improvements in gait, such as longer stride length and faster walking speed (Dalla Bella, 2020; Ghai et al., 2018; Ye et al., 2022).

Rhythms are also impacted in language related impairments, such as dyslexia, aphasia, stuttering, and Developmental Language Disorders (DLD), a neurodevelopmental disorder characterized by impairment in learning, understanding, and producing language (Tallal et al., 1997). These language difficulties cannot be attributed to other neurodevelopmental or neurological conditions (including learning disabilities, hearing loss, autism, …) nor to extenuating circumstances such as limited exposure to language. It was shown that individuals with dyslexia and DLD show temporal processing deficits, particularly in tasks requiring rhythm and timing, such as speech and music. In speech, children with DLD present impaired cortical tracking of speech (Nora et al., 2024). Whereas in music, DLD individuals have difficulties to produce musical rhythms (Fiveash et al., 2021; Kreidler et al., 2023; Ladányi et al., 2020). Individuals with DLD also often meet diagnostic criteria for dyslexia (Bishop & Snowling, 2004). Recent theory postulates that the risk for developmental speech/language disorders could be correlate with rhythmic abilities, individuals with poor rhythm would be at

higher risk for developmental speech/language disorders. (**Figure 1.7**). As such, rhythm-based interventions also represent a promising avenue of research for the improvement of language perception and production skills, within the general population but also to those affected by aphasia, dyslexia, DLD, and stuttering (Fiveash, et al., 2023; Ladányi et al., 2020). Specifically, techniques involving rhythmic pacing, auditory-motor integration, and singing have been shown to facilitate speech production in patients with aphasia (Stahl et al., 2011; Stahl & Kotz, 2014). Furthermore, analogous methodologies have been recommended for use with children diagnosed with ASD (Wan et al., 2011) and ADHD (Jackson, 2003; F. Zhang et al., 2017).

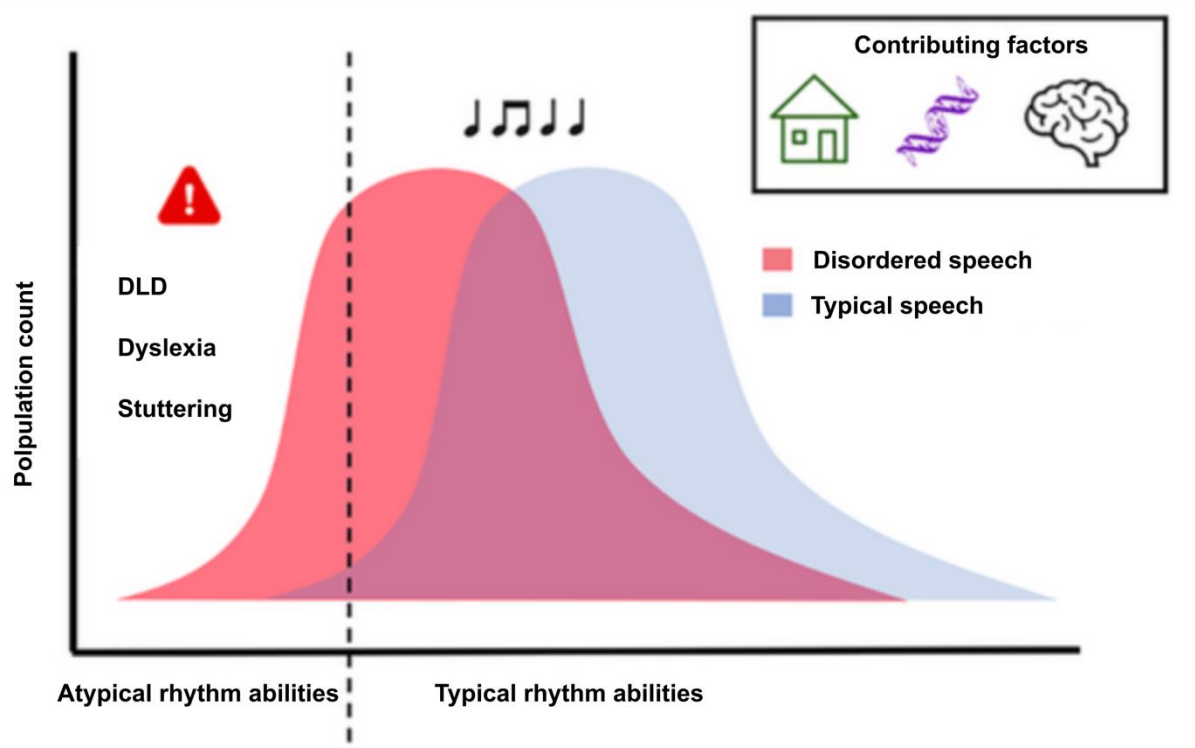

Figure 1.7: Atypical rhythm theory posits that individuals with poorer rhythmic abilities are at higher risk for developmental speech/language. Adapted from (Ladányi et al., 2020).

1.3.2 What is dyslexia?

Dyslexia is a neurodevelopmental disorder that impairs an individual's ability to read, write and spell. Individuals with dyslexia often have difficulty deciphering words, understanding the

meaning of sentences and spelling correctly. Diagnostic criteria according to ICD-10 (International Classification of Diseases, 10th revision, 2008) are : the presence of persistent and significant difficulties in the acquisition and use of academic skills, particularly in reading and writing, which cannot be explained by an overall developmental delay or by environmental factors, difficulties which may appear during the period of early development (as early as learning to read between the ages of 5 and 7), difficulties resulting in academic performance significantly below what is expected for the child's chronological age, despite adequate instruction, educational opportunities and normal intelligence for the child. The difficulties observed in individuals with dyslexia cannot be more appropriately or explanatorily attributed to another developmental disorder, a medical or neurological disorder, sensory or motor problems, or an oral language acquisition deficit. However, the diagnosis is not trivial because many comorbidities are associated with dyslexia such as dysphasia, dyspraxia, attention deficit disorder with or without hyperactivity (ADHD), dysgraphia, dyschronia, dysorthographia, dyscalculia or even specific oral language disorders such as DLD (Habib, 2003; Kaplan et al., 2001). Consequently, the diagnosis of dyslexia is made when these criteria are met, and after excluding other potential causes of learning difficulties. These criteria have been the subject of debate for many years, as they exclude, by definition, the possibility of diagnosing dyslexia in children who have not received the necessary educational opportunities and resources, as well as in those suffering from mental retardation unrelated to reading (Elliott & Grigorenko, 2014).

In particular, dyslexia can be characterized and identified in childhood by a certain difficulty in identifying the sounds associated with letters (i.e., grapheme-phoneme correspondence), which can make reading complex and slow, and can also make spelling words laborious, as it requires switching between sounds and letters. This disorder can also affect word processing and cause errors in text comprehension (Lyon et al., 2003; Shaywitz & Shaywitz, 2005). Diagnosis of dyslexia requires a full speech and language assessment, including reading, writing and other tests of underlying cognitive processes: phonological, memory and visuo-spatial. The prevalence of dyslexia is a matter of debate in scientific research (Miles, 2004; Wagner et al., 2020) but can be broadly estimates from 5 to 9% (Francks et al., 2002; Pennington & Bishop, 2009; Peterson & Pennington, 2012; Yang et al., 2022), though diagnosis is more common in boys than girls (Shaywitz et al., 1990). The difficulty of diagnosing this disorder is accentuated by its numerous comorbidities and the low sensitivity of dyslexia to non-specific tests. Diagnosis and follow-up by a speech therapist often becomes difficult outside childhood, as the patient tends to adopt dyslexia-specific compensation strategies in later life. These strategies

may include avoiding tasks that highlight the disorder, visual memorization of words, or using global recognition techniques when reading rather than purely phonetic decoding (Cole et al., 2024; Kirby et al., 2008; Rello et al., 2013). In addition, numerous studies of dyslexic university students have revealed significant deficits in various cognitive aspects. These include difficulties in phonological processing, notably deficits in phoneme detection and phonemic decoding tasks (Cole et al., 2024; Pennington et al., 1990), as well as impaired naming speed and marked reading deficits. In addition, these comparative studies have revealed deficits in spelling, writing and mathematics in dyslexic individuals (Angelelli et al., 2004; Cole et al., 2024; Simmons & Singleton, 2008). Other research has also highlighted executive function disorders in dyslexic subjects, characterized by prolonged reaction times indicating a reduced capacity for inhibition (Barbosa et al., 2019; Reiter et al., 2005; Varvara et al., 2014). Deficits can also be observed in the coordination of eye movements during saccades, affecting binocular coordination and visual attention (Biscaldi-Schäfer et al., 2000; Bucci et al., 2008, 2012; Jainta & Kapoula, 2011; Kirkby et al., 2008; Seassau et al., 2014) but also in the processes involved in verbal working memory, visuo-spatial memory and sustained attention (Cole et al., 2024; Jeffries & Everatt, 2004; Smith-Spark et al., 2003; Smith-Spark & Fisk, 2007). These findings highlight the diversity of deficits often observed in association with dyslexia in diagnosed individuals.

An increasing number of studies indicate that dyslexia is not just a reading or phonological disorder; but is also related to challenges in processing sensory information over time, characterized by deficits in perceiving the temporal order of auditory and visual stimuli (Farmer & Klein, 1995; Habib, 2021; Meilleur et al., 2020; Tallal, 2004; Tallal et al., 1993). Children and adults with dyslexia exhibit robust deficits in temporal tasks whether they are explicit (judgments on duration/ temporal order and simultaneity (Casini et al., 2017; Tallal et al., 1993; Tallal & Piercy, 1973) or implicit (phoneme discrimination based on durational contrast (Casini et al., 2017), and show affected electrophysiological mismatch negativity response to duration deviants sounds (Corbera et al., 2006; Huttunen-Scott et al., 2008; Stefanics et al., 2011). Furthermore, temporal discrimination abilities of infants and children have been able to predict subsequent language skills (Benasich & Tallal, 2002; Ozernov-Palchik et al., 2018; Plourde et al., 2017; Steinbrink et al., 2014). Rhythm perception is also known to be impacted in dyslexia (Bégel et al., 2022; Overy et al., 2003; Ozernov-Palchik et al., 2018). Literature has also shown the contextual advantage of rhythmic rehabilitation in the case of language disorders. Research suggests that both short-term rhythmic stimulation and long-term rhythmic training can produce

beneficial outcomes for children with dyslexia (Colling et al., 2017; Cumming et al., 2015; Muneaux et al., 2004). Evidence indicates that brief interventions, such as the presentation of rhythmic music excerpts prior to naturally spoken statements, can improve the grammatical processing of spoken sentences (Bedoin et al., 2016; Ladányi et al., 2021; Przybylski et al., 2013). Furthermore, sustained engagement in activities, particularly musical training focused on rhythmic processing, has been shown to be effective in enhancing phonological awareness and reading skills among children with dyslexia (Flaugnacco et al., 2015) but also improve sentence repetition with children with DLD (Fiveash, Ladányi, et al., 2023). Thus, these converging evidence from the literature seems to suggest a strong link between rhythms and certain pathology, especially in language disorders such as dyslexia. A better understanding of how rhythms are affected in dyslexia is crucial to better comprehend how the healthy and pathological brain can use rhythmic contexts to enhance perception.

1.3.3 The Dyslexia brain

Dyslexia is recognized by a wide consensus as a neurological disorder with a genetic origin (Démonet et al., 2004; Galaburda et al., 2006; Ramus, 2003). Dyslexia is characterized by auditory and phonological deficits implying that dyslexic people have great difficulty in segmenting words into phonological subunits (e.g., syllabic units) (Cole et al., 2020; Shaywitz & Shaywitz, 2005) as reading acquisition depends heavily on the ability to segment the acoustic signal into a sequence of perceptually discrete linguistic units. Current research suggests a connection between central hearing impairment and dyslexia, characterized by difficulties in decoding and interpreting auditory messages amongst noise, stemming from dysfunction in the central auditory system rather than from deafness. For instance, dyslexics can correctly distinguish a speech signal in silence, but their perception is impaired in the presence of noise, leading to speech degradation and poor comprehension associated with altered speech tracking (Destoky et al., 2022; Ziegler et al., 2009).

It has been hypothesized that this deficit in the processing of sensory information in individuals with dyslexia could originate from a wider impairment in the temporal sampling of rhythmic contexts (Bégel et al., 2022; Goswami et al., 2016; Overy et al., 2003; Ozernov-Palchik et al., 2018; Thomson & Goswami, 2008). Dyslexic have altered abilities to follow auditory rhythms, for instance in speech, dyslexics show impaired cortical tracking of speech in the right

hemisphere that is associated with phonemic deficits (Destoky et al., 2022; Di Liberto et al., 2018). To accurately anticipate the timing of speech units, the brain is believed to utilize oscillatory patterns to generate temporal expectations based on the rates of syllable and word presentation, thereby influencing speech comprehension (Bree et al., 2021; Guiraud et al., 2018; Kösem et al., 2018). This mechanism is supposedly based on oscillatory mechanisms in particular low frequency neural oscillations in the delta and theta ranges, which have been identified as essential for the temporal processing of speech (Giraud & Poeppel, 2012; Kösem & van Wassenhove, 2017) that follow syllable and phonemic units in speech. Therefore, rhythmic deficits in dyslexia could originate from deficit in neurophysiological tracking mechanisms carried by neural oscillations. Several studies support this idea (Goswami, 2011, 2018), demonstrating for example that neural tracking of auditory regularities is diminished in adults with dyslexia and that enhanced neural tracking of statistical structures has been associated with improved spelling skills (Ringer et al., 2024). Other studies also support that individuals with dyslexia show reduced synchronization of neural oscillations with external stimuli, notably within the delta and theta frequency ranges, when compared to neurotypical participants (Fiveash et al., 2020; Guiraud et al., 2018a; Hämäläinen et al., 2012; Leong & Goswami, 2014, 2014; Molinaro et al., 2016; Soltész et al., 2013; Thomson et al., 2006; Thomson & Goswami, 2008). This impairment in brain oscillations to synchronize with temporally expected events in speech could indicate an altered neural entrainment (Calderone et al., 2014) therefore indicating a wider deficit in temporal prediction abilities in dyslexia.

Research suggests that there is a temporal processing deficit in individuals with dyslexia, which is associated with impairments in neural entrainment mechanisms. However, the relationship between these impairments and deficits in temporal predictive mechanisms has not yet been fully clarified. Additionally, the response of individuals with dyslexia to temporally variable sound sequences remain uncertain.

The next four chapter will cover the following aspects:

Chapter 2 will examine the influence of contextual variability on temporal predictability and will critically assess the concept of rhythmicity. The findings indicate that temporal predictions can be established even in probabilistic contexts, although the ability to make such predictions diminishes as the variability of the temporal context increases.

Chapter 3 delves into the neural mechanisms underlying these predictions across various temporal contexts. We investigated scenarios involving periodic stimulation, where neural mechanisms are thought to be based on neural entrainment, as well as probabilistic and random distributions (i.e., that lack predetermined statistical rules within a temporal framework). The findings indicate that the temporal context influences the evoked responses, with neural tracking of the stimulus rate enhancing in more regular contexts, thereby offering valuable insights into the neural mechanisms associated with probabilistic contexts.

In Chapter 4, we explored the impact of temporal predictability effects on individuals with dyslexia, highlighting a potential connection between dyslexia and challenges in processing temporal regularities within sensory contexts.

Finally, Chapter 5 provides a general discussion on the impact of temporal context on temporal predictions mechanisms and perception.

Chapter 2:

IMPACT OF TEMPORAL VARIABILITY OF THE SENSORY CONTEXT ON PERCEPTION

2.1 Introduction

2.1.1 Motivation

In this experiment we tested a range of temporal variability conditions and compared the temporal predictability benefits from the temporal regularities present in these sensory contexts. Reasons to investigate the effects of temporal variability on sensory perception were the following:

- Perception of sensory events is known to be improved when their timing is fully predictable in time. Indeed, dynamic attending theory suggest that predicting the timing of future sensory events allows to allocate cognitive resources at the expected time of occurrence, and therefore facilitates the sensory processing of these upcoming stimuli (Large & Jones, 1999; Nobre et al., 1999).

- However, little is known about how the temporal variability in a sensory context affect perception. Most works have been done on determinist sequences, as when auditory stimulation is periodic (Cravo et al., 2013; Jaramillo & Zador, 2010; Lawrance et al., 2014; Morillon et al., 2016; Rimmele et al., 2011), when temporal intervals are repeated (Breska & Deouell, 2017), or when the temporal intervals are slowly decreasing or increasing at a predictable pace (Cope et al., 2012; Morillon et al., 2016).

- From a naturalistic point of view, temporal contexts are rarely fully isochronous nor deterministic. Speech acoustic signals in particular presents complex statistical temporal regularities (Singh et al., 2003; Cummins, 2012; Varnet et al., 2017) that are supposedly used to form temporal expectations and influence language comprehension (Tillmann, 2012; Jadoul et al., 2016; Kösem & Van Wassenhove, 2017; Kösem et al., 2018; Aubanel & Schwartz, 2020). Thus, it is unclear to what extent probabilistic temporal predictions influence the discrimination of sounds per se. The aim of this study is therefore to investigate how the temporal statistics of auditory stimulation influences ongoing auditory perception, specifically when the temporal context is not fully predictable in time.

2.1.2 Experiment

In this experiment, we adapted the active oddball paradigm of (Morillon et al., 2016) in which participants were asked to detect deviant sounds that where embedded in 3 min-long sound sequences masked by a continuous white noise. Visual cues indicating whether it was a target were synchronized to appear simultaneously with the sounds. A “red circle” visual cue indicated a target, and that the participant had to respond to this trial by pressing a button. A “white cross” cue indicated a standard trial of the context and that participants did not have to respond to this trial. When the “white cross” was presented on the screen, the synchronized sound was always a standard sound whereas when the “red circle” was presented, the synchronized sound could either be a standard or a deviant sound (with equal 50% probability). We manipulated the temporal intervals between sounds so that the Stimulus-Onset-Asynchrony (SOA) between each sound of the sequence was drawn from Gaussian distributions. The distributions had the same mean (500 ms; 2Hz) but different standard deviations (STD): from 0 ms (periodic) to 150 ms STD. If participants are able to use the temporal statistics present in the probabilistic

sequences, we expect that discrimination of the target sounds should be better in more regular sequences. Thus, in this experiment we question the range for which temporal variability of the context still allow temporal predictability effects.

2.1.3 Summary of the results

Results suggest that temporal predictions can be setup in aperiodic probabilistic context and that auditory discrimination performance progressively declines as the temporal variability of the context increases. Specifically, our data suggests that temporal predictions benefit auditory perception until the variability of temporal context reaches a STD threshold of 10–15% of the mean SOA of the distribution. Moreover, these temporal prediction effects can be set up quickly from the local temporal statistics of the context. Both local and global statistics interact, as local temporal statistics from three intervals can begin to influence the perception of an upcoming sound. Therefore, this work suggests that temporal prediction mechanisms are robust to temporal variability, and that temporal predictions built on sensory stimulations that are not purely periodic nor temporally deterministic can influence auditory perception.

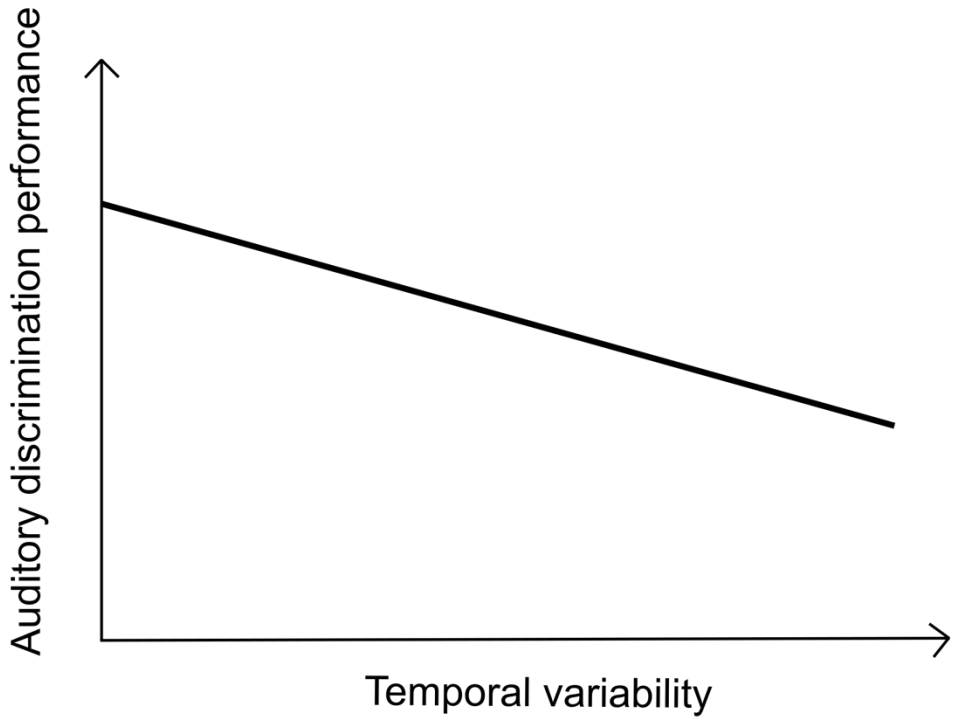

Figure 2.1: Summary of the results. Auditory performance in our task linearly decreased as the temporal variability in the sensory contexts increased.

2.2 Article

Bonnet, P., Bonnefond, M., & Kösem, A. (2024). What is a rhythm for the brain? The impact of contextual temporal variability on auditory perception. Journal of Cognition, 7(1)

What is a Rhythm for the Brain? The Impact of Contextual Temporal Variability on Auditory Perception

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ABSTRACT

Temporal predictions can be formed and impact perception when sensory timing is fully predictable: for instance, the discrimination of a target sound is enhanced if it is presented on the beat of an isochronous rhythm. However, natural sensory stimuli, like speech or music, are not entirely predictable, but still possess statistical temporal regularities. We investigated whether temporal expectations can be formed in non-fully predictable contexts, and how the temporal variability of sensory contexts affects auditory perception. Specifically, we asked how "rhythmic" an auditory stimulation needs to be in order to observe temporal predictions effects on auditory discrimination performances. In this behavioral auditory oddball experiment, participants listened to auditory sound sequences where the temporal interval between each sound was drawn from gaussian distributions with distinct standard deviations. Participants were asked to discriminate sounds with a deviant pitch in the sequences. Auditory discrimination performances, as measured with deviant sound discrimination accuracy and response times, progressively declined as the temporal variability of the sound sequence increased. Moreover, both global and local temporal statistics impacted auditory perception, suggesting that temporal statistics are promptly integrated to optimize perception. Altogether, these results suggests that temporal predictions can be set up quickly based on the temporal statistics of past sensory events and are robust to a certain amount of temporal variability. Therefore, temporal predictions can be built on sensory stimulations that are not purely periodic nor temporally deterministic.

KEYWORDS: Temporal predictions; auditory perception; probabilistic temporal contexts; temporal statistics; rhythmicity perception

INTRODUCTION

Temporal predictions are believed to play a key role in the way we process sensory information (Jones, 1976; Schroeder & Lakatos, 2009; Arnal & Giraud, 2012; Nobre et al., 2012). Predicting the timing of future sensory events allows to allocate cognitive resources at the expected time of occurrence, and therefore facilitates the sensory processing of these upcoming stimuli (Large & Jones, 1999; Nobre et al., 1999). As a consequence, the perception of sensory events is improved when their timing is fully predictable. Auditory discrimination performances are also improved when the temporal context of the stimulation is deterministic, as when auditory stimulation is periodic (Cravo et al., 2013; Jaramillo & Zador, 2010; Lawrance et al., 2014; Morillon et al., 2016; Rimmele et al., 2011), when temporal intervals are repeated (Breska & Deouell, 2017), or when the temporal intervals are slowing decreasing or increasing at a predictable pace (Cope et al., 2012; Morillon et al., 2016).

However, from a naturalistic point of view, temporal contexts are rarely fully isochronous nor deterministic. Speech acoustic signals in particular presents complex statistical temporal regularities (Singh et al., 2003; Cummins, 2012; Varnet et al., 2017) that are supposedly used to form temporal expectations and influence language comprehension (Tillmann, 2012; Jadoul et al., 2016; Kösem & Van Wassenhove, 2017; Kösem et al., 2018; Aubanel & Schwartz, 2020). How temporal predictions occur in non-fully predictable temporal contexts such as speech and music and how they influence auditory perception is still under debate (Jadoul et al., 2016; Herbst & Obleser, 2017, Zoefel & Kösem, 2022). During speech listening in particular, temporal prediction mechanisms are put forward as an important mechanism that would contribute to acoustic segmentation and enhanced processing of relevant auditory information (Giraud & Poeppel, 2012; Meyer et al., 2019; Peelle & Davis, 2012; Zoefel & Kösem, 2022). In line with this, temporal predictability based on rhythmic cues present in the signal, specifically on the average speech rate, influences speech perception (Dilley & Pitt, 2010; Kösem et al., 2018). Yet, speech processing also requires to take into account probabilistic temporal variations in syllable and word durations naturally present in languages (Jadoul et al., 2016; Varnet et al., 2017; Ten Oever & Martin, 2021). Probabilistic inference of sensory timing influences explicit temporal judgments of auditory events (Cannon, 2021; Doelling, 2021), tapping (Cannon, 2021), warned reaction time tasks (Los et al., 2017), responses times during auditory discriminations tasks (Herbst & Obleser, 2017). However, it is unclear to what extent probabilistic temporal predictions influence the discrimination of sounds per se. The aim of this

study is therefore to investigate how the temporal statistics of auditory stimulation influences ongoing auditory perception, specifically when the temporal context is not fully predictable in time. Additionally, the perception of rhythmicity, here defined as the perception of how temporally regular the sound sequences are, is known to vary across participants (Geiser et al., 2009; Krause et al., 2010; Repp, 2010; Fiveash et al., 2022). Subjective perceived rhythmicity may have an influence on the way temporal predictions are formed (Doelling & Poeppel, 2015*)*: if participants rely on an internal model of temporal predictions that differs from external timing, maximal auditory discrimination performance would occur when participants judge the temporal context to by maximally predictable, and not necessarily when the external context is regular. We therefore also explored whether auditory perception is influenced by the subjective perception of the contextual temporal structure.

To do this, we used an auditory oddball paradigm adapted from the study of Morillon and colleagues (Morillon et al., 2016). Participants were asked to detect deviant sounds that where embedded in 3 min-long sound sequences. The Stimulus-Onset-Asynchrony (SOA) between each sound of the sequence was drawn from Gaussian distributions. The distributions had the same mean (500 ms) but different standard deviations (STD): from 0 ms (periodic) to 150 ms STD (Fig. 2.2B). Results suggest that (i) temporal predictions can be formed in aperiodic probabilistic context, though auditory discrimination performance progressively declines with the temporal variability of a context, (ii) these temporal prediction effects are set up quickly from the local temporal statistics of the context. Therefore, this work suggests that temporal prediction mechanisms are robust to temporal variability, and that temporal predictions built on sensory stimulations that are not purely periodic nor temporally deterministic can influence auditory perception.

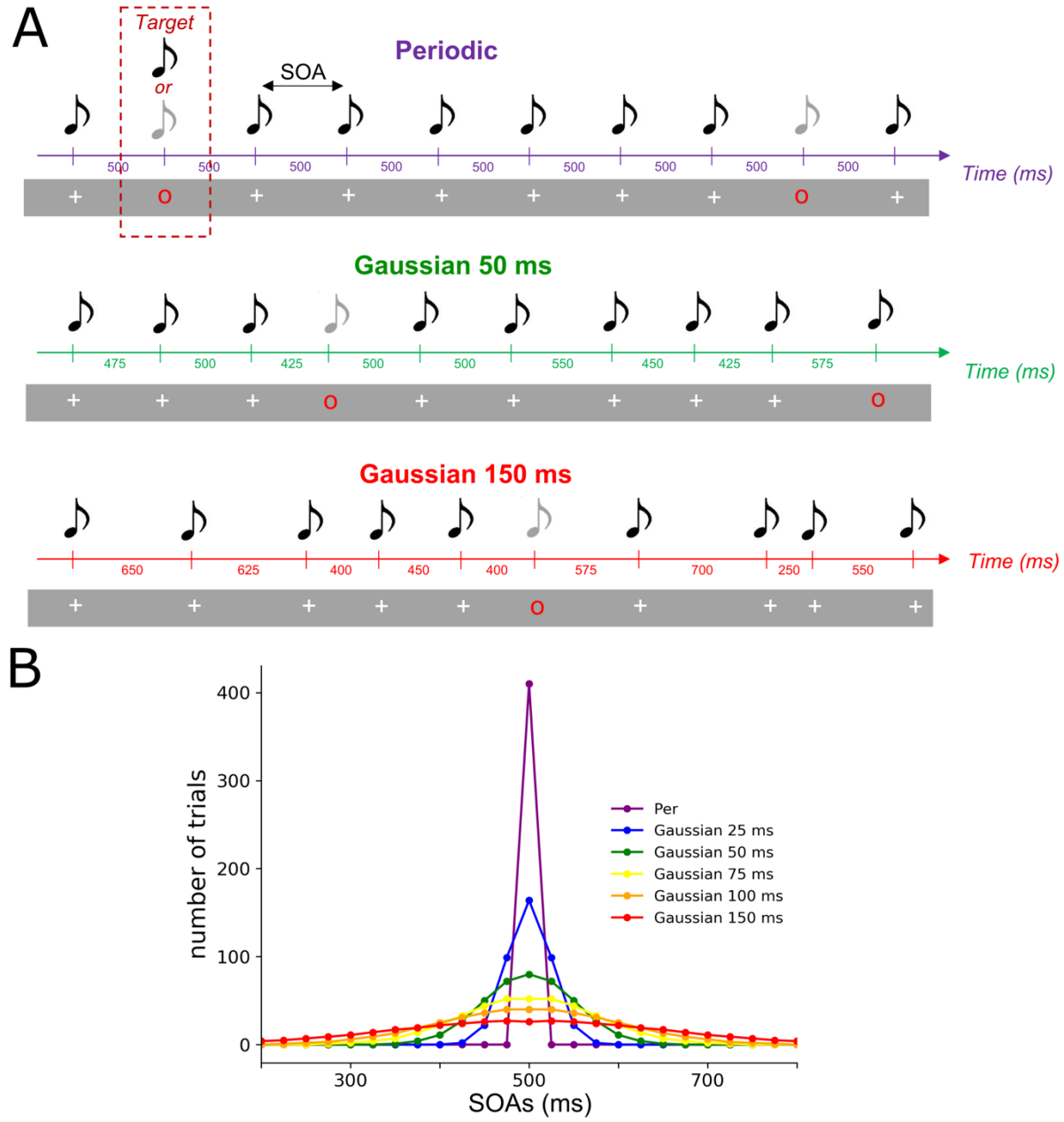


Figure 2.2: Experimental design. (**A**) Example of three sequences of different temporal STD used in this experiment. Each sequence consisted of a stream of simultaneous auditory and visual stimuli. A standard stimulus corresponded to a 440 Hz pure tone co-occurring with a white cross. Occasionally a red circle appears in the stream indicating a target stimulus, on which participants had to discriminate between a standard (440 Hz) and deviant (220 Hz) pure tone. (**B**) Distribution of SOAs in each sequence. For each sequence, the distributions of the SOAs were drawn of Gaussian distributions with equals means (500 ms) but distinct STDs. Six conditions were designed: from 0 (periodic) to 150 ms of STD with data points built from 100 ms to 900 ms and spaced from 25 ms.

MATERIALS AND METHODS

Participants. Twenty-three participants (11 females, mean age = 25.6 years, 3 left-handed) took part in the experiment. Participants reported no history of neurological or psychiatric disease, normal hearing and normal or corrected-to-normal vision. Four participants had outlier data and were excluded from data analysis: one participant responded at chance level throughout the experiment, three participants had outlier subjective rhythmicity ratings of the sequences (±1.5 interquartile range of regression scores) (Fig. 2S1). Therefore, nineteen participants were included for the analysis. The study was approved by an ethical committee (CPP) and all participants signed a written consent and received payment for their participation.

Stimuli. Participants heard sequences of pure tones, that were either a standard sound (corresponding to a pure 440 Hz sound) or a deviant sound (pure 220 Hz sound). The sounds were presented via headphones for 100 ms (with 5 ms ramp-up and ramp-down in volume). With each sound, visual cues were presented via a digital display (1600, 1024 resolution; 120 Hz refresh rate) and were displayed in front of them (70 cm) in the center of the screen for a duration of 100 ms. Visual cues were synchronized to appear simultaneously with the sounds. A "red circle" visual cue indicated a target and that the participant had to respond to this trial by pressing a button (Fig. 2.2A). A "white cross" cue indicated a standard trial of the context and that participants did not have to respond to this trial. When the “white cross” was presented on the screen, the synchronized sound was always a standard sound whereas when the “red circle” was presented, the synchronized sound could either be a standard or a deviant sound (with equal 50% probability). The “red circle” stimulus was used to indicate to the participant that the sound was a target stimulus and that an answer was required. With this manipulation, we could make sure that the response of the participant was referring to the last cued sound, and not to any other sound from the sequence (which is presented continuously at a relatively fast rate around 2 Hz). In the absence of the visual cue, we could not unambiguously decipher to which sound the participant was reacting to. In addition to the pure tones, broadband white noise was presented continuously to make the task more difficult. The signal-to-noise ratio between pure tones and white noise was adjusted individually via a staircase procedure (see Procedure). All stimuli were generated and presented via the Psychophysics-3 toolbox.

Procedure. The experiment was composed of 12 blocks of 3 min 30 s. Each block consisted of a sequence of auditory sensory stimuli masked in constant noise. Participants had to discriminate the sound when a red visual cue was presented on the screen (target trial) (Fig. 2.2A). To vary the temporal regularities of the context, the SOAs between the sounds of each block was drawn from distinct distributions. In the Periodic condition, the SOA was fixed at 500 ms. For the Gaussian conditions, the SOAs were drawn from Gaussian distributions with distinct STDs of 25 ms, 50 ms, 75 ms, 100 ms and 150 ms (Fig. 2.2B). The SOAs data points used to build these gaussian distributions were spaced out every 25 ms to allow accurate sampling of these conditions. Both standards and target trials were drawn from these distributions. Each block consisted of 410 trials including 56 target trials. Between two target trials, a minimum of 4 standard sounds and a maximum of 10 standard sounds (uniform distribution) could occur. The target trials could not appear in the first 10 trials of the sequence. Two blocks were presented for each condition and the block order was pseudo-randomized so that the same condition was not presented twice in succession. Therefore, 112 target trials were obtained for each condition.

After each block, the subjective perception of the rhythmicity of the temporal context was assessed: participants were asked to rate the global rhythmicity of the sequence. We specifically asked to rate whether the sounds in the sequence were presented at a regular pace on a scale from 0 (totally not rhythmic) to 10 (totally periodic). Before the main experiment, a staircase procedure was performed to adjust the signal-to-noise ratio (SNR) so that the average sound discrimination performance was within ~80% correct responses (mean SNR = -14.9 dB, within [-16.0, - 13.7] dB range). These SNRs are slightly higher than previously reported detection thresholds of pure tones (around -17 dB) (McPherson et al., 2022). We think for this reason that participants were able to hear both standards and deviant sounds and that our task relied on pitch discrimination. In the staircase, 75 sounds were displayed with periodic SOAs (500 ms) and targets trials could appear every ~2-3 tones.

Data analysis. Generalized linear mixed models (GLMMs) were computed using lme4 (version 1.1-28) (Bates et al., 2014) with R 4.1.2 (2021-11-01), on both the subject's responses (1 for a correct response, 0 if incorrect, binomial distribution) and subject's response times (gamma distribution) as dependent variables. We first included the global temporal STD (global STD, continuous variable) as fixed effect, and the factor Subject as a random effect. Stepwise models comparison was done using the likelihood ratio test, and Type II Wald chi-square tests were used to assess the best model fit, and the significance of fixed effects (Bates et al., 2014; Luke,

2017). For subjects' responses, the best model only included the Subject random intercept (as adding the random slope did not significantly improve the model's explained variance: Chi-square = 2.72, p =0.2557). For the response times, the best model included both random intercepts and random slopes. To evaluate the difference in performance between each Global STD condition in our experiment, we then performed post-hoc tests using the emmeans package version 1.7.4.1. For this we considered Global STD as a categorical factor and compared each Global STD level (0, 25, 50, 75, 100, 150 ms) using Tukey multiple comparison correction. As exploratory analyses, we investigated the impact of the subjective perception of rhythmicity on performances. To do this, we compared the first models to a new model that included the predictor Rhythmicity Rating (gaussian distribution) as additional fixed effect. We also investigated the correlation between Global STD and Rhythmicity Rating. For this, Rhythmicity Rating was considered as a dependent variable and Global STD as fixed effect, and Subject as Random effect.

We also investigated how the recent temporal statistics in the non-periodic sequences impacted performance (i.e. based on the statistical distribution of the SOAs between the last N sounds before target presentation). To do this, we computed for each participant 2-D plots representing the discrimination accuracy and response times according to the STD and mean of the N previous SOAs. Specifically, we computed the mean and STD of the local SOA distribution drawn from the N previous SOAs before each target trial (with N ranging from 1 to 7 SOAs for the mean SOA, and N ranging from 2 to 7 SOAs before target trial for the SOA STD). We then binned target trials per SOA distribution mean (from 400 to 600 ms SOA mean, with a sliding window of ±20 ms length) and per SOA distribution STD (from 10 ms to 100 SOA STD, with a sliding window of ±10 ms length). Bins containing less than 5 trials per participant were excluded from further analysis. For each bin, we computed the average accuracy and response time across trials. We obtained a 2-D plots representing how the mean and STD of the 2/3/4/… last SOAs impacted accuracy and response times for each participant. We investigated whether, across participants, performances would be relatively better or worse depending on the mean or STD of the local temporal statistics. To test this, we therefore Z-scored the 2-D plots for each participant and applied cluster-based permutation statistics (using MNE version 1.0.3) to the z-scored data (Maris & Oostenveld, 2007). One sample t-tests against zero were computed for each sample. Adjacent samples with a p-value associated to the t-test of 5% or lower were selected as cluster candidates. The sum of the t-values within a cluster was used as the cluster-level statistic. The reference distribution for cluster-level statistics was computed by performing 1000 random sign-flipping permutations of the data. Clusters were considered significant if the

probability of observing a cluster test statistic was below the 2.5-th quantile and above the 97.5-th quantiles for the reference distribution. The choice of the cluster permutation tests was done to solve multiple comparison testing, and was motivated by the fact that we had two-dimensional data whose adjacent samples were correlated in both dimensions (i.e. we expected that samples with close mean SOA and close SOA STD would lead to similar performances; similarly, we expected that the computation of the mean and STD of the N preceding SOAs would also correlate with the mean and STD of the N-1, N-2 SOAs, and so forth). Additionally, cluster-based non-parametric permutation testing allows to capture nonlinear effects (expected to occur for mean SOA effects in particular). Finally, to further evaluate the relative contribution of global and local temporal STD on performances, we ran GLMMs that included both Global STD and the Local STD (from the N previous SOAs, N rating between 2 to 7), and the last SOA before target presentation as predictors of subject's response and response times (Table S1).

RESULTS

Temporal variability impacts auditory discrimination accuracy and response times

We tested the effect of the temporal variability of auditory sequences on auditory accuracy and on response times. Participants auditory discrimination significantly decreased as a function of contextual temporal variability (main effect of the factor Global STD ($\chi 2(1) = 14.574$, $p = 0.0001$)). Discrimination accuracy was highest in the periodic context, and progressively decreased with increasing global temporal STD (accuracy decreased by 0.6% every 25 ms). Contrasting each global STD condition between one another, post-hoc tests revealed that accuracy in the periodic condition was statistically different from the more aperiodic condition (difference % correct responses Periodic - Gaussian 150 = 4.28%, $p = 0.0061$). Moreover, performance was also statistically different between the contexts Gaussian 25 and Gaussian 150 (difference % correct responses Gaussian 25 - Gaussian 150 = 3.76%, $p = 0.0262$). These results suggest that the percentage of correct responses is higher in conditions with less variable contexts even if they are not completely periodic (e.g., in the Gaussian 25 condition) (Fig. 2.3A).

Response times were also significantly affected by the temporal STD of the context (main effect of the factor Global STD ($\chi 2(1) = 115.47$, $p < 0.0001$)). Response times were faster in temporal

contexts with low variability and progressively slowed as the global temporal STD increased (response times increased by 5 ms as the context variability increased by 25 ms). Post-hoc tests showed that the three conditions with the lowest temporal variability: Periodic, Gaussian 25 and Gaussian 50 were statistically different from the three conditions with the highest temporal variability: Gaussian 75, Gaussian 100 and Gaussian 150 (difference response times (Periodic – Gaussian 75 = -20.2 ms, $p < 0.0001$); (Periodic – Gaussian 100 = -21.6 ms, $p < 0.0001$); (Periodic – Gaussian 150 = -21.2 ms, $p < 0.0001$); (Gaussian 25 – Gaussian 75 = -20.8 ms, $p < 0.0001$); (Gaussian 25 – Gaussian 100 = -22.1 ms, $p < 0.0001$); (Gaussian 25 – Gaussian 150 = - 21.8 ms, $p < 0.0001$); (Gaussian 50 – Gaussian 75 = -19.3 ms, $p = 0.0001$); (Gaussian 50 – Gaussian 100 = -20.7 ms, $p < 0.0001$); (Gaussian 50 – Gaussian 150 = -20.3 ms, $p = 0.0003$). Results on response times suggest that there is a gap between contexts with low temporal variability and contexts with global temporal STD that exceed 75 ms (Fig. 2.3C).

The more variable the auditory sequence, the more variable the target stimuli's SOA. It could therefore be possible that the preceding results only reflect the impact of target's SOA variability, and not of the overall temporal context. In particular, perception is subject to temporal hazard rate, so that auditory discrimination performances improve the longer you wait for the stimulus (Herbst & Obleser, 2019), and reversely, auditory perception performance could decrease drastically for shorter SOAs. To alleviate these effects, we restricted our analyses to all targets whose preceding SOA were of 500 ms only. We still observed similar effects of temporal context as when all SOAs were included. Participants auditory discrimination significantly decreased as a function of contextual temporal variability (main effect of the factor Global STD ($\chi 2(1) = 14.490$, $p = 0.0001$)). Contrasting each global STD condition between one another, post-hoc tests revealed that accuracy in the periodic condition was statistically different from the condition Gaussian 75 ms and from the condition Gaussian 100 ms (difference % correct responses Periodic - Gaussian 75 = 7.50 %, $p = 0.0174$; Periodic - Gaussian 100 = 8.04 %, $p = 0.0371$). Condition Gaussian 25 ms was also significantly different from the conditions Gaussian 50 ms, Gaussian 75 ms, and Gaussian 100 ms (difference % correct responses Gaussian 25 - Gaussian 50 = 8.27 %; $p = 0.0036$; Gaussian 25 - Gaussian 75 = 10.59 %; $p = 0.0004$; Gaussian 25 - Gaussian 100 = 11.13 %; $p = 0.0013$). These results suggest that when we took only the SOA at the mean of the distributions (500 ms) auditory accuracy was also better in low variability conditions (e.g., periodic and Gaussian 25 ms) compared to conditions with more variability in the context (e.g., Gaussian 75 and 100 ms) (Fig. 2.3B).

For the response times, there was also a significant main effect of the factor Global STD ($\chi 2(1) = 77.926$; $p < 0.0001$). Response times were also faster in temporal contexts with low variability and progressively slowed as the global STD increased. Post-hoc tests show that the Periodic condition was different from the Gaussian distributions above 50 ms STD (Periodic – Gaussian 50 = -19.6 ms, $p < 0.0218$; Periodic – Gaussian 75 = -41.1 ms, $p < 0.0001$; Periodic – Gaussian 100 = -38 ms, $p < 0.0001$; Periodic – Gaussian 150 = -21.5 ms, $p < 0.0218$). RTs in Gaussian 25 ms and Gaussian 50 ms were also significantly different from the Gaussian 75 ms and Gaussian 100 ms conditions (Gaussian 25 – Gaussian 75 = -43.3 ms, $p < 0.0001$; Gaussian 25 – Gaussian 100 = -40.2 ms, $p < 0.0001$; Gaussian 50 – Gaussian 75 = -21.4 ms, $p < 0.0432$; Gaussian 50 – Gaussian 100 = -18.3 ms, $p < 0.0001$). RTs in the conditions Gaussian 100 and Gaussian 150 were also statistically different (Gaussian 100 – Gaussian 150 = -16.4 ms, $p < 0.0288$). Results on response times with the SOA at 500 ms only also shows differences between low variability contexts (e.g., Periodic, Gaussian 25 ms or 50 ms) and contexts with more variability in the global temporal STD (Fig. 2.3D).

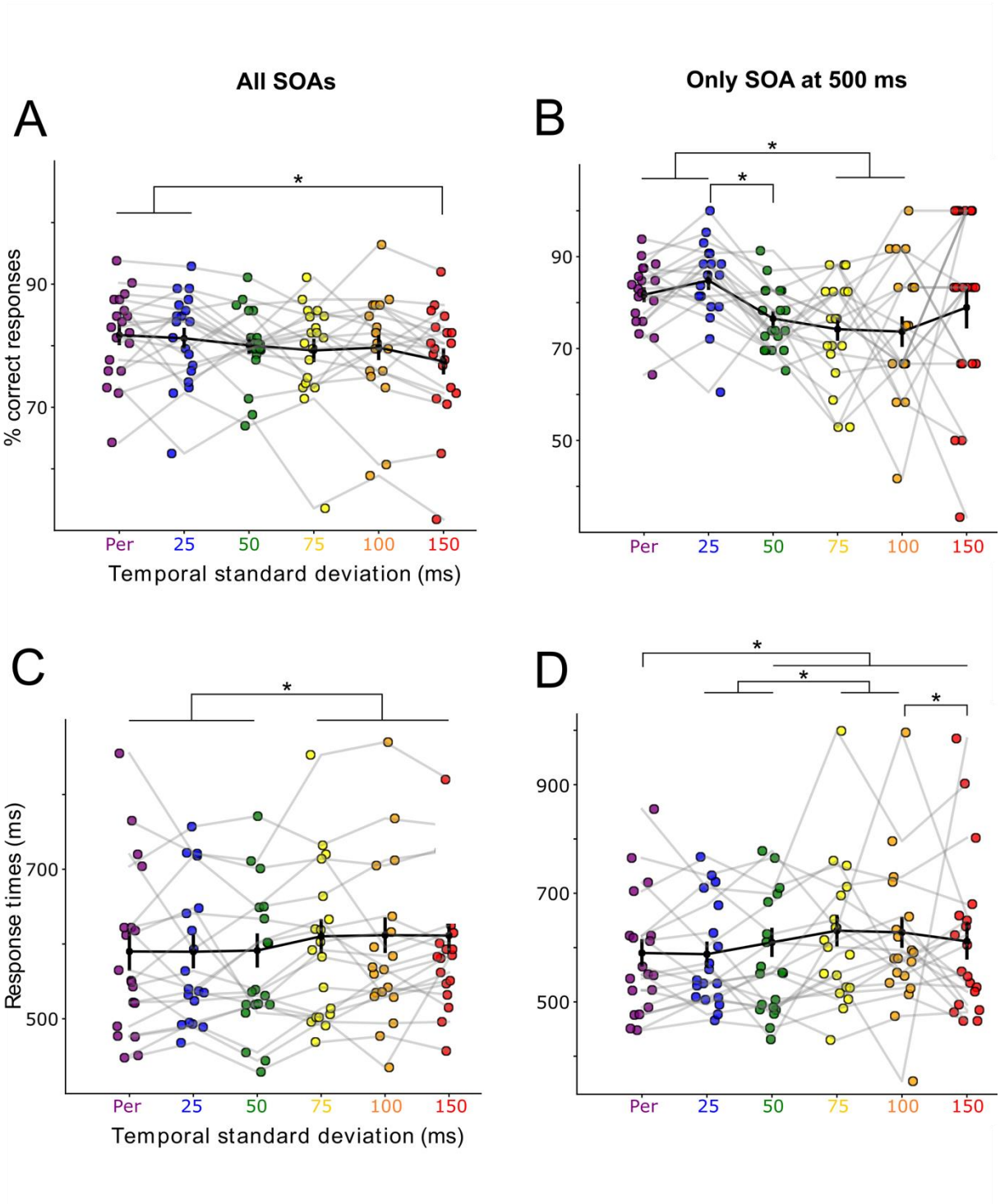


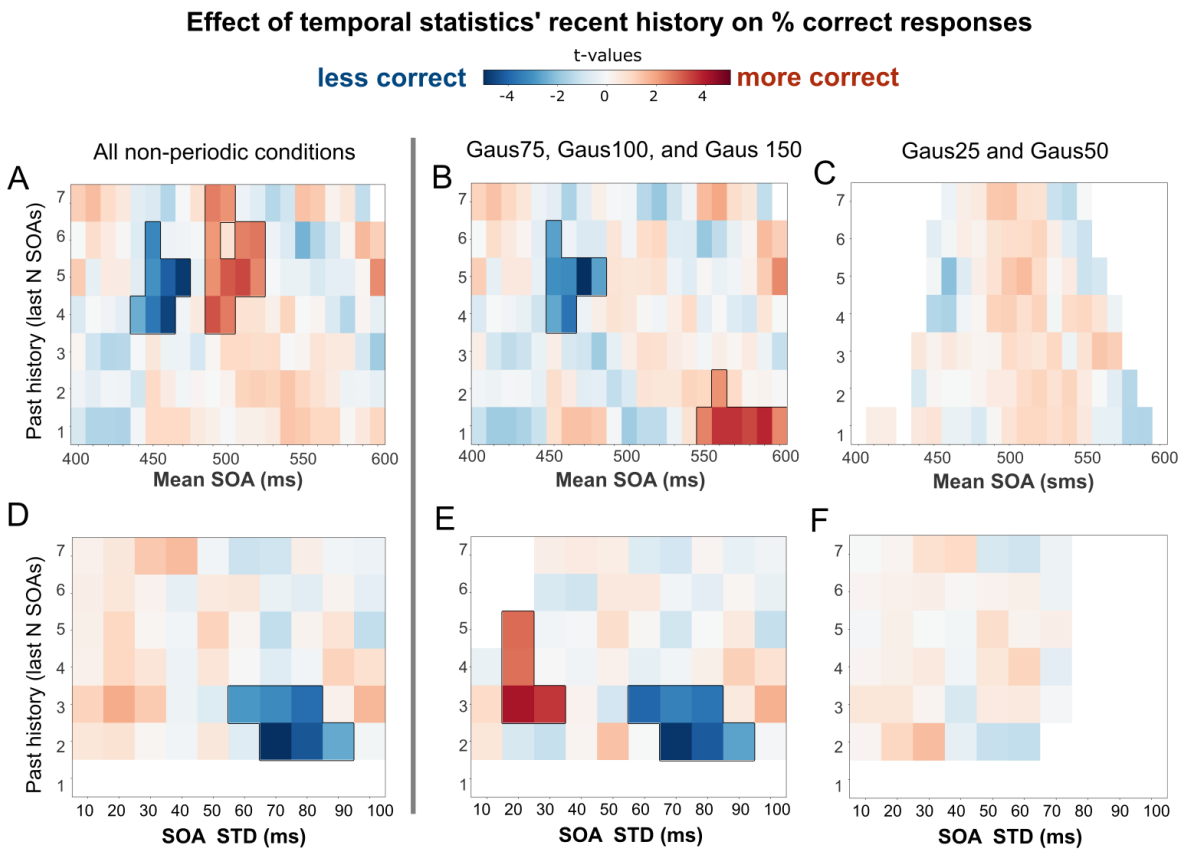
Figure 2.3: Auditory deviant discrimination is influenced by the temporal variability of the sound sequences. (**A**) Percentage of correct responses and (**C**) Response times as function of the standard deviation of SOAs in the auditory sequences. Each color dot represents a participant. Black dots represent the average across participants. Error bars indicate the Standard Error of the Mean (SEM) and stars indicate significant differences ($p < 0.05$). (**B**) Percentage of correct responses and (**D**) Response times restricted to target trials presented at SOA = 500 ms (mean of the distributions).

Statistical temporal predictions occur rapidly

We further investigated the effect of temporal statistics' recent history in auditory discrimination performances. Specifically, we computed, across all targets in non-periodic sound sequences, the mean and the STD of the distribution of the N-previous SOAs before a target trial (with N ranging from 1 to 7 SOAs for the mean SOA, and N ranging from 2 to 7 SOAs before target trial for the SOA STD), and we asked how the temporal statistics of the N previous SOAs impacted the perception of the target trial. When data in all non-periodic sound sequences were aggregated, auditory discrimination performance was significantly influenced by the mean SOA of N-previous sounds: discrimination accuracy was significantly relatively better when the mean of the last N SOAs was around 500 ms and was significantly worse when the mean of the last N SOAs was around 450 ms (Fig. 2.4A). Moreover, there was a significant effect of preceding local STD on accuracy, performance was relatively worse when the STD of the last SOAs was high (relative decrease in performance most prominently observed for STD around 60-90 ms) (Fig. 2.4D). Response times were not significantly affected by the mean SOA of local context (though the direction of the effect is consistent with the working hypothesis, with a relatively shorter RT when the mean of the last SOAs was around 500 ms) (Fig. 2.4G). Furthermore, when the STD of the last SOAs was low, responses times were significantly faster, and when the local STD was wider response times were significantly slower (Fig. 2.4J).

Data were pooled across all non-periodic sound sequences to maximize the number of trials per bin. Yet, by the way auditory sequences were designed, more target trials in the less temporally variable auditory sequences (e.g. Gauss25 and Gaus50 conditions) had a low STD of the N-previous SOAs, compared to the more variable sound sequences. To limit the effect of global context, we performed the same analyses by dividing the data into two groups: low-temporal variability (Gaus25 and Gaus50) and high-temporal variability (Gaus75, Gaus100, and Gaus150). Grouping the sequences into 2 groups allowed us to have a minimum of trials for each bin of interest. Pooling the data across the more temporally variable conditions (Gaus75, Gaus100 and Gaus150 conditions), performances followed similar observed patterns as across all non-periodic sound sequences: both local SOA mean and STD significantly influenced the discrimination accuracy. Discrimination accuracy was significantly relatively better when the last SOA (past history of N = 1) was longer. Accuracy was significantly lower when the SOA mean of the previous SOAs was lower than the expected mean 500 ms SOA (Fig. 2.4B). Moreover, accuracy was significantly higher when the STD of the previous SOAs was low and was significantly lower for larger STDs (Fig. 2.4E). No significant clusters were found on responses times (Fig. 2.4HK).

For the less variable conditions (Gaus25 and Gaus50 conditions), no significant effects of the mean SOA were observed, though the effects were in the expected direction: accuracy was higher, and RTs were faster when the mean SOA was around the expected 500 ms (Fig. 2.4CI). We observed no conclusive pattern of local STD on accuracy (Fig. 2.4F). However, contrary to our expectations, response times were relatively slower when local temporal variability was low and faster when the local temporal variability was high (Fig. 2.4L). Considering that the analysis compares the relative change in performance per participant as function of local SOA mean and STD, it is possible that the relative change in performance is less important in the low-variable conditions than for the more variable conditions.


Effect of temporal statistics' recent history on % correct responses
t-values
less correct
more correct
-4 -2 0 2 4
All non-periodic conditions
Gaus75, Gaus100, and Gaus 150
Gaus25 and Gaus50
A
B
C
D
E
F
Past history (last N SOAs)
Mean SOA (ms)
Mean SOA (sms)
SOA STD (ms)
400 450 500 550 600
10 20 30 40 50 60 70 80 90 100
1 2 3 4 5 6 7

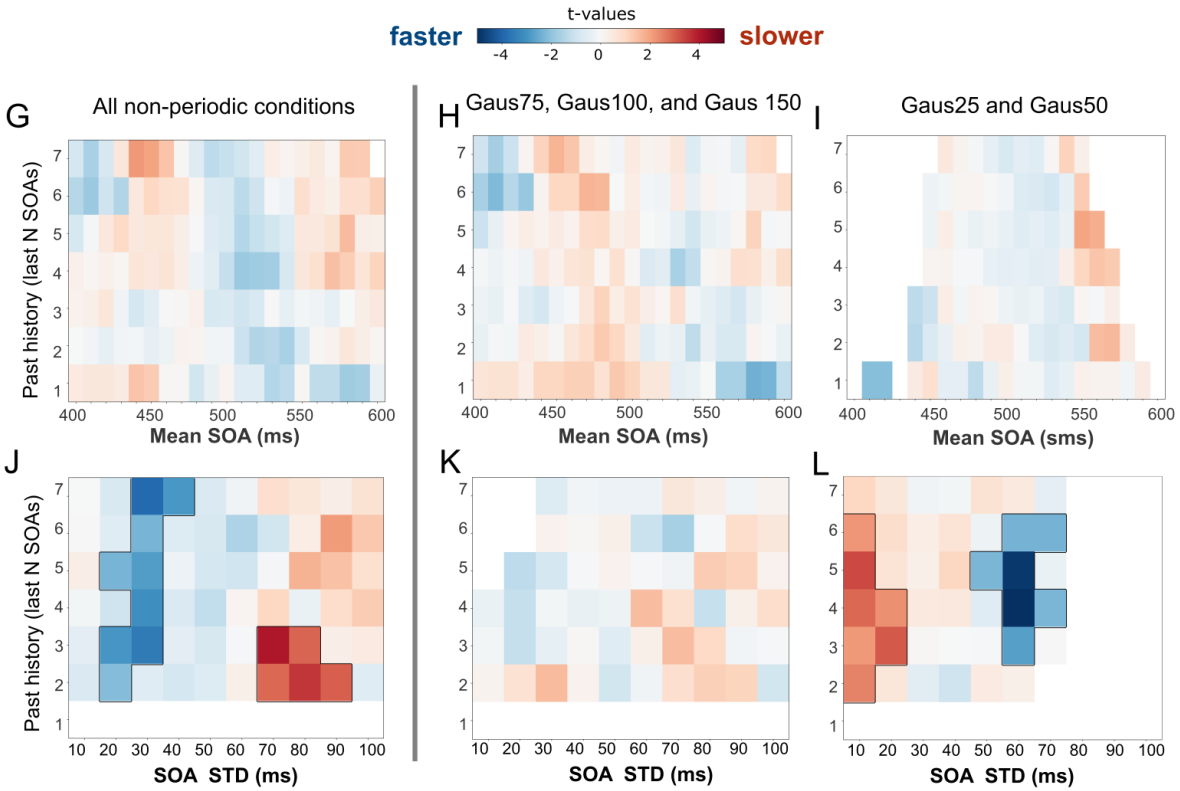

Effect of temporal statistics' recent history on response times
t-values
faster
slower
-4 -2 0 2 4
All non-periodic conditions
Gaus75, Gaus100, and Gaus 150
Gaus25 and Gaus50
G
H
I
J
K
L
Past history (last N SOAs)
Mean SOA (ms)
Mean SOA (sms)
SOA STD (ms)
400 450 500 550 600
10 20 30 40 50 60 70 80 90 100
1 2 3 4 5 6 7

Figure 2.4: Effect of local temporal SOAs' statistics on perception. The figures illustrate whether the relative performance of participants was affected by the mean and STD of the previous N SOAs. Specifically, we computed the mean and STD of the local SOA distribution drawn from the N previous SOAs before each target trial (with N ranging from 1 to 7 SOAs before target trial for mean SOA, and from 2 to 7 SOAs before target trial for SOA STD). We then binned target trials per SOA distribution mean (from 400 to 600 ms SOA mean, with a sliding window of ±20 ms length) and per SOA distribution STD (from 10 ms to 100 SOA STD, with a sliding window of ±10 ms length). Bins containing less than 5 trials per participant were excluded from further analysis. For each bin, the average accuracy and response time across trials was computed, and then z-scored across participants. The obtained 2-D plots represent whether accuracy and response times were relatively higher or lower depending on the mean and STD of the 2/3/4/… last SOAs. Data were aggregated for either (**A, D, G, J**) all non-periodic contexts, (**B, E, H, K)** the more variable temporal sequences (Gaus75 and higher), and (**C, F, I, L)** the less variable temporal sequences (Gaus25 and Gaus50 conditions). The color label represents the one sample t-test value against zero for each sample. Black lines denote significant clusters (transparency is applied to non-significant areas). Due to the low variability in conditions Gaus25 and Gaus50 some bins are left white (empty) because the number of trials was not sufficient to be representative (<5).

To further evaluate the relative contribution of global and local temporal STD on performances, we ran GLMMs that included both global STD and the local STD (from the N previous SOAs, N rating between 2 to 7), and the last SOA as predictors of subject's response and response times. The models revealed an interplay between local and global STD effects. The local STD of the N previous SOAs did not have a significant influence on correct responses when N = 2, while the global STD significantly biased perception. However, for N previous SOAs between 3 and 4 items, we observed that the local STD significantly influenced the subject's response, while the influence of the global context relatively diminished (Fig. 2.5, Supp. Table S1). Similar patterns were observed for response times (Supp. Table S1). This suggests that the local STD could influence performances, and that the observed effect of global STD could partially be explained by the local influence of previous few SOAs.

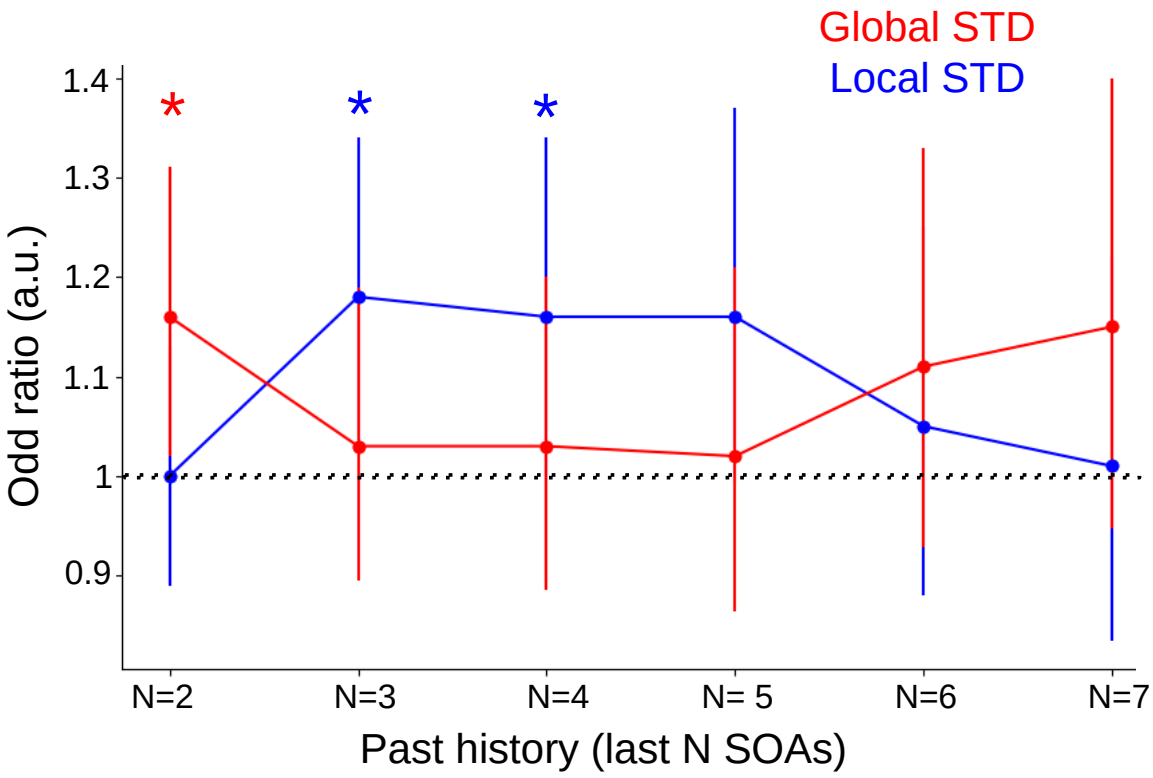


Figure 2.5: Interplay between local and global temporal SOAs' STD on perception. We ran GLMMs that included both global STD and the local STD (from the N previous SOAs, N rating between 2 to 7) as predictors of subject's response. The red line denotes the odds ratios of the global STD effect, the blue line denotes the odds ratio of the local STD effect, when local effects are computed with the N previous SOAs, N ranging from 2 to 7. An odds ratio superior to 1 means that participants were more correct for low STD trials than for high STD trials. Bars denote 95% confidence intervals, if the confidence interval is above 1 then the observed STD effects had a significant influence on the subject's response. The models revealed an interplay between local and global STD effects. The local STD of the N previous SOAs did not have a significant influence on correct responses when N = 2 or N > = 5, while the global STD significantly biased perception. However, for N previous SOAs between 3 and 4 items, we observed that the local STD significantly influenced the subject's response, while the influence of the global

Altogether, these results suggest that participants integrated the temporal statistics of the global sound sequences. Furthermore, it suggests that the temporal predictions effects at hand were not related to hazard rate. We also investigated whether recent temporal variability affected performances. Both accuracy and response times were affected by local temporal variability: accuracy was significantly improved, and response times were faster when the local temporal variability was low; conversely accuracy was lower and response times are significantly slower when the local temporal context was highly variable. These findings suggest that temporal expectations form quickly, within a few numbers of sounds in the sequence.

Link between subjective perception of rhythm and auditory discrimination performance. We also asked participants to subjectively rate their perception of the rhythmicity of each sound sequence. After each sequence, participants rated from 0 (totally arrhythmic) to 10 (totally periodic) the rhythmicity of the sequence of sounds. Participants rated low-variability sequences as more rhythmic: rhythmicity rating was negatively correlated with the temporal variability of context (main effect of the factor Global STD on Rhythmicity Rating as dependent variable: ($\chi 2(1) = 43.364$; $p < 0.0001$)) (Fig. 2.6A). Global STD and Subjective rating being highly correlated, Rhythmicity Rating also correlated with the participant's discrimination accuracy (main effect of Rhythmicity Rating on subjects' responses: ($\chi 2(1) = 14.84$; $p = 0.0001$)) (Fig. 2.6B). Yet, inter-subject variability in rating was observed, with some participants rating non-periodic sequences as more rhythmic than periodic sequences (Fig. 2.6C). We therefore investigated whether rhythmicity rating could be a predictor of participants performances, specifically whether adding the Rhythmicity Rating as factor with the model fit would explain away more variance in auditory discrimination performance. However, this was not the case: comparing statistical models with the likelihood ratio test, adding the Rhythmicity Rating as a fixed effect in the model did not significantly improve the data fitting for the percentage of correct responses ($\chi 2(1) = 3.24$; $p = 0.072$) nor the response times ($\chi 2(1) = 0.3054$; $p = 0.624$).

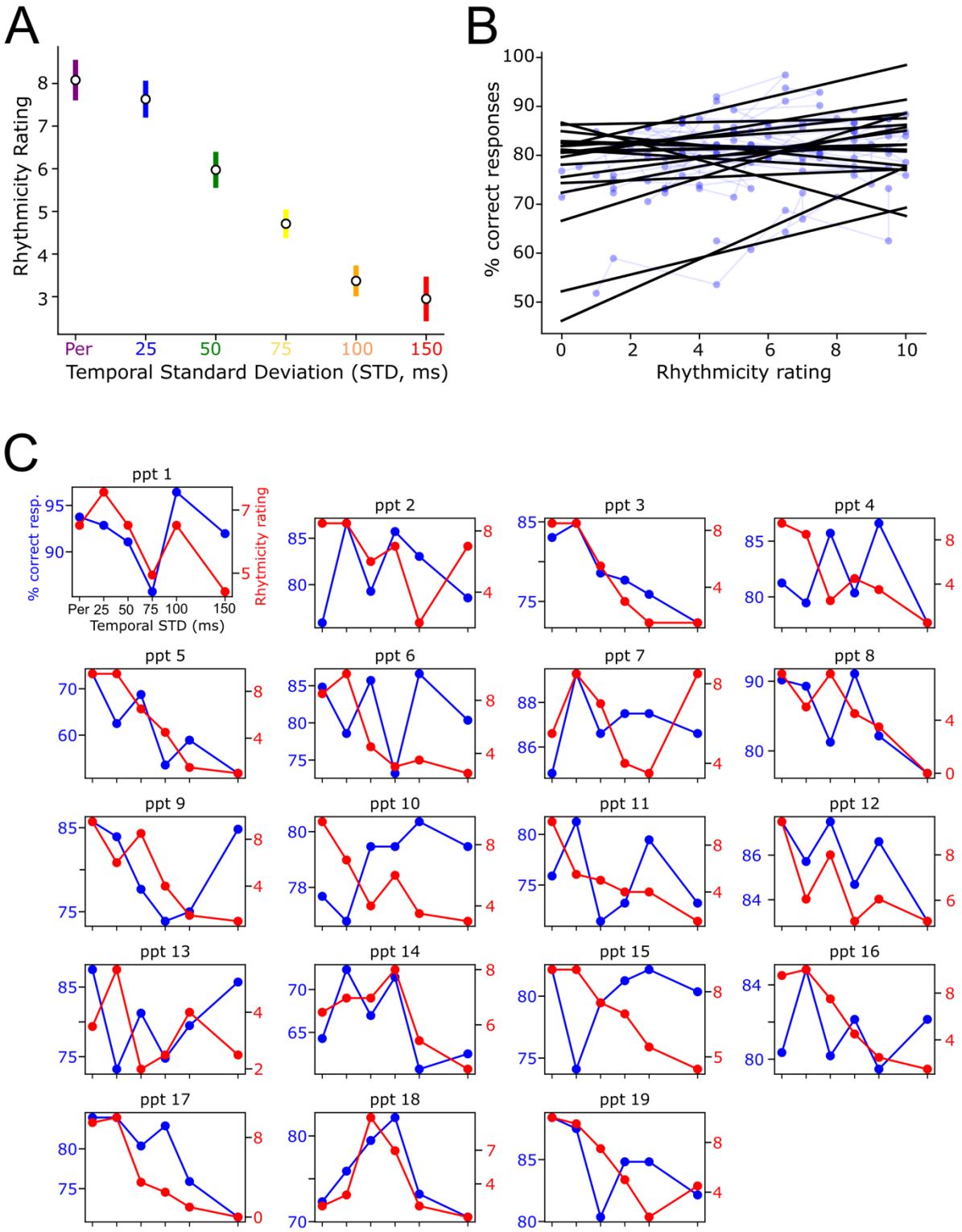


Figure 2.6: Link between subjective perception of rhythmicity and auditory performances. (A) Means of participant's ratings of the degree of rhythmicity present in the temporal contexts. (B) Positive correlation between the rating and the percentage of correct responses. Each point and the corresponding regression line represent a single participant. (C) Individual correlations between percentage of correct responses and rhythmicity ratings. Each figure represents a participant's data. Blue lines denote the percentage of correct response as a function of temporal standard deviation of sound sequences. Red lines denote the subjective rating of rhythmicity of each sound sequence.

DISCUSSION

The aim of this study was to investigate the impact of temporal prediction mechanisms on auditory perception in probabilistic temporal contexts. For this, participants were asked to discriminate deviant sounds in auditory sequences, whose SOAs between consecutive sounds were drawn from distinct gaussian distributions. All distributions had the same average SOA (500 ms) but different STDs (from 0 ms up to 150 ms). Auditory perception was influenced by the probabilistic temporal regularities of the sound sequences. Deviant discrimination accuracy was highest and response times were fastest when the deviant sounds were presented in periodic sequences as compared to non-periodic sequences, in line with previous findings (Morillon et al., 2016). However crucially, temporal context also influenced auditory discrimination in the non-periodic sound sequences. Deviant discrimination performances slowly decreased when the temporal variability of the auditory sequences increased. Auditory deviant perception was optimal at the average of the SOA distribution of the sequences, suggesting that both influenced by the mean SOA of sequences and by the temporal variability of the last sounds prior to target.

Probabilistic timing influences auditory perception

This study emphasizes that the temporal variability of the context impacts auditory performance. These findings are in line with the literature that shows that auditory perceptual sensitivity is enhanced when stimuli are presented within periodic streams of sensory events (Rimmele et al., 2011; Henry & Obleser, 2012; Cravo et al., 2013; Ten Oever et al., 2014; Morillon et al., 2016; Ten Oever et al., 2017) or when the temporal context is deterministic (Cope et al., 2012; Morillon et al., 2016; Breska & Deouell, 2017). Our findings further suggest that auditory perception relies on probabilistic inference of events timing. Target discrimination accuracy slowly degraded with increasing temporal variability of sound sequences. Response times showed a plateau effect, where a similar increase in response times duration was observed for the more variable contexts from 75 ms STD as compared to contexts with SOA variability below 75 ms STD. When data were restricted to targets presented at the mean SOA of the distribution, we observed that discrimination performances (both in terms of accuracy and RTs) were relatively better for periodic and for low-temporally variable sound sequences as compared to more temporally variable sequences (of standard deviation above 50 ms/75 ms, i.e. 10-15% of the mean SOA of the distribution). The persistence of contextual effects when restricting analyses to targets presented at the same SOA (500 ms) shows that the effect of

temporal context on auditory perception cannot be explained by the sole influence of the last SOA between the target and the preceding sound. In particular, these results cannot be influenced by hazard rate effects (i.e. relatively better performances when targets stimuli occur later than expected, and poorer performances when the target stimuli arrive before than expected (Luce, 1986; Nobre & Van Ede, 2018). Furthermore, these results also rule out the hypothesis that participants only assume a 500-ms SOA, and are surprised when it is not met. If our contextual effects only relied on the assumption of a 500-ms SOA, we would observe similar performances for all targets with a preceding 500ms SOA. However, we do see that the discrimination performance of these targets decreased when the global temporal context was more temporally variable. We argue that these observations result from probabilistic temporal predictions mechanisms, i.e. that the participant forms an internal model of the distribution of SOAs. Specifically, temporally predictable contexts would give an advantage in target auditory discrimination versus no advantage for no predictable contexts: in a low temporal variability context, participants can leverage temporal predictions to anticipate stimulus arrival, thereby enhancing auditory perception. However, in temporally variable contexts, there is no reliable temporal cues in order to predict the timing of the target sound, therefore temporal predictability cannot benefit auditory discrimination. This suggests that perception is not only influenced by the probabilistic inference of the mean SOA between sounds, but also by the amount of temporal variability of the context.

The effects of probabilistic timing of sensory context have previously been observed on response times (Cannon, 2021; Herbst & Obleser, 2017; Herbst & Obleser, 2019; Grabenhorst et al, 2019; Grabenhorst et al., 2021). In these studies, participants either performed auditory discrimination tasks (Herbst & Obleser, 2017; Herbst & Obleser, 2019), tapping (Cannon, 2021), or "set-go" tasks (Grabenhorst et al., 2019, 2021). The temporal distribution of the foreperiod before the target stimuli influenced response times in both tasks. Importantly, like in this current study, temporal expectancy mechanisms were not uniquely driven by the hazard rate of events, but were also sensitive to the probability of events timing so that response times were fastest when events occur around the mean of contextual temporal probability distribution. Our results further show that not only response times, but also auditory perceptual sensibility is influenced by the temporal probabilities of contextual information. They also highlight that the time required to implement temporal predictions mechanisms based on contextual temporal probabilities is relatively short (temporal statistics from the previous 3 SOAs can already bias

target perception and response times) and depends on the degree of confidence in the temporal regularities of the context.

Knowing that the perception of rhythmic cues in auditory signals is variable across individuals (Potter et al., 2009, Obleser et al., 2017) and could depend on several factors, such as the participant's musical expertise (Geiser et al., 2009), we examined whether participants accurately perceived the amount of temporal variability in the sound sequences, and whether this impacted their performances. Participants accurately assessed the amount of temporal regularity in the sound sequences, as their subjective rating of temporal regularity slowly decreased with increased temporal STD of the context. Interestingly, individual variability in the ratings were observed, so that certain participants rated more variable temporal contexts as more rhythmic. However, subjective variations in the perception of rhythmic cues did not significantly add explanatory power to the auditory performances.

Putative neural mechanisms behind probabilistic temporal predictions

The present findings have implications for current theories and frameworks linking low-frequency neural oscillations to temporal prediction mechanisms in auditory perception. The neural entrainment theory postulates that external rhythms can entrain endogenous neural oscillations, which reflect periodic fluctuations in excitability of neuronal populations (Jones & Boltz, 1989; Large & Jones, 1999; Schroeder & Lakatos, 2009; Cravo et al., 2013). According to this view, neural excitability fluctuations temporally align to the periodic external stream so that the period of high neural excitability coincides with the beat of the external stimuli. A direct prediction of the neural entrainment theory is that perception should be optimal when stimuli are periodic enough to entrain neural oscillations, and when target sensory events occur on beat with the entrained neural oscillation. Here, we do actually report that temporal prediction mechanisms do not only account for purely periodic stimuli but are also robust to a certain amount of temporal variability. Specifically, we found that temporal predictions benefit auditory perception until the variability of temporal context reaches a STD threshold of 10-15% of the mean SOA of the distribution. It is possible that the neural entrainment theory, tested in periodic contexts, could generalize to more complex temporal predictions observed in hierarchically structured rhythms (e.g., speech or music). Importantly, this would explain why temporal properties of speech signals, which are not periodic (Nolan & Jeon, 2014) but are still based on probabilities of occurrence, influence the perceived duration of speech segments and neural dynamics in auditory cortices (Kösem et al., 2018). Interestingly, a recent computational

model reports that neural oscillators can handle a certain degree of temporal variability: Stuart–Landau neural oscillatory models are still able to synchronize to temporally variable stimuli, with SOAs drawn from Gaussian distributions with standard deviations going up to 20% of the mean SOA (Doelling & Assaneo, 2021). Empirically, neural entrainment is observable for stimuli that are not fully isochronous (Calderone, 2014; Lakatos et al., 2008; Herrmann et al., 2016; Kösem et al., 2018). Yet, it is still unclear what exact degree of temporal variability entrainment mechanisms can handle. Interestingly, local variations of sounds sequences' timing can affect neural entrainment to the delta range (Herrmann et al., 2016): entrained delta oscillations to a temporally variable sound sequences were shown to fluctuate in amplitude over the course of the sequence. Importantly, the phase of entrained delta oscillations was indicative of sound deviant discrimination, but only when the delta entrainment was strong. It is possible that, in this experiment, epochs with high delta oscillatory activity were corresponding to periods where the sound sequences were sufficiently temporal regular and predictable so that entrainment could occur, while epochs with low delta activity were reflecting failure of neural oscillatory activity to entrain to more temporally variable contexts (Herrmann et al., 2016).

Alternatively, the temporal predictions mechanisms observed in periodic and probabilistic contexts could rely on low-frequency dynamics, but would not obviously reflect neural entrainment per se. Evidence for this hypothesis is that low-frequency neural dynamics are shown to reflect temporal predictions in non-entrained sensory context, e.g. when temporal predictions rely on memory-based patterns (Wilsch et al., 2015; Daume et al., 2021; Herbst, Stefanics, et al., 2022; Breska & Deouell, 2017). However, it is possible that memory-based predictions and temporal contextual predictions may rely on different co-existing neural mechanisms (Bouwer et al., 2020; Bouwer et al., 2022). The results of this study also support the view that predictive probabilistic timing is more than hazard rate, and that it also relies on the probability density function of the timing of previous sensory events. As such, the mechanisms related to hazard rate and contextual temporal predictions could be dissociated and have different mechanistic origins. While hazard rate processing seems to rely on motor regions (Herbst et al., 2018; Cui et al., 2009), contextual probabilistic timing may involve a different distributed neural architecture, including early sensory areas (Bueti et al., 2010; Herbst et al., 2018).

In our study, we presented visual cues in synchrony with the auditory sounds. The visual cue was indicating the target sound, so as to make sure that the response of the participant was

referring to the target, and not to any other sound from the sequence. A limitation from this manipulation is that visual timing could potentially have affected the temporal precision of the observed auditory effects, considering that the visual event timing can interact with the perception of auditory event timing (Di Luca & Rhodes, 2016), and that event timing of visual events are usually judged with less precision than auditory events (Di Luca & Rhodes, 2016; Zalta et al., 2020), though audition is known to dominate the temporal judgments of audiovisual stimuli (Wilsch et al. 2020), e.g. during rhythmic stimulation where perceived audiovisual rates are usually shifted towards the auditory rate (Wada et al., 2003; Welch et al., 1986). Visual timing also interacts with neural entrainment mechanisms, so that visual stimuli can modulate the phase of entrainment of auditory cortices (Lakatos et al., 2008; Kösem et al., 2014). We cannot fully conclude whether the observed temporal predictions mechanisms rely on unimodal or crossmodal mechanisms. However, the present results provide evidence that temporal predictive mechanisms influence auditory perception in implicit probabilistic temporal contexts, and that they are robust to some amount temporal variability.

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SUPPLEMENTARY MATERIAL

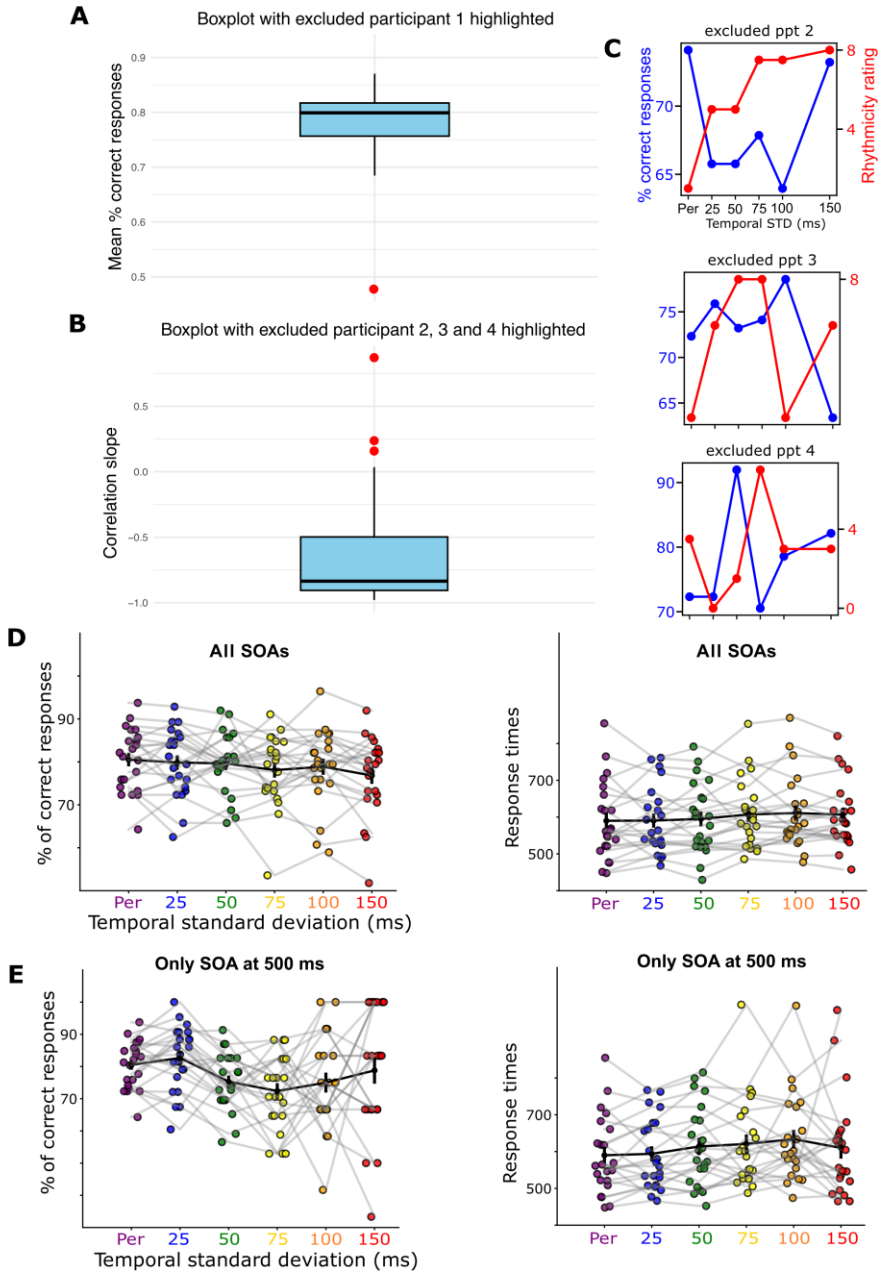

Figure 2.S1: Data exclusion criteria. Four participants had outlier data and were excluded from data analysis. (A) one participant responded at chance level throughout the experiment (highlighted in red) (B) three participants had outlier subjective rhythmicity ratings of the sequences (±1.5 interquartile range of regression scores, highlighted in red). (C) Response and rhythmicity rating of the three excluded participants from (B). (D-E) Including the three participants from (B) does not influence the main patterns of results. (D) We still observe a main effect of the global Temporal STD on the correct responses ($\chi2(1) = 12.17$, $p = 0.00048$) and on response times ($\chi2(1) = 17.909$, $p < 0.0001$). (E) When we restrict the analysis to targets presented at 500 ms SOAs, we also have a main effect of global Temporal STD on the correct responses ($\chi2(1) = 14.49$, $p = 0.00014$) and on response times ($\chi2(1) = 26.468$, $p < 0.0001$).

Model: Dependent variable ~ GlobalSTD + LastSOA + LocalSTD + (1+ GlobalSTD | Subject)

Local STD from N previous SOAs

N = 2

	Dep. Var.: subject's responses				**Dep. Var.: response times**			
Groups	Name	Variance	SD	Corr	Name	Variance	SD	Corr
Subj	(Intercept)	0.1285	0.3585		(Intercept)	0.00183	0.04278	
	global STD	1.2459	1.1162	0.48	Global STD	0.04278	0.21018	-0.39
Residual						0.09853	0.31390	
Fixed effects:								
	Estimate	**SE**	**Z value**	**Pr(>|z|)**	**Estimate**	**SE**	**t value**	**Pr(>|t|)**
Intercept	1.15013	0.15962	7.205	**< 0 .001**	0.61127	0.02786	21.938	**< 0.001**
Global STD	-1.46183	0.63695	-2.295	**0.02173**	0.19790	0.09112	2.172	**0.0299**
Last SOA	0.75670	0.25905	2.921	**0.00349**	-0.03023	0.01765	-1.713	**0.0868**
Local STD	-0.02454	0.60973	-0.040	0.96790	-0.02721	0.04182	-0.651	0.5153

N = 3

Groups	Name	Variance	SD	Corr	Name	Variance	SD	Corr
Subj	(Intercept)	0.1285	0.3584		(Intercept)	0.001828	0.04276	
	Global STD	1.2599	1.1224	0.48	Global STD	0.044112	0.21003	-0.39
Residual						0.098496	0.31384	
Fixed effects:								
	Estimate	**SE**	**Z value**	**Pr(>|z|)**	**Estimate**	**SE**	**t value**	**Pr(>|t|)**
Intercept	1.1712	0.1582	7.401	**< 0 .001**	0.61008	0.02789	21.876	**< 0.001**
Global STD	-0.3017	0.7222	-0.418	0.67615	0.10619	0.09370	1.133	0.2571
Last SOA	0.7147	0.2556	2.796	**0.00518**	-0.02779	0.01783	-1.558	0.1192
Local_STD	-1.6233	0.6676	-2.431	**0.01504**	0.10590	0.04669	2.268	**0.0233**

N = 4

Groups	Name	Variance	SD	Corr	Name	Variance	SD	Corr
Subj	(Intercept)	0.1285	0.3585		(Intercept)	0.001829	0.04277	
	Global STD	1.2569	1.1211	0.48	Global STD	0.044133	0.21008	-0.39
Residual						0.098534	0.31390	
Fixed effects:								
	Estimate	**SE**	**Z value**	**Pr(>|z|)**	**Estimate**	**SE**	**t value**	**Pr(>|t|)**
Intercept	1.1635	0.1584	7.347	**< 0 .001**	0.61070	0.02787	21.909	**< 0.001**
Global STD	-0.3167	0.7827	-0.405	0.68574	0.14078	0.09642	1.460	0.144
Last SOA	0.7336	0.2559	2.867	**0.00414**	-0.02911	0.01773	-1.642	0.101
Local STD	-1.4981	0.7434	-2.015	**0.04387**	0.05331	0.05210	1.023	0.306

N = 5								
Groups	Name	Variance	SD	Corr	Name	Variance	SD	Corr
Subj	(Intercept)	0.1285	0.3585		(Intercept)	0.001829	0.04276	
	Global STD	1.2559	1.1206	0.48	Global STD	0.044066	0.20992	-0.39
Residual						0.098528	0.31389	
Fixed effects:								
	Estimate	**SE**	**Z value**	**Pr(>|z|)**	**Estimate**	**SE**	**t value**	**Pr(>|t|)**
Intercept	1.1714	0.1587	7.380	**< 0 .001**	0.60997	0.02788	21.876	**< 0.001**
Global STD	-0.2257	0.8598	-0.262	0.79294	0.10573	0.09941	1.064	0.288
Last SOA	0.7175	0.2567	2.795	**0.00519**	-0.02765	0.01780	-1.553	0.120
Local STD	-1.5221	0.8197	-1.857	0.06333	0.09259	0.05737	1.614	0.107
N = 6								
Groups	Name	Variance	SD	Corr	Name	Variance	SD	Corr
Subj	(Intercept)	0.1285	0.3585		(Intercept)	0.001829	0.04276	
	Global STD	1.2478	1.1171	0.48	Global STD	0.044017	0.20980	-0.39
Residual						0.098540	0.31391	
Fixed effects:								
	Estimate	**SE**	**Z value**	**Pr(>|z|)**	**Estimate**	**SE**	**t value**	**Pr(>|t|)**
Intercept	1.1553	0.1592	7.255	**< 0 .001**	0.61020	0.02788	21.885	**< 0.001**
Global STD	-1.0614	0.9234	-1.149	0.25039	0.09016	0.10255	0.879	0.3793
Last SOA	0.7475	0.2579	2.898	**0.00375**	-0.02811	0.01780	-1.580	0.1142
Local STD	-0.4897	0.8996	-0.544	0.58616	0.10752	0.06287	1.710	0.0872
N = 7								
Groups	Name	Variance	SD	Corr	Name	Variance	SD	Corr
Subj	(Intercept)	0.1285	0.3585		(Intercept)	0.001829	0.04277	
	Temporal STD	1.2460	1.1162	0.48	Temporal STD	0.044062	0.20991	-0.39
Residual						0.098546	0.31392	
Fixed effects:								
	Estimate	**SE**	**Z value**	**Pr(>|z|)**	**Estimate**	**SE**	**t value**	**Pr(>|t|)**
Intercept	1.1505	0.1595	7.214	**< 0 .001**	0.61024	0.02788	21.888	**< 0.001**
Global STD	-1.4124	0.9912	-1.425	0.15418	0.09790	0.10643	0.920	0.358
Last SOA	0.7561	0.2586	2.924	**0.00345**	-0.02807	0.01778	-1.579	0.114
Local STD	-0.0722	0.9585	-0.075	0.93996	0.09454	0.06823	1.386	0.166

SD; standard deviation; SE, standarderror; Corr, correlation

Table 2.S1: Models summaries of local statistics vs global statistics influences on subject's responses and subject's response times

Chapter 3:

THE EEG MARKERS OF TEMPORAL PREDICTIONS IN PROBABILISTIC CONTEXTS

3.1 Introduction

3.1.1 Motivation

The Chapter 2 has explored the benefits of temporal predictions on auditory perception in probabilistic contexts and has highlighted that temporal predictions mechanisms are robust to certain amount of temporal variability. Chapter 3 further explores the putative neural mechanisms underlying temporal predictions in probabilistic contexts.

Neural entrainment theory suggests that brain oscillations can align with the onset of expected events so that when a new sensory event occurs, if it arrive on the previous beat, his perception will be optimal (Schroeder & Lakatos, 2009). The significance of neural oscillations in temporal prediction has been demonstrated in experimental paradigms where the onset of sensory events were temporally predictable because the stimulation was either periodic, or target onsets were cued in time (e.g., Breska & Deouell, 2017; Herbst, Stefanics, et al., 2022; Stefanics et al., 2010). However, as we discussed in Chapter 2, temporal predictions can also occur in probabilistic sensory contexts. In this chapter, we reproduced the experimental paradigm of Chapter 2 in an EEG experiment where we could compare the neural markers of temporal prediction in probabilistic contexts with different levels of temporal regularities.

3.1.2 Experiment

To achieve this objective, we used the same paradigm explained in Chapter 2, retaining only four different temporal contexts to maximize the number of trials in each condition. We included a periodic condition, a condition with low variability in the context (i.e., gaussian 25 ms, where we demonstrated in Chapter 2 that temporal predictability benefits were similar to periodic sequences). We also included more variable probabilistic contexts (i.e., gaussian 150 ms) and we designed a new condition where the SOA in the sequences were draw from a uniform distribution between 100 and 900 ms. We were motivated to design this new sequence because we wanted to maximize temporal variability as much as possible within the physical constraints of our paradigm.

If neural oscillations are relevant for temporal predictions mechanisms in more naturalistic contexts, we should expect that neural oscillatory activity would be preserved for temporally predictable sound sequences, even in the presence of temporal variability. Moreover, the strength of brain oscillatory tracking to the expected rhythm should indicate how temporally predictable a sound is, and thereby impacting its perception.

3.1.3 Summary of the results

Behavioral results support the previous findings presented in Chapter 2, indicating better performances in terms of both auditory discrimination and response times for the more temporally regular sequences. The temporal context also influenced the evoked responses to the target sounds: targets presented in more regular sound sequences showed increased ramping activity post-target onset, higher N2-P2 amplitude and more pronounced P300 amplitude. Moreover, 2Hz brain oscillatory dynamics varied with the level of temporal predictability of the sound sequences with higher power at 2Hz in more regular conditions. Importantly, we observe variations of 2Hz-power within the sound sequences. Periods of high 2Hz power were associated with faster discrimination of sound deviants, suggesting a link between brain oscillatory dynamics and behavior. Altogether, these results suggest that temporal variability of the sensory context affects both the synchronization between brain and auditory rhythms and the response to individual sounds of the sequences, ultimately influencing auditory perception.

3.2 Article

The neural mechanisms of temporal prediction in probabilistic sensory contexts (in preparation)

The neural mechanisms of temporal prediction in probabilistic sensory contexts

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ABSTRACT

Current theories link observed neural oscillatory dynamics to temporal predictions mechanisms. These theories propose that neural oscillations indicate cyclic fluctuations in excitability that align with the onset of expected events in time. Such alignment occurs in the presence of periodic auditory streams and when the temporal intervals between sounds are fully predictable. This phenomenon is associated with enhanced sound discrimination when the targets are presented at the expected timing. However, in more naturalistic environments as speech or music, while being temporarily regular, sensory events may also occur with a certain amount of temporal variability. If neural oscillations are relevant for temporal predictions mechanisms in more naturalistic contexts, we should expect that neural oscillatory activity would be preserved for temporally predictable sound sequences even in the presence of temporal variability, and that the strength of brain-sound synchronization would indicate how temporally predictable a sound is, and therefore impact its perception. To test this, we ran an EEG experiment where participants were asked to discriminate between standard and deviant sounds that were embedded in 3 min-long sound sequences. The Stimuli Onset Asynchrony (SOA) of the sequences were drawn from distributions with the same mean (500 ms) but distinct distribution profiles: periodic, Gaussian distributions with 25 ms and 150 ms SD, uniform distribution. Behavioral results support previous findings showing better behavioral performances in both auditory discrimination and response times for the more temporally regular sequences. The temporal context also influenced the evoked responses to the target sounds: targets that were presented in more regular sound sequence showed increased ramping activity post-target onset, higher N2-P2 response and more pronounced P300 amplitude. Moreover, 2Hz- brain oscillatory dynamics varied with the level of temporal predictability of

the sound sequences with higher power at 2Hz in more regular conditions. Importantly, we observed variations of 2Hz-power within the sound sequences. Periods of high 2Hz power were associated with faster discrimination of sound deviants, suggesting a link between brain oscillatory dynamics and behavior. Altogether, these results suggest that temporal variability of the sensory context affects both the synchronization between brain and auditory rhythms and the response to individual sounds of the sequences, ultimately influencing auditory perception.

INTRODUCTION

Temporal predictions are thought to play a prominent part in the processing of sensory information (Arnal & Giraud, 2012; Jones, 1976; Nobre et al., 2012; Schroeder & Lakatos, 2009). Predicting when sensory events will occur allows for better allocation of cognitive resources, improving the processing of incoming stimuli (Jones & Boltz, 1989; Large & Jones, 1999; Nobre et al., 1999). Understanding the mechanisms of temporal prediction is thus central for models of cognitive and neural processing. The dynamic attending theory (DAT) suggests that in the presence of temporally expected sensory input, temporal attention would synchronize with the temporally expected stimulus onsets. The resulting attentional temporal sampling mechanisms would help to drive attention toward moments of high stimulus probability (Jones, 1976, 2004; Jones & Boltz, 1989; Large & Jones, 1999). A potential neural implementation of the DAT involves the recruitment of low-frequency neural oscillations (Henry & Herrmann, 2014; Schroeder & Lakatos, 2009). In this view, oscillations reflect the modulation of neural excitability (Lakatos et al., 2005) and can constrain perceptual excitability with periods of high and low excitability, leading to moments of increased probability of detection as well as instances with a higher likelihood of overlooking sensory stimuli (Schroeder & Lakatos, 2009; VanRullen & Koch, 2003).

In line with the DAT, the significance of neural oscillations in temporal prediction has been demonstrated in experimental paradigms where the onset of sensory events can be anticipated using a temporal cue. Notably, it was found that delta oscillations (1- 4 Hz) exhibit an increase in phase concentration and amplitude when the target is cued temporally (Breska & Deouell, 2017; Herbst, Stefanics, et al., 2022; Stefanics et al., 2010). These phase effects were also correlated with evoked potentials such as the contingency-negativity variation (CNV) that is a potential peaking at on-beat times and resolve immediately after (Breska & Deouell, 2014; Praamstra et al., 2006; Walter et al., 1964). This early negative shift is a component present in

tasks involving stimulus timing and can be interpreted as an index of expectancy for an upcoming stimulus (Breska & Deouell, 2014, 2017; Miniussi et al., 1999). Post-stimulus evoked activity is also influenced by temporal expectations. The mismatch negativity (MMN), a component related to the prediction error commonly measured in oddball paradigms with a peak at 150-250ms from change onset (Näätänen et al., 2007), showed higher amplitude when the sound deviant occurred on the expected beat but was weaker when the deviance occurred off-beat (Bouwer et al., 2014). Moreover, the P300 component, a well know ERP (Polich, 2007) dominated by the delta-band component (Bernat et al., 2007; Ergen et al., 2008; Ishii et al., 2009; Schürmann et al., 2001) show greater amplitude when the target events are cued and can be predicted (Miniussi et al., 1999; Stefanics et al., 2010).

The significance of neural oscillations on temporal predictions have also been shown when they synchronize to the rhythmic sensory context. Auditory discrimination performances improve when the target sound sequences are presented on a periodic sequence (Cravo et al., 2013; Jaramillo & Zador, 2010; Lawrance et al., 2014; Morillon et al., 2016; Rimmele et al., 2011). Furthermore, behavioral measures correlate with the synchronization strength between low-frequency neural oscillatory activity and external sensory rhythms (Cravo et al., 2013; Henry et al., 2014; Henry & Obleser, 2012). According to neural entrainment models, endogenous oscillations can be entrained (i.e., through period correction and phase alignment) to an external stream such that optimal phases align with on-beat times of the rhythmic stimuli (Haegens & Zion Golumbic, 2018; Lakatos et al., 2008; Obleser & Kayser, 2019). Neural entrainment mechanisms underlying temporal predictions are thought fundamental because many sensory stimuli are supposedly rhythmic (Obleser et al., 2017; Schroeder & Lakatos, 2009). Nevertheless, these rhythms are far from isochronous or deterministic. This is particularly true for natural sound sequences, such as music and speech. Speech acoustic signals in particular presents complex statistical temporal regularities (Cummins, 2012; Singh & Theunissen, 2003; Varnet et al., 2017) that are postulated used to form temporal expectations and influence language comprehension (Aubanel & Schwartz, 2020; Jadoul et al., 2016; Kösem et al., 2018; Kösem & van Wassenhove, 2017; Tillman, 2012). Therefore, speech processing requires taking into account probabilistic temporal variations in syllable and word durations naturally present in languages (Jadoul et al., 2016; Ten Oever & Martin, 2021; Varnet et al., 2017).

Probabilistic inference regarding sensory timing impacts explicit temporal judgments of auditory events (Cannon, 2021; Doelling & Assaneo, 2021), as evidenced by tapping (Cannon,

2021), warned reaction time tasks (Los et al., 2017), and response times during auditory discrimination tasks (Herbst & Obleser, 2017). Additionally, research indicates that temporal predictions established through probabilistic inference also affect auditory discrimination performance (Bonnet et al., 2024). Yet, it remains uncertain how neural entrainment functions in contexts characterized by temporal variability (Haegens & Zion Golumbic, 2018; Lakatos et al., 2019; Obleser & Kayser, 2019; Zoefel & Kösem, 2024). Previous research has indicated that entrainment may occur in probabilistic contexts (Herrmann et al., 2016). However, this study was limited to auditory sequences with minimal temporal variations. It is important to note that neural entrainment may not occur consistently, as it can be influenced by the degree of temporal variability in the incoming sensory information (Herrmann et al., 2016). Our prior behavioral study demonstrated that the advantages of temporal regularity in auditory discrimination may diminish when the temporal variance of the stimuli onset asynchronies (SOAs) exceeds 10%-15% of the mean SOA (Bonnet et al., 2024).

In this study, we employed EEG to examine neural entrainment to sound sequences with varying degrees of temporal variability, as well as the impact of this entrainment on behavioral responses and the neural response to sounds. If neural oscillations play a significant role in temporal prediction mechanisms in probabilistic settings, we would anticipate that both auditory perception and neural oscillatory activity are affected by the temporal variability of the context and that neural oscillatory entrainment measures correlate with behavior. Additionally, we also expect that the temporal variability of the sound sequences influences evoked responses to target sounds, including the post target-onset ramping activity (related to CNV resolution in response to the expected timing of the target), MMN, and P300 responses.

MATERIALS AND METHODS

Participants. Twenty-nine participants (17 females, mean age 23.39 years, everyone right-handed) took part in the experiment. Participants reported no history of neurological or psychiatric disease, normal hearing and normal or corrected-to-normal vision. The study was approved by an ethical committee (CPP) and all participants signed a written consent and received payment for their participation.

Stimuli. The experimental design was adapted from (Morillon et al., 2016) and (Bonnet et al., 2024). Participants heard sequences of pure tones, that were either a standard sound

(corresponding to a pure 440 Hz sound) or a deviant sound (pure 220 Hz sound). The sounds were presented via headphones for 100 ms (with 5 ms ramp-up and ramp-down in volume). With each sound, visual cues were presented via a digital display (1920, 1080 resolution; 120 Hz refresh rate) and were displayed in front of them (130 cm) in the center of the screen for a duration of 100 ms. Visual cues were synchronized to appear simultaneously with the sounds. A "red circle" visual cue indicated a target, and that the participant had to respond to this trial by pressing a button on a keyboard (the buttons associated with the standard or deviant responses were reversed halfway through subject recruitment to control for possible laterality bias). A "white cross" cue indicated a standard trial of the context and that participants did not have to respond to this trial (Fig. 3.1A). When the “white cross” was presented on the screen, the synchronized sound was always a standard sound whereas when the “red circle” was presented, the synchronized sound could either be a standard or a deviant sound (with equal 50% probability). The “red circle” stimulus was used to indicate to the participant that the sound was a target stimulus and that an answer was required. With this manipulation, we could make sure that the response of the participant was referring to the last cued sound, and not to any other sound from the sequence (which is presented continuously at a relatively fast rate around 2 Hz). In the absence of the visual cue, we could not unambiguously decipher to which sound the participant was reacting to. In addition to the pure tones, broadband white noise was presented continuously to make the task more difficult. The signal-to-noise ratio between pure tones and white noise was adjusted individually via a staircase procedure (see Procedure). All stimuli were generated and presented via the Psychophysics-3 toolbox.

Procedure. The experiment was composed of 16 blocks of 3 min 30 s. Each block consisted of a sequence of auditory sensory stimuli masked in constant noise. Participants had to discriminate the sound when a red visual cue was presented on the screen (target trial) (Fig. 3.1A). To vary the temporal regularities of the context, the Stimuli Onset Asynchrony (SOAs) between the sounds of each block was drawn from distinct temporal distributions. In the Periodic condition, the SOA was fixed at 500 ms. For the Gaussian conditions, the SOAs were drawn from Gaussian distributions with distinct Standard Deviations (STDs) of 25 ms, 150 ms and a last condition with a Uniform distribution of the SOAs (between the range of 100 – 900 ms) (Fig. 3.1B). The SOAs data points used to build these gaussian distributions were spaced out every 25 ms to allow accurate sampling of these distributions. Both standards and target trials were drawn from these distributions. Each block consisted of 416 trials including 56 target trials. Between two target trials, a minimum of 5 standard sounds and a maximum of 10 standard

sounds (uniform distribution) may occur. The target trials could not appear in the first 10 trials of the sequence. Four blocks were presented for each temporal distribution and the block order was pseudo-randomized so that the same distribution was not presented twice in succession. Therefore, 224 target trials were obtained for each temporal distribution. After each block, the subjective perception of the rhythmicity of the temporal context was assessed: participants were asked to rate the global rhythmicity of the sequence. We specifically asked to rate whether the sounds in the sequence were presented at a regular pace on a scale from 0 (totally not rhythmic) to 10 (totally periodic). We also asked them after each block to rate their feeling about their performance in the preceding sequence from 0 (random answers) to 10 (feeling about 100% accurate). Before the main experiment, a staircase procedure was performed to adjust the signal-to-noise ratio (SNR) so that the average sound discrimination performance was within ~80% correct responses (mean SNR = -13.6 dB, within [-15.5, - 9.7] dB range). These SNRs are slightly higher than previously reported detection thresholds of pure tones (around -17 dB) (McPherson et al., 2022). We think for this reason that participants were able to hear both standards and deviant sounds and that our task relied on pitch discrimination. In the staircase, 75 sounds were displayed with periodic SOAs (500 ms), and targets trials could appear every ~3-6 tones.

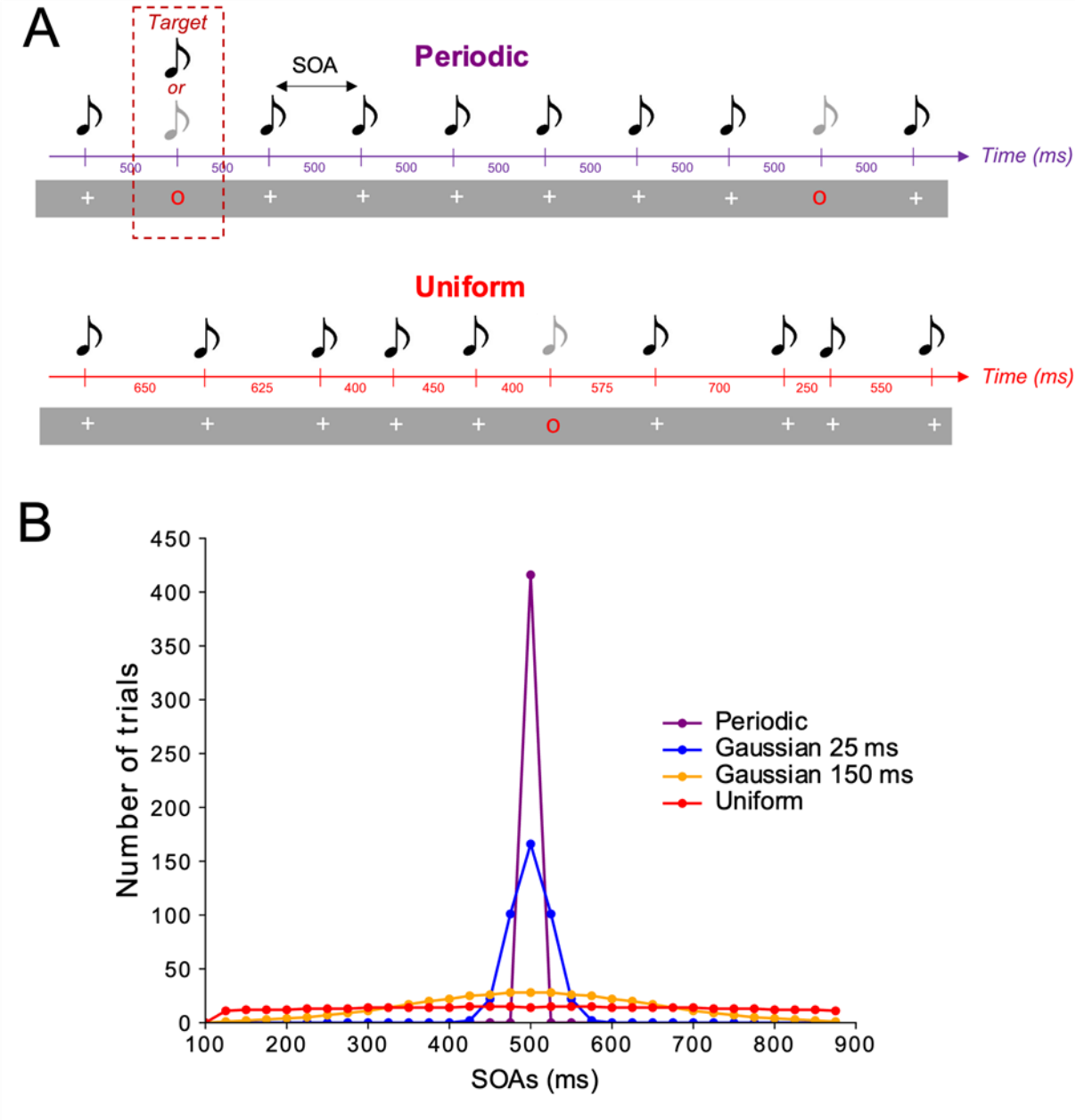

Figure 3.1: Experimental design. (**A**) Example of two sequences of different temporal distribution used in this experiment. Each sequence consisted of a stream of simultaneous auditory and visual stimuli. A standard stimulus corresponded to a 440 Hz pure tone co-occurring with a white cross. Occasionally a red circle appeared in the stream indicating a target stimulus, on which participants had to discriminate between a standard (440 Hz) and deviant (220 Hz) pure tone. (**B**) Distribution of SOAs in each sequence. For each sequence, the distributions of the SOAs were drawn of Gaussian distributions with equals means (500 ms) but distinct temporal variability. Four conditions were designed: from periodic (0 ms STD) to uniform distribution (with SOAs bounded between 100 ms to 900 ms).

Behavioral data analysis. Generalized linear mixed models (GLMMs) were computed using lme4 (version 1.1-28) (Bates et al., 2014) with R 4.1.2 (2021-11-01), on both the subject's responses (1 for a correct response, 0 if incorrect, binomial distribution) and subject's response

times (gamma distribution) as dependent variables. We first included the temporal distribution (categorical variable with 4 ordered levels: per, gaus 25, gaus 150 and uni) as fixed effect, and the factor Subject as a random effect. In both case, subjects' responses, or response times as dependent variable, we included the random intercepts only because if we added the random slopes, we obtained too complex random effects structures leading to a singular fit error. By removing the random slopes, we ensured that variance-covariance matrices could be estimated accurately, minimizing the risk of incorrect convergence and improving the robustness of statistical inferences (Barr, 2013; Bates et al., 2015; Matuschek et al., 2017). Stepwise models comparison was done using the likelihood ratio test, and Type II Wald chi-square tests were used to assess the best model fit, and the significance of fixed effects (Bates et al., 2014; Luke, 2017). To evaluate the difference in performance between each temporal distribution condition in our experiment, we then performed post-hoc tests using the emmeans package version 1.7.4.1 and we used Tukey multiple comparison correction.

EEG recording and preprocessing. EEG was recorded continuously from 64 pre-amplified Ag/AgCl electrodes, using an Active 2 system (BioSemi) mounted on an elastic cap according to the extended 10-20 system. Additional electrodes were placed on the left and on the right mastoids. The EEG signal was sampled at a rate of 1024 Hz. Preprocessing was conducted on MNE-Python (version 1.0.3) using the following pipeline: referencing offline with the mean between the two mastoids, band-pass filter between 0.5 Hz – 100 Hz, the signal was then segmented into epochs of 4s length (-2s before the target occurrence and 2s after), these epochs were then submitted to an automated artifact rejection toolbox called autoreject (version 0.4.2) (Jas et al., 2016, 2017) with a first step of autoreject that aims to search for bad signal in the epochs, correction of ocular artifacts using an independent component analysis (ICA) (Jung et al., 2000) based on typical scalp topography and time course was done on epochs ignoring the segments marked as 'bad' by the previous step 1 of autoreject. The first step of autoreject only goal was to improve the performance of the ICA algorithm and autoreject solution wasn't apply on epochs at this stage. After rejection of artefacts with the ICA, another step of autoreject was done and applied on epochs (mean number of ICA rejected by subject = 3.2; STD = 2.2; mean percentage of bad segments after the preprocessing: 4.1%; STD: 4.8).

ERP analysis. For ERP analysis, epochs were cropped into 1.2 s length (-0.6, 0.6 ms) around the target onset. A period of 100 ms before target onset (-0.1, 0 ms) was used as a baseline. Epochs were then re-filtered with a 35 Hz low-pass filter (firwin method, Hamming window

for attenuation). Importantly, in order to reduce the influence of the evoked activity of the previous and following sounds within the target window, we restricted the analyses to the targets for which both the SOA between the previous sound and target, and the SOA between the target and next sound was higher than 400 ms (i.e. trials where no sound was presented within the [-400 ms, 400 ms] time window surrounding target onset). We analyzed the ERPs within the Region Of Interest (ROI) that was most sensitive to auditory discrimination. For this, we contrasted the ERP response to deviant and standard sounds, and we selected the 15 channels that showed strongest response to the difference (deviant – standard) within the pre-defined post-target onset [150 – 250 ms] window based on the literature of the MMN (Näätänen et al., 2007). For subsequent analyses on ERPs we used either this previously described time window, either a time window of [300 – 500 ms] post-target onset that is a window commonly used to analyze the P300 (Gonsalvez et al., 2007; Polich, 1986, 1987), or a third time window of [0 – 150 ms] in which we had post-target onset ramping activity. For the sake of clarity, we will refer to these time windows as: post-target ramping activity, MMN and P300 in the remainder of this article.

We then computed LMMs using lme4 (version 1.1-28) on the mean EEG amplitude within the ROI in these three time windows: post-target ramping activity time window; MMN time window; and P300 time window) as dependent variables (normal distributions), and the temporal distribution (categorical variable with 4 ordered levels: per, gaus 25, gaus 150 and uni), the correctness (categorical variable with 2 levels: correct response or incorrect response), and the deviance (categorical variable with 2 levels: standard target or deviant target) as fixed effects, and the factor Subject as a random effect was added in the models.

Power analysis.

We analyzed power spectral density (PSD) in the range of 1 Hz to 15 Hz on epochs of length 3s (-1.5, 1.5) in the ROI using the PSD welch MNE function (sampling frequency = 1024; fmin = 1 Hz; fmax = 15 Hz; n_fft = 3*sampling frequency; n_overlap = 0; hamming window). We computed both the total PSD (on all epochs) and evoked PSD (after epochs averaging per participant). We extracted the total and evoked PSD at 2Hz, and we investigated using LMMs the impact of temporal distribution (fixed effect) on 2Hz power, with Subject as a random effect. We furthermore investigated whether the 2Hz power within trials or across individuals could predict auditory discrimination performances (percentage of correct response and RT). For this, we sorted trials of individuals according to 2Hz power in each distribution and we binned trials in 10 categories from bin 0 (10% of trials with lowest 2Hz power) to bin 9 (10% of trials with

highest 2Hz power). We ran a GLMM on both the subject's responses (binomial distribution) and subject's response times (gamma distribution) as dependent variables, we included the 2Hz power decile and the temporal distribution as fixed effects, we added the factor Subject as a random effect in the model.

RESULTS

TEMPORAL VARIABILITY IMPACTS AUDITORY DISCRIMINATION ACCURACY AND RESPONSE TIMES

We tested the effect of the temporal variability of auditory sequences on auditory accuracy and on response times. Participants auditory discrimination significantly decreased as a function of contextual temporal variability (main effect of the factor Temporal distribution ($\chi2(3) = 97.01$, $p < 0.001$)) (Fig 3.2A). Discrimination accuracy was highest in the periodic context, and progressively decreased with increasing temporal variability. Contrasting each temporal distribution condition between one another, post-hoc tests revealed that accuracy in the periodic condition was statistically different from the more aperiodic conditions (difference % correct responses Periodic – Gaussian 150 = 5.68%, $p < 0.001$, and Periodic – Uniform = 5.82%, $p < 0.001$). Moreover, performance was also statistically different between the contexts Gaussian 25 and the two more aperiodic conditions (difference % correct responses Gaussian 25 – Gaussian 150 = 4.77%, $p < 0.001$, and Gaussian 25 – Uniform = 4.91%, $p < 0.001$). These results suggest that the percentage of correct responses is higher in conditions with less variable contexts even if they are not completely periodic (e.g., in the Gaussian 25 condition) (Fig. 3.2A). Response times were also significantly affected by the temporal distribution of the context (main effect of the factor Temporal distribution ($\chi2(3) = 39.42$, $p < 0.001$)) (Fig. 3.2C). Response times were faster in temporal contexts with low variability and progressively slowed as the temporal variability increased. Post-hoc tests showed that the two conditions with the lowest temporal variability: Periodic and Gaussian 25 were statistically different from the two conditions with the highest temporal variability: Gaussian 150 and Uniform (difference response times (Periodic – Gaussian 150 = –17.5 ms, $p = 0.001$); (Periodic – Uniform = –13.4 ms, $p = 0.002$); (Gaussian 25 – Gaussian 150 = –15 ms, $p < 0.001$); (Gaussian 25 – Uniform = –10.9 ms, $p = 0.001$).

We also show that these effects cannot fully be attributed to hazard rate, i.e. that auditory discrimination performances improve the longer you wait for the stimulus (Herbst & Obleser, 2019), reversely, auditory perception performance could decrease drastically for shorter SOAs. To alleviate these effects, we conducted the same analysis but restricted to all targets whose preceding SOA were contained in a range of 425 to 575 ms. With this subset we can have a substantial number of trials under each condition while maintaining small SOA deviation from mean of the global distributions. We still observed similar effects of temporal context on auditory discrimination as when all SOAs were included. Participants auditory discrimination significantly decreased as a function of contextual temporal variability (main effect of the factor Global STD ($\chi2(3) = 60.64$, $p < 0.001$)) (Fig. 3.S1A). These results suggest that when we took only the SOAs around the mean of the distributions (500 ms) auditory accuracy was also better in low variability conditions (e.g., Periodic and Gaussian 25 ms) compared to conditions with more variability in the context (e.g., Gaussian 150 ms and Uniform). For the response times, there was also a main effect of the factor Global STD ($\chi2(3) = 17.56$; $p < 0.001$) (Fig. 3.S1B).

We also investigated the effect of local temporal variability on auditory perception as in (Bonnet et al., 2024). We observed that the temporal statistics of recent history (from the last 3 SOAs before the target onset) can influence perception (Fig. 3.S2).

Lastly, we observed that the participants' performances were different between standard and deviant sound detection. In the experiment deviant sounds were very less likely to occur in the sequences (~13% probability) thus deviant occurrence was surprising and had led to differences in the behavioral auditory discrimination performances. The mean percentage of correct response for deviant targets was 67.6% compared to 81.7% for the mean percentage of standard targets (main effect of the factor Deviance on the auditory discrimination ($\chi2(1) = 643.2$, $p < 0.001$, no interaction between factor Temporal distribution and Deviance ($\chi2(3) = 2.66$, $p = 0.447$). On RT, the mean RT for deviant targets was 608 ms that was faster than the mean RT of standard targets around 642 ms (main effect of the factor Deviance on the response times ($\chi2(1) = 474.0$, $p < 0.001$) and a significant interaction between factor Temporal distribution and Deviance ($\chi2(3) = 185.52$, $p < 0.001$).

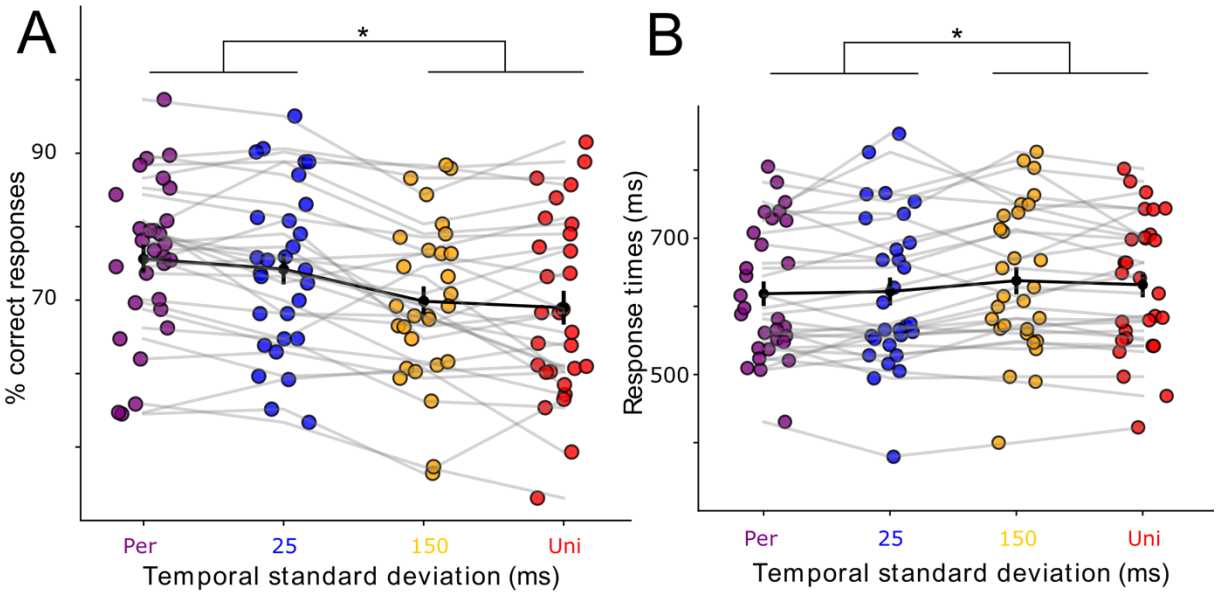

Figure 3.2: Auditory deviant discrimination is influenced by the temporal variability of the sound sequences. (A) Percentage of correct responses and (B) Response times as function of the standard deviation of SOAs in the auditory sequences. Each color dot represents a participant. Black dots represent the average across participants. Error bars indicate the Standard Error of the Mean (SEM), and stars indicate significant differences ($p < 0.05$).

ERPs RESPONSES TO TEMPORAL CONTEXT, AUDITORY DEVIANCE AND CORRECTNESS

In this study we aimed to understand how the temporal context influences the evoked response to target sounds within predefined ROI that respond maximally to the auditory deviance within the MMN related time window ([150 – 250 ms] post target) (Fig. 3.3 A-B). We also tested in this model the effect of the deviance (whether the target sound was a standard sound of a deviant) and the correctness (whether participants discriminated the target correctly).

Post-target ramping activity *time window (0 – 150 ms)*

We observed a significant effect of Temporal distribution, Deviance, and Correctness on the mean amplitude within the first 150 ms post target onset (main effect of the factor Temporal distribution ($\chi2(3) = 72.95$, $p < 0.001$), main effect of the factor Deviance ($\chi2(1) = 4.10$, $p = 0.048$), and main effect of the factor Correctness ($\chi2(1) = 10.84$, $p < 0.001$) (Fig. 3.3ACD).

Contrasting each temporal distribution condition between one another, post-hoc tests revealed that evoked amplitudes were more negative in the periodic and gaussian 25, these two conditions were statistically different from the more aperiodic conditions (difference amplitude Periodic – Gaussian 150 = 0.80 μV, $p < 0.001$, Periodic – Uniform = 1.04 μV, $p < 0.001$), and (difference amplitude Gaussian 25 – Gaussian 150 = 0.68 μV, $p = 0.001$, Gaussian 25 – Uniform = 0.93 μV, $p < 0.001$) (Fig. 3.3C). We didn't find any interaction between the factors Temporal distribution and Deviance (no main effect of the interaction between Temporal distribution and Deviance ($\chi2(1) = 0.86$, $p = 0.835$) and no interaction between the temporal context and correctness (no main effect of the interaction between Temporal distribution and Correctness ($\chi2(1) = 1.83$, $p = 0.609$). However, we found an interaction between the factor deviance and correctness (main effect of the interaction between Correctness and Deviance on the ramping activity ($\chi2(1) = 4.71$, $p < 0.030$)) (Fig 3.S3A), and a triple interplay between all factors (main effect of the interaction between the factors Temporal context, Deviance and Correctness, on the ramping activity ($\chi2(1) = 10.77$, $p = 0.013$)) (Fig 3.3E). More specifically, the effect of standard targets when correctly discriminated, was linear with a diminution of amplitude with increase temporal variability, for deviant targets that were incorrectly discriminated (i.e., perceived as a standard) we found a similar pattern with decrease evoked amplitude with increase temporal variability. Interestingly, for deviant correctly perceived and standard incorrectly discriminated (i.e., perceived as a deviant) the patterns looked like a plateau effect with better evoked amplitude for more regular contexts.

MMN time window (150 – 250 ms)

As expected, we observed a stronger negativity for the deviant targets compared to standard targets within the [150 – 250 ms] time window (main effect of the factor Deviance on the MMN mean amplitude ($\chi2(1) = 6.72$, $p = 0.009$)). Within this time window, we also observed a significant effect of the temporal context (main effect of the factor Temporal distribution on the evoked amplitude ($\chi2(3) = 47.89$, $p < 0.001$)) (Fig. 3.3C). Contrasting each temporal distribution condition between one another, post-hoc tests revealed that evoked amplitudes in the periodic and gaussian 25 conditions were statistically different from the more aperiodic conditions (difference amplitude Periodic – Gaussian 150 = 0.64 μV, $p < 0.001$, Periodic – Uniform = 1.12 μV, $p < 0.001$), and (difference amplitude Gaussian 25 – Gaussian 150 = 0.47 μV, $p = 0.016$, Gaussian 25 – Uniform = 0.95 μV, $p < 0.001$).

While Correctness was not significantly affecting evoked responses (no main effect of the factor Correctness: $\chi2(1) = 1.20$, $p = 0.247$)), we found a significant interaction between the factor

deviance and the factor correctness (interaction between the factor Deviance and Correctness on the evoked amplitude within the [150 – 250 ms] time window: ($\chi2(1) = 8.68$, $p = 0.003$)). Post hoc tests show that evoked amplitudes were more negative when participants correctly responded, when participants were incorrect the evoked response during the [150 – 250 ms] window could not dissociate between standard and deviant tones (Fig. 3.S3B). No interactions were found between the temporal distribution and the deviance ($\chi2(3) = 0.54$, $p = 0.25$), between the temporal context and correctness ($\chi2(3) = 8.68$, $p = 0.908$) or between the three factors: temporal distribution, deviance and correctness ($\chi2(3) = 3.03$, $p = 0.387$).

P300 time window (300 –500 ms)

All three factors (temporal distribution, Deviance, and Correctness) significantly influenced the P300 component (main effect of the factor Temporal distribution ($\chi2(3) = 107.26$, $p < 0.001$), main effect of the factor Deviance ($\chi2(1) = 47.77$, $p < 0.001$), and main effect of the factor Correctness ($\chi2(1) = 15.83$, $p < 0.001$) (Fig. 3.3ACD). Contrasting each temporal distribution condition between one another, post-hoc tests revealed that P300 responses in the periodic and gaussian 25 conditions were statistically different from the more aperiodic conditions (difference amplitude Periodic – Gaussian 150 = 1.07 µV, $p < 0.001$, Periodic – Uniform = 1.57 µV, $p < 0.001$), and (difference amplitude Gaussian 25 – Gaussian 150 = 1.15 µV, $p = 0.001$, Gaussian 25 – Uniform = 1.64 µV, $p < 0.001$).

We also found a significant two-way interaction between the factors deviance and correctness (interaction between Deviance and Correctness : ($\chi2(1) = 26.43$, $p < 0.001$) (Fig 3.S3B), but the interaction between the temporal context and deviance was not significant (no main effect of the interaction between Temporal context and Deviance : ($\chi2(3) = 3.39$, $p = 0.335$), as the interaction between the temporal context and correctness (no main effect of interaction between Temporal context and Correctness : ($\chi2(3) = 2.20$, $p = 0.531$). The three-way interaction was marginally significant (three-way interaction between temporal distribution, Deviance, and Correctness ($\chi2(1) = 7.20$, $p = 0.066$)).

These findings suggest that the temporal regularity of the context influences the early and late processing of the target sound, and later influences participants correctness.

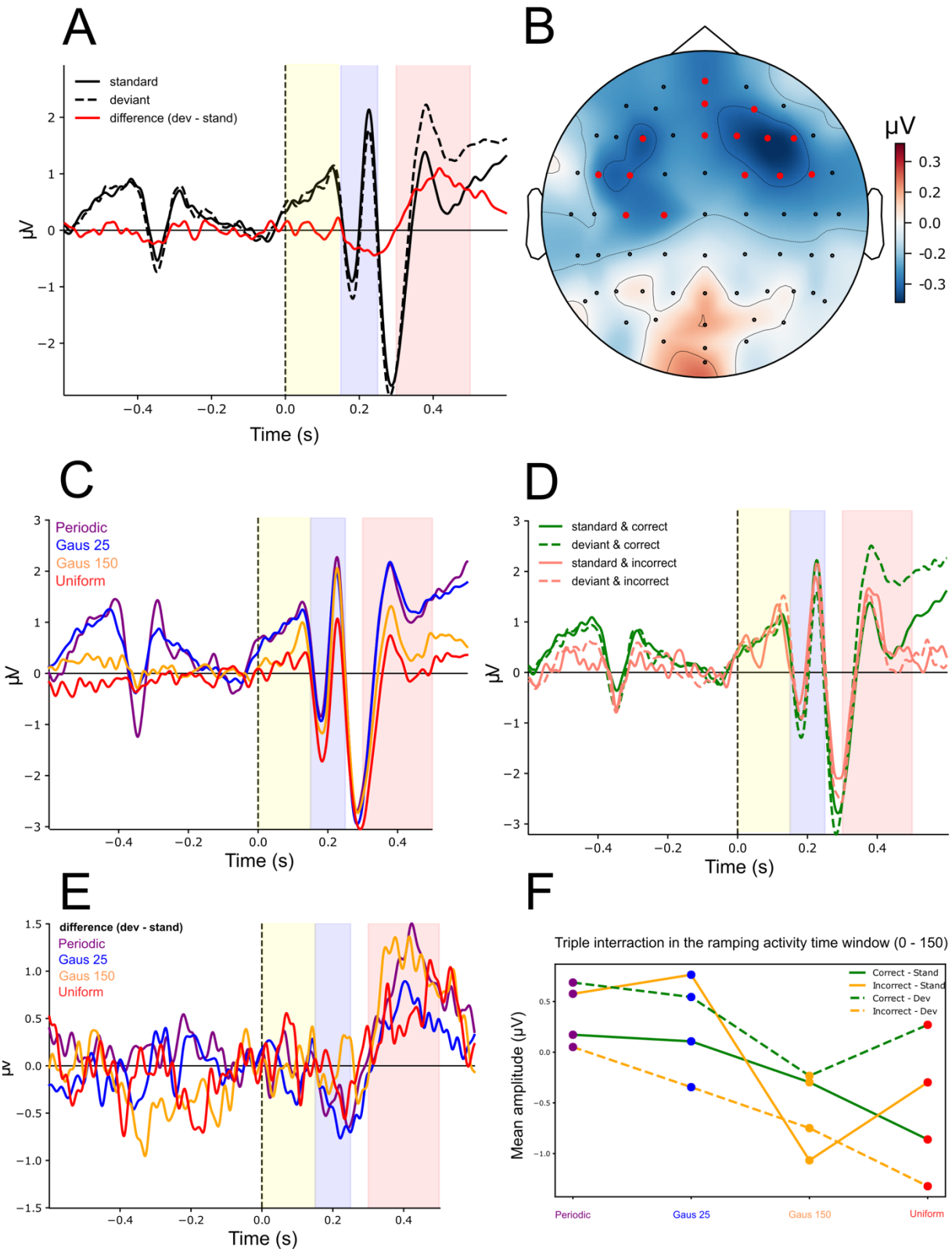

Figure 3.3: Effects of Deviance (standard or deviant sounds) on ERPs components (A). Contrast between standard and deviant is represented with the red line. The ROI used for all the subsequent ERPs analyses was plotted in (B). ROI was calculated by taking the 15 channels responding the best to the contrast (deviant – standard) with the

more amplitude negativity averaged in the time window of [150 - 250 ms] post target onset. ERPs in the different temporal distributions was plotted over time in (C) and ERPs for the conditions of Deviance (standard or deviant sound) and Correctness (whether a correct or incorrect response was given for this trial) were shown in (D). The plot (E) represents the difference deviant minus standard for each temporal context. Colored shadings represent temporal windows of interest. (F) The triple interaction between Correctness, Temporal context and the Deviance in the early post-target ramping activity. We found a significant effect of the interaction between these three factors.

2HZ POWER IS SIGNIFICANTLY HIGHER IN MORE REGULAR CONDITIONS AND CORRELATE WITH BETTER BEHAVIORAL RESPONSES

We first tested in a model whether the power at the mean sound sequence rate (2Hz) was influenced by the variability of the temporal context. We showed that total 2 Hz power was higher in the more regular conditions (main effect of the factor Temporal distribution on the 2Hz power ($\chi2(1) = 92.72$, $p < 0.001$)). Post-hoc tests revealed that power at 2Hz in the periodic and gaussian 25 conditions were statistically different from the more aperiodic conditions (difference amplitude Periodic – Gaussian 150 = 0.99 μV^2, $p < 0.001$, Periodic – Uniform = 1.00 μV^2, $p < 0.001$), and (difference amplitude Gaussian 25 – Gaussian 150 = 0.77 $\mu V,^2$ $p = 0.001$, Gaussian 25 – Uniform = 0.78 μV^2, $p < 0.001$) (Fig. 3.4 A-C).

Then, we investigated whether 2Hz power could be a predictor of target discrimination. To do this, we sorted trials of individuals according to 2Hz power in each distribution and we binned trials in 10 categories from bin 0 (10% of trials with lowest 2Hz power) to bin 9 (10% of trials with highest 2Hz power). we extended the statistical models of behavioral performance (Fig. 3.2), and we added the factor 2Hz power decile as an additional fixed effect. In the model on correct responses adding the 2Hz power decile did not significantly improve the model's explained variance: $\chi2(4) = 4.18$, $p = 0.382$, and did not improve the model's fit on correct response ($\chi2(1) = 0.05$, $p = 0.816$) (Fig. 3.5A). However, in the model on RT, adding the 2Hz power decile significantly improve the model's explained variance: $\chi2(4) = 24.58$, $p < 0.001$ and the main effect was significant (main effect of the 2Hz decile on the RT ($\chi2(1) = 17.36$, $p < 0.001$)). We additionally, observed an interaction between the 2Hz power and the temporal context (interaction between the factor 2Hz power decile and temporal distribution on the RT ($\chi2(3) = 58.09$, $p < 0.001$)). Periodic condition seems to be more influenced by the 2Hz power decile than in the temporally variable contexts (Fig. 3.5B).

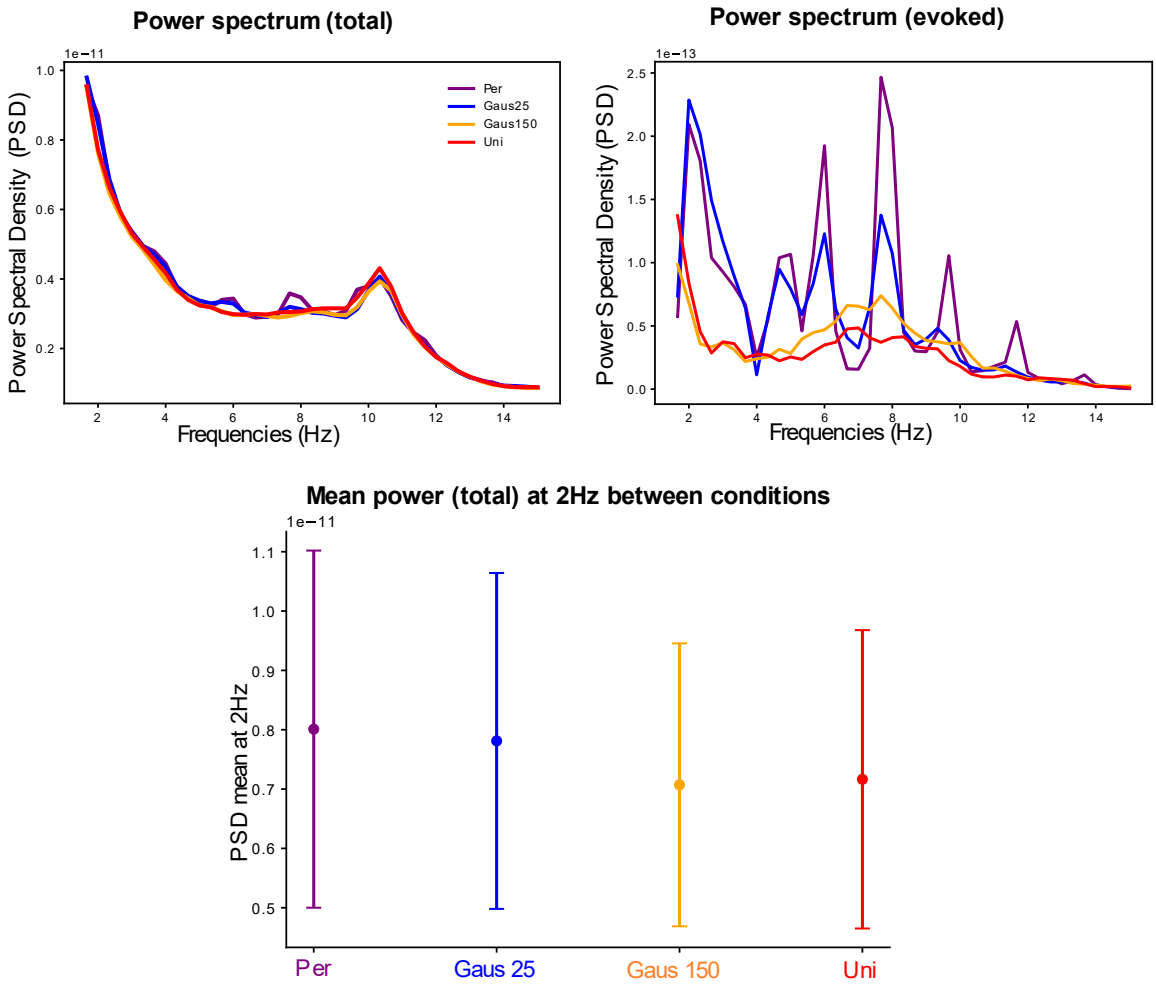

Figure 3.4: Power Spectral Density (PSD) was higher in more regular conditions. (A) Power spectrum (total) calculated from single-trial time series using a PSD, and subsequent averaging across trials. (B) Mean evoked amplitude spectrum (averaged across channels) from a PSD calculated from trial-averaged time series. (C) Histogram of PSD means and STD in each condition.

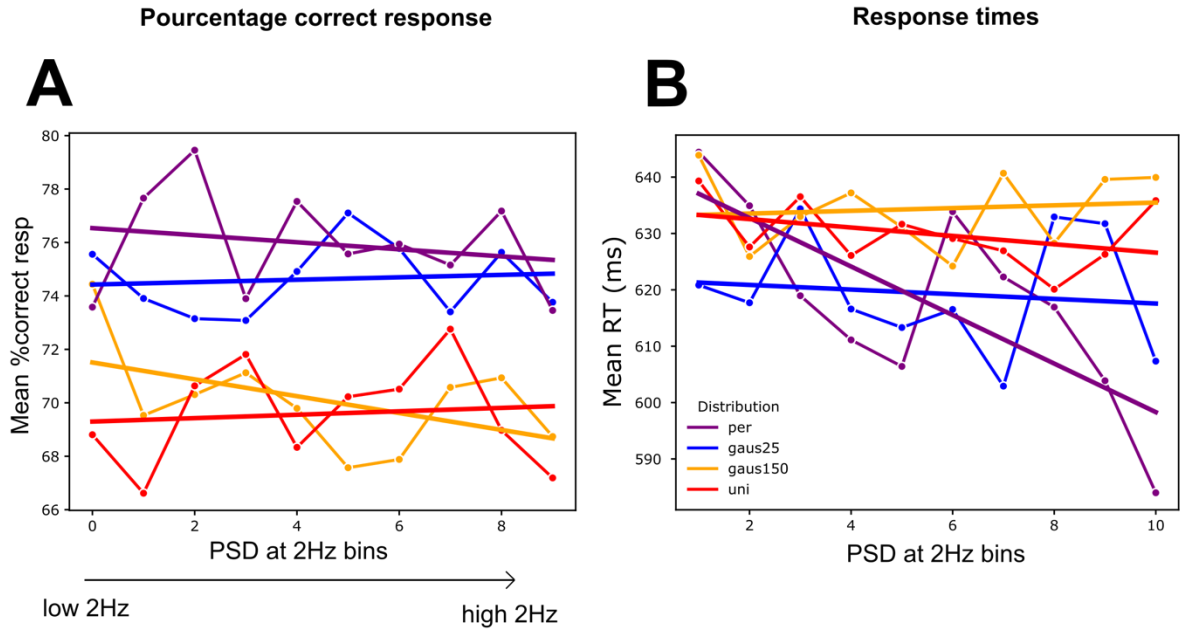

Figure 3.5: 2Hz power effects on behavioral performances. Power at 2Hz was binned by subject accordingly to amplitude (in 10 categories from bin 0 (10% of trials with lowest 2Hz power) to bin 9 (10% of trials with highest 2Hz power)) and plotted by distribution for the mean percentage of correct response (A) or mean RT (B). Linear slopes were added to the plot. The mean of the 2Hz amplitude by participant and by condition was then calculated and plotted for the mean percentage of correct response (C) and mean RT (D).

DISCUSSION

We here investigated the neural mechanisms underlying temporal predictions in probabilistic temporal contexts. Overall, the results first replicate previous behavioral effects (Bonnet et al., 2024): participants have more correct auditory deviance discrimination and faster response times in both periodic sound sequences and sequences with small temporal variability (i.e., gaussian SOA distribution with a standard deviation of 25 ms), as compared to sounds sequences that are more temporally variable. The behavioral results therefore confirm that temporal predictions are robust to a certain amount of temporal variability. Analyses on local temporal statistics further show that temporal predictions can be implemented quickly building on the temporal variability of previous sounds. We further showed that temporal context influences the evoked responses to target sounds: targets presented in more regular sound sequences showed increased ramping activity after target onset, a stronger amplitude around [150 – 250] ms post stimulus onset response (i.e., higher N2-P2) and more pronounced P300

amplitudes. Notably, the influence of temporal context on the evoked response did not impact the response to deviances; specifically, the MMN response to deviant targets compared to standard targets remained unaffected by temporal context. This indicates that the processes related to pitch discrimination and predictive mechanisms operate concurrently. However, within the first 150 milliseconds following target onset, we observe a significant triple interaction among temporal context, target type, and the accuracy of participants' responses. This finding suggests that temporal expectations may play a role in the initial response to targets, potentially influencing participants' perception and the accuracy of their responses. In addition, brain oscillatory dynamics at 2 Hz varied with the level of temporal predictability of the sound sequences, with higher power at 2 Hz in the more regular conditions. We observed significant variations in power at 2 Hz within sound sequences. The findings indicate that stronger 2 Hz power in the periodic condition was correlated with faster discrimination of deviant sounds, highlighting a connection between brain oscillatory dynamics and behavioral responses. Overall, these results suggest that temporal variability in sensory context impacts both the synchronization of brain and auditory rhythms and the responses to individual sounds within sequences, ultimately affecting auditory perception.

No interaction between "what" and "when" sound processing at MMN time window (150-250) ms and P300 time window

In our experiment, we conducted a discrimination task requiring participants to detect changes in subtitle pitch. As anticipated, we observed a more pronounced negative response to deviant sounds compared to standard sounds within the 150 to 250 ms time window. This effect is typically associated with mismatch negativity (MMN), which reflects the prediction error to the unexpected deviant sound. (Näätänen et al., 2007). Although in our study we had both visual and auditory stimuli, we argue that only auditory deviance had led to this MMN effect because the same visual stimulus was used for target presentations and was not indicative of the pitch (50% of the time the target could be a standard sound, and 50% of the cases it was a deviant sound). We show that deviancy effects were only visible when the target sound was correctly perceived. When participants failed to discriminate between standard and deviant sounds, evoked responses to standard and deviant tones were no longer distinguishable, supporting the idea that mismatch responses can reflect whether a trial will be correctly perceived or not (Amenedo & Escera, 2000; Näätänen, 1995; Näätänen & Alho, 1997). Indeed, even small changes in temporal deviance were shown to modulate mismatch negativity amplitude (Kisley et al., 2004) and temporal regularity was shown to facilitates attentive processing of deviance

(Schwartze et al., 2011). Importantly, in our study, we did not observe any interaction between the processing of deviant pitch and the processing of temporal context in the MMN time window. The undifferentiated manner in which temporal context influenced the evoked sounds suggests that the mismatch resulting from pitch variations and the surprise arising from uncertainty in temporal intervals may be addressed by distinct parallel brain processes.

The effect of the temporal context on P300 component was also shown in this study. P300 responses were higher in more regular contexts. Literature proposes that P300 rely to a conscious stimuli perception and link P300 to task difficulty, probability of occurrence and inter-stimulus interval suggesting overall that P300 rely to sound processing with higher P300 when the sound processing was easy (Gonsalvez et al., 2007; Miniussi et al., 1999; Polich, 1986, 1987; Stefanics et al., 2014). This would suggest that higher P300 responses in more regular contexts could be due to the globally better perception of targets sounds.

Interaction between "what" and "when" sound processing at post-target ramping activity time window [0-150] ms

In our experiment, early (*[0-150] ms)* post-target onset activity was influenced by the temporal regularities in the sensory context. ERP amplitude at this time window was higher in the more predictable temporal contexts as compared to the more unpredictable temporal contexts. We therefore interpret these results as a reflection of the contingent negative variation (CNV). The CNV is an ERP component that occurs during the period between a warning stimulus and a target stimulus. It is known to index the temporal expectancy between warning and target stimuli (Breska & Deouell, 2014, 2017; Miniussi et al., 1999). The CNV is composed of a negative deflection that occurs between the onset of the warning signal and stops at the expected arrival of the target stimulus, and a positive deflection that marks the temporal resolution that starts at the expected arrival of the target (Breska & Deouell, 2014, 2017). In our experiment, we expected that a CNV should be observed within each temporal interval of the sound sequences, because on average sounds occur with an expected temporal interval of 500 ms. However, we also predicted that the CNV amplitude should decrease for the more temporally variable contexts when temporal predictions become less reliable. We interpret the presence of stronger ramping activity post-target onset in the more temporally predictable conditions as a consequence of the resolution pattern of the CNV. The higher ramping amplitude in more regular contexts would result from a higher CNV resolution suggesting higher temporal expectations in these conditions. This result is in line with (Breska & Deouell, 2017) paper showing that CNV can be build up even in no periodic contexts.

Importantly, the CNV resolution would also reflect the subsequent perception of the target stimulus, as its amplitude is also correlated to the target type and correctness of participants' responses. These results suggest that temporal predictions could influence target processing very early and can influence the correctly discrimination of the target sound.

Neural tracking of sound sequences dynamics influences response times

We investigated the 2Hz power surrounding the target sounds in our paradigm, as a marker of neural tracking to the main rhythm in the sound sequence (as the expected temporal interval in all sequences is of 500 ms). We show that the variability in temporal context in our sequences impacted the observed 2Hz power. As expected, higher 2Hz power was observed for the more temporally regular sequences. The higher 2 Hz power between the sound sequences, could mostly reflect evoked response activity, as more temporally regular sounds would lead to more regular evoked responses and stronger neural tracking (Kösem & van Wassenhove, 2017; Obleser & Kayser, 2019). We therefore analyzed fluctuations in the 2 Hz response within the same sound sequences as in (Herrmann et al., 2016), and test to what extent changes in neural tracking correlate with changes in behavior. We show that neural tracking to the sound sequences at 2 Hz correlated response times, with faster response times in trials with stronger 2Hz power. However, the observed correlation between trial-by-trial 2 Hz power and response times was only observable for periodic sequences. The neural tracking of the stimulation rate is thought to rely to entrainment mechanisms and is supposed to explain this perceptual improvement in periodic condition. However, this effect is only visible on response times. In our previous study, the effect of temporal variability on behavioral performance also showed stronger effects on the response times (Bonnet et al., 2024). Therefore, our study failed to show a generalization of neural entrainment in probabilistic contexts as in (Herrmann et al., 2016). Time frequencies fluctuations are still being analyzed but are also expected to variate with the level of temporal predictability of the sound sequences.

Conclusion

Altogether, this present study explored neural mechanisms behind temporal predictions in probabilistic contexts. Behavioral findings replicated prior results, showing that participants had better auditory discrimination and faster response times in more regular sound sequences or those with minimal temporal variability. Temporal predictions were thus confirmed to be robust to certain levels of variability. Furthermore, evoked responses to target sounds were shown to be influenced by temporal context, with more regular sequences producing increased

ramping activity, higher N2-P2 response and stronger P300 amplitudes. Additionally, our findings indicate that temporal predictions play a significant role in the early processing of sounds, subsequently affecting their perception. Our study also suggests that there are distinct processing pathways for temporal and pitch-related deviations. Finally, this paper highlights that neural tracking is enhanced in more regular sound sequences and correlates well with response times in the periodic condition only, which may imply the existence of separate temporal prediction mechanisms for periodic and probabilistic contexts.

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SUPPLEMENTARY MATERIALS:

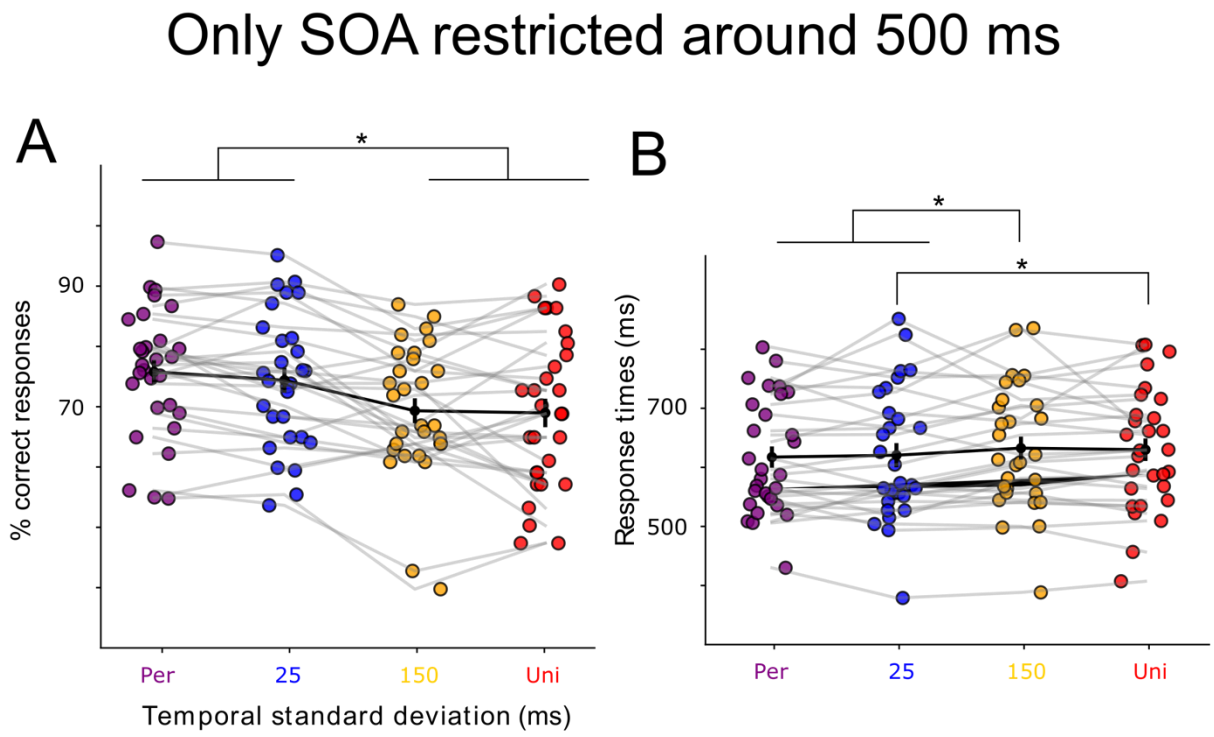
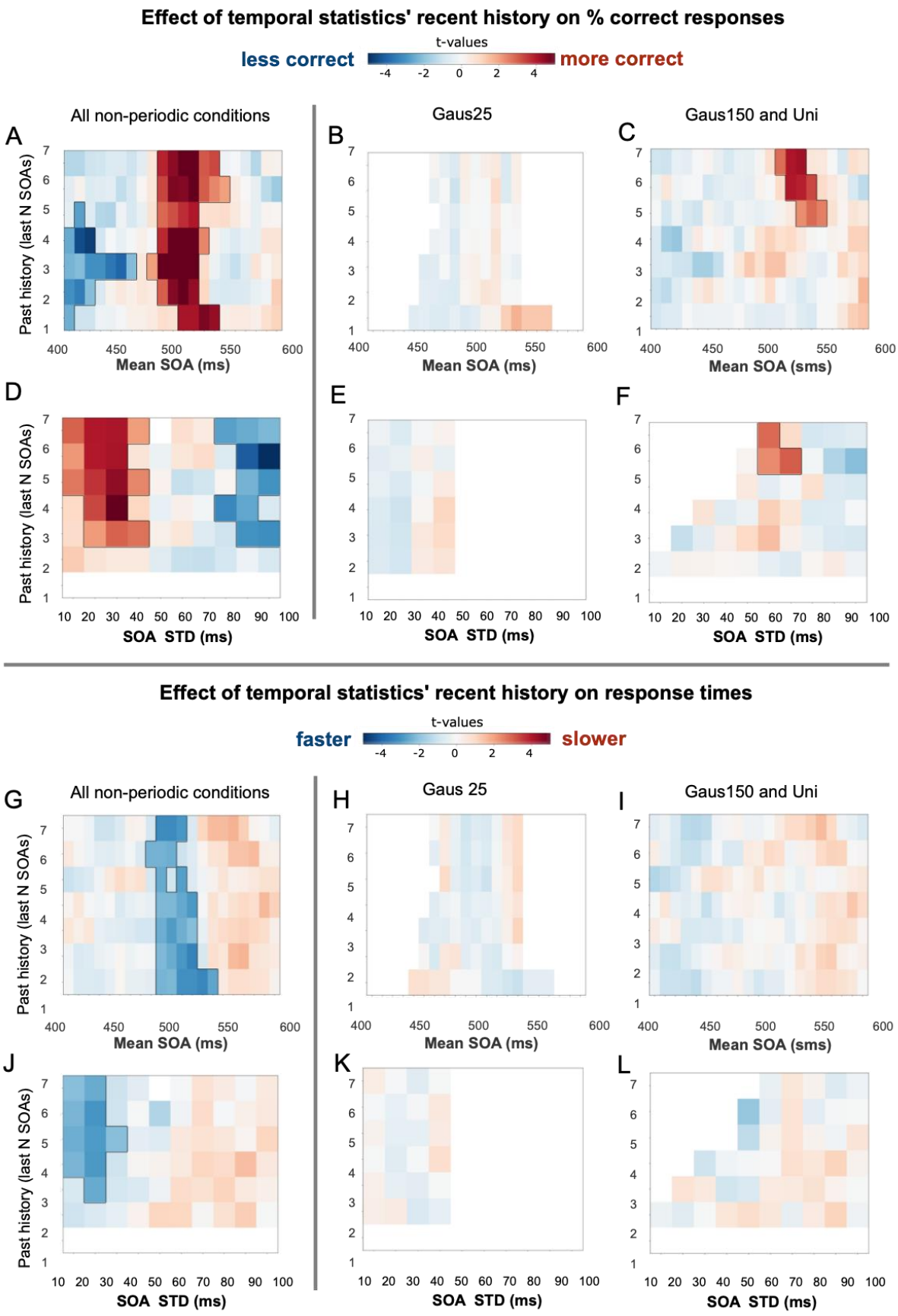


Figure 3.S1: Auditory deviant discrimination is influenced by the temporal variability of the sound sequences restricted to target trials presented at SOA = [425, 575] ms. (A) Percentage of correct responses. Contrasting each global STD condition between one another, post hoc tests revealed that accuracy in the periodic condition was statistically different from the more aperiodic conditions (difference % correct responses Periodic – Gaussian 150 = 6.52%, $p < 0.001$, and Periodic – Uniform = 6.00%, $p < 0.001$). Condition Gaussian 25 ms was also significantly different from the two more aperiodic conditions (difference % correct responses Gaussian 25 – Gaussian 150 = 5.61%; $p < 0.001$, and Gaus 25 – Uniform = 5.09%, $p < 0.001$). (B) Response times. Post-hoc tests showed that responses times were faster in temporal contexts with low variability: Periodic and Gaussian 25 were statistically different from the condition Gaussian 150 (difference response times (Periodic – Gaussian 150 = –14.1 ms, $p = 0.015$); (Gaussian 25 – Gaussian 150 = –11.6 ms, $p = 0.002$); and Gaussian 25 was also different from the more aperiodic condition (Gaussian 25 – Uniform = –11.1 ms, $p = 0.045$). Each color dot represents a participant. Black dots represent the average across participants. Error bars indicate the Standard Error of the Mean (SEM) and stars indicate significant differences ($p < 0.05$).


Effect of temporal statistics' recent history on % correct responses
t-values
less correct
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All non-periodic conditions
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D
E
F
Past history (last N SOAs)
Mean SOA (ms)
Mean SOA (sms)
SOA STD (ms)
Effect of temporal statistics' recent history on response times
t-values
faster
slower
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All non-periodic conditions
Gaus 25
Gaus150 and Uni
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L
Past history (last N SOAs)
Mean SOA (ms)
Mean SOA (sms)
SOA STD (ms)

Figure 3.S2: Effect of local temporal SOAs' statistics on perception. The figures illustrate whether the relative performance of participants was affected by the mean and STD of the previous N SOAs. Specifically, we computed the mean and STD of the local SOA distribution drawn from the N previous SOAs before each target trial (with N ranging from 1 to 7 SOAs before target trial for mean SOA, and from 2 to 7 SOAs before target trial for SOA STD). We then binned target trials per SOA distribution mean (from 400 to 600 ms SOA mean, with a sliding window of ±20 ms length) and per SOA distribution STD (from 10 ms to 100 SOA STD, with a sliding window of ±10 ms length). Bins containing less than 5 trials per participant were excluded from further analysis. For each bin, the average accuracy and response time across trials was computed, and then z-scored across participants. The obtained 2-D plots represent whether accuracy and response times were relatively higher or lower depending on the mean and STD of the 2/3/4/… last SOAs. We applied cluster-based permutation statistics (using MNE version 1.0.3) to the z-scored data (Maris & Oostenveld, 2007). One sample t-tests against zero were computed for each sample. Adjacent samples with a p-value associated to the t-test of 5% or lower were selected as cluster candidates. The sum of the t-values within a cluster was used as the cluster-level statistic. The reference distribution for cluster-level statistics was computed by performing 1000 random sign-flipping permutations of the data. Clusters were considered significant if the probability of observing a cluster test statistic was below the 2.5-th quantile and above the 97.5-th quantiles for the reference distribution. Data were aggregated for either **(A, D, G, J)** all non-periodic contexts, **(B, E, H, K)** the less variable temporal condition (Gaus25), and **(C, F, I, L)** the more variable temporal sequences (Gaus150 and Uniform conditions). The color label represents the one sample t-test value against zero for each sample. Black lines denote significant clusters (transparency is applied to non-significant areas). Due to the low variability in conditions Gaus25 some bins are left white (empty) because the number of trials was not sufficient to be representative (<5).

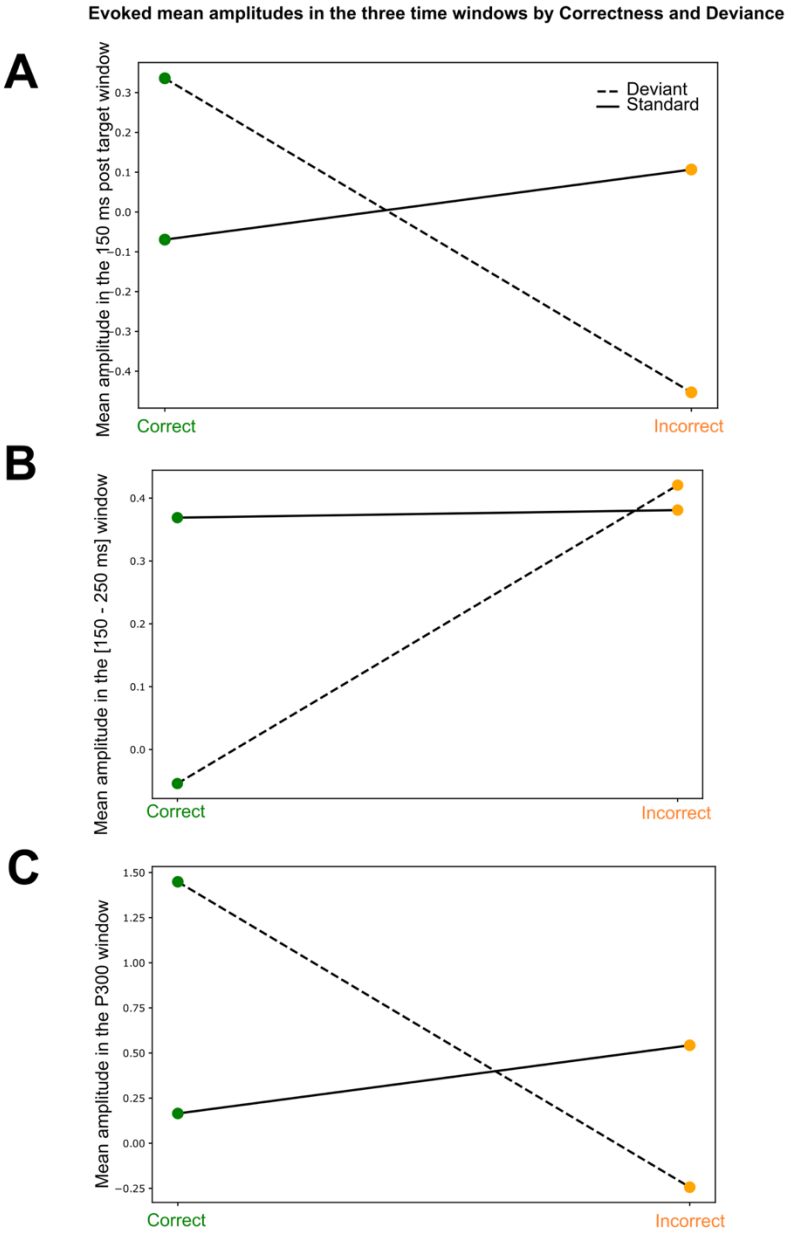

Figure 3.S3: The interactions between Correctness and the Deviance on the ERPs (A) in the early post-target ramping activity we found an effect of the interaction between these two factors and post hoc contrasts highlight that evoked to deviant sounds were significantly higher in correct compared to incorrect trials (deviant correct – deviant incorrect = 0.79 µV, p = 0.008). Moreover, the contrast between deviant and standard evoked when correct was marginally significant (deviant correct – standard correct = 0.40 µV, p = 0.0569). (B) in the second time window of [150 – 250 ms], post hoc tests showed that effects of the deviance were visible only on correct responses trials (deviant correct – standard correct = -0.42 µV, p = 0.014). Additionally, the correctness effect on deviant trials was close to significance (deviant correct – deviant incorrect = -0.47 µV, p = 0.062) (C) in the P300 time window post hoc contrasts shown that deviant sounds correctly discriminated led to higher P300 response than standard sounds also correctly discriminated (deviant correct – standard correct = 1.28 µV, p < 0.001). Moreover, deviant sounds correctly discriminated produced higher P300 response than deviant sounds incorrectly discriminated (deviant correct – deviant incorrect = 1.69 µV, p < 0.001). Moreover, deviant sounds that were correctly discriminated resulted in higher P300 responses than standard sounds that were incorrectly discriminated (deviant correct - standard incorrect = 0.91 µV, p = 0.001)

Chapter 4:

IMPAIRED TEMPORAL PREDICTIONS IN DYSLEXIA

4.1 Introduction

4.1.1 Motivation

In this third experiment, we were motivated to test the hypothesis of a temporal predictability deficit in dyslexia and thus to adapt our paradigm with dyslexic and control participants for the following reasons:

- Dyslexia is characterized by auditory and phonological deficits (Cole et al., 2020; Shaywitz & Shaywitz, 2005).

- A growing body of literature suggests that dyslexia is associated with difficulties in processing sensory information over time (Farmer & Klein, 1995; Habib, 2021).

- Individuals with dyslexia often show pronounced deficits in temporal tasks and temporal discrimination abilities in children can be predictive of their future language skills (Benasich & Tallal, 2002; Ozernov-Palchik et al., 2018).

- The rhythmic deficits observed in dyslexia may stem from impairments in neurophysiological tracking mechanisms associated with neural oscillations (Goswami,

2011, 2018). Supporting this, several studies have found that individuals with dyslexia exhibit diminished synchronization of neural oscillations with external stimuli, particularly in the delta and theta frequency ranges, when compared to neurotypical peers (Fiveash et al., 2020).

Therefore, understanding how these temporal prediction mechanisms function in the presence of irregularities is essential for grasping their impact on continuous auditory and speech processing. This present chapter aims to explore the operation of temporal prediction mechanisms within probabilistic auditory contexts specifically in individuals with dyslexia.

4.1.2 Experiment

We employed the same experimental design outlined in Chapter 2 and tested two adult groups: one with dyslexia and one without. In this design, participants were asked to discriminate between standard and deviant sounds that were embedded in 3 min-long sound sequences. The Stimuli Onset Asynchrony (SOA) of the sequences were drawn from distributions with the same mean (500 ms) but distinct distribution profiles: periodic and Gaussian distributions from 25 ms to 150 ms STD. If temporal predictions mechanisms are affected in dyslexia, we expect to find differences on behavioral measures between our two groups (dyslexia versus control), specifically the temporal context variability is expected to influence less auditory performances in individuals with dyslexia.

4.1.3 Summary of the results

The temporal contexts differently affected auditory discrimination performances of participants between the dyslexia and control groups. Dyslexic participants demonstrated lower accuracy in identifying target sounds within auditory sequences, as evidenced by a higher number of incorrect responses and longer response times relative to controls. Moreover, the responses from participants with dyslexia indicated a reduced sensitivity to the temporal context of the sequences, whereas the control group demonstrated shorter response times for sequences that were more temporally regular (and therefore, more predictable). These findings suggest a

possible connection between dyslexia and deficits in temporal prediction abilities, which may ultimately influence auditory perception.

4.2 Article

Impaired temporal prediction mechanisms in dyslexia (in preparation)

Impaired temporal prediction mechanisms in dyslexia

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ABSTRACT

To effectively analyze speech signals, it is crucial to decompose the acoustic signal into recognizable linguistic units. The processes involved in speech segmentation includes the ability to detect and predict temporal regularities present within auditory signals. However, these processes might be compromised in individuals with dyslexia. Using an auditory discrimination task, this study examined the effects of temporal context and related temporal predictions in both dyslexic participants and matched control participants. Here, we used an oddball task, pure tones were presented in sequences, and participants were requested to identify the pitch of a target stimulus, which was indicated by a visual cue. The temporal intervals among the sounds varied in regularity across the sequences, thereby creating contexts with different levels of temporal predictability. The results indicated significant effects related to the temporal context on the discrimination of target sounds and to the participant group (dyslexic versus control). Control participants responded faster in sequences that were temporally more regular (and thus more predictable), while dyslexic participants showed a diminished sensitivity to the temporal context of the sequences. Dyslexic also participants demonstrated lower accuracy in identifying target sounds within auditory sequences, as evidenced by a higher number of incorrect responses and longer response times relative to controls. These findings imply a potential link between dyslexia and deficits in temporal prediction abilities, which may impact auditory perception.

Keywords: auditory perception, context, temporal prediction, dyslexia, language, rhythm

INTRODUCTION

Dyslexia is a neurodevelopmental disorder that affects an individual's capacity to read, write, and spell. Research suggests that dyslexia is unlikely to occur as a standalone deficit; rather, it may stem from a combination of multiple risk factors (Pennington, 2006; van Bergen et al., 2014). Reading acquisition depends on the ability to segment the acoustic signal into a sequence of perceptually discrete linguistic units. As a consequence, dyslexia has been characterized by phonological deficits (Cole et al., 2020; Shaywitz & Shaywitz, 2005), as well as to deficits in processing auditory information over time (Farmer & Klein, 1995; Habib, 2021; Meilleur et al., 2020; Tallal, 2004). Children and adults with dyslexia exhibit robust deficits in temporal tasks whether they are explicit (judgments on duration/ temporal order and simultaneity (Casini et al., 2017; Tallal et al., 1993; Tallal & Piercy, 1973) or implicit (phoneme discrimination based on durational contrast (Casini et al., 2017), electrophysiological mismatch negativity response to duration-deviants sounds (Corbera et al., 2006; Huttunen-Scott et al., 2008; Stefanics et al., 2011). Furthermore, temporal discrimination abilities of infants and children predicted language skills later in development (Benasich & Tallal, 2002; Ozernov-Palchik et al., 2018; Plourde et al., 2017; Steinbrink et al., 2014).

A particular emphasis has been placed on examining the capacity to process auditory rhythms (Bégel et al., 2022; Overy et al., 2003; Ozernov-Palchik et al., 2018). Music and speech, in particular, contain sequences of auditory signals that demonstrate various forms of rhythmicity (Ding et al., 2017; Fiveash et al., 2021). The temporal regularity of sensory sequences is believed to significantly impact the perception of the sequences, as it creates temporal expectations and facilitates the processing of sensory stimuli that align with the rhythm (Jones, 2019; Large & Jones, 1999; Nobre et al., 2012). This processing facilitation is thought to arise from the synchronization between external sensory rhythms and low-frequency neural oscillations (Cravo et al., 2013; Herbst & Obleser, 2017; Miniussi et al., 1999; Schroeder & Lakatos, 2009; Wilsch et al., 2020). Low-frequency neural oscillations in the Delta (1–4 Hz) and Theta (4–8 Hz) ranges have been identified as essential for the temporal processing of

speech (Giraud & Poeppel, 2012; Kösem & van Wassenhove, 2017). They have been shown to build temporal expectations based on syllable and word presentation rates, which influence speech comprehension (Bree et al., 2021; Guiraud et al., 2018; Kösem et al., 2018). Therefore, rhythmic deficits in dyslexia could originate from deficit in neurophysiological tracking mechanisms carried by neural oscillations (Goswami, 2011, 2018). In line with this hypothesis, several reports have shown that individuals with dyslexia exhibit reduced synchronization of neural oscillations with speech, music, and tone sequences particularly within the delta (1-4 Hz) and theta (4-8 Hz) frequency ranges when compared to neurotypical participants (Fiveash et al., 2020; Guiraud et al., 2018; Hämäläinen et al., 2012; Leong & Goswami, 2014, 2014; Molinaro et al., 2016; Soltész et al., 2013; Thomson et al., 2006; Thomson & Goswami, 2008).

Acoustic features of speech demonstrate statistical temporal regularities; while still encompassing a range of variations (Cummins, 2012; Jadoul et al., 2016; Singh & Theunissen, 2003; Varnet et al., 2017). Understanding the functioning of temporal prediction mechanisms in the presence of irregularities is therefore crucial to understand their impact in continuous speech processing. A recent behavioral study in adults indicated that temporal predictions can develop in contexts that are less predictable (Bonnet et al., 2024). The findings revealed improved auditory discrimination performance in temporally regular (periodic) contexts as well as in temporally more variable environments, indicating that probabilistic temporal prediction of rhythm is indeed feasible. The present study aimed to investigate the operation of temporal prediction mechanisms within a probabilistic auditory context in individuals with dyslexia and matched control participants. To achieve this, we employed the same experimental paradigm of (Bonnet et al., 2024) (see Fig. 4.1). Participants were asked to discriminate between standard and deviant sounds that were embedded in 3 min-long sound sequences. The Stimulus Onset Asynchronies (SOA) between the sounds of the sequences were drawn from distributions with the same mean (500 ms) but distinct distribution profiles: periodic and Gaussian distributions from 25 ms to 150 ms STD. If temporal predictions mechanisms are affected in dyslexia, we expect to find differences on behavioral measures between the two groups (dyslexia vs. control) and the temporal context variability is expected to influence auditory performances differentially depending on the group.

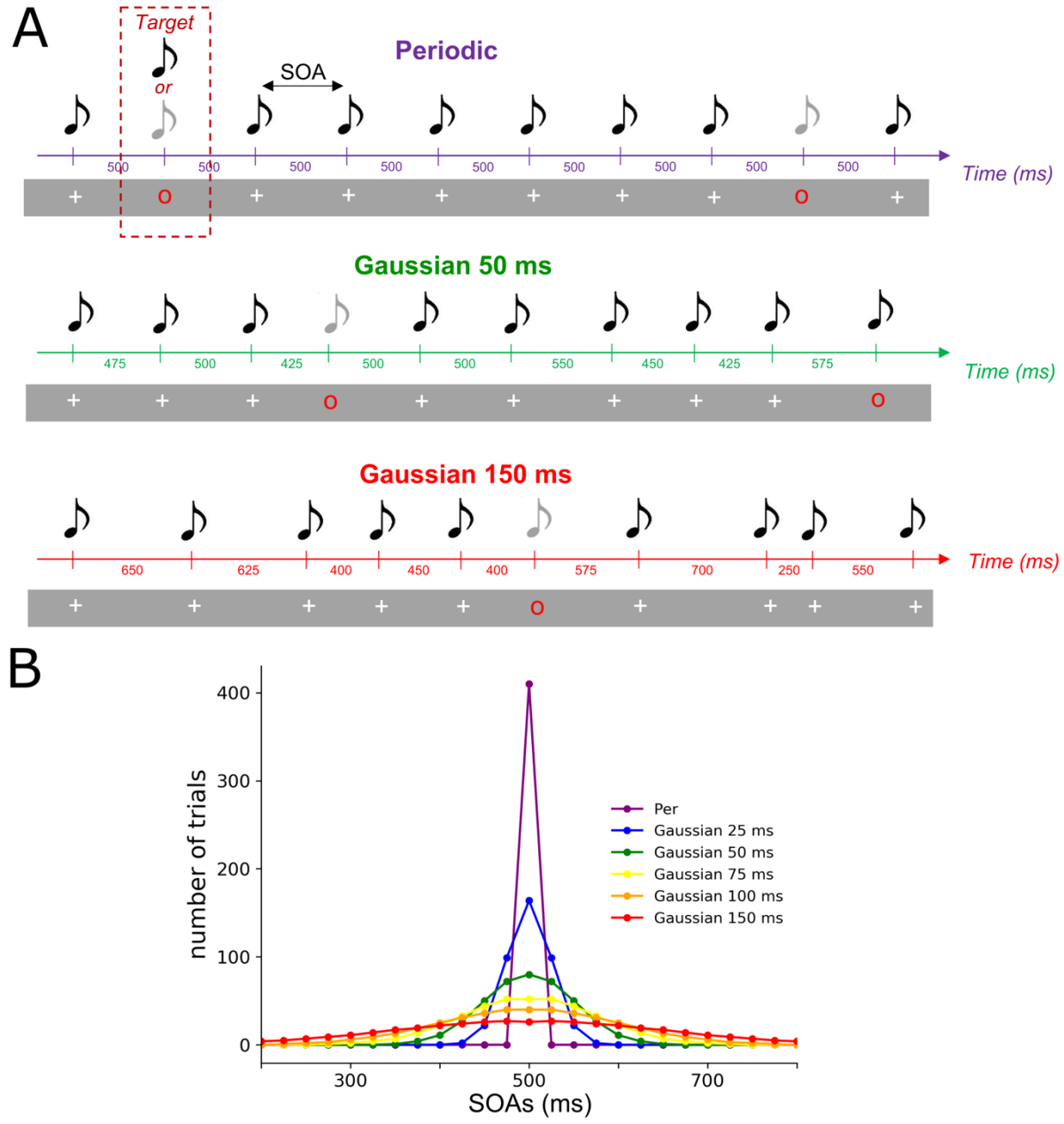

Figure 4.1: Experimental design. (A) Example of three sequences of different temporal standard deviations (STD) used in this experiment. Each sequence consisted of a stream of simultaneous auditory and visual stimuli. A standard stimulus corresponded to a 440 Hz pure tone co-occurring with a white cross. Occasionally a red circle appears in the stream indicating a target stimulus, on which participants had to discriminate between a standard (440 Hz) and deviant (220 Hz) pure tone. **(B) Distribution of SOAs in each sequence.** For each sequence, the distributions of the SOAs were drawn of Gaussian distributions with equals means (500 ms) but distinct STDs. Six conditions were designed: from 0 (periodic) to 150 ms of STD with SOAs drawn from 100 ms to 900 ms and spaced from 25 ms.

METHODS

Participants

27 dyslexic participants (19 female, mean age (M) = 24.12, standard deviation (STD) = 6.31) and 22 control participants (15 females, M = 24.14, STD = 4.16) took part in this experiment. Participants diagnosed with dyslexia were required to have received their diagnosis from a speech therapist. All participants were screened to exclude any hearing problems, neurological or psychiatric disorders, and engagement in music or dance activities, either currently or in the past. Furthermore, volunteers were included only when they reported the absence of other known learning disorders commonly associated with dyslexia, including attention deficit disorder with or without hyperactivity (ADHD), and other DYS- disorders such as dyscalculia, dysorthographia, and dyspraxia. Prior to the main experiment, volunteers completed an ADHD symptom screening questionnaire (ASRS-v1.1) (Kessler et al., 2005), as this comorbidity may impact task performance independently of dyslexic disorder (Calderone et al., 2014a; Gabrieli, 2009). Following the results of our ADHD test (ASRS-v1.1) (Kessler et al., 2005), one dyslexic participant presenting a too elevated ADHD score was excluded from the analyses. Thus, 48 participants were included in the study. The study was approved by an ethics committee (CPP 220 B17), and each participant signed an informed consent form before starting the experiment.

Questionnaires

Prior to the main experiment, control and dyslexic participants completed various questionnaires to assess dyslexia, ADHD and IQ.

To assess reading difficulties in adults, a sub-part of the ECLA 16+ test (Gola-Asmussen et al., 2010) was used. The ECLA 16+ is a tool designed to screen adults for dyslexia in French. Four sub-sections of the test were retained for this study:

I. *L'Alouette.* This read-aloud test indicates reading speed and errors. The results obtained were compared with the mean, standard deviation and percentiles according to the participant's age (Lefavrais, 1967, 2005) (Lefavrais 1967, 2005)
II. *Word dictation*. A dictation test with 10 regular words, 10 irregular words and 10 pseudowords was used to investigate participant's lexical and phonological writing difficulties.

III. *Initial phoneme deletion test*. This test of phonological awareness analyzes the ability to distinguish syllables and phonemes, and to manipulate them deliberately (e.g. “cliché” -> “liché”).

IV. *Spoonerism test*. This phonological memory test requires you to isolate and swap the first phoneme of each word, presented in pairs (e.g. “dossier”-“massage”), and to produce the resulting words (e.g. “mossier”-”dassage”).

To assess IQ, volunteers completed a simplified version of the Raven Matrices test (Bilker et al., 2012) (9-item version A11, B12, C4, C12, D7, D12, E1, E5, E7). The Raven Matrices are a multiple-choice intelligence test consisting of matrices to be completed with progressive difficulty (QI SPM; Standard Progressives Matrices - Raven, 1936)).

In addition, each participant completed an ADHD symptom screening questionnaire (ASRS-v1.1) (Kessler et al., 2005). This questionnaire consists of 18 questions aligned with the DSM-IV-TR criteria and provides a list of symptoms that may indicate the presence of ADHD. Part A of the questionnaire is the fundamental component for screening with the ASRS v1.1, while Part B offers additional insights to guide therapeutic follow-up. The responses to the six questions in Part A are the most indicative for making a diagnosis of ADHD and constitute the best tool for screening this disorder. Data from participants who scored above 4 in Part A of the test were excluded (1 DYS participant).

Stimuli

The stimuli presented in the main experiment were identical to those used by (Bonnet et al., 2024). Sound sequences were delivered alongside continuous white noise. The stimuli consisted of standard tones (pure tones at 440 Hz) and deviant tones (pure tones at 220 Hz) (see Figure 4.1). When a white cross was displayed, the synchronized auditory stimulus was always a standard sound. When a red circle appeared, participants were required to respond which sound they heard by pressing a key on the keyboard (left key for a standard sound and right key for a deviant sound). The inter-stimulus intervals (SOAs) between the sounds of the sequence were drawn from distinct Gaussian distributions of the same mean (500 ms) but of distinct standard deviation (STD). Six types of sequences with different SOA distributions were presented: periodic condition (with 0 ms standard deviation), and gaussian distributions with 25 ms, 50 ms, 75 ms, 100 ms, and 150 ms STD for the standard deviation. Each sequence comprised 410 tones, with 56 of them synchronized with the red circles (targets). Between two targets, a

minimum of four and a maximum of ten standard tones were presented. All stimuli were generated and presented using Psychopy-3 software.

Procedure

After having completed the questionnaires, participants were placed in a soundproof experimental room to participate in the experiment. Each participant was seated approximately 70 cm from a computer screen and wore headphones. The experiment began with a staircase adjustment procedure lasting about five minutes: the staircase procedure aimed to ensure that the participant understood the instructions and to adjust the sound intensity of the target sounds to an optimal level. By adjusting the loudness of the stimuli and modifying the signal-to-noise ratio between the sound sequences and the white noise, we established a condition that resulted in an average performance of approximately 80% correct pitch discrimination responses of targets. In the staircase, 75 targets sounds were displayed in auditory temporally irregular sequences were SOAs were drawn from a gaussian distribution with 150 ms STD, and targets trials could appear every ~3-6 tones. The mean SNR across participants was of -13.89 dB, within [-15.89, - 9.58] dB range. The SNRs are slightly higher than previously reported detection thresholds of pure tones (around -17 dB) (McPherson et al., 2022). We think for this reason that participants were able to hear both standards and deviant sounds and that our task relied on pitch discrimination.

Once the staircase had been completed, the experiment started. The experimental phase consisted of 12 blocks, each block lasting three and a half minutes. These blocks included sound sequences associated with visual cues (a white cross and a red circle). For each block, participants were asked to respond when they saw a red circle on the screen and judge whether the sound heard through the headphones was deviant or standard by using the keys on the keyboard. Between each block, participants were allowed to take breaks to maintain optimal alertness and concentration throughout the experiment. Two blocks per condition were presented to participants in a pseudo-randomized order to prevent the same condition from occurring twice in succession. After completing each block, participants were asked to evaluate (1) their perception of the overall rhythmicity of the block they had just heard on a scale from 0 (non-periodic) to 10 (completely periodic), and (2) their own performance in the previous block on a scale from 0 (random choice) to 10 (very good). Before the main experiment, a staircase procedure was performed to adjust the signal-to-noise ratio (SNR) so that the average sound discrimination performance was within ~80% correct

Statistical analyses

Statistical analysis of the data was conducted using R Studio (R 4.1.2 (2021-11-01). Student's t-tests and chi-square tests were performed to compare the demographics of each group. For the auditory detection task, results were evaluated in terms of the percentage of correct responses and reaction times. A generalized linear mixed model (GLMM) using lme4 (version 1.1-28) (Bates et al., 2014) was employed, incorporating the fixed effects of the Group condition (Dyslexic, Control), the context's Temporal STD (a continuous variable ranging from 0 ms to 150 ms), their interaction, and Subject was included as a random factor.

RESULTS

Demographics

No significant difference was observed between the Dyslexics and Control groups regarding gender balance ($\chi 2$ (1) = 0.006, p = 0.94), age (t (46) = -0.204, p = 0.84; dyslexics: M = 24.14, STD = 4.19; controls: M = 24.46, STD = 6.38), and IQ as indicated by the final Raven matrix score (t(46) = 1.332, p = 0.190) (controls: M = 115.65, STD = 6.16; dyslexics: M = 112.18, STD = 10.84). Regarding years of post-baccalaureate study, a significant difference was observed between the groups (t(46) = 2.256, p = 0.029). The control subjects had more years of study (M = 3.36 years, STD = 1.50) than dyslexic subjects (M = 2.39 years, STD = 1.50); however, this difference remained small, less than 1 year. Finally, although the participant with a score indicative of an ADHD disorder was excluded, a significant difference for ADHD scores between dyslexics and controls was observed (part A) (t(46) = -3.800, p < 0.001). Dyslexic participants scored higher in the ADHD test (M = 2.81, STD = 1.17) than controls (M = 1.46, STD = 1.30).

For ECLA scores, a significant difference was observed on the *Alouette* reading test (t(46) = -5.277, p < 0.001), with slower reading speed and more errors for dyslexic subjects (error-corrected Alouette reading time: M = 146.5 s, STD = 37.0) compared to controls (M = 101.6 s, STD = 15.9). Similar results were obtained on the initial phoneme deletion test, in terms of both task completion time and score. Dyslexics were slower than control participants (t(46) = -3.84, p < 0.001; controls: M = 33.9s, STD = 10.0; dyslexics: M = 48.1s, STD = 14.7) and scored lower (t(46) = 3.942, p < 0.001; controls: M = 9.1, STD = 1.4; dyslexics: M = 6.8, STD = 2.4). For the spoonerism test, dyslexics were also slower to complete the task (t(46) = -5.454, p < 0.001; controls: M = 85.2 s, STD = 32.9; dyslexics: M = 159.0 s, STD = 55.7) and performed

with a lower score ($t(46) = 3.515$, $p < 0.001$; controls: M = 19.2, STD = 0.8; dyslexics: M = 15.8, STD = 4.6). Word dictation scores were also different between control and dyslexic groups. On all three dictations ("regular words", "irregular words", "pseudo-words"), dyslexics made significantly more errors than controls (Regular words: $t(46) = -4{,}42$, $p < 0.001$, dyslexics M= 2.7, STD = 1.8; controls: M = 0.9, STD = 1.0. Irregular words: $t(46) = -5{,}60$, $p < 0.001$; dyslexics: M = 5,7, STD = 1,2; controls: M = 2.7, STD = 1.9. Pseudowords: ($t(46) = -2{,}47$, $p = 0{,}017$; dyslexics: M = 1.6, STD = 1.2; controls: M = 0.9, STD = 0.8).

Auditory discrimination task

Dyslexic participants overall performed more poorly than did the controls. Dyslexics had less correct responses (78.2% (SEM=8.09) than did controls (84.6% (SEM=7.69) (Fig. 4.2A, main effect of the factor Group: $\chi2\ (1) = 6.97$; $p = 0.008$), i.e. a difference of 6.4% between the groups. The variability of the context did not significantly affect correct responses (no main effect of the factor Temporal STD: $\chi2\ (1) = 6.19$; $p = 0.288$), and no interaction was observed between Group and Temporal STD ($\chi2\ (5) = 1.80$; $p = 0.875$), suggesting that the accuracy of Dyslexics and Controls did not differ as a function of the temporal variability of the stimuli.

Dyslexic participants responded slower to the target sounds than Controls (Fig. 4.2B, main effect of the factor Group: $\chi2\ (1) = 203.94$; $p < 0.001$). Control participants had a mean RT of 637 ms (SEM=51.02), while dyslexic participants had a mean RT for all conditions of 666 ms (SEM=55,14), i.e. a difference of 29 ms between the groups. Importantly, the variability of the temporal context influenced response times. Participants responded faster when the targets were embedded in more temporally regular sequences (main effect of Temporal STD: $\chi2\ (1) = 947.16$; $p < 0.001$), and a significant interaction between Group and Temporal STD was observed (interaction Group * Temporal STD: $\chi2\ (5) = 110.39$ $p < 0.001$): the impact of temporal variability on response times was less pronounced in the dyslexia group than in the control group (RT decrease linearly with the temporal context: - 6.975 ms each 25 ms of temporal context in the control group whereas in dyslexia group RT decrease by – 3.525 ms) (Fig. 4.2D).

Importantly, the observed results cannot be explained by absolute auditory discrimination thresholds, as participants staircases' SNR thresholds (leading to an average target pitch discrimination performance of 80% in temporally irregular sound sequences) were comparable across groups (fig. 4.2C).

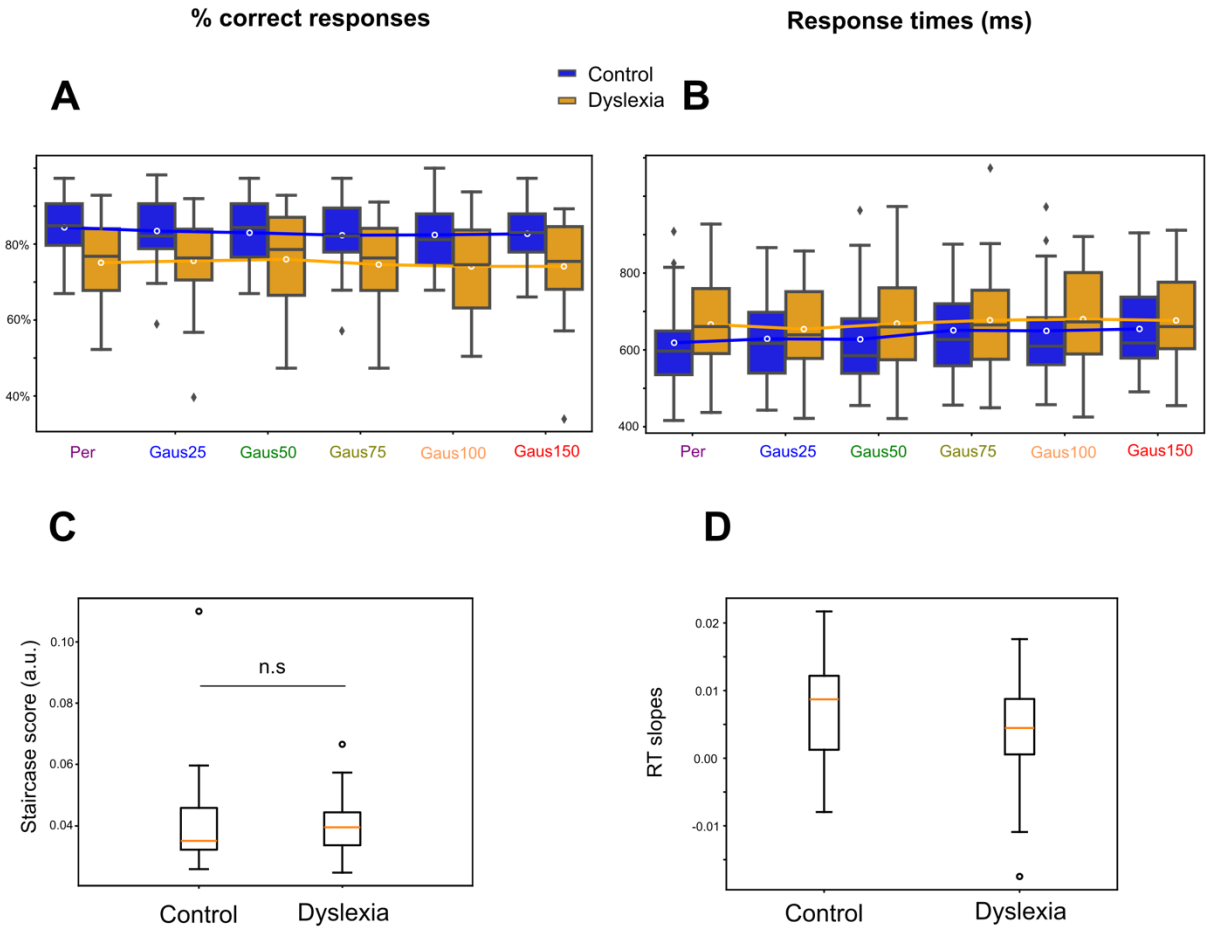

Figure 4.2: Auditory discrimination is affected by dyslexia. (A) Percentage of correct responses and (B) Response times as function of the standard deviation of SOAs in the auditory sequences. Colors represent the control and dyslexia groups. Box plots are illustrated for each distribution and group and represent the dispersion with the first quartile, median, and third quartile. The line plots link the means between the distributions. (C) Boxplot of staircase scores in the two groups, reflecting the SNR used in the experiment. No differences in the SNR between the groups were observed, suggesting that the results in the main experiment cannot be explained by absolute auditory discrimination thresholds. (D) Boxplots by groups with the coefficients of regressions of the evolution of RT as a function of temporal context by subject. RTs of control participants were more strongly affected by the temporal context (more positive RT slopes) than the dyslexics participants.

DISCUSSION

Temporal predictions are relevant also in speech processing and dyslexia. This works aimed to assess the ability of dyslexics to use probabilistic temporal regularities. The results of the controls in this present study provides converging evidence, in line with our previous research

(Bonnet et al., 2024), that variability in temporal context has a significant impact on auditory discrimination performance. Participants showed slower response times to target sounds when engaged with sound sequences that featured greater temporal variations. Importantly, our analysis revealed a significant disparity between the two group of participants. Dyslexic individuals demonstrated lower accuracy and slower pitch discrimination of the target sounds, across all presented temporal sequences, when compared to control volunteers. Furthermore, the influence of temporal variability on response times exhibited a distinct pattern for each group. Control participants exhibited a stronger influence of temporal variability on their response times than dyslexics; specifically, as the temporal variability of a sequence increased, their response times became longer. Conversely, dyslexic participants demonstrated a diminished effect of temporal context variability on their perception of target sounds. These findings suggest that individuals with dyslexia may encounter greater challenges in processing sounds presented in sequences, and unlike control participants, they derive less advantages from temporal context regularity.

Temporal prediction deficits in dyslexia

The present findings can be interpreted in the context of temporal deficit theories related to dyslexia (Goswami, 2011, 2018; Tallal et al., 1993). Our findings indicate a significant overall deficit among dyslexic participants in the speed of discriminating deviant sounds across various sound sequences, despite these individuals demonstrating comparable perceptual thresholds to the control group in the staircase procedure. This aligns with recent research suggesting that individuals with dyslexia may experience a generalized difficulty in processing sound structures (Ringer et al., 2024). Furthermore, these findings are in line with the impaired anchoring deficit theory (Ahissar et al., 2000, 2006; Daikhin et al., 2017). The impaired anchoring deficit theory proposes that, in typical neurological functioning, repeated exposure to a specific auditory reference enhances the ability to discriminate an unexpected deviant sound. However, individuals with dyslexia seem to possess a compromised mechanism, resulting in reduced advantages from such repetition. This may account for the overall decrease in auditory discrimination performance observed in our study, as control participants likely benefitted from the repetition of standard tones when identifying deviants, while dyslexic participants did not experience the same level of advantage.

We further investigate the influence of temporal prediction precision on auditory perception and identify an impairment of this ability in individuals with dyslexia. Our findings indicate

that temporal variability affects response times in control groups, with quicker responses associated with more temporally predictable sequences. In contrast, this effect is less evident in the dyslexic group, suggesting that their response times are less influenced by the temporal variability of the sequences. This implies that dyslexic participants may not utilize temporal prediction cues as effectively as their control counterparts, responding independently of the temporal context. It remains ambiguous whether these outcomes are indicative of a deficit in sensory processing or a limitation in temporal attention. This could align with the sluggish attentional shifting theory, which posits that when dyslexic individuals encounter rapid stimulus sequences, their automatic attention system struggles to disengage promptly from one stimulus to move on to the next (e.g., Hari et al., 1999, 2001; Hari & Kiesila, 1996; Helenius et al., 1999; Lallier et al., 2010; Ruffino et al., 2014).

Effect of music (rhythmic) training on auditory perception

Our findings do not fully align with those of Bonnet et al. (2024). Whereas the preceding study reported effects on both accuracy of responses and response times, the present data indicates an effect of temporal variability only in response times, including among control participants. One potential explanation for this effect could be the role of musical practice. In the present study, we purposely included volunteers who had no musical experience. The results of this study demonstrates that individuals without musical training may exhibit diminished temporal prediction abilities. Musical practice is known to influence perception of rhythm (Tallal & Gaab, 2006), and neural tracking to rhythms (Musacchia et al., 2008). Musical practice also influences speech perception, particularly in dyslexics (Overy, 2006; Przybylski et al., 2013; Thomson et al., 2013). It is therefore possible that musical practice, particularly training aimed at enhancing rhythm perception, may offer a valuable method for addressing speech perception difficulties, particularly those associated with dyslexia. However, it is important to acknowledge that while musical training can improve speech processing abilities, it does not completely eliminate the risk of reading disorders. As a result, individuals who have undergone musical training may still encounter ongoing challenges associated with dyslexia (Bishop-Liebler et al., 2014; Zuk et al., 2017).

Limitations

The analysis of demographics data revealed a significant difference in the number of years of post-baccalaureate education between the two groups, although this difference was small (under one year of difference between the two groups). Furthermore, variations in ADHD scores were

noted among the groups. It is essential to emphasize that the volunteers selected for the study demonstrated test scores indicating the absence of potential ADHD comorbidity. However, the average test scores of participants with dyslexia were found to be higher than those of the control group. This observation may suggest that individuals with dyslexia face more significant attentional challenges compared to their peers. The influence of the visual component on auditory perception was not assessed in our experimental protocol, nor was it evaluated in relation to the predictions of the sensory stimuli presented, encompassing both visual and auditory elements. Consequently, we cannot dismiss the possibility that the outcomes of our experiment may arise from multimodal mechanisms rather than being solely associated with the auditory component.

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Chapter 5:
GENERAL DISCUSSION

5.1 Summary of the findings

As outlined in the introduction, external rhythmic stimulation can be beneficial for sensory perception, as it enables temporal prediction and facilitates the inference of when the next relevant sensory event will take place. However, little is known about the underlying mechanisms and the range at which a temporal context can still be considerate as enough rhythmic to effectively utilize the contextual temporal regularities.

This question is particularly relevant for natural auditory processing, and speech in particular, because:

(1) Speech is not isochronic; rather, it contains complex statistical temporal regularities (Cummins, 2012; Singh & Theunissen, 2003; Varnet et al., 2017). If temporal expectations influence language comprehension (Kösem et al., 2018; Kösem & van Wassenhove, 2017; Tillman, 2012), how does the brain cope with auditory structures that exhibit temporal variability to form such predictions ?

(2) Speech comprehension relies on the analysis of temporal cues to process the acoustic signals into meaningful linguistic information, as evidence by several behavioral and neurophysiological findings (Giraud & Poeppel, 2012; Meyer et al., 2020; Peelle & Davis, 2012). Temporal predictability effects, based on average speech rate information, is known to influences speech perception (Dilley & Pitt, 2010; Kösem et al., 2018; Reinisch et al.,

2011; van Bree et al., 2021). It has been postulated that neural oscillations support these temporal prediction mechanisms, in the same way they have been postulated to support the rhythmic contextual advantage of non-verbal sequences. This would operate via neural entrainment to speech acoustics, which optimizes neural excitability, ensuring it is appropriately high or low in anticipation of incoming stimuli (Arnal & Giraud, 2012; Lakatos et al., 2008, 2013; Schroeder & Lakatos, 2009). Yet, in speech, sensory context deviates from isochrony, such as many other naturalistic contexts, and the occurrence of linguistic events follow statistical rules without being temporally fully predictable (Cummins, 2012; Singh & Theunissen, 2003; Varnet et al., 2017). Can neural entrainment still subsist in such temporally variable contexts? Is neural entrainment mechanistically relevant to build temporal predictions in such scenarios?

(3) Deficit in timing and rhythm perception is present in individuals with dyslexia. Dyslexics children and adults present difficulties in their abilities to process auditory rhythms (Bégel et al., 2022; Goswami et al., 2016; Overy et al., 2003; Ozernov-Palchik et al., 2018; Thomson & Goswami, 2008) and altered cortical tracking to auditory rhythms (Calderone et al., 2014; Destoky et al., 2022; Di Liberto et al., 2018). Is it unclear whether these deficits originate from impairment of temporal prediction per se. Are temporal prediction mechanisms affected in dyslexia, specifically in the presence of probabilistic sound sequences?

The research conducted in this thesis sought to address these questions. In Chapter 2, we used an auditory oddball experiment in which participants listened to different sound sequences where the temporal interval between each sound was drawn from gaussian distributions with distinct standard deviations. We showed that the ability to discriminate a deviant pitch sound in the sequence (measured with both discrimination accuracy and response times) decreased linearly with increasing temporal context variability. In addition, sound sequences with a temporal variability of up to 10-15% relative to the average temporal interval still offer similar advantages in terms of discrimination response time, whereas for temporal contexts with higher variabilities, temporal predictability benefits were significantly lower and dissociable from more regular contexts. This suggest that a temporal deviation from strict isochrony in a sensory context still allow predictability benefits. Importantly, the results of Chapter 2 were replicated in Chapter 3 and 4 (though in Chapter 4 the effect of temporal variability were only significant on response times). Finally, in Chapter 2 we also demonstrated that these temporal regularities

in sensory contexts can be captured at the local level, auditory discrimination performance was optimal at the average of the probabilistic distributions and when the standard deviation contained in the few previous sounds was low suggesting that both global temporal regularities and local variability of the last sounds prior to target influence the prediction of an upcoming event.

In the Chapter 3 of this thesis, we performed an EEG study with an experimental design adapted from Chapter 2. Results show that evoked responses to target sounds were influenced by the temporal context of the stimulation. Periodic and probabilistic auditory sequences with low temporal variability both induced greater post-target ramping activity, higher N2-P2 response and stronger P300 amplitude with no differences observed between these two temporal contexts. Conversely, evoked responses significantly differ when the temporal variability of the auditory sequences deviated from isochrony by more than 30%. Specifically, post-target ramping activity, which we interpret as a reflection of the contingent negative variation (CNV) (an ERP component that occurs during the period between a warning stimulus and a target stimulus) was diminished in these more irregular contexts suggesting a lower expectation about the temporal expectancy between warning and target stimuli. In addition, N2-P2 amplitudes in these contexts are more negative, which could reflect increased surprisal response to the *timing* of targets, as they depart more often from the expected timing (500 ms). Furthermore, these results are also consistent with the observed lower P300 amplitudes, pointing to greater difficulties in processing target sounds in sensory contexts with high temporal variability. Importantly, we did not find an interaction between the effect of temporal predictability on evoked responses and the mismatch response to deviant pitch, suggesting parallel processes. Chapter 3 also demonstrated that neural tracking of the stimulation rate (i.e., 2 Hz) is stronger in Periodic and low-variance temporal contexts than in more variable temporal contexts. Nevertheless, the 2 Hz neural tracking only correlated with behavioral performance in Periodic contexts.

Finally, in the Chapter 4 we tested the benefits of temporal predictability in probabilistic contexts with a population of dyslexics and controls. Findings show that dyslexic individuals demonstrated lower discrimination accuracy of the target sounds and slower response times, across all presented temporal sequences, when compared to control volunteers. Furthermore, the influence of temporal variability on response times exhibited a distinct pattern for each group. Control participants exhibited a more significant influence of temporal variability on

their response times; specifically, as the temporal variability of a sequence increased, their response times became slower. Conversely, dyslexic participants demonstrated a diminished effect of temporal context variability on their response time. These findings suggest that individuals with dyslexia may encounter greater challenges in processing sounds presented in sequences, and unlike control participants, they seem to derive less advantages from the regularity of temporal context.

Altogether, the findings of this thesis indicate that temporal prediction mechanisms exhibit resilience to temporal variability. Additionally, the research suggests that both periodic and probabilistic contexts may share certain neural markers linked to predictability. Furthermore, the study proposes that temporal prediction mechanisms may be modified in individuals with dyslexia. Overall, this thesis highlights the significance of temporal structure in sensory processing and its impact on behavior and neural activity.

5.2 The importance of temporal predictions in speech processing

5.2.1 Temporal prediction in natural speech

Throughout this thesis, our findings illustrate the utility of temporal prediction mechanisms in elucidating the rhythmic contextual advantages of naturalistic stimuli, such as speech. We demonstrated that deviations from strict isochrony can still provide temporal predictability benefits and influence subsequent neural activity, enabling the brain to track the rhythmic structure of the stimuli. We propose that, similar to our paradigm involving probabilistic contexts, speech is inherently temporally predictable. Despite some variability, the average timing of its constituent elements is generally predictable. Linguistic structures, such as phrases (0.6 – 1.3 Hz), words (1.8 – 3 Hz), syllables (2.8 – 4.8 Hz), and phonemes (8 – 12.4 Hz), exhibit fluctuations within specific frequency ranges. Additionally, even the variability of speech timing can be predictable; for instance, a reduction in speech rate is often a reliable indicator of an upcoming noun (Seifart et al., 2018), and the duration of an arriving syllable can aid in predicting the timing of adjacent syllables (Greenberg, 1999; Greenberg et al., 2003).
Notably, deviations from this apparent rhythmicity in speech can impact auditory perception. For instance, some words are not perceived if the surrounding speech is too slow or too fast

(Dilley & Pitt, 2010), that can also affect the meaning of words depending on the context (Bosker, 2017; Kösem et al., 2018). We argue that, because of this observable predictability in speech, temporal predictions can be made using previous timing speech cues. Thus, this effect of speech rate can be interpreted in the same way as our results. When a deviation from the expected timing occurs (i.e. when the speech rate changes or, in our case, when the statistical rule changes), then this deviation from the expected timing produces a mismatch in the prediction, which is reflected with an altered auditory perception.

It might also be interesting to consider that temporal prediction mechanisms in speech could occur via multiple time scales, and through distinct speech cues to anticipate when new elements will occur. Speech is a complex and evolving signal that conveys important acoustic and linguistic information over time. As such, the neural analysis of speech necessitates the parallel processing of these continuous information across various time scales (Poeppel, 2003). The brain is able to track speech structures over time suggesting a putative role of the neural dynamic to carry the continuous information present in speech (Giraud & Poeppel, 2012). Conveying the information of speech would be then useful to the parallel chunking of these different levels of language to help the comprehension (Ghitza, 2011). In the three experiments of this thesis, we employed a paradigm with a stimulation rate of 2 Hz, which aligns with the frequency range of words in spoken language. We highlighted that at this time scale, probabilistic temporal predictions could occur. Nevertheless, it would be fruitful to pursue a more in-depth investigation into the implications for additional temporal dimensions in speech, such as syllables or phonemes, and to ascertain whether this finding can be extrapolated to other frequency ranges.

5.2.2 Interaction between “what and “when” predictions

Predictions, in speech, can be made continuously on both the timing of an upcoming event (i.e., temporal prediction, predicting the “when”) but also on the linguistic element that will follow (i.e., predicting the “what”). The neural activity is thought to reflect a representation of speech elements. Following this view, temporal prediction through the modulation of neural activity may enhance the processing of linguistic structures during speech. However, when expectations are not fulfilled, the brain generates prediction errors (which are thought to signal the need to update the brain’s model of the world) (Fitz & Chang, 2019). Both types of predictions (i.e.,

'what' and 'when' predictions) when deviating from the expectation could lead to prediction errors. For example, semantic errors during language task comprehension are thought to provoke a negative evoked potential 400 ms after the arrival of the error (N400) (Kutas & Federmeier, 2011) whereas a positive evoked potential is trigger 600 ms after a syntactic error (P600) (Gouvea et al., 2010). Moreover, the neural activity carrying speech information is believed to occur very early. From 50 ms after a temporal cue the neural activity reflects a representation of stressed words that contributes to generate predictions to evaluate linguistic prosodic information (Zora et al., 2023). Mismatch effects can also occur when changes in the spatial (i.e. location), spectral ('what': loudness, frequency, or timbre) or temporal ('when': durations, or inter-onset interval) dimension of repeated sounds (Näätänen et al., 2007).

In speech, if features predictability is manipulated, for both types of predictions ('what' and 'when'), a MMN is elicited around 200 ms, suggesting that both what and when information can generate the same evoked mismatch response around the same time (Emmendorfer et al., 2020; Honbolygó et al., 2004). In this thesis, our results first indicates that the 'what' predictions (i.e. pitch, either standard or deviant pitch target) can elicit a MMN. Interestingly, our results also indicates that temporal variability (i.e., 'when' predictions) of a sensory context can affect the evoked in the same MMN time window. We highlighted that even two probabilistic temporal contexts (with 5% or 30% of temporal standard deviation from the mean of the gaussian) had led to different N2-P2 evoked responses, with more negative evoked amplitudes for the more variable temporal contexts. This result could reflect increased surprisal response to the *timing* of targets, as they depart more often from the expected timing (500 ms). Thus, in our task higher variability in the temporal intervals could have led to higher prediction errors. This finding is consistent with a paper showing that reversing the syllables (i.e., reversed speech), and thus affecting the expected timing of speech elements also elicited early negative component that curiously matched the spatiotemporal features of the MMN (Boulenger et al., 2011). Importantly, in our study, we demonstrate that the responses to temporal deviancy and pitch deviancy do not interact with one another. This indicates that temporal expectations influence the processing of sounds regardless of their pitch, potentially enhancing auditory processing in a non-specific manner.

5.2.3 Temporal prediction is impaired in language disorder

During an animated conversation, the speed of speech can differ considerably from one speaker to another. As discussed in the previous section, speech rate is an important parameter that affect our understanding of speech flows (Bosker, 2017; Dilley & Pitt, 2010; Kösem et al., 2018). For people with language difficulties, following the speaker speech rate can be a particularly challenging task. Language-disordered children exhibit difficulties in perceiving rapid acoustic sequences and struggle to process fast-rate speech compared to typically developing children (Guiraud et al., 2018; Lubert, 1981). Reversely, slowing speech rate improves auditory comprehension in children with language disorders supposedly by freeing up attentional resources (Campbell & McNeil, 1985). In this thesis, we discussed results where both typical and dyslexia participants faced varying temporal contexts. Overall auditory performances of dyslexics were lower than controls, suggesting a global deficit to process the contextual temporal regularities. Our results are in line with the hypothesis of a temporal sampling deficit in language disorders (Bégel et al., 2022; Goswami et al., 2016; Overy et al., 2003; Ozernov-Palchik et al., 2018; Thomson & Goswami, 2008).

Our results are also consistent with the idea of a statistical learning deficit in dyslexia. Research has accumulated evidence that dyslexia is linked to a broader perceptual deficit, which influences an individual's capacity to process regularities in sensory input and to utilize these regularities to improve auditory perception efficiency (Ahissar, 2007; Ahissar et al., 2000; Daikhin et al., 2017). This concept (also called the impaired anchoring deficit theory) is substantiated by findings indicating that impaired perceptual processing is evident not only with speech stimuli but also with non-linguistic sound materials. For example, studies have shown that, compared to healthy control participants, individuals with dyslexia exhibited diminished behavioral responses to stimulus repetition in perceptual tasks, such as tone frequency discrimination (Ahissar et al., 2006; Gertsovski & Ahissar, 2022). Furthermore, neural adaptation to various types of repeated auditory stimuli, including voices and tones (Jaffe-Dax et al., 2018; Jainta & Kapoula, 2011; Perrachione et al., 2016), as well as phoneme categories (Ozernov-Palchik et al., 2022), was also found to be less pronounced in individuals with dyslexia. Particularly, there were significant impairments in processing more complex statistical regularities, such as the extraction of transitional probabilities in sequences of syllables or tones (Gabay et al., 2015) and the learning of distributional information, including the frequencies of occurrence of specific syllables (Kimel et al., 2022) or bimodal distributions along a continuum between two non-native phonemes (Vandermosten et al., 2019).

Moreover, individuals with dyslexia and languages disorders were hypothesized to have perceptual difficulties in processing slower temporal modulations in speech (< 10 Hz), (Cumming et al., 2015; Goswami, 2011) as illustrated by rhythmic tapping tasks to a slow beat (Thomson et al., 2006; Thomson & Goswami, 2008). This is consistent with our paradigm where we used a slow stimulation rate of 2 Hz. We did not test for faster stimulation rate but according to the proposal of Tallal & Piercy, we make the assumption that a small adaptation of our paradigm with higher stimulation rates (e.g., using musical stimuli) should also highlight a deficit in the sequential processing of rapidly-arriving acoustic cues (Tallal & Piercy, 1973), specifically at the phonemic rate that was described in children with language disorders (Tallal, 2004) and that could be reflected in an altered temporal organization of brain activity (Heim et al., 2011).

Event-related potentials associated to auditory prediction are attenuated in adults with dyslexia compared with controls participants. Several studies indicated that prediction errors to the 'what' such as pitch, or phoneme elicit a diminished MMN (Corbera et al., 2006; Cunningham, 2020; Daikoku et al., 2023; Schulte-Körne et al., 1998; Stoodley et al., 2006). Additionally, predictions related to the 'when' (i.e., referring to the durations between temporal cues) also result in a reduced MMN in individuals with dyslexia (Corbera et al., 2006; Stefanics et al., 2011). These findings points to an early-level auditory-system deficit, in particular, auditory-discrimination dysfunction, in this disorder (Kujala & Näätänen, 2001).
The P300 component is also impacted in dyslexia, both latency and amplitude show abnormalities in this ERP component (Papagiannopoulou & Lagopoulos, 2017). P300 is often used as an effective tool to evaluate central auditory nervous system's structural and functional integrity and auditory attention in children with phonological deficits and reading, writing alterations (Mendonça et al., 2013). This difference in the sensory processing compared to controls in the MMN and in the P300 component is also present in individuals with DLD (Leppänen & Lyytinen, 2009) and these alterations are thought to reflect fundamental processing deficiencies. Moreover, other studies indicate that when listening to rhythmic sequences, the CNV is reduced in dyslexics (Soltész et al., 2013) suggesting less preparatory brain activity. Altogether, the altered neural markers associated with temporal prediction mechanisms appear to indicate a general deficit in the ability to form expectations among individuals with language disorders. It would be valuable to apply our EEG study with adult dyslexics. We anticipate that both the prediction of sound pitch (i.e., either standard or deviant) and the prediction of temporal intervals (i.e., based on varying temporal contexts) will yield a

diminished MMN response in individuals with dyslexia compared to control participants. We also anticipate a diminished P300 component, linked to attention and difficulty to process the sounds. We hypothesize that the CNV should also be lower in dyslexics, reflecting overall altered neural markers of temporal predictability.

Oscillatory activity is supposedly also affected in language disorders. There is evidence of impaired rhythmic processing in dyslexia that could originate from a deficit in tracking mechanisms carried by neural oscillations (Goswami, 2011, 2018). Recent research has shown reduced neural tracking of artificial words within a structured syllable stream in individuals with dyslexia. In addition, there is a positive correlation between the strength of neural tracking at the word rate and phonological awareness (Zhang et al., 2021). Another recent study also highlighted that the neural tracking of auditory regularities is reduced in adults with dyslexia while enhanced neural tracking of statistical structures has been linked to improved spelling abilities (Ringer et al., 2024). Other studies also support that individuals with dyslexia show lower synchronization of neural oscillations with external stimuli, notably within the delta and theta frequency ranges, when compared to neurotypical participants (Fiveash et al., 2020; Guiraud et al., 2018; Hämäläinen et al., 2012; Leong & Goswami, 2014, 2014; Molinaro et al., 2016; Soltész et al., 2013; Thomson et al., 2006; Thomson & Goswami, 2008). Therefore, these convergence evidence indicating deficits in the neural tracking of temporally expected events could indicate altered neural mechanisms of temporal prediction in language disorders (potentially through neural entrainment) (Calderone et al., 2014). Once again, we predict that, if we carry out our experiment with EEG, we will observe reduced neural tracking of auditory sequences in individuals with dyslexia.

5.3 Neural mechanisms underlying probabilistic temporal predictions

5.3.1 Temporal prediction is a key component of perception, and temporal variability is pervasive to most ecological stimuli

Our results, in line with previous studies, emphasize that human brain can benefit from statistical temporal regularities of a context to better predict in time and thus optimize

perception. This statement implies that the brain needs to build a comprehensive model of the world with probabilistic inferences of what and when events can occur. Studies supports the idea that the brain is sensitive to statistical regularities in sensory input across multiple time scales (Baldeweg, 2006; Bendixen et al., 2009; Garrido et al., 2009, 2013; Ulanovsky et al., 2004; Wacongne et al., 2011; Winkler, Denham, et al., 2009; Yaron et al., 2012; J. Zhao et al., 2013), indicating that the brain is attuned to the statistical aspects of sensory stimulation. Moreover, neuronal activity was found to be associated with the predictability of auditory input, reflecting both deterministic patterns and the entropy within random sequences (Barascud et al., 2016; Hu et al., 2024; S. Zhao et al., 2024). This offers substantial neurophysiological evidence of the brain's ability to automatically encode higher-order statistical information from sensory input.

Recent studies utilizing artificial neural networks have demonstrated that, akin to the behavior of neurons in the primary visual and auditory cortices, simulated neurons generally exhibit heightened responsiveness to features that change over time. Both artificial networks designed to predict sensory input and the human brain exhibit a preference for similar types of stimuli, specifically those that are effective in aiding the anticipation of future information. (Singer et al., 2018, 2023). This suggests that the brain does not efficiently represent all incoming information equally; instead, it selectively represents sensory inputs that help in predicting the future. In this view, the brain prioritizes the different features of sensory events and selects those which in the past have been most informative about the state of future sensory events, (i.e., which features have been the best predictors of the future). This implies that the brain is a prediction machine and continuously make inferences about future events (Bubic et al., 2010; Knill & Pouget, 2004). Computationally, this generative model of the brain’s environment may be expressed within a Bayesian framework. Such frameworks leverage Bayesian belief updates to explain how one may refine prior expectations in the light of sensory likelihoods (Barniv & Nelken, 2015; Friston & Kiebel, 2009; Körding & Wolpert, 2006; Millidge et al., 2021; Sato et al., 2007) The resulting (updated) model of the world then makes predictions about incoming stimuli. Note that, because exact Bayesian posterior computation is intractable in most practical cases, these frameworks often rely on approximations to compute the updated posterior. These approximations are usually based on the error term between the predicted and the observed stimuli (Millidge et al., 2021) with supporting evidence in neurophysiology (Iglesias et al., 2013).

Temporal variability is as key element of every natural stimulation and the Bayesian framework is a nice way to integrate this notion in cognitive models of perception by adjusting the strength of the prediction based on the confidence term (i.e., how well you can be sure about the sensory data: the noisier the sensory stimulation, the smaller the associated confidence). Neuroscience definitions of confidence tend towards the notion that brains encode information using probabilistic distributions at the neuronal population level (Meyniel, et al., 2015). This idea is well illustrated in a study where the Bayesian predictive inferences nicely described the transition between sequences of unfolding sounds with different statistics (i.e., varying pitch of sounds in the sequences) and modulation of brain activity followed the belief updating within the brain (Zhao et al., 2024). By linking the computational model outputs to observed brain responses, this study reveal that transition-related dynamics correlate with 'precision' (i.e., the confidence in predicted sensory signals) highlighting the relationship between the brain's statistical tracking and response dynamics. Other works confirmed this idea, by demonstrating that during learning, humans not only refine a model of their environment, but also derive an accurate sense of confidence from their inferences. Human performance aligns with optimal probabilistic inference, where subjective confidence is influenced by environmental uncertainties. Additionally, confidence grows with the number of observations during stable periods. These findings suggest that humans inherently possess a quantitative sense of confidence in abstract environmental parameters, which appears to be a fundamental aspect of the learning process (Maheu et al., 2019; Meyniel, et al., 2015).

This framework fits well with our results suggesting that the human brain is able to grasp the probabilistic regularities of the context to make inference on the likelihood of a new sensory event. Brain models of perception try to predict whether a sound will be perceived or not, and update their beliefs based on perceived errors between predicted and observed outcomes. In our task, results suggests that we could explain participants data by building a Bayesian model of perception to predict human performance using both the global level of statistics present in sound sequences as well as the local statistics of the N previous sounds before the target occurrence. This intuition is supported by previously approaches (Maheu et al., 2019) suggesting that the brain processes sequences by performing statistical inferences at multiple scales, and leveraging multiple computational subsystems. Moreover, another recent study (Hu et al., 2024) confirmed our finding that temporal prediction mechanisms can occurred rapidly based on very few previous events. In that study, the subjects were able to detect a regular pattern from only three previous events. This was reflected in the cortical tracking with higher

sustained activity in the regular context, confirming the influence of multiscale statistical regularities on sensory perception.

However, the evoked results presented in Chapter 3 could present departure from the predictive coding framework (Friston, 2002, 2005). According to this framework, high-entropy contexts present more challenges for the brain to model the world, thus resulting in lower confidence predictions and reduced prediction errors when encountering deviations from the (small) expectations (Lumaca et al., 2019). In contrast, in our findings we observed more negative N2-P2 amplitudes for the more variable temporal contexts, which potentially reflect increased surprisal response to the *timing* of targets, as they depart more often from the expected timing. Thus, in our task higher variability in the temporal intervals could have led to higher prediction errors. We interpret these apparent conflicting views as a distinction between high-entropy contexts and variable contexts but still containing regularities that can be useful to orient attention toward expected timings. In Lumaca study, they used very short sequences (between 1.3 and 1.6 s long) where no clear statistical rules could emerge, reversely our study was designed to let emerge probabilistic rules (if the brain was able to catch it) that could help to predict in time. According to this interpretation, when mismatch about the expected timing was met in probabilistic contexts, the brain interprets this as an error. This error occurred less often when the sensory contexts are more regular. Whereas in high entropy contexts, when you can't make expectation in time, the brain habituates to the entropy and lose confidence in its predictions, so that less prediction errors are elicited in the brain activity. This interpretation of these apparent conflicting results also suggests that even in our more variable contexts, participants were still able to use the small temporal regularities present in the sensory context.

5.3.2 Can neural oscillations entrain to naturalistic stimulations?

Neural entrainment is supposedly tolerant to timing variability and observable for stimuli that are not fully isochronous (Barczak et al., 2018; Breska & Deouell, 2017; Calderone et al., 2014; Doelling et al., 2019; Herrmann et al., 2016; Kösem et al., 2018; Lakatos et al., 2008, 2019; Obleser et al., 2017) just as human rhythm perception (Carlsen & Witek, 2010). However, an open debate on the literature emphasizes the actual need to test whether these non-fully regular contexts directly stimulate the endogenous brain oscillations (i.e., entrainment), or rather elicits a series of evoked potentials independently of intrinsic oscillatory activity (i.e., neural tracking

of the stimulation) (Zoefel, et al., 2018). This need for clarification of the terminology relating to neural entrainment has been proposed to designate entrainment in the narrow sense when referring to endogenous oscillatory processes, and entrainment in the broad sense when referring to alignment of brain and stimulus when unclear underlying process (Obleser & Kayser, 2019). Is it still uncertain, whether entrainment in the narrow sense could be the mechanism underlying temporal predictions in naturalistic stimulations. In the case of naturalistic stimulations such as speech, some data have demonstrated that neural fluctuations induced by the external stimuli can persist a few cycles after the end of the stimulation. For instance, low-frequency sustained activity persisting after a change in the speech rate (Kösem et al., 2018). Such speech echoes outlasting the external stimulation provides evidences toward entrainment in the narrow sense in non-periodic contexts (Kösem et al., 2018; van Bree et al., 2021). Finally, another argument in favor of such putative 'true' entrainment in speech comes from FFR studies, frequency-following response (FFR) is an index of neural periodicity encoding that can provide a vehicle to study entrainment in frequency ranges relevant to speech and music processing. Repeated syllables over time induced FFR for up to 40 ms at subcortical levels and even longer durations at cortical levels suggesting that neural entrainment, at least during repeated speech elements, could be useful for the encoding of sounds (Coffey et al., 2021). In natural contexts of spoken speech for instance with a constant syllable rate, this neural echo alignment with the expected timings can be mechanistically very relevant for the brain to produce expectations. However, is it to note that other studies points to a more mitigate effect of such speech echoes on auditory perception (L'Hermite & Zoefel, 2022; Vilà-Balló et al., 2022).

Recently, a convincing paper tried to reconciliate the Bayesian and the neural entrainment frameworks (Doelling et al., 2022). In this paper, Doelling and colleagues, demonstrated that, in a timing estimation paradigm where participants were asked to track pseudo-rhythmic tone sequences, the participants behavioral performances could be predicted by a Bayesian model. Then, they showed that, using a frequency adaptive oscillator model that spontaneously adapts his frequency based on the stimuli rate, they also successfully modeled participant performances. This finding bridges the gap between these two apparently distinct approaches to the study of temporal predictions. Additionally, this particularly relevant study makes the prediction that neural entrainment mechanism (modeled by adaptive oscillators) should adapt to sensory contexts with temporal variability. Indeed, adaptive oscillators are not metronome and are tolerant to a certain range of temporal variability. Stuart–Landau neural oscillatory

models are still able to synchronize to temporally variable stimuli, with SOAs drawn from Gaussian distributions with standard deviations going up to 20% of the mean SOA. Although this subsequent deviation from periodicity, the oscillator still peaks at the expected time and phase at this time is highly concentrated across repeated simulations. (Doelling & Assaneo, 2021). Thus, although neural oscillators are physically constrained by their eigenfrequency (e.g., auditory system, (Obleser & Kayser, 2019; Pesnot Lerousseau et al., 2021)), oscillators are also flexible to a certain range of temporal variability, suggesting that rhythmic inferences could be constrained by the inherent physical limits of oscillators themselves (Doelling et al., 2022). We presented evidence in this thesis, that probabilistic distributions can be inferred by the human brain up to a temporal standard deviation of 15-20%. Altogether, these works supporting the idea that rhythmic inferences could be carried by adaptive neural oscillators that can physically handle a certain range of temporal variability and then, when this temporal variability becomes too high, fail to synchronize with external stimuli rates.

In this thesis, we provided evidence about a neural tracking at the stimulation rate (i.e., 2 Hz power) in non-periodic contexts, specifically, when the temporal intervals were based on probabilities of occurrence. We observed that neural tracking is more pronounced in contexts with higher regularity, while a decrease in temporal regularities leads to a reduction in neural tracking. These findings align with the research conducted by Herrmann and colleagues, which revealed that entrained delta oscillations occur in response to temporally variable sound sequences, with fluctuations in amplitude throughout the sequences (Herrmann et al., 2016). Notably, the phase of entrained delta oscillations was found to be indicative of the ability to discriminate sound deviants, but this was only evident when delta entrainment was robust (Herrmann et al., 2016). Our study did not fully replicate this effect. As mentioned in Chapter 3, we did not find a correlation between neural tracking strength and the percentage of correct responses. Conversely, we observed an effect on response time (RT), where trials with greater neural tracking exhibited faster overall RT. Additionally, we identified an interaction between neural tracking and temporal context, indicating that the relationship between strength in neural tracking and RT was predominantly observed for periodic auditory sequences. Therefore, our findings warrant caution in interpreting neural tracking (or entrainment) as the underlying neural mechanism for generating temporal predictions in probabilistic settings, as the only correlation between neural oscillatory activity and behavior was observed in response to periodic sequences. Future investigations into phase coherence will be beneficial for further exploring this question, with the expectation that inter-trial phase coherence (ITPC) at the point

of target arrival will be stronger in regular contexts. Moreover, we anticipate that this phase coherence will correlate with behavioral responses, including improved accuracy and faster RT, when phase alignment occurs at the time of target arrival.

5.3.3 Are neural entrainment mechanisms necessary to elucidate the rhythmic advantages in perception?

While our findings can be partially understood within the neural entrainment framework, the evidence supporting neural entrainment in naturalistic contexts remains limited and indirect. Various studies have attempted to evaluate the causal effects of neural tracking on speech comprehension but have yielded inconsistent results (Dai et al., 2022; Kösem et al., 2023; Zoefel & VanRullen, 2016). The primary challenge in addressing this complex issue lies in distinguishing between evoked activity that recurs due to the rhythmicity of the stimulus and endogenous entrained activity (Zoefel et al., 2018). While the neural entrainment theory may provide insights into periodic contextual advantages, it is important to consider that alternative mechanisms might also contribute to these effects.

First, even if neural tracking does not reflect entrainment in the strictest sense, it can still be a valuable measure of statistical learning (e.g., in syllable streams) (Sjuls et al., 2024). Therefore, while neural tracking may not be a definitive proof of neural entrainment, it can still reflect a mechanism for temporal predictions in periodic and probabilistic contexts that depend on low-frequency dynamics. Supporting this hypothesis, low-frequency neural dynamics have been shown to reflect temporal predictions in non-entrained sensory contexts, particularly when those predictions rely on memory-based patterns (Wilsch et al., 2015; Daume et al., 2021; Herbst, et al., 2022; Breska & Deouell, 2017). Nevertheless, it remains possible that memory-based predictions and temporal contextual predictions could rely on distinct yet co-existing neural mechanisms (Bouwer et al., 2020; Bouwer et al., 2022).

Other mechanisms of temporal inference have been put forward, that do not rely on neural tracking mechanisms, and could alternatively explain our results. Neural oscillations in the beta band (~20 Hz) has been shown to reflect predictive timing (Arnal et al., 2011; Arnal & Giraud, 2012). A recent paper has explored the concept of confidence implementation in the brain and presented evidence that confidence about the prediction modulate the arousal (i.e., orient

temporal attention to the expected timing) and the beta oscillations, suggesting a supposedly important role for the stabilization of confidence (Meyniel, 2020). Thus, this suggest that the confidence about prediction would modulate the intrinsic properties of the brain state. Such brain mechanism for rhythmic inferences would also support an idea of prediction errors carried by the neural activity. When sensory data deviates from established rhythmic inferences, it produces surprise signals that can be detected in neuronal activity (e.g., mismatch negativity effects, characterized by vigorous neuronal responses to unexpected stimuli). These prediction error signals may serve as effective indicators of rhythmic inference mechanisms.

Additionally, the implication of the attentional system may be advantageous in directing temporal attention to anticipated timing locations. Alpha oscillations could play a critical role in this process by facilitating top-down control to manage attention (Samaha et al., 2015). Alpha oscillations have been put forward as useful instrument for sensory selection (Bonnefond & Jensen, 2012; Jensen et al., 2012; Samaha et al., 2015), as the phase of alpha oscillation can determine whether a stimulus is perceived. Specifically, there is a greater likelihood of missing sensory stimuli during periods of heightened alpha activity (Busch et al., 2009; VanRullen, 2016). Therefore, this rhythmic inference mechanism may leverage the attentional system through top-down control to calibrate alpha oscillations in alignment with both attended and unattended events.

Consequently, it is not trivial to disentangle between entrainment or top-down attentional effects in our data. Future analyses of alpha-beta oscillations may help to elucidate this question in addition to phase coherence analyses. We do not rule out the possibility that these two mechanisms are part of the same general mechanism in the brain enabling statistical inferences to help the brain predict the future. In summary, neural activity reflecting prediction errors appears to be a good marker of rhythmic inferences and provides clues to the contextual benefits of rhythmicity on perception. Finally, further work is needed to unravel these mechanisms and study the brain structures involved in temporal predictions in rhythmic contexts.

5.4 Conclusion

The human brain is sensitive to temporal regularities history and can take advantage from these regular patterns to optimize the sensory perception. This benefit of temporal predictability decreases rapidly as the temporal variability in the sensory context increase. Our work provides evidence that the temporal predictability based on context influences both evoked responses to target sounds as well as neural tracking. We also posited that dyslexia may be associated with a deficit in temporal prediction abilities, which could impact auditory and language perception. Finally, we discussed the implications of these results for the neural mechanisms of temporal predictions. Overall, this thesis provides elements to discuss further the mechanisms allowing temporal prediction in both the typical and pathologic human brain.

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