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# How to best assess duration perception in the lab and the wild?: an exploratory journey into measuring time perception in train travels, and challenging the automaticity of duration deviance with neuroimaging

Yvan Nedelec

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Yvan Nedelec. How to best assess duration perception in the lab and the wild?: an exploratory journey into measuring time perception in train travels, and challenging the automaticity of duration deviance with neuroimaging. *Neurons and Cognition [q-bio.NC]*. Sorbonne Université, 2024. English. NNT: 2024SORUS157 . tel-04825388

**HAL Id: tel-04825388**

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# Thesis manuscript of Sorbonne Université

Doctoral school n°158 “Cerveau, Cognition, Comportement”

Presented and defended publicly by

Yvan Nédélec

## **How to best assess duration perception in the lab and the wild?**

**An exploratory journey into measuring time perception in  
train travels, and challenging the automaticity of duration  
deviance with neuroimaging**

Directed by Dr. Virginie van Wassenhove

Defended the 07/06/2024 in front of the jury composed of:

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# Acknowledgments

First of all, I would like to thank the members of the jury, Pr. Sylvie Droit-Volet, Dr. Anne Caclin, Dr. Florian Waszak, and Dr. Valérie Gyselinck, for the time and effort required to evaluate my work. This precious time was taken out of their own research, which makes me even more grateful.

I would also like to thank the members of my annual thesis follow-up committee, Dr. Hedderik van Rijn and Dr. Christophe Lopez, for the many pieces of advice they gave me on my work, but also on how to organize the life of a young researcher.

I don't have the words to clearly express my gratitude to Virginie van Wassenhove, without whom all my work would never have existed. Thank you for trusting me with this PhD. I thank you for guiding my thinking, supporting, and motivating me when necessary. Finally, I thank you for sharing your knowledge and experience with me, and for all the enriching discussions we've had.

I thank all the members of the Cognition and Brain Dynamics team, with whom I have shared this scientific adventure:

Sophie, thank you for the many discussions that enabled me to constantly improve my work, but also for your encouragement.

Leila, thank you for your help with the technical aspects, but also mainly for sharing your daily good humor.

William, thank you for giving me the basic knowledge required for a cognitive neuroscientist.

Christina, thank you for your help with the analyses (MMN and questionnaire), but above all for sharing your vision of research and for your many tips.

Camille, thank you for your energy, your passion, your rigor and precision, and for your friendship which helped me through the hardest times and to finalize this PhD.

Marianna, thank you for forcing me to clarify my thoughts by thinking out loud with you, and sharing our respective questions. Thank you also for all the time we spent together outside science.

Valentine, thank you for your quick wit, constant good humor, and precise thinking, all of which have greatly contributed to my work. Thank you for all the moments and discussions we shared, whether scientific or simply to remake the world.

Raphaël, thank you for your immense help with the various experiments we carried out together, but above all for all the discussions and little moments in between these experiments.

Anna, thank you for your calm and for your philosophical wisdom, which helped me to refine my scientific thinking.

Yunyun, thank you for your explosiveness, your good humor, and your critical mind which allows you to question even the smallest parameter.

Harish, thank you for being my 1st PhD companion, and for sharing with me the best (but also the worst) moments of a PhD.

I would also like to thank all the former members of the team with whom I've worked, from near and far: Dragana, Izem, Paul, Diane, Anna, Tad, Ignacio, Mathias, Cyril, Elisa, Robert, and all the others.

I thank the WildTimes consortium, for the scientific discussions, but also the good atmosphere around this project: Valérie, Simon, Thong, Simone, Guillaume, Elise, Archana, and Emile.

I thank the entire Neurospin staff for their warm welcome, and especially the UNIACT nurses who helped us so much in recruiting participants.

I would also like to take this opportunity to thank all the participants in my studies. They are real adventurers who give us a little of their time to further our research.

I thank all my colleagues at UNICOG, and especially those I am happy to call friends:

Tiffany, thank you for this adventure and all the moments shared. Your invaluable help in drafting this manuscript will almost make me forget your betrayal when you moved office!

Théo, thank you for always being ready to help, scientific or otherwise, and for all our discussions. Thank you for all the moments outside science, which I hope to continue sharing for a long time to come.

Lorenzo, thank you for being the best office neighbor (despite your rare appearances), and for sharing your joy and friendship.

Alexandre, thank you for always being ready to share the difficult moments we go through, and for your example of stoicism in coping with them.

Science is a beautiful discipline, transcended by the people who dedicate themselves to it, and my greatest joy in this doctorate is to have met them and forged links with them.

Je remercie mes ami.e.s, les anciens comme les nouveaux, qui m'ont aidé à traverser cette aventure, de près comme de loin.

Manu, merci d'être mon 3<sup>ème</sup> frère. Un de mes rares regrets de ce doctorat est de n'avoir pas pu passer plus de temps à tes côtés (ce que je compte bien changer).

Lise, merci pour ton amitié que je chéris. Tu es un exemple d'organisation, de précision et de résilience. Merci aussi pour tes retours et encouragements sur ce manuscrit.

PA, merci. J'ai rencontré très peu de personnes comme toi, toujours prêtes à discuter et essayer de comprendre l'autre indépendamment de son propre point de vue. C'est un plaisir pour moi de te connaître et de te côtoyer.

Rémi, merci pour cette nouvelle amitié qui a été un vent de fraîcheur (et de studiosité) crucial pour les derniers mètres de ce doctorat.

Je remercie également mes ami.e.s de longues date : Camille, Leslie, Benjamin, et tous les autres.

Je remercie ma famille pour son soutien et son amour, qui est une source d'énergie indispensable dans toutes situations. Je remercie mes grands-parents : Mamina (Catherine), Mamie (Anic), Papy (Jean) qui ont toujours été des exemples que j'espère atteindre un jour.

Je remercie également ma belle-famille qui est tout aussi supportrice et toujours prête à me venir en aide : Céline, Max, Laurence, Stéphane, Valérie, Léa, Balqis.

Je remercie ma (plus si) petite sœur Angèle, pour son courage, son originalité et sa bienveillance qui m'inspire chaque jour.

Je remercie mon grand frère Lucas, avec qui j'ai partagé un si grand nombre d'expériences, et qui est toujours resté attentif et a veillé sur moi.

Je remercie mon grand frère Gabriel, qui a si souvent été, et continuera d'être, un exemple à suivre, qui surveille de loin, mais de manière attentive, l'évolution de ses petits frères et sœur.

Je ne le dis pas assez, mais j'espère que vous le savez, je vous aime.

Je remercie mon papa, Frédéric, de m'avoir transmis ton goût pour la recherche et ta curiosité, qui ont été mes outils les plus utiles pour ce doctorat. Merci pour tous tes conseils, ton soutien, et ton amour. Je t'aime.

Je remercie ma maman, Christine, de me soutenir de manière indéfectible et de toujours croire en moi (bien plus que moi-même). Tu es un exemple de bravoure, de sensibilité, et de sagesse, que je chercherai toujours à atteindre. Je t'aime.

Je remercie mon amour, Charlotte, qui partage ma vie et m'épaule au quotidien. Merci pour ton énergie, ton engagement, et ta capacité de tout remettre en question qui me permet de toujours m'améliorer. Merci de m'avoir sorti du moment le plus difficile. Merci pour tout ce que tu m'apportes, et bien plus, je t'aime.

# Abstract

Temporal cognition refers to our ability to estimate and use temporal information ranging from a scale of milliseconds to several hours. Although a large amount of experimental work has been performed in the laboratory to identify which factors (e.g., attention, emotion) influence our perception of duration, it is unclear whether these results generalize to our daily-life experiences. This fundamental and historical issue in experimental psychology refers to the “real-world or lab” dilemma, whereby laboratory constraints required to obtain reliable behavioral measurements question their ecological validity. My thesis work confronts this dilemma by aiming at exporting laboratory experiments used for duration perception research to an ecological and urban context: train travels.

In the lab, I first used electroencephalography (EEG) to explore and titrate a neural marker of automatic duration coding, the mismatch negativity (MMN). The MMN automatically detects deviances and has been reported for changes in duration. Herein, I wanted to use the MMN as an implicit and automatic marker of duration coding for use in trains. I tested several experimental protocols to characterize and replicate the duration MMN, including testing different duration scales (N = 23) in rhythmic or non-rhythmic contexts (N = 29). However, my work challenges the robustness of the previous duration MMN reports and discusses whether prior experimental work truly made the case for the existence of a duration MMN.

In the train, using a questionnaire approach, I explored the estimation of duration, distance, and speed and their relationship during train journeys (N = 247). I found that participants correctly estimated the elapsed duration and the distance traveled, exhibiting a regression effect near the halfway point of the travel. Participants were less accurate for speed estimates, that did not predict duration nor distance estimates from the other magnitude. Additionally, sensory information available onboard had little effect on duration and distance estimation. Instead, several results suggest that distance was estimated using duration and the *a priori* knowledge of the journey, supporting the use of a temporal cognitive map.

In sum, my PhD thesis shows examples of the benefits of the ecological approach, ranging from challenging accepted findings to discovering new specific observations from everyday life. This work opens new avenues of research, both in the laboratory and in more ecological contexts, which will provide a better understanding of duration perception mechanism.

# Résumé

La cognition temporelle fait référence à notre capacité à estimer et utiliser des informations temporelles allant de quelques millisecondes à plusieurs heures. Bien qu'un grand nombre de travaux expérimentaux aient été réalisés en laboratoire pour identifier les facteurs (par exemple, l'attention, l'émotion) qui influencent notre perception de la durée, il n'est pas certain que ces résultats s'appliquent à nos expériences de la vie quotidienne. Cette question fondamentale et historique en psychologie expérimentale renvoie au dilemme "monde réel vs laboratoire", selon lequel les contraintes de laboratoire nécessaires à l'obtention de mesures comportementales fiables remettent en question leurs validités écologiques. Mon travail de thèse confronte ce dilemme en visant à exporter des expériences de laboratoire utilisées pour la recherche sur la perception de la durée dans un contexte écologique : les voyages en train.

En laboratoire, j'ai d'abord utilisé l'électroencéphalographie (EEG) pour étudier et titrer un marqueur neuronal de l'encodage automatique de la durée, la négativité de discordance (MMN). La MMN détecte automatiquement les changements dans l'environnement sensoriel et a été rapportée pour des changements de durée. Ici, je cherchais initialement à utiliser la MMN comme marqueur implicite et automatique de l'encodage de la durée afin de l'utiliser dans les trains. J'ai testé plusieurs protocoles expérimentaux pour caractériser et reproduire la MMN de la durée, notamment en testant différentes échelles de durée ( $N = 23$ ) dans des contextes rythmiques ou non rythmiques ( $N = 29$ ). Mes résultats remettent en question la robustesse des travaux précédents sur la MMN de la durée. Cette observation corrobore avec ma revue de littérature qui examine si les précédentes études ont réellement démontré l'existence d'une MMN de la durée.

Dans la situation écologique d'un train, à l'aide d'un questionnaire, j'ai étudié l'estimation de la durée, de la distance et de la vitesse, ainsi que leur relation au cours d'un voyage en train ( $N = 247$ ). J'ai constaté que les participants estimaient correctement la durée écoulée et la distance parcourue, avec un point de régression situé vers la moitié du trajet. Les estimations de vitesse étaient moins précises et ne permettaient pas de prédire les estimations de durée ni de distance à partir de l'autre magnitude. De plus, les informations sensorielles disponibles à bord du train ont eu très peu d'effet sur les estimations de durée et de distance. Au contraire, plusieurs autres résultats suggèrent que la distance a été estimée à partir des estimations de durée et les connaissances *a priori* du voyage. Cela soutient l'hypothèse que les participants ont utilisé un mécanisme de carte cognitive temporelle, plutôt qu'un mécanisme de magnitude basé sur les sens, pour leurs estimations.

En résumé, mon doctorat montre des exemples de l'apport de l'approche écologique en neuroscience cognitive, allant de la remise en question des résultats couramment acceptés dans la littérature, à la découverte de nouvelles observations spécifiques à des contextes de la vie de tous les jours. Ces travaux ouvrent de nouvelles pistes de recherche en laboratoire et en contexte plus écologique, qui permettront de mieux comprendre les mécanismes de représentation de la durée, afin de préciser l'organisation et la représentation du temps de manière plus globale.

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# Preface

This Preface aims to first provide the context into which I conducted my PhD. Then, I present the personal interest and motivations I had when I started this PhD. After briefly introducing the initial plan of the PhD, I describe the actual work that was done throughout my PhD. I spell out the organization of the manuscript and finally state the scientific questions and objectives of this work. It is written in a more personal format than the other chapters, which follow a more classical scientific writing.

## 0.1. The WildTimes context

My PhD was part of the ambitious WildTimes research project (Project-ANR-18-CE22-0016), funded by the French National Research Agency (ANR). Although the rapid development of transport modes in the last century has changed our travel possibilities, and therefore potentially our conceptions of accessible traveled durations and distances, our knowledge of how we perceive space and time in these contexts is rather poor. The WildTimes project aimed to pave the way towards understanding space and time perception during real-world navigation and initiate how the human brain may map them during complex journeys. In very concrete terms, the project proposed to carry out cognitive neuroscience experiments in a real-life situation, such as a train journey.

## 0.2. Motivations

Within this project, my first point of interest was the innovative "Wild" approach, i.e. doing experiments outside the laboratory. As my Master's degree was more engineering-oriented, I knew very little about how cognitive neuroscience studies have been conducted in the laboratory so far. However, I had the desire (and intuition) to conduct experiments close to our everyday lives. It is only after the start of my Master's internship, that I discovered that the generalization of cognitive neuroscience results from the lab is often questioned, a dilemma coined "real-world vs. lab", which I discuss in Chapter 3 and the General Discussion. In addition to conducting behavioral tasks in the "real-world", there was also the proposal and possibility of a technical challenge by making electroencephalographic (EEG) recordings during a train journey.

My second point of interest in this project concerned the perception of time. My first interrogation on this topic came during a classic visual and auditory perception course. While learning about the classical sensory illusions, I wondered about those moments when time seems to pass faster or slower and, as a result, whether time should be considered as a perceptual process as well. This questioning led me to discover Virginie's team and her research program. During my Master's internship with the team, I became aware of the complexity and importance of the study of time for cognitive neuroscience. This convinced me to embark on this PhD journey.

### 0.3. Initial plan

The initial aim of my PhD was to characterize the perception of time (mainly duration as discussed in Chapter 1) and its different phenomenologies during an ecological context such as a train journey. To this end, I had initially planned to carry out various time perception tasks (endogenous/exogenous, implicit/explicit, see Chapter 1 for definitions) to capture variations in our perception of time through ecological factors such as the moment of travel (waiting time/travel time), sensory information (optic flow & acceleration), or expectations and uncertainties (expected travel time & delay).

More concretely, I had first planned to characterize implicit time perception as a function of optic flow orientation using a passive EEG task such as the duration MMN (but see Chapters 1-2) and an active task such as the foreperiod. I then planned to characterize endogenous and exogenous explicit time perception at various moments of the journey (waiting time/transport time) using duration production and temporal bisection tasks, respectively (or potentially spontaneous tapping or synchronized/continuous tapping tasks). It is work that I had already started during my Master's internship. Finally, I had also planned to develop a task to measure and disentangle the notion of the speed of the passage of time from perceived duration during a train journey.

### 0.4. Studies conducted during the PhD

As with most PhDs, preliminary results and external hazards largely influenced the progress and work carried out during my PhD. However, the financial support from the CEA (that extended my contract) and the flexibility of my doctoral school allowed me to pursue in proper conditions my deviating work from the original plan. First of all, preliminary laboratory results made me question the very existence of a duration MMN (that is not questioned after a first glimpse at the literature), which led me to a literature review specifically on duration MMN (Chapter 1) and three empirical studies (Chapter 2, Annex 5.2, acquired but unanalyzed data mentioned in Chapter 2). Second, the COVID-19 pandemic crisis made data acquisition onboard trains complicated and uncertain for several months, reducing the number of experiments carried out on trains. Thanks to the help of interns and research engineers from the team, we were nonetheless able to collect data across train journeys on questionnaires (Chapter 3), resting-state EEG

(Bordas et al., in prep.), and time perception tasks for the WildTimes project (foreperiod, tapping continuation, duration production, violation of temporal expectation and speed of the passage of time judgment). I was involved in designing some of the studies, helped organizing and collecting the data, and I analyzed some of them (questionnaires, duration production). Additionally, I had the wonderful opportunity to work with a Master's student and contributed to the design of her published study (co-authored, Annex 5.3). In this study, we disentangled the estimation of duration from the speed of the passage of time by manipulating event density.

## 0.5. Manuscript organization

In agreement with my Ph.D. mentor, my manuscript is written as a sum of journal articles. The discontinuity between the laboratory studies on MMN (Chapters 1-2, Annex 5.1-5.2) and the onboard questionnaire study (Chapter 3), as well as the differences in methodology, seem to lend themselves better to this format. Those works are nonetheless all investigating how durations are computed and perceived. I humbly try to develop common reflections in introductory chapter paragraphs and my General Discussion (chapter 4).

To make this manuscript easier to read, an introductory paragraph before each chapter will provide a quick reminder of the chapter's context, objectives, and content. It may seem like redundancy in a full reading, but I hope it will make it easier to pick up information quickly and read each chapter independently.

## 0.6. Scientific questions and objectives

The main questions investigated in my PhD were:

- ❖ Are there enough data to claim that duration is coded in the MMN process?
- ❖ When an empty duration change is specifically tested, do we observe an MMN potential?
- ❖ How are durations estimated in an ecological context such as a train journey, and are they influenced by the available sensory information onboard?

Here are the main associated objectives of each chapter:

- ❖ Chapter 1 sets out the theoretical framework I use to study time in cognitive neuroscience. Then, throughout a literature review, I put forward that there is insufficient empirical data to assert the existence of mismatch negativity (MMN) for duration change detection.
- ❖ Chapter 2 demonstrates that using careful methodology for the study of MMN, no robust evidence for MMN to duration detection change is observed. I complement this observation with a careful assessment of the limitations of published findings and my own work.
- ❖ Chapter 3 explores an *In Situ* and in the “wild” experimental design assessing travelers’ estimation of duration distance and speed during a train journey. Based on empirical observations, I discuss the possibility that travelers’ duration estimates are inferred from knowledge rather than sensory estimates, appealing to a temporal cognitive map of train journeys.
- ❖ Chapter 4 briefly summarizes each empirical work, and discusses the links between studies, additional thinking, and/or observations from the research work of my PhD.

# Chapter 1 – Of duration perception and MisMatch Negativity (MMN)

This chapter aims to set out the theoretical framework I use to study time in cognitive neuroscience and to demonstrate that there is insufficient empirical data to assert the existence of a duration MMN, by means of a literature review. I originally intended to use the duration MMN as an implicit marker of duration perception onboard trains to test if we could measure any change in duration perception in the absence of an explicit duration estimation of the participant. First, I spell out my theoretical framework of cognitive neuroscience. Second, I describe the classical taxonomy of time perception, and then propose an alternative named temporal cognition based on a more concrete operationalization of time-related brain processes. Third, I introduce the MMN potential and briefly describe the current understanding of this automatic brain response. Fourth, I explain the main challenges for the study of duration changes in the MMN process and announce the three main points to consider when reviewing MMN articles of duration. Fifth, I describe more specifically the studies that allow us to discuss the effects of the direction of deviance, the existence of particular duration thresholds in this process, and the importance of distinguishing the notion of duration from temporal expectation in the MMN studies. Lastly, I conclude that there is currently insufficient evidence demonstrating the duration MMN and propose an experimental design to remedy this.

## 1.1. Introduction

In this first part of the chapter, I start by spelling out my theoretical framework stating why the understanding of how the brain processes time is important in cognitive neuroscience. Then, I present the classical taxonomy of time in cognitive neuroscience and provide my opinion on how we could clarify it. Next, I discuss whether the duration is a good candidate for the representation of time in the brain. Finally, I propose to study whether the brain automatically processes duration to investigate whether duration is a basic material and format for the representation of time.

### 1.1.1. Background and theoretical framework

The existence of a spiritual substance, often named soul, that enables the control of our bodies to interact with the surrounding world, is probably one of mankind's oldest questions. Even before the first written traces of philosophical reflection on the topic, the observation of funeral rites could already be considered evidence of a belief in a spiritual existence beyond matter, which would depart from the body - made of biological matter - when an individual dies (Wickens, 2014). However, the scientific study of the soul, often termed psyche in philosophical thinking and which encompasses mental activities, is very recent. In this section, I make a brief summary of the history of the study of the soul (i.e. the mind) and state why I think understanding time in cognitive neuroscience is necessary.

While our ancestors continuously believed that the soul was closely linked to the heart, the description of brain lesions directly impacting human behavior by Thomas Willis, father of neurology, in the mid-17th century, popularized and disseminated the idea of a close link between soul and the brain (Gazzaniga et al., 2006). The emergence of computer sciences and information theories in the mid-20th century, at the origin of the cognitive revolution, allowed the beginning of a research program enabling the scientific study of the soul, as the mind (Núñez et al., 2019). In this research project, coined cognitive sciences, the mind can be seen as a set of mental processes that can be described by representations and operations (Cummins, 2000). The increasing discoveries of neurology, and its expansion into neuroscience, confirmed the key role of the brain in controlling the body and mental processes (Gazzaniga et al., 2006). As the relationship between the mind and the brain becomes more and more evident, all

scientific studies of the mind-brain relationship now fall under the umbrella of the cognitive neuroscience discipline.

To explain the mapping of the external reality into mental processes through the brain, the concept of representation is needed. Representation is a loaded term, and there are still ongoing debates about what authors are referring to according to their backgrounds (Fallon et al., 2023). Herein, the way I use representation follows the definition of Randy Gallistel: “The brain is said to represent an aspect of the environment when there is a functioning isomorphism between some aspect of the environment and a brain process that adapts the animal's behavior to it” (Gallistel, 1990). Thus, a functioning isomorphism is a process that maps entities, relations, and operations between two systems, the represented and the representing. For the brain, it would consist of defining a mapping between the external reality and its electrochemical activities that would reflect the external entities, but also their relations and operations.

Our goal, as cognitive neuroscientists, is to understand the mind-brain relationship rather than just describe it (Krakauer et al., 2017). However, it is unlikely that the “simple” description of brain processes will lead to an understanding of the mind. Observing brain processes to understand the mind could be seen as observing the internal pieces and mechanics within a windmill. It is unlikely that by observing those internal mechanics, we could understand the complete functioning of the windmill. This problem is called the Leibniz’s gap, describing a gap between the concepts we use to describe the mind and those we use to describe the brain (Cummins, 2000). To bridge this gap, we usually focus on the output of the mind-brain relationship, often reduced to specific behaviors in animal or human research. To guide my research work, and jump over Leibniz’s gap, I use the three-level analysis proposed by David Marr, developed to study any complex information-processing systems (Marr, 2010). The first level is the computational goal, e.g. the behavior that we want to study resulting from the mind-brain relationship. We could think of milling grain for the windmill as an illustration. The second level is the algorithm, e.g. what are the entities and the operations to realize a given behavior. In our illustration, this would be the operations needed to create and apply forces on grains, to grind them and turn it into flour. The third level is the implementation, e.g. what are the bio-physical substrates of the entities and operations, hence generally the brain structures and processes. This would be the mechanics and the wind blades shape in our illustration on the windmill.



I just discussed that one approach to understanding the mind is to decompose it into different modules, responsible for different behaviors. However, all behaviors happen over time, yet their temporal dimension is often set aside when we investigate a peculiar behavior. The brain itself, by its intrinsic activity, possesses its own dynamic. How time is tracked, stored, and used in any behavior is therefore crucial to understanding the mind-brain relationship and developing a complete theoretical proposal of the mind, and the brain (Buonomano, 2017).

### 1.1.2. The study of time in the mind: temporal cognition

While time seems a familiar and shared concept across mankind, as soon as we want to explain it, we face its complex nature, as formulated by Saint Augustine in the fifth century (Hippo., 1841, p. 338). The origin and the nature of time is a controversial topic investigated by philosophers and physicists that we can trace back to the fourth century, and its first physical measurement to 4 000 years BC (*Introducing Time – Icon Books*, s. d.). Time, as a word and concept, is used in many scientific domains, but results in a polysemy that makes the very notion of time even fuzzier (*TimeWorld Temps – Rencontres scientifiques mondiales*, s. d.; van Wassenhove, 2023). To clarify the notion of time and how it is used across disciplines, we need to make the effort to clearly spell out what aspect of time we are working on. For example, the theory of relativity is incompatible with the global notion of present across the universe (Carlo, 2017), but it needs to be clarified whether cognitive neuroscientists should also take into account those aspects of time (Buonomano & Rovelli, 2023). Hence, in this section, I first briefly describe the current taxonomy of time that can be found in the literature of cognitive neuroscience and then discuss the framework I used to approach time in the mind-brain, named temporal cognition.

For cognitive neuroscientists (with an evolutionary perspective), I would say that the question of time could be reduced to “simply” how the mind-brain keeps track of the time passing, stores temporal information, and uses it for higher-level computations to guide and plan behaviors for interacting with our dynamic world. We do not need to ask ourselves what is the nature and origin of physical time, the truth of the notion of a global present, or whether time passage is just an illusion. We are interested in the different possibilities of how physical temporal information is represented, and therefore used, by the mind-brain resulting in a subjective time. The physical reality of

temporal information, that we are interested in, is the one that can be measured with physical devices, often labeled as objective time (van Wassenhove, 2023).

The study of time in the mind-brain usually falls under the umbrella of time perception, whose aim is to study subjective time, which refers to the sensation of time (Matthews & Meck, 2016). This view is mainly inherited from William James, where the sensation of time deviated into the sensation of time-as-duration (Myers, 1971). The influence of psychophysics (Fechner, 1860) required to define what was the appropriate stimulus to study the sensation of time, i.e. to define the physical quantity from which the sensation of time arises when converted into brain signals. Quite intuitively, and also linked to the notion of the specious present (what is the now of consciousness, or what is the duration of now in the mind), it fell onto duration (van Wassenhove, 2017). In other words, the question of time perception became reduced, in a way, to “how does the brain measure time interval?” (Droit-Volet, 2018). The taxonomy of time perception developed in cognitive neuroscience, which I usually encountered in my readings, is mostly based on the methodology used (Droit-Volet & Wearden, 2003; Matthews & Meck, 2016; Grondin, 2017).

The first distinction that can be found in time perception is whether it is implicit or explicit (Nobre & van Ede, 2023). Implicit time perception refers to behavioral tasks that do not require a specific time judgment or estimation, but that will benefit from processing temporal information, typically a time interval. Explicit time perception refers to behavioral tasks where participants are asked to make an explicit judgment of temporal information, such as estimating, (re)producing, or classifying (between long and short) a duration. Whether implicit and explicit time perception rely on similar or distinct neuronal bases is currently being tested (Herbst et al., 2022). Although implicit timing involves more than just measuring a duration, such as hazard rate, synchronizing with a rhythm (Nobre & van Ede, 2018), or timing the motor commands (Grondin, 2010), it is often also considered part of time perception mechanisms (Nobre & van Ede, 2023).

The second distinction that can be found, under explicit time perception, is between prospective and retrospective judgments (Grondin, 2017). In studies of time perception, participants can be instructed in advance that they will have to estimate/judge the duration of a stimulus (or between stimuli), which refers to prospective judgment. In other studies, participants can be presented with a single time

interval without any clear instruction about time. Only after the presentation, they are instructed to estimate the duration, which refers to retrospective judgments (Grondin, 2010). Prospective judgments are described as being influenced by perceptual, attentional, and short-term memory processes, while retrospective judgments are described as relying much more on long-term memory processes (Matthews & Meck, 2016). For practical and quantitative reasons, it is easier to study prospective judgments than retrospective ones scientifically, since “pure” retrospective judgments can only be asked once per participant in a testing session. However, retrospective judgments are more likely to be closer to our daily-life estimation of duration and, hence, probably much more ecologically valid (Azizi et al., 2023).

The last distinction to be made in time perception is about the time scale under investigation (Grondin, 2017). It is unlikely that the representation of time at the circadian timescale would involve the same representation of time at the millisecond timescale (Fig. 1.1A). Distinct time scales can be defined based on the ways in which psychological factors such as attention and memory impact duration judgment (Rammsayer & Lima, 1991), or when the scalar variability is disrupted (Grondin, 2014). Personally, I would argue that the most classical thresholds of time scale are the 200 ms, the 1.2 s, and minute boundaries. Durations below 200 ms fall within the temporal window of integration, a temporal window that allows the processing of speech (Poeppel, 2003) and integration of (non)simultaneous sensory signals (van Wassenhove et al., 2007). Duration information at this scale can directly impact and influence how the brain (re-)construct stable speech percepts (van Wassenhove et al., 2007). Perceived durations below 1.2 s are more influenced by sensory processing and attentional processes while those above are more influenced by long-term memory processes (Thibault et al., 2023). Perceived durations at the minute/hour scale are related to memory processing and the subjective feeling of time passing (Droit-Volet, 2018).

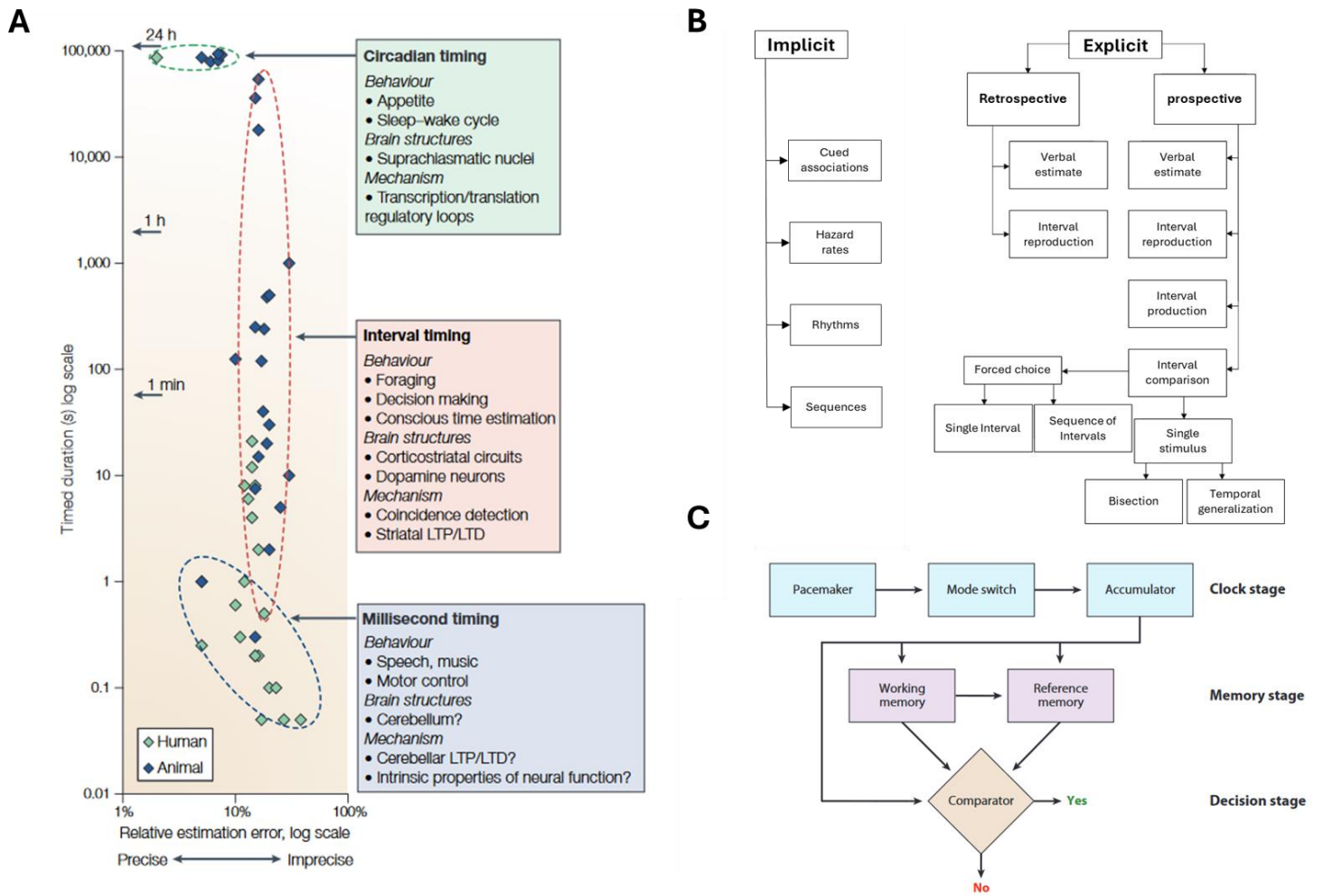
While this taxonomy is a useful starting point for categorizing and refining the methodology used by each research group interested in time, we can note a few limitations that, in fact, blur the research questions we are after. First, all researchers must agree on all the categories and share their exact same definitions (that are not intuitive, keeping in mind that cognitive neuroscience arose from the merging of 6 disciplines (Núñez et al., 2019)) along with making the effort to situate their work among it. Second, additional categories such as endogenous and exogenous timing could

be considered, which would encompass all the already defined categories (van Wassenhove et al., 2019). Third, within each category, we also need to define the diverse experimental paradigms used to quantify time perception (e.g. duration estimation, duration (re)production, temporal bisection, see Fig. 1.1B for more examples). Moreover, the necessary operations underlying these experimental paradigms should be clearly explained and reminded. This also raises the question of how to interpret a result in terms of associated phenomenology obtained in one paradigm (does an overestimation correspond to a feeling of duration passing more slowly?) and its generalization to other paradigms (should an underestimation due to one factor, measure with a duration estimation, necessarily induce an overproduction if the same factor tested is manipulated in a duration production task?). In a similar vein, the role and interactions of the other major mental functions (e.g. attention, working memory, or decision-making) with each of the paradigms need to be clearly spelled out. Finally, this taxonomy mostly focuses on time perception and its phenomenology in terms of duration. Other operations (simultaneity, order, perception of rhythm and synchronization with it, expectation of a future event, ordering of past and future events on a chronological map, etc.) could lead to different phenomenologies than duration (but still linked to the broad notion of time).

By reducing the question of time in the mind-brain to the time perception, largely focusing on duration perception, the computational goals and operationalizations of time, along with its associated phenomenology, are unclear. By unclear, I mean that they do not allow the clear distinction of computational goals, algorithms and implementations to study them, as proposed in the tripartite hypothesis of D. Marr (Marr, 2010). Clearer operationalizations for time could be found with parallelization of how space has been studied (Issa et al., 2020). The representation of space in the brain has been studied by examining various functions and behaviors related to space, such as navigation using path integration, egocentric positioning of landmarks, and computation of distances and so on. Each function can then be tested separately with potentially distinct neuronal computations and dedicated working hypotheses (van Wassenhove, 2023). As described in van Wassenhove (2023), an inspiring framework is coming from artificial intelligence, where J. F. Allen (Allen, 1983) described what are the necessary temporal relations between two time intervals. This operationalization suggests that a coordinate system that codes events “moment” (by timestamping) and extracts the

distance (duration) between events could provide a parsimonious system for humans (and animals in general) to navigate through time (van Wassenhove, 2023), as suggested by the interval and phase sense proposed by Randy Gallistel (1990). Therefore, all the operations and phenomenologies related to this mapping process of time constitute temporal cognition (among which time perception belongs). Throughout the rest of this manuscript, I try to avoid time perception, but when I use it, I refer to duration perception (how time intervals are measured by the mind-brain), unless otherwise specified (e.g. time perception literature that refers to the broad literature of time perception, not specifically the literature of duration perception). Pushing this reasoning to the extreme, I even think that it would be beneficial to eliminate the use of the word “time” in scientific studies and instead utilize the specific operationalization relevant to each study. Funny note: even if the Cognition and Brain Dynamics team seems to agree with this proposal, we have barely succeeded in removing the word time from our discussions. From this effort, I believe that a new, more informational, and less confusing taxonomy could arise for (young) researchers interested in temporal cognition.

That duration perception is only a part of temporal cognition does not tarnish its importance, attested by the (humble) fact that my work mostly focuses on it. All in all, what I wanted to discuss here is that the term time perception is unspecific and carries a lot of implicit assumptions that were not immediately clear to me when I dove into this research program. One possibility, to help future young researchers, could be to replace time perception with temporal cognition along with a clear operationalization of the behavior of interest at the beginning of each scientific article.



**Fig. 1.1:** A: time scales across behaviors (adapted from Buhusi & Meck, 2005). Specific behaviors occur at different time scales. It is unlikely that the brain uses the same representation of time across those different time scales. In their review, Buhusi & Meck disentangle three time scales: millisecond, interval, and circadian timing. B: Classical taxonomy of time perception (adapted from Grondin, 2010). Duration perception is often classified as explicit or implicit. Among explicit duration estimations, researchers distinguished prospective from retrospective estimations. Each category has a different set of paradigms. C: Schematic representation of the internal clock model (from Allman et al., 2014).

### 1.1.3. The issue of coding duration

Although duration perception is only one aspect of temporal cognition, understanding how the brain can actively measure time intervals (durations) remains a necessity. It could provide evidence of how time is quantified and can become, from a dimension that structures information in the brain, a representational content for consciousness (van Wassenhove, 2017) as witnessed by the large amount of work dedicated to it (Grondin, 2017, usually under the name of time perception, as discussed above). One major assumption in duration perception is that duration is the actual format of representation for time. This perception-based approach makes the strong *a priori* that duration would be a feature of the sensory world in the same way the amplitude of a sound or the luminance of a visual patch would be. It follows that the problem is framed as a perceptual issue of “how is the brain accurately encoding lapses of time?”, whereas I contend that the problem is a computational one and should be framed as “how is the brain accurately measuring and codes for lapses of time?”. Herein, I discuss whether the duration should be considered as the basic material and format for time representation and emphasize that we need to be careful, when we study duration representation, to escape the “signifier is not the signified” problem (van Wassenhove, 2023).

Perceived duration differs across sensory modalities (van Wassenhove et al., 2008), is highly subjective and malleable leading to numerous temporal illusions (Eagleman, 2008), influenced by a wide range of factors such as attention (Matthews & Meck, 2016), emotional state (Droit-Volet, 2013), tasks demand (Politi et al., 2018). Those behavioral observations suggest that perceived durations do not follow the linear objective time (van Wassenhove, 2009), and therefore not encoded as any other sensory feature, but rather as the result of a higher-level process. A duration can be defined as the quantity of elapsed time constituting an event or separating two sensory events, respectively filled and empty time intervals. Successful psychological models accounting for duration perception have been built on the internal clock model (Allman et al., 2014; Treisman, 1963). In the latest version of this model, a pacemaker produces ticks at a rate modulated by arousal. These ticks are registered in an accumulator, gated by attentional control to regulate the count. The resulting count is compared to a reference duration stored in memory (Fig. 1.1C). While a tremendous amount of work has been conducted on behavioral duration perception in animals (Gibbon et al., 1984; Tallot & Doyère,

2020) and humans (Buhusi & Meck, 2005; Grondin, 2017), possible neuronal implementations for duration perception remain debated.

Several electrophysiological studies found evidence for neurons firing both for a sensory feature and for a specific duration in the sensory cortex. Neurons firing with a sustained activity or firing at the offset of stimulus presentation with a duration tuning curve have been found in the visual cortex (Duysens et al., 1996) and the auditory cortex (Qin et al., 2009). While it was demonstrated recently that inhibiting those offset responses in the auditory cortex impairs duration discrimination in mice (Li et al., 2021), the link between these accurate neuronal temporal markers and our subjective experience of duration remains to be demonstrated (van Wassenhove, 2009). Furthermore, duration-tuned neurons are also found in non-sensory brain areas such as the parietal cortex (Leon & Shadlen, 2003; Nieder et al., 2006) and neurons encoding objective, not subjective, elapsed time can be found in the striatum (Toso, Fassihi, et al., 2021). Using human non-invasive neuroimaging studies, it was demonstrated that neural populations sensitive to objective duration are, again, not restricted to sensory areas, such as the right supramarginal gyrus in the parietal lobule (Hayashi et al., 2015) and the supplementary motor area (Protopapa et al., 2019). It was recently suggested that those duration-tuned neuronal populations are related to the subjective experience of duration rather than the objective duration (Hayashi & Ivry, 2020), but this could also simply be explained by an inter-individual sensibility of duration perception. Hence, the observation of signals correlating with duration (or the onset and offset etc.) cannot be directly considered as proof that this signal is the representation of the subjective duration.

The problem we face here is that we assume that duration selectivity neurons (or any neurons selective to temporal information) would be the implementation of the duration representation used by the brain. If we take the example of color perception, this means that we would expect neurons to turn blue when they code for blue. This is obviously not the case. Blue is coded by neurons that convert the information received on the retina and transmit the resulting signal to a decoding center responsible for the phenomenology of the color blue. In cognitive neuroscience, it is usually unlikely that the signifier is the signified (van Wassenhove, 2023). For the perception of duration, we need to distinguish between temporal information signals (which could be all neurons, given their activity over time) and those actually responsible for coding duration. This



problem as been already described and labeled the two-way non-identity problem (van Wassenhove, 2009).

#### 1.1.4. Automatic coding to investigate possible format of representation

I have just mentioned that finding a correlation between neural signals and temporal information (e.g. duration, onset, offset) is not a sufficient proof to consider that this information is indeed represented by the brain. To investigate whether a neuronal signal codes for duration, it seems more appropriate to examine mechanisms that involve operations on durations, than simply correlating with it. However, we would have to face the difficulty of proving that we are indeed in the presence of a mechanism specific to the information studied (duration in our case) and not just specific to the operation. For example, Ofir & Landau (2022) recently found an electrophysiological response following both the objective duration, and also the subjective appreciation of it (classifying it as shorter or longer than a reference), by using a temporal bisection task. Hence, the electrophysiological response they found can indeed be considered as coding for duration, since it does not simply capture the objective part of duration. Thus, these findings are additional evidence that we are capable of measuring durations and comparing them (as suggested by internal clock models), hence representing them, but it does not necessarily imply that duration is the basic format of time representation.

Knowing the extraordinary capacity of human to create and manipulate (thus to abstract) information, asking participants to perform a specific task (e.g. classifying duration as short and long) does not necessarily target the underlying format of representation of a concept (e.g. time representation). Hence, asking participants to consciously perform an operation (requiring a representational stage), such as classifying a duration, does not allow us to claim that duration is the underlying format of time representation, as hypothesized in internal clock models.

Added to the fact that the signifier is not the signified, studying whether the duration is one of the formats of time representation is therefore even more challenging. I propose that understanding whether an information can be considered a good candidate for the format of representation can be achieved by studying automatic operations performed on this information. In scenarios where conscious processing or attention is not required, the identification of a signal associated with a manipulation of the hypothesized format of representation (duration in our case) may provide

preliminary evidence that such information is readily accessible to the brain. This suggests its potential reusability for representing more complex concepts, such as time for duration. Notably, since the 1960s, the phenomenon of Mismatch Negativity (MMN) has been recognized as a neuronal marker of automatic encoding, offering a valuable tool for exploring such automatic operations. In the next part, I outline the current comprehensive understanding of the MMN, suggest how we could use it to investigate whether duration is automatically coded by the brain, and discuss the evidence required to state that duration is indeed coded in the MMN process.

## 1.2. MisMatch Negativity (MMN) as a marker for automatic operations in the brain

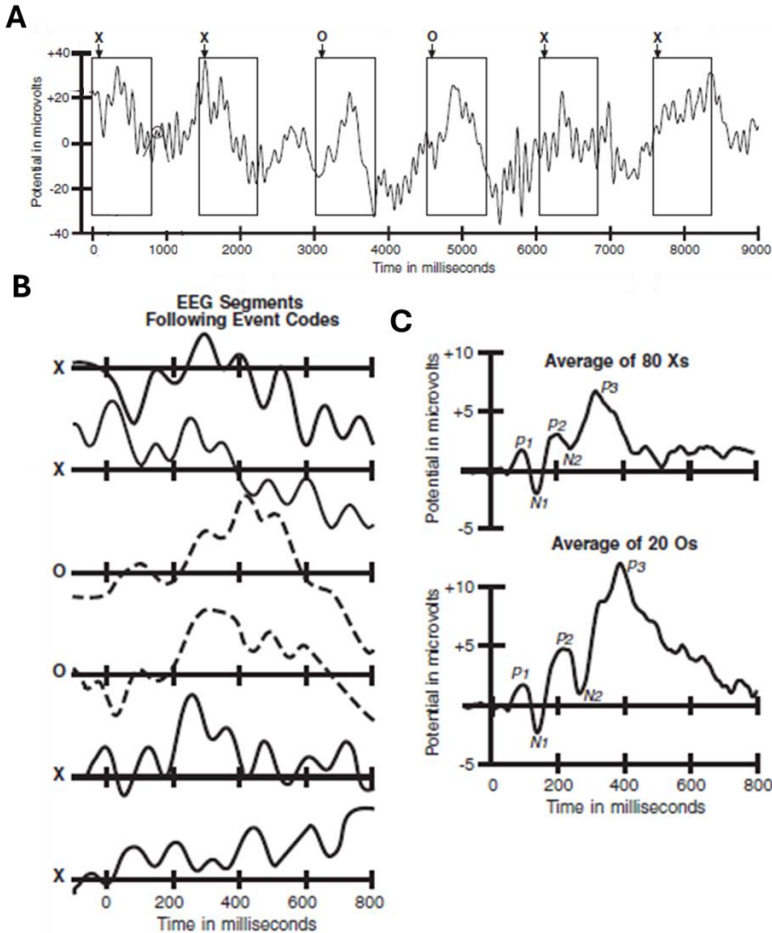
In this second part of the chapter, I will first introduce the Mismatch Negativity (MMN) potential and argue why it is typically considered a marker of automatic change detection in the brain. Second, I discuss the specific case of the duration MMN. I highlight three important aspects to be kept in mind when reading about duration MMN, together with a few methodological considerations from existing literature.

### 1.2.1. The MMN evoked response

To study whether duration is automatically coded by the brain, and therefore accessible as a format to represent time, I turned to Mismatch Negativity (MMN). In the seventies, an Event-Related Potential (ERP), a brain response time-locked to an event that we can measure with EEG, has been described as a marker for automatic coding, since it is observed even when participants are not specifically focusing on the presented event (Näätänen et al., 2012). In this section, I first briefly explain the ERP technique and introduce the oddball paradigm. Then, I mention how the MMN potential was discovered and the seminal studies demonstrating it for a change in duration. Last, I describe the general description of the MMN potential.

The ERP technique is a method to investigate time-locked neuronal activity elicited by the presentation of a stimulus in EEG recordings. It requires the repeated presentation of a stimulus, to average the EEG time-lock responses and emphasize the specific response of this stimulus, the so-called ERP (Fig. 1.2A). For example, it has been shown that the presentation of a sound elicits a specific sequence of positive and

negative ERPs, called auditory ERP and labeled as P1, N1, P2, N2 waves (Fig. 1.2C, stimulus X). In ERP studies, a long lasting and important question is “How does selective attention (specifically paying attention to one stimulus and not the others) impact the processing of sensory stimuli?”. Back in the seventies, the group of Hillyard (1973) found that the amplitude of the auditory N1 was amplified for a rare and different target stimulus compared to a repetitive standard stimulus, when participants were asked to specifically focus on one ear. This paradigm is now called the oddball paradigm, where participants are asked to detect a specific rare target stimulus (called deviant, O in Fig. 1.2C) in a stream of standard stimuli (called standard, X in Fig. 1.2C).



**Fig. 1.2: Illustration of the ERP technique (adapted from Luck, 2014).** A: Illustration of the EEG raw data at one electrode. X and O correspond to the presentation of different sounds. Rectangles are time-locked windows to stimuli (named epochs) used for the averaging process of the ERP technique. B: Each line corresponds the stimulus epoch from A. In the ERP technique, the epochs of X are averaged to remove the noise from the time-locked brain activity resulting from the presentation and processing of the stimulus. C: Evoked Response Potentials (ERPs) of the X and O stimuli.

Another group of researchers, led by Näätänen, proposed that the effect observed by Ford & Hillyard was resulting from the presentation of target stimuli in a stream of standard stimuli instead of selective attention. In their own data (1978), they found an increase of the auditory N1 for the presentation of deviant stimuli, independently of whether they are attended to. They interpreted this negative potential as arising from the mismatch between the memory trace of the standard, not corresponding to the response of the deviant. The group of Näätänen named this potential the MisMatch Negativity (MMN, see Fig. 1.3A for an illustration of the MMN potential). A decade later, the same group demonstrated that the MMN potential was also found when the target stimulus was changing in sound duration (i.e. filled time interval, as I will discuss later on) (Näätänen et al., 1989, Fig. 1.3B). Even though there was evidence, even before the term MMN was coined, from the group of Hillyard (Ford & Hillyard, 1981), the group of Näätänen showed later on that the MMN potential was also found when there is a transient change in the Inter-Stimulus Interval (ISI) (i.e. empty time interval) (Näätänen, Jiang, et al., 1993). Whether there is enough evidence to claim that both filled and empty time intervals are coded in the MMN process is the goal of review in the next part (1.3) of this chapter.

To observe MMN potentials, a passive (where participants ignore stimuli by watching a movie for example) oddball paradigm is sufficient, but also prevents the contamination of the MMN by other ERP components, such as the N2b observed for active detection of deviants (Schröger, 1998a). The automaticity of the MMN was first supported by its elicitation in the absence of attention to the stimuli (Näätänen et al., 1978) and during sleep (Atienza & Cantero, 2001) and coma (Fischer et al., 1999). To reliably observe the MMN, around 100 deviants are required per participant, with a probability not greater than .15, but several deviants can be presented in one block to reduce the total experiment duration (Deacon et al., 1998). To visualize and quantify the MMN potential, the differential wave “deviant-standard” (subtracting the ERP of the standard from the ERP of the deviant) is computed. To control for refractoriness and observe a “true” MMN, a control block can be used where deviants and standards are presented with equal probabilities (therefore not deviant nor standards anymore in those control blocks Schröger, 1998b).

The auditory MMN potential is a negative waveform, arising between 100 to 200 ms after the onset of a change, elicited by changes in any low-level or higher and more abstract feature (Näätänen et al., 2012, Fig. 1.3A) with a fronto-central topography (for audition). It has been observed for any sensory modality but has been more extensively studied in the auditory modality. Generally, it has been observed that the amplitude of the MMN increases with the decreasing probabilities of the deviant, and increases when the difference between the standard and the deviant increases (until it reaches a plateau, Winkler, 2007). In the two following sections, I briefly describe the type of deviance that elicits the MMN, the debated hypothesis underlying the MMN process, and the specific challenges to study duration MMN.

### 1.2.2. Type of deviance eliciting the MMN, and its underlying theories

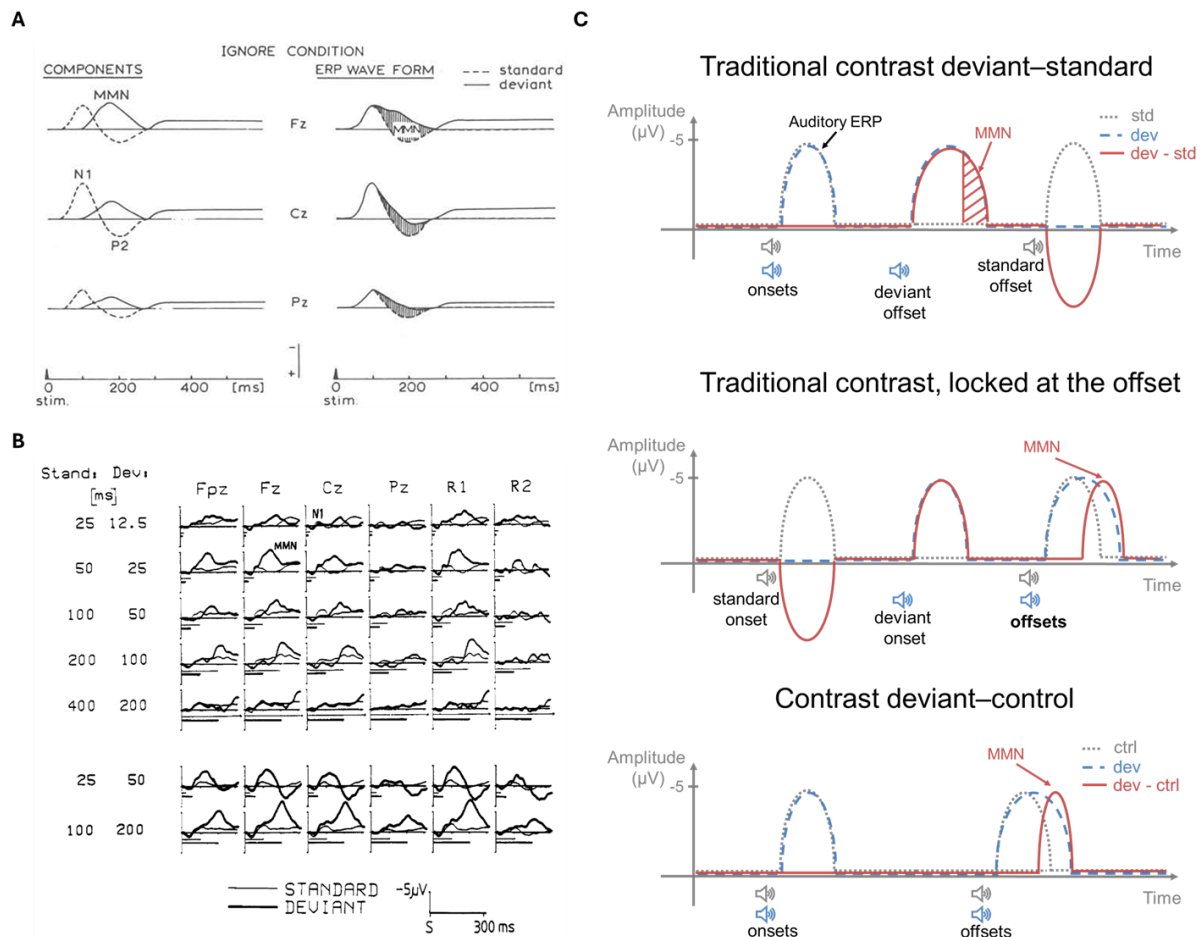
Initially described in the auditory modality, homologs of the auditory MMN have been observed in other sensory modalities since the 2000s (Näätänen et al., 2012). By homolog, I mean that we also find an automatic response linked to a deviant stimulus within a stream of standards. Whether these different responses across sensory modalities share common neuronal bases is still under investigation. Visual MMN has a parieto-occipital topography (Pazo-Alvarez et al., 2003). Intracranial data suggest that the somatosensory MMN has generators directly in the somatosensory cortex as well as in the frontal cortex (Spackman et al., 2010), and a recent study has shown a frontal topography for a duration change in the tactile modality (Isenstein et al., 2024). Olfactory MMN has a slower latency (~500 ms) and a parietal topography (Krauel et al., 1999). The fronto-central topography (with an inversion at the mastoids) of the auditory MMN is thought to rely on the existence of two generators, the first in the supra-temporal auditory cortex (Hari et al., 1984) and the second in the frontal cortex (hypothetically linked to the redirection of attention) (Giard et al., 1990; Rosburg et al., 2005). In the rest of my review, I will specifically focus on the auditory modality unless specified otherwise. This is because audition is the sensory modality that underwent the most parametric studies, especially for the specific case of duration changes, that provide most of the available data to discuss whether duration is coded automatically in the MMN process.

The MMN discovery, with changes in auditory intensity and frequency (Näätänen et al., 1978), first suggested that the auditory cortex simply encoded the first-order

physical characteristics of a repeated stimulus. An MMN was indeed observed for a change in intensity (Näätänen, Paavilainen, et al., 1993), sound frequency (Sams et al., 1985), spatial location (Paavilainen et al., 1989), and sound duration (Näätänen et al., 1989). This might have suggested that duration is encoded by the brain in a similar way to any other physical sensory feature (despite having no duration receptors). However, subsequent studies have shown that higher-level and more abstract features can also be coded by the MMN process. MMNs have been observed for pattern changes such as sequential rule, combinatory-rule, stream segregation, and violation of music-syntactic analysis (for a complete review, see Näätänen et al., 2010). More than a simple physical deviance feature detector of sensory cortices, the MMN process can even code for complex regularities and abstract rules. It suggests that, while early papers of the MMN considered sound duration part of the low-level sensory features, we cannot consider anymore the fact that the observation of a duration MMN classifies duration into a low-level feature, and that duration processing could be the result of higher-level computation than simple physical measurement. The conditions and type of deviance eliciting an MMN are at the core of the hypotheses underlying the MMN process.

The first hypothesis that was proposed as the underlying mechanism of the MMN is the release from refractoriness or N1 adaptation hypothesis (Näätänen, 1990; Jääskeläinen et al., 2004). In the N1 adaptation hypothesis, the MMN potential is seen as an enhanced N1 potential for the rare deviant compared to the strongly refracted N1 potential of the frequently presented standard. Methodology improvements to take into account refractoriness, and the observation of more abstract regularities eliciting MMNs led to the second hypothesis called the memory-mismatch or model-adjustment hypothesis (Näätänen & Winkler, 1999). Here, it is hypothesized that, in addition to the enhanced N1, deviants elicit an additional ERP component, which reflects the difference between the being processed deviant stimulus and the memory trace of the repeated standard. To reconcile the first two hypotheses, a third hypothesis was proposed, based on the predictive coding framework (Winkler, 2007; Garrido et al., 2009). The predictive coding framework predicts the adjustment of an internal model of the current stimulation (i.e. model-adjustment hypothesis) by plastic changes in synaptic connections (i.e. N1 adaptation hypothesis). This third hypothesis based on predictive coding is currently the most accepted to explain the underlying MMN process (Wacongne et al., 2012). Importantly to my reasoning, each hypothesis proposes that an

operation (comparison) is made automatically by the brain, suggesting that the information that is being compared is already somehow accessible to the brain. In the next section, I describe the key point to study whether duration changes are coded in the MMN process and a few methodological aspects that should be kept in mind.



**Fig. 1.3: Historical observation of duration MMN and illustration of the possible MMN contrast.** A: Illustration of the auditory and the MMN potentials (from Näätänen & Picton, 1986). They are usually disentangled by computing the differential wave deviant-standard. B: First duration MMN (from (Näätänen et al., 1989). During the presentation of a series of sounds with the same duration (referred to as 'standard' sounds), the introduction of a shorter sound (referred to as a 'deviant' sound) elicited a negative potential observable at the Fz electrode. C: Schematic illustration of the computation of empty time intervals (delimited by two sharp sound) differential wave. Top: If ERPs are not relocked to the offset of the deviant duration, the MMN potential will not be disentangled from the auditory potential. Middle: With empty intervals, ERPs need to be relocked at the offset of durations. However, it will not take into account the effect of refractoriness (see Chapter 2, Fig. 2.4). Bottom: Using a control block, where the deviant duration is presented equiprobably with the standard (and therefore not a deviant anymore), allows to avoid both the re-locking at offset and the effect of refractoriness.

### 1.2.3. Key points to investigate duration MMN

Although some links between the MMN and duration perception have been discussed (Macar & Vidal, 2004; Ng & Penney, 2014; van Wassenhove et al., 2019), no real efforts have been made to comprehensively synthesize the observations from MMN elicited by changes in duration. In this section, I develop key points to keep in mind when we investigate MMN and more specifically duration MMN.

As stated above, when we study duration, we need to distinguish between filled and empty time intervals. It is well known in the duration perception domain, that the content of the interval will impact the perceived duration. In a filled interval (e.g. a sound lasting a few milli/seconds), the duration will always be confounded with sensory integration allowing participants to respond not only based on temporal information but also according to non-temporal ones, the major one being sound intensity (Rammsayer et al., 1991). That is why empty intervals (e.g. a silent interval delimited by two sharp auditory sounds) are traditionally favored in duration perception studies. In the absence of sustained sensory stimulation, the brain must find something else to count. It is therefore highly probable that differences between the processing of filled and empty time intervals can be found. Surprisingly, most of duration MMN papers focus on filled intervals (probably because the question of duration was not central to their interest). Even though filled and empty intervals could be processed differently by the brain, it is interesting to investigate how both could be coded in the MMN process. Below the distinction between filled and empty intervals, I would argue that there are three key points to keep in mind if we want to claim that duration is indeed coded in the MMN process: the direction of deviance, the thresholds of duration scales, and the distinction between duration information and temporal expectation.

The direction of deviance refers to whether both a deviant shorter than the standard and a deviant longer than the standard elicit an MMN. In the MMN literature, testing a shorter deviant is referred to as a decrement in duration and testing a longer is referred to as an increment in duration. If not both a shorter, and a longer deviant elicit an MMN, we cannot conclude whether the information carried by the MMN potential is related to the change in duration itself, and not simply a surprise signal indicating a change in the auditory information, without access to the nature of that change. There



are obvious distinctions between shorter and longer deviants that could lead to distinct processing such as short deviants have simultaneous information of deviance and duration while longer deviants have first information of deviance (at the offset of the standard duration), and then information about duration (at the offset of the longer deviant duration). Orthogonal to the question of duration MMN, testing the direction of deviance is an interesting topic for the MMN as it could provide information on the nature of the comparison being made. A predictive coding account of the MMN implies a quantitative relationship between the MMN amplitude and the residual error of the comparison. If the MMN amplitude scales with the arithmetic difference between the deviant and the standard, it could imply that the brain has already a metric system to quantify the stimuli (and their residual error). If the MMN amplitude scales with the ratio deviant/standard, it could imply that the residual error is computed according to the standard scale, as it is traditionally seen in sensory perception, and a minimum constant ratio should exist to elicit the MMN potential (cf. Weber's law). The actual operation underlying the residual error computation is rarely spelled out in most of the MMN papers or implicitly given. To study which operation underlies the MMN process, a parametric manipulation of the deviance could be tested and the resulting MMN amplitude could be fitted with different models based on the distinct hypothesized operations. The goodness of fit along with the slope could then be compared to favor one or the other operation. Note that this type of reasoning was targeted in my first MMN study (Annex 5.1, 5.2), but the null results led me to refine my hypotheses and first test a simpler design (chapter 2).

The thresholds of the duration scales refer to critical time points that could delimit different duration scales under which duration is processed differently by the brain. As stated above, there are likely three thresholds that might affect perceived duration, from which two fall into the duration tested in the MMN studies, the ~200 ms and the ~1.2 s thresholds. The ~200 ms threshold delimits the Temporal Window of Integration (TWI), below which temporal information is crucial to (re-)construct stable percepts (van Wassenhove et al., 2007), but that can be manipulated to yield specific temporal illusions such as the temporal recalibration or the rabbit illusion (Eagleman, 2008; Grabot et al., 2021). The ~1.2 s threshold delimits the duration below which they are more perceptually processed and above which they are more cognitively processed (Rammsayer & Lima, 1991). Psychophysics investigations showed that the scalar

variability ratio (coefficient of variation) starts to increase for intervals longer than 1.2 s (Grondin, 2012).

The last point to discuss is the distinction of duration information from temporal expectation. There is plenty of evidence that the temporal structure of the environment (such as a constant rhythm) can be internalized allowing one to predict when future events will appear (Nobre & van Ede, 2018). If we are interested in the duration *per se*, we need to make sure that duration is the only temporal information that the brain can track and code in the MMN process. If other temporal regularities (such as steady rhythm resulting from constant ISI) can be tracked than the duration of interest, they constitute supra-temporal cues that prevent us from knowing what is coded by the brain. As I discuss below, a large amount of duration MMN contains supra-temporal cues, therefore confounding duration information. Although these three points overlap each other, they will be used as a structure for the next part of this chapter, but many studies will be discussed in each of those points, as they cannot be fully separated, and were not specifically tested in isolation from each other.

There are a few methodological aspects that should be kept in mind when results from MMN studies are under review, and that were not always respected or specified in each article. The first, not specific to duration, is related to the ratio of deviant/standard used in the averaging process of the ERP and the refractoriness of the N1 potential with the repetition of the standard. If the traditional contrast deviant–standard is used, the number of standards used to compute the ERP (of the standard) should match the number of deviants to have equal signal/noise ratios for the deviant and the standard in the averaging process of the ERP. However, this traditional contrast will not take into account the refractoriness induced by the repetition of the standard in the oddball paradigm. To observe a “genuine” MMN, it is now advised to use control blocks where deviants and standards are presented along with many other stimuli in an equiprobable fashion (Schröger, 1998b). With such control blocks, the differential wave deviant–control can be computed (Jacobsen & Schröger, 2003). Surprisingly, while this methodological issue has been known since the late nineties, even very recent studies are not using this appropriate methodology (Thibault et al., 2023; Isenstein et al., 2024). For duration changes, the use of the contrast deviant–control is even more appropriate to avoid artificial ERP components created by the subtracting process. Another possibility is to at least lock the ERPs of the deviant and the standard at the offset of the

duration (corresponding to the onset of deviation, Fig. 1.3C). The second is to be careful about when the baseline is done and when is the onset of deviance, specifically if the latency of the MMN is of interest. The baseline should always be done before the start of the presented duration, as ramping activity could develop throughout the processing of a stimulus leading to different baseline levels if stimuli don't have the same duration. Duration changes don't have the same onset of deviance for shorter and longer deviants. If one is interested in the latency of the MMN, this is especially important to consider. Again, the use of the deviant-control contrast is very well suited in this case. Papers containing those methodological problems might still be presented shortly for documentation but will not be discussed further.

### 1.3. Specific review of the duration MMN

In the third part of the chapter, I review the duration MMN articles according to the three points raised in the previous section: the direction of the duration deviance, the different thresholds of duration scales in duration MMN, and the impact of temporal expectation on duration MMN.

#### 1.3.1. Deviance direction

In this section, I review the articles that provide information about the deviance direction in duration MMN. Whether shorter and longer deviants than standards elicit an MMN is the first point to investigate whether duration is coded in the MMN process. Although there are clear distinctions between the two (such as the onset of deviance and duration information), it is unclear whether they should be considered similar deviances.

For filled interval, it was demonstrated and replicated qualitatively, quite early, that MMN can be elicited by both a shorter and longer tone duration when standard durations are below 200 ms (Näätänen et al., 1989; Catts et al., 1995). By qualitatively, I mean that the methodology to compute the differential wave is not correct, as they did not compare deviant and standards of the same duration. A few years later, Amenedo and her colleagues confirmed the observation of duration MMN for shorter and longer deviants and found that the MMN amplitude was linearly following the logarithm of the deviance for both (Amenedo & Escera, 2000). Similarly, when shorter and longer deviant

durations are presented in the same block, both elicit an MMN potential with a standard duration of 100 ms (Jaramillo et al., 2000). With a standard duration above 200 ms, deviants longer than the standards do not elicit an MMN (Takegata et al., 2008). This was replicated by a parametric study specifically testing the effect of deviance direction across different standard durations (Colin et al., 2009). Colin and her colleagues tested several standard durations (100; 150; 200; 250 ms), each with two types of duration deviants (+/- 50% of deviance). No MMN was elicited by the longer deviant of their longest standard duration (deviant 375 ms; standard 250 ms).

For empty intervals, very few studies tested the effect of deviance direction on the MMN potential. Most of the studies investigated deviants shorter than standards, and not longer. In the seminal study of Ford & Hillyard (not an MMN study *per se*), an MMN-like potential was observed when a constant rhythm (600 ms ISIs) was disrupted with an occasional shorter ISI of 300 ms, but it was not the case when the constant rhythm (300 ms ISIs) was disrupted occasionally with a longer ISI of 600 ms (Ford & Hillyard, 1981). Surprisingly, the deviant longer than the standard of an empty interval was completely put aside by the community after this study. There are only two studies that tested deviants longer than standards, but with a specific methodology. Instead of using a constant rhythm that would be occasionally disrupted by a shorter or longer ISI, they used trains of four empty intervals (Sable et al., 2003; Lai et al., 2011). The first three empty intervals are the standards and the last is a deviant (or a standard). With such a design, constituted of a higher-order sequence, a negative potential was found following the presentation of deviants longer than standards. Though this result seems appealing, the methodology to compute the differential wave is not correct. Although they compare responses from the deviant to the same duration as a standard, the train of the previous empty interval is not the same. This implies that they are each following a different rhythmic stimulation. It is highly probable that the baseline level is not similar for the deviant and the corresponding standard (as I discuss in chapter 2).

The direction of deviance has only been properly tested for filled intervals. While deviants shorter than standards elicit an MMN, deviants longer than standards do not. For durations below 200 ms, we clearly find a response to a deviant longer than standard (Colin et al., 2009), but this is not the case for durations above 200 ms. This observation smoothly introduces the possible existence of a threshold around 200 ms, which I discuss in the next section.

### 1.3.2. Thresholds of duration scale

In this section, I review the articles that provide information about the possible existence of thresholds for duration MMN (see 1.2.3.). I specifically focus on the threshold of ~200 ms and the threshold of ~1.2 s. The notion of TWI (for the ~200 ms), and empirical results from the perception of duration (for the ~1.2 s) suggest us to hypothesize the existence of such thresholds for the MMN process.

For filled intervals, we have already seen that longer deviant does not elicit an MMN when the standard duration reaches ~200 ms (Takegata et al., 2008; Colin et al., 2009). Few other studies tested a longer standard duration scale, but only for deviant shorter than standard. When a constant ISI is used between the tested durations, shorter deviant elicits an MMN for standard durations of 400 (Sysoeva et al., 2006), 800, and 1600 ms (Näätänen et al., 2004). The amplitude of the MMN at those longer standard duration scales is lower. Interestingly, when a variable ISI is used, no MMN is observed at all, for standard durations of 667 (Grimm et al., 2006) and 1000 ms (Grimm et al., 2004). The fact that MMN amplitude largely decreases for standard durations longer than 400 ms, or that no MMN is observed in the absence of supra-temporal cues, suggests a possible threshold around 400 ms for processing durations accompanied also by asymmetrical processing of shorter and longer deviants.

For empty intervals, there is no data available for longer deviants across different standard duration scales. However, shorter deviants have been studied across many different standard durations, ranging from 120 (Kujala et al., 2001) to 1500 ms (Brannon et al., 2004). In between, reliable MMNs for shorter deviant have been found for the standard duration of 610 ms (Hari et al., 1989) and 800 ms (Nordby et al., 1988a). No clear change in the MMN amplitude is observed across those different standard durations, contrary to what we observed for filled intervals below and above 400 ms. It is worth noting that all those studies used infrequent disruption of a constant rhythm, rather than a specific manipulation of empty interval. The existence of a threshold was not investigated with longer deviant, but data from omission MMN can provide additional information on this topic. To some extent, the omission of a stimulus in a sequence can be related to longer deviant duration, as it can inform us whether the brain actually tracked the standard duration and detect whenever it has elapsed. Omission MMN has been extensively used to study the length of the TWI. Several studies

refined the length of the TWI, converging to 150 ms above which no omission MMN is found (Tervaniemi et al., 1994; Yabe et al., 1997, 1998). An ECoG study replicated a similar result by finding an omission response for 100 ms but not for 1200 ms (Hughes et al., 2001). Interestingly, the use of a train of five empty intervals managed to restore the observation of an omission MMN for a standard duration of 330 ms (above the TWI, Salisbury, 2012).

Taken together, no study investigated the effect of 200 ms and 1.2 s thresholds on the MMN specifically. However, the pattern of results across studies suggests the existence of a threshold of 200 ms for filled and empty intervals above which longer deviant or the omission of a stimulus do not elicit MMNs anymore. Additionally, a possible threshold around 400 ms can be hypothesized for filled interval, above which no MMN is observed. However, supra-temporal cues seem to allow the retrieval of the MMN process above those thresholds. It introduces the impact of temporal expectation on the MMN process and the necessity to disentangle it from duration to specifically investigate duration MMN which I discuss in the next section.

### 1.3.3. Duration information and temporal expectation

In this section, I review the specific impact of temporal expectation on the two previous points raised above. It was surprising, to me, to discover that most of the published duration MMN papers did not disentangle duration information from temporal expectation. Temporal expectation refers to mechanisms of internalizing the temporal regularities of the environment to predict and facilitate the processing of a future event (Nobre & van Ede, 2018). If one is interested in duration information *per se*, one needs to make sure that duration is the only temporal regularity that the brain can track. The major source of temporal regularity that is often under looked in studies is whether researchers used constant ISI between the durations they manipulated.

For filled intervals, only one group made sure to use variable ISIs between the durations of interest (Grimm et al., 2004, 2006). As stated above, they did not find an MMN for shorter deviant at a long standard duration scale. The use of constant ISIs, in another similar study, allowed retrieval of an MMN at this long duration scale (Näätänen et al., 2004). This suggests that the additional temporal regularity coming from the constant ISI facilitates the automatic detection of duration deviance in the MMN process.

For empty intervals, no one tested duration manipulation in the absence of temporal expectation. The majority of studies used infrequent disruptions (early or late, but mostly early as already discussed above) of a constant rhythm with fixed ISIs. Three studies used trains of four/five empty intervals, the last interval being shorter or longer than the previous ones (Sable et al., 2003; Lai et al., 2011; Salisbury, 2012). Interestingly, the use of those higher-order regularities also facilitated the observation of MMN. However, the methodology to perform differential waves in those studies is not sufficient to fully consider those results. One study used pairs of sounds to delimit empty time intervals, but they also used constant inter-pair intervals, meaning that the empty time intervals delimited by sounds were not the only source of temporal regularity.

Those results (Sable et al., 2003; Salisbury, 2012) suggest that temporal expectation facilitates the process of deviance duration detection. This is partially supported by results showing a decrease in MMN amplitude with rhythm entropy, manipulated by the increasing the number of distinct time interval in a sequence (Lumaca et al., 2019; Knight et al., 2020). However, the differential waves used are not completely satisfactory to fully consider this result since they used the traditional deviant – standard contrast, not taking into account effect of refractoriness. The facilitation of the MMN process by temporal expectation is in line with the facilitation of perceiving/ discriminating/reacting to stimuli by temporal expectation observed in behavioral task (Nobre & van Ede, 2018). It is therefore very surprising that little efforts have been made to disentangle temporal expectation and duration information in the MMN process.

	Filled Interval	Empty Interval
Deviance direction	<p>Näätänen et al., 1989 Catts et al., 1995 Jaramillo et al., 1999 Amenedo &amp; Escera, 2000 Jaramillo et al., 2000 Takegata et al., 2008 Colin et al., 2009 Peter et al., 2010</p>	<p>Ford &amp; Hillyard, 1981 Sable et al., 2003 Lai et al., 2011</p>
Thresholds & duration scale	<p>Naatanen et al., 2004 Grimm et al., 2004 Grimm et al., 2006 Sysoeva et al., 2006 Takegata et al., 2008 Colin et al., 2009</p>	<p>Näätänen, Jiang, et al., 1993 Kujala et al., 2001 Brannon et al., 2004 Brannon et al., 2008</p>

**Table 1.1: Classification table of duration MMN (omission MMN are not included).** Red color indicates a differential wave methodology not suited to study duration. Green color indicates a differential wave methodology close to be suited to study duration changes. Light color indicates supra-temporal cues in the study (e.g. constant ISI). Dark color indicates studies that specifically tested duration. Strikingly, we can note that there are only two studies for filled interval that tested duration specifically, and none for empty interval.

## 1.4. Conclusion

In the last part of the chapter, I first briefly summarize the major observations from the literature on duration MMN, then give my current opinion on those data, and finally propose a few protocols to fully answer this question.

### 1.4.1. Not enough evidence to say that duration is coded in the MMN process

The goal of this short review was to investigate whether there is enough available data to claim that duration is indeed coded in the MMN process. Most of the studies used filled intervals, and the few studies that used empty intervals have only tested disruption of constant rhythm rather than duration *per se*. Hence, whether empty intervals are automatically coded in the MMN process has never been tested. This is surprising given the fact that duration MMN has been discussed by researchers from duration perception (Macar & Vidal, 2004; Ng & Penney, 2014; van Wassenhove et al., 2019). As discussed in the first part of this chapter, whether duration is automatically coded by the brain or requires psychological concepts such as attention, to be computed by the brain



constitutes a foundation of the proposed psychological models for duration perception. It provides an opportunity for a series of studies to investigate this question.

Even in studies with filled intervals, most confuse duration information with temporal expectation. However, it has been observed that supra-temporal cues can facilitate the process of automatic deviance detection. Therefore, it is important to differentiate between duration information and temporal expectation in future studies.

Among these studies, a distinction can still be made between duration scales. Short standard durations (below 400 ms) tend to induce MMNs more easily than long standard durations. Additionally, there is a difference in detecting shorter and longer deviants, which is closely linked to the existence of a threshold (around 200 ms). There are no clear studies demonstrating an MMN for deviants longer than a standard duration of 200 ms.

To determine if duration information is coded in the MMN process, it is necessary to reconduct studies while clearly separating and parametrically testing the notions of deviance direction, duration thresholds, and the distinction of duration information from temporal expectation. The following section proposes an experimental protocol that could provide data to answer this question.

#### 1.4.2. Suggestion of protocols

To fill the gap and resolve the lack of well-controlled data describing duration MMN, I propose a design that can be carried out for both filled and empty time intervals. Firstly, we need to test for the effect of deviance direction, using a shorter and a longer deviant. Next, we need to consider the possibility of a threshold and test two different standard durations (a short one below 200 ms and a longer one above 400 ms). To avoid supra-temporal cues confounding the tested durations, the ISIs must be sufficiently variable. To compute the differential waves to highlight the MMN, we need to use control blocks in which all our durations are presented equiprobably (with additional durations). This will enable us to subtract the classic response of these durations, when they are not a deviant, from the response of the deviant durations, and to take into account the effect of refractoriness. The number of stimuli in the control blocks should match the number of deviants in the MMN blocks to ensure a similar signal-to-noise ratio for responses across MMN and control blocks.

Further studies could then be conducted to test the effect of constant ISI or the effect of attention for example. The nature of the operation performed by the MMN could be tested by examining several deviants in both directions, as suggested in section 2.3. This data could help determine whether duration is automatically coded by the brain and, if so, what can be deduced about the nature of its representation.

The following chapter presents an empirical study on the MMN of empty time interval following the proposed design.

## Chapter 2 – Empirical study of empty time interval MMN

This chapter<sup>1</sup> aims to demonstrate that, when the correct methodology for studying an empty time interval change is used, no empty time interval MMN is observed. This chapter follows the classic structure of Introduction - Materials & Methods - Results - Discussion. However, elements of discussion can also be found in the Results section, as I felt this was more appropriate for understanding the logical unfolding of my demonstration. In the Introduction, I justify the importance of the existence of an empty time interval MMN. In the Materials & Methods, I detail the method I used to test it. In the Results, I begin by demonstrating that it is necessary to use the deviant-control contrast when using empty time intervals to test the existence of the duration MMN, using the example of a 600 ms long standard duration. I then suggest that no duration MMN is observed when using the deviant-control contrast, for both a long standard duration of 600 ms and a short standard duration of 100 ms (but the absence of an observation do not demonstrate the absence of effect). Finally, I show that to test rhythmic sequences of several empty time intervals (as has been tested in the literature), special control blocks are required, but in any case, we no longer test specifically duration. To follow-up this work, I acquired a new set of data, where I removed the rhythmic blocks, added frequency deviants as a control to the observation of MMN, and added blocks with selective attention to frequency or duration deviance.

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<sup>1</sup>This chapter is a scientific article close to be submitted. This version was adapted to the thesis format.

# The duration Mismatch Negativity (MMN): an empirical revision using empty time intervals

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## 2.1. Introduction

The study of how we perceive time is one of the most ancient branches of experimental psychology (James, 1886). The conception of time as an entity that we can perceive shifted the study of time to “how do we measure time interval” (Myers, 1971; Matthews & Meck, 2016; Droit-Volet, 2018). The ability to track the duration of external events is, indeed, fundamental for any organism to interact with its environment (Michon, 1998). Among the various psychological models proposed over the last decades, the most successful ones are based on the internal clock model, which describes how duration may be coded by the mind (Creelman, 1962; Treisman, 1963; Gibbon, 1977). In the latest version of the internal clock (Allman et al., 2014), a pacemaker produces ticks at a rate modulated by arousal; these ticks are registered in an accumulator, itself gated by an attentional switch that switches on and off the accumulation of ticks (Zakay & Block, 1996). The resulting count from the accumulator is compared to a reference duration stored in working memory or long-term memory. The attentional module of this model plays an important part in delimiting and regulating the latency of the onset and the offset of the interval to be timed (van Wassenhove et al., 2008). While this psychological model is powerful in explaining behavioral results (Buhusi & Meck, 2005), its neuronal implementation remains debated (Allman et al., 2014; Tallot & Doyère, 2020). To claim that this measure of time interval is at the core of how the mind represents time is a strong assertion, that comes with a lot of implicit assumptions.

While the brain does not have clear time receptors, there is now plenty of evidence of neurons sensitive to duration. Inhibiting activity in the auditory cortex impairs duration discrimination in mice (Li et al., 2021), and manipulating

somatosensory cortical activity influences the perceived duration of tactile stimuli (Toso, Fassihi, et al., 2021; Reinartz et al., 2024). However, duration-tuned neurons can be found in non-sensory brain areas such as the parietal cortex (Leon & Shadlen, 2003; Nieder et al., 2006), the striatum (Toso, Reinartz, et al., 2021), the right supramarginal gyrus in the parietal lobule (Hayashi et al., 2015) and the supplementary motor area (Protopapa et al., 2019). Therefore, one can ask whether those duration signals are the ones actually used by the brain to represent duration, and even time on a larger scale (van Wassenhove, 2009). To test whether information is represented and directly accessible to the brain, one can turn to automatic operations (see 1.1.3. & 1.1.4.)

To assess whether duration is automatically coded (and therefore represented) by sensory systems in the absence of attention, we can test whether a change in duration can elicit a mismatch negativity (MMN) response. In humans, the MMN, recorded with electroencephalography (EEG), is elicited by an infrequent stimulus in a stream of standard stimuli. The MMN is a negative response between 100 to 200 ms following the presentation of the deviant stimulus (Näätänen et al., 2012). Crucially, this response is considered automatic as it is readily observed in the absence of attention directed to the stimuli (Näätänen et al., 1978). Infrequent changes in stimulus duration have been demonstrated to induce an MMN (Näätänen et al., 1989), thereby suggesting that duration may be coded and readily used by the brain in the absence of attentional orientation to time.

However, we contend that several confounding factors in duration MMN preclude the firm conclusion as to the existence of a duration-specific MMN. First, most studies used filled time intervals in which the presence of a sensory stimulus delineates the tested duration. For instance, many used a pure tone lasting a specific duration in the auditory modality (Amenedo & Escera, 2000; Näätänen et al., 2004; Grimm et al., 2006; Takegata et al., 2008; Colin et al., 2009). As the duration of stimuli is well known to be proportional to the logarithm of its intensity (Berglund et al., 1969; Fraisse, 1984), when using filled intervals, the duration code may result from temporal integration of other sensory features (i.e. loudness) as opposed to timing *per se* (Rammsayer & Lima, 1991). Recent work indeed describes such time-intensity trade-offs in sensory systems (Toso, Fassihi, et al., 2021). To overcome this confound, time research has long advocated the use of “empty time intervals”, which, in the audition, can take the form of a gap in noise

(e.g. Abel, 1972) or a silence between two transient sounds. Therefore, we should turn to empty time interval MMN since we are interested in “pure” duration.

Second, to state that it is indeed the duration that is coded in the MMN process and not simply a signal of surprise resulting from prediction error, we need to test both shorter and longer deviants. Indeed, the direction (shorter or longer) of the subjective duration estimation is of particular interest when the effect of a factor (e.g. repetition, probability, or expectation) is studied (Pariyadath & Eagleman, 2007; Cai et al., 2015; van Wassenhove & Lecoutre, 2015). Moreover, testing shorter and longer durations can provide additional insight into how the time interval is measured (Ofir & Landau, 2022). In the MMN process, testing shorter and longer deviants will allow us to infer if the length of the time interval actually matters, and that it is not simply a surprise signal. Among the few empty time interval MMN studies, a seminal work found that the N1-P2 amplitude only increased when the stimulus arrived earlier than expected (shorter), but not when the stimulus arrived later than expected (longer) (Ford & Hillyard, 1981). This observation illustrates this point: whether the MMN reflects the complete measure of the time interval is unclear. Following this initial observation, much research focused primarily on duration changes that were shorter than the standard duration. In follow-up studies, shorter deviants have been tested for standards as low as 120 ms (Kujala et al., 2001) and as high as 1500 ms (Brannon et al., 2004, 2008). Longer empty deviants were tested in only two studies but with a specific design related to the third and the fourth points (Sable et al., 2003; Lai et al., 2011). If the duration in the MMN process is only measured until the standard duration has elapsed, we would expect a response at the offset of the expected standard duration when the deviant is longer. Note that this could suggest a mechanism of temporal expectation, coding for when the duration of the standard has been violated. In this framework, longer deviant empty time intervals would then be closer to an omission of the standard stimulus than to a comparison of duration. When an omission paradigm was used, an MMN was reported for durations up to 150 ms in an isochronous rhythm (Yabe et al., 1998) and up to 300 ms when an isochronous sequence of stimuli was used (Salisbury, 2012), a difference probably related to the fourth point.

Third, empty time interval MMN were only tested with rhythmic input, hence the duration information is fully confounded with temporal expectation. Temporal

expectation refers to mechanisms that enable us to internalize the temporal structure of the environment, in order to predict when future events will happen (Nobre & van Ede, 2018). If one is interested in the duration *per se*, one needs to make sure that duration is the only temporal information that the brain can track. Any other temporal regularities, such as rhythmic stimulation, can constitute supra-temporal cues that will facilitate the processing of stimuli features, such as pitch or duration. Empty time interval changes were either tested by an occasional disruption of an isochronous rhythm at a random location (Ford et al., 1982; Näätänen et al., 1993) or by a change in the last Inter-Stimulus Interval (ISI) of an isochronous sequence of five stimuli (Sable et al., 2003; Lai et al., 2011). The difference between the two designs is that the latter has an additional regularity compared to the temporal expectation. When a sequence of five ISI is used, the position of the deviant is always the same (Sable et al., 2003; Lai et al., 2011; Salisbury, 2012), meaning that the brain can also internalize when the deviance appears. It seems to restore the observation of MMN for longer empty deviants (Sable et al., 2003; Lai et al., 2011) and omission above the TWI (Salisbury, 2012). However, such a design requires to have an adequate control to compute the differential wave, which constitutes the fourth point.

Fourth, many studies did not use the appropriate methodology to compute differential waves with empty time intervals. It is now well documented in neuroscience that the amplitude of an auditory evoked response increases with the length of the preceding ISI (Davis et al., 1966; Hari et al., 1987; Budd & Michie, 1994; Loveless et al., 1996; Todd et al., 2000). This effect is interpreted as resulting from a refractory period of more than 10 s causing the attenuation of the evoked response amplitude to a stimulus repeated, within less than 10 s. If the responses of different objective empty time intervals are compared such as we do with differential waves deviant-standard (e.g. a deviant of 420 ms and a standard of 600 ms), it is highly probable that the difference in refractoriness might induce artificial responses (as we demonstrate in the results 2.3.3). To prevent this, control blocks with an equiprobable presentation of all the tested durations should be used (Jacobsen & Schröger, 2003). Then, the differential wave should be done between the deviant and the same objective duration from the control block (e.g. a deviant of 420 ms and a control of 420 ms). We refer to this differential wave as deviant – control (reduced to DEV – CTRL) in the rest of the article.

Last, the MMN quantification has been mostly done by extracting the amplitude of the ERP over a specific time window, at a specific electrode (usually Fz). State-of-the-art analyses of ERP now rely on spatio-temporal clusters (Maris & Oostenveld, 2007). This statistical tool allows us to take into account the multiple problem comparison, which corrects the significance of our statistical test based on the number of electrodes and time points we have.

Taken together, “pure” empty time interval MMN has never been tested. In this EEG study, our first goal was to replicate the literature by showing the elicitation of a duration MMN by testing changes of empty time intervals embedded in a rhythmic structure. Our second goal was to demonstrate the existence of a duration MMN in the absence of a rhythmic structure and avoid the confounding factor of temporal expectation. Additionally, we used control blocks to overcome the effect of refractoriness. We also investigated two different time scales by using standard stimuli of 100 ms and 600 ms. We hypothesized that because durations below 200 ms are building blocks of perception (Poeppel, 2003; van Wassenhove et al., 2007), they may elicit an MMN, whether embedded in a rhythmic sequence or not, and whether deviants are short or long. Duration at that scale can be manipulated by the brain and yield specific temporal illusions such as temporal recalibration or rabbit illusion (Eagleman, 2008; Grabot et al., 2021). To the contrary, in the absence of a task durations above 200 ms would elicit an MMN only in rhythmic sequences, possibly only for shorter deviants, as temporal regularities and expectations will facilitate tracking changes in duration. This article focuses on the good practices for investigating empty time interval MMN. It is important to note that even very recently published works still present some of those methodological constraints (Isenstein et al., 2024, Thibault et al., 2023).

## 2.2. Materials & Methods

### 2.2.1. Participants

Twenty-nine volunteers (19 women, mean age = 23.7 +/- 4.4 years old) took part in the study and received monetary compensation for their participation. All were self-declared right-handed. All declared normal-to-corrected vision, normal hearing, and no neurological or psychiatric disorders. Before participating, each participant was



informed about the study and signed a consent form validated by the Ethics Committee on Human Research at Neurospin (CPP number 100049, Gif-sur-Yvette, France) in agreement with the Declaration of Helsinki (2013).

Using a previous study reporting the amplitude values of duration MMN (Lai et al., 2011), a power analysis using G-power (3.1.9.6) estimated a sample size of 15 participants. However, we targeted 30 participants considering we used state-of-the-art spatio-temporal cluster t-tests correcting for multiple comparisons (Maris & Oostenveld, 2007) as compared to the one-way ANOVA at a chosen electrode at a specific latency window (Lai et al., 2011).

### 2.2.2. Procedure

After participants were equipped with the EEG cap (~30 min), they were comfortably seated 60 cm away from the computer screen in a testing room. They were told that the experiment would last approximately 1h30, divided into six blocks, with small breaks in between each block. During each block, participants were instructed to watch a silent movie and to ignore the sounds that were played in their ears via headphones. The participants could take small breaks in between each recording block.

### 2.2.3. Stimuli

The stimuli were constructed and delivered with the Psychtoolbox (Brainard, 1997) on Matlab 2019a, with a Dell Latitude E6530 portable computer. The stimuli were empty time intervals delimited by two white noise bursts (5 ms duration each with 2.5 ms ramping (rise and fall), Fig. 2.1). The loudness of noise bursts was adjusted at a comfortable hearing level, on a per individual basis. In each condition, there were two types of DEV stimuli, one shorter (DEV-, -30% of STD duration) and one longer (DEV+, +30% of STD duration) than the standard empty time interval. The STD was presented with a probability of 0.83 (corresponding to 770 stimuli), and each deviant with a probability of 0.083 (corresponding to 77 stimuli each). In the short duration scale condition, the STD was 100 ms, the DEV- was 70 ms, and the DEV+ was 130 ms. In the long duration scale condition, the STD was 600 ms, the DEV- was 420 ms, and the DEV+ was 780 ms.

#### 2.2.4. Task

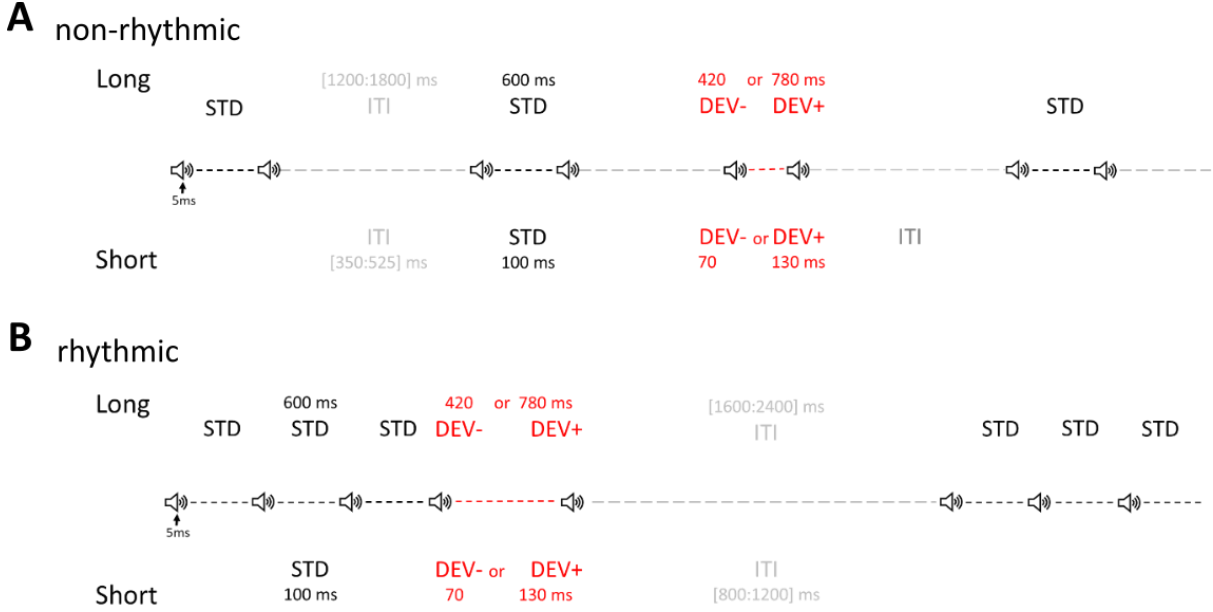
The task was designed and run on Matlab 2019a using Psychtoolbox (Brainard, 1997). The experiment was a classical auditory oddball, with frequent standard (STD) stimuli and occasional deviants (DEV). The experimental design was a 2 (deviant direction: DEV-, DEV+) x 2 scale (duration scale: short, long) x 2 (sequence type: rhythmic, non-rhythmic) within factorial design (Fig. 2.1). The deviance direction was a two-level factor where the deviant could be shorter (DEV-) or longer (DEV+) than the standard. The duration scale was a two-level factor where the STD could be 100 ms (short condition) or 600 ms (long condition). The sequence type was a two-level factor where empty time intervals were presented either rhythmically (rhythmic condition, Fig. 2.1B) or non-rhythmically (non-rhythmic condition, Fig. 2.1A). Besides the four experimental conditions, there were two control conditions (short and long), in which stimuli were all presented equally, resulting in 6 different blocks presented in random order.

In the non-rhythmic conditions, empty time intervals were presented sequentially, with random Inter-Trial Intervals (ITIs) selected from a uniform distribution ranging from 350 ms to 525 ms for the short condition and from 800 ms to 1200 ms for the long conditions to prevent supra-temporal cueing (Fig. 2.1A). Non-rhythmic conditions started with at least 10 STD, and there was at least 2 STD between each DEV (Schröger, 1998b).

In the rhythmic conditions, stimuli were presented in sequences of 4 consecutive empty time intervals. Hence, STD consisted of four 100 ms (short condition) or 600 ms (long condition) empty intervals (Fig. 2.1B). DEV consisted of three STD durations (100 ms or 600 ms) followed by a last DEV duration. In the rhythmic conditions, random ITIs were selected from a uniform distribution ranging from 800 ms to 1200 ms for the short conditions and from 1600 ms to 2400 ms for the long condition. All the conditions parameters are summarized in Table 1.1.

In the control conditions, STD and DEV were presented equiprobably in a random order, with ITIs similar to the non-rhythmic conditions. We added a shorter empty time interval to prevent an MMN-like response for the control of our DEV- (Jacobsen & Schröger, 2003). The two added empty intervals were 50 ms and 300 ms for the short and long conditions, respectively. Brain responses to these two stimuli were disregarded

from the analyses. Those control conditions allowed us to compute the auditory obligatory evoked response to each of our empty time intervals (termed CTRL in the rest of the article) in the absence of a standard/deviant relationship. We named CTRL- the response of the empty time interval in the control condition to the duration corresponding to DEV-, CTRL the one corresponding to the STD, and CTRL+ the one corresponding to DEV+.



**Fig. 2.1: Illustration of the non-rhythmic (A) and rhythmic (B) conditions.** A: In the non-rhythmic condition, the empty time intervals were presented sequentially, separated by variable Inter-Trial Intervals (ITIs, in light grey). There were at least two standards (STD) between each deviant (DEV). B: In the rhythmic condition, the empty time intervals were presented as sequences of 4 consecutive empty intervals, separated by variable ITIs (light grey). The last empty time interval of the sequence was either an STD or DEV. Orthogonally to rhythmic and non-rhythmic conditions, we tested two duration scales (short and long). The STD duration was 100 ms in the short condition, and 600 ms in the long condition. Additionally, in each condition, there were two deviants, one shorter (DEV-) and one longer (DEV+) than the STD of +/- 30% of duration, respectively. It resulted in a 2x2x2 within-participants design, where each combination of conditions was tested in a separate block.

Duration scale	Stimuli		Standard (ms)	Deviant (ms)		Inter-Trial Interval (ms)	
	non-rhythmic	rhythmic		STD	DEV- (-30%)	DEV+ (+30%)	non-rhythmic
Short	Empty interval separated by random ITIs	Sequences of 4 empty intervals separated by random ITIs	100	70	130	350-525	800-1200
Long			600	420	780	1200-1800	1600-2400

**Table 2.1. Parameters of task conditions.**

### 2.2.5. EEG recordings & preprocessing

EEG recordings were performed with a high-density 64 channels waveguard cap (ANT Neuro, Enschede, Netherlands) and an EEGoPro amplifier (ANT Neuro, Enschede, Netherlands) with a sampling frequency of 1 kHz. A low-pass filter of 260 Hz was applied online during data acquisition. No online high-pass filter was used, and the recording was DC. The online reference electrode was CPz. A vertical EOG was placed above the left eye to record eye movements and blinks. Impedances of all channels were set below 20 k $\Omega$  before the recording session. They were systematically checked throughout the experiment and corrected to below 20 k $\Omega$  if and when needed.

Data were pre-processed and analyzed using the MNE-python software v1.0.2 (Gramfort, 2013). Bad electrodes were identified manually, removed from the analysis (mean 2.48 per participant across conditions), and interpolated at the end of the preprocessing. On a separate version of the data, we applied a notch filter of 50 Hz and we performed an Independent Component Analysis (ICA) to identify and remove blink and eye movement artifacts from our raw data. Ocular artifacts were corrected by rejecting ICA components that most correlated with detected EOG events (mean ICA component rejected per participant across conditions = 1.94).

Clean raw EEG data were re-referenced to the global average, band-pass filtered from 1 Hz to 30 Hz using a Finite Impulse Response filter, applied twice (forward and backward to make it non-causal, Gramfort, 2013).

Our analysis used epochs locked to the onset of the empty time interval. In the non-rhythmic conditions, data were locked to the onset of the time interval from -50 ms

to 490 ms for the short conditions, and from -50 ms to 1140 ms for the long condition. In the rhythmic conditions, data were locked to the onset of the empty time interval of interest, which was the last empty time interval of the sequence. This empty time interval was epoched from -50 ms to 350 ms for the short and from -50 ms to 1140 ms for the long conditions time scale.

No baseline correction was applied as the lower band of the band-pass filter was set to 1 Hz. Epochs with amplitude exceeding 100  $\mu$ V were discarded (mean percentage of rejected epochs across conditions = 1.48% +/-2.35).

### 2.2.6. Differential wave computation & statistical analyses

For each participant, epochs of each condition were averaged separately: DEV- (mean epoch number: 75.9 +/-1.9), DEV+ (mean epoch number: 75.8 +/-1.9), and STD (following two standards in non-rhythmic conditions, mean epoch number: 143.9 +/-2.8; in rhythmic conditions and controls, mean epoch number: 75.9 +/-1.9).

To ensure that each white noise burst elicited a clear and classical auditory evoked response (N1, P1), we ran spatio-temporal cluster analyses on the evoked responses grand-average across participants to quantify whether spatio-temporal cluster analysis could disentangle those evoked responses (see Fig. 2.S1-S2 for the grand average evoked responses).

To compute the differential waves, we first recentered epochs at the offset (second white noise burst) of the time interval of interest (for rhythmic conditions, it corresponds to the last time interval of a sequence). We, then, performed two kinds of differential waves. In the first one, we computed a differential wave by subtracting the response of STD from the response of DEV (DEV-STD). In the second one, we computed differential waves by subtracting the response of the CTRL from the response of DEV (DEV-CTRL). Although the differential wave DEV-CTRL is now the accepted way to look at duration MMN responses (Jacobsen & Schröger, 2003; Kujala et al., 2007), recent studies still use the DEV-STD contrast (Thibault et al., 2023; Isenstein et al., 2024).

For statistical quantification, we performed spatio-temporal cluster-based permutations to identify where and when the differential waves would differ from zero

and to highlight MMN responses. This method allows one to take care of the multiple comparisons problem (inflation of type 1 error with repetition of statistical tests), usually encountered with the multidimensional characteristic of neuroscience data (Maris & Oostenveld, 2007). We used a threshold for inclusion in the cluster test of  $p < 0.01$  and a final acceptance threshold of  $p < 0.05$ . In the plots, the shaded area around the evoked responses corresponds to the standard error of the mean across participants.

To quantify the effect of refractoriness, we computed a subject-wise linear regression between the amplitude of the evoked responses and the time interval length for each sensor and each time point. Then, we performed spatio-temporal cluster analysis on the regressions betas to test where and when we would find significant linear regressions. This analysis is an adaptation of the analysis developed by Gauthier (2019) to investigate signed or absolute regression patterns across their experimental conditions.

## 2.3. Results & Discussion

We first looked at the auditory evoked responses for each condition to check that each white noise elicited a clear evoked response. At the long condition, each white noise (onset and offset) elicited clear obligatory auditory evoked responses (P1, N1, P2; Fig. 2.S1). At the short condition, the auditory evoked responses of the first white noise (onset of the time interval) overlapped with the responses of the second white noise (offset of the time interval; Fig. 2.S2). Hence, we first focused on the long duration scale condition to demonstrate that the appropriate contrast for duration MMN is DEV-CTRL and not DEV-STD. Then, we focused on the short condition only with the DEV-CTRL contrast.

### 2.3.1. Long duration scale: DEV- but not DEV+ elicit an MMN-like potential with the contrast DEV-STD

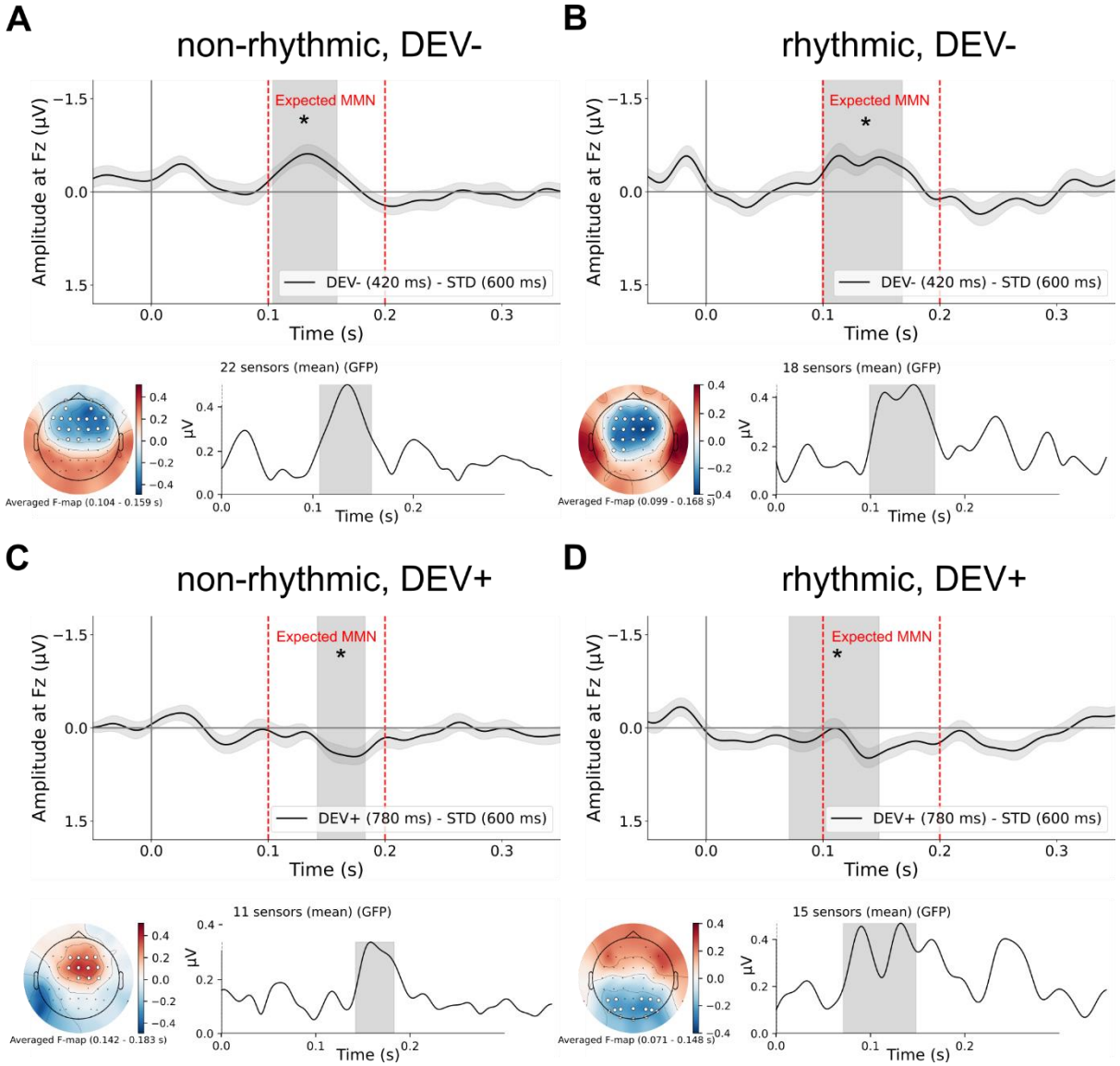
The historical and traditional contrast DEV-STD have been extensively used with empty time interval MMN, and even recently in duration MMN studies (Thibault et al., 2023; Isenstein et al., 2024). To replicate studies using such a contrast, we performed this contrast for each deviant (DEV-, DEV+) separately in both the rhythmic and the non-rhythmic conditions. A significant negative cluster in frontocentral electrodes at the

expected MMN time window was found for DEV- (non-rhythmic: number of electrodes = 22, time window = 104-159 ms,  $p = 0.003$ , Fig. 2.2A; rhythmic: number of electrodes = 18, time window = 99-168 ms,  $p = 0.001$ , Fig. 2.2B). Those negative clusters fall right in the expected MMN time window, with topographies close to the one classically described for the MMN. For DEV+, we found a significant positive cluster in frontocentral electrodes in the non-rhythmic condition (number of electrodes = 11, time window = 142-183 ms,  $p = 0.034$ ) and a significant negative cluster in occipitoparietal electrodes in the rhythmic condition (number of electrodes = 15, time window = 71-148 ms,  $p = 0.008$ ). Those positive clusters also fall in the expected MMN time window, but the topographies are inverted compared to DEV-, and hence inverted compared to the classical MMN topography.

The observation of an MMN-like potential for DEV- but not for DEV+ replicates previous observations found for rhythmic stimuli (Brannon et al., 2004, 2008; Ford & Hillyard, 1981; Lai et al., 2011; Näätänen et al., 1993) and extends it to a non-rhythmic condition with empty time intervals. To the best of our knowledge, this is the first observation of an MMN-type potential when the change in duration comes only from a deviance of an empty time interval, with no other supra-temporal cues (such as a rhythmic stimulation).

However, the fact that DEV+ elicited a positive potential in a similar time window and not a negative one as expected by the MMN, challenges the interpretation that this response is an MMN at all. However, whether this response is an MMN, or another response does not matter if this response still codes for the detection of a duration change. A bold interpretation could be that negativity and positivity could code for a shorter and a longer deviance. Another competing hypothesis to the encoding of the duration is the encoding of temporal expectation. In this case, we could expect a specific response at the offset of a shorter duration (DEV-, what has been observed) and at the offset of the expected duration (STD) when the duration is longer (DEV+). Moreover, the coding of temporal expectation would also explain MMN potentials observed by the omission of a sound. The omission of a stimulus would be a similar situation as to the moment where the offset of a standard empty time interval is omitted if the deviant is longer. The violation of the elapsed standard duration would be sufficient to elicit an MMN. Therefore, we investigated whether we could find a response at the offset of the

standard, within the response of the longer deviant. It has been shown that omission can elicit an MMN for duration above the TWI when a rhythmic stimulation with sequences of empty time intervals is used (Salisbury, 2012), just like we did.



**Fig. 2.2: Differential waves DEV-STD at the long duration scale and significant clusters in the expected MMN time window.** A: DEV- in the non-rhythmic condition. B: DEV- in the rhythmic condition. C: DEV+ in the non-rhythmic condition. D: DEV+ in the rhythmic condition. In each panel, the upper figure corresponds to the grand average amplitude at the Fz electrode of the contrast DEV-STD, time-locked at the offset (second white noise burst of the empty time interval). Red dashed lines delimit the expected MMN time window from 100 to 200 ms. The lower figure corresponds to the topography of the amplitude average across the duration of the cluster and the time series of the global field average across the electrodes of the cluster. The grey-shaded areas correspond to the significant time windows.

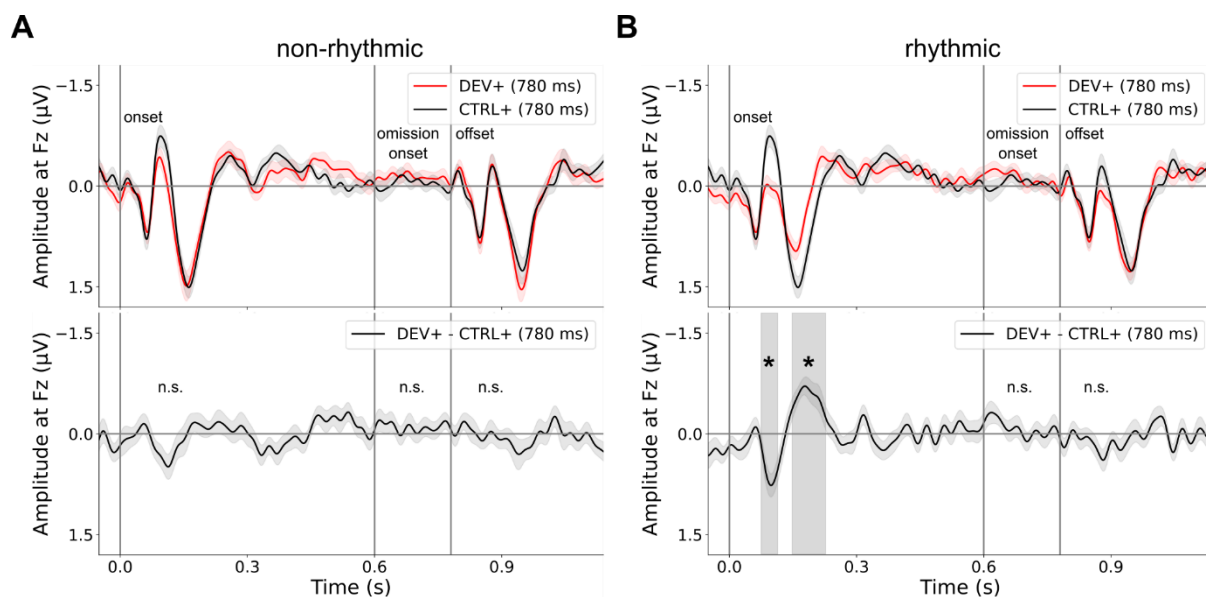


### 2.3.2. Long duration scale: DEV+ does not elicit a response at the STD offset

To test for a response at the offset of the STD in the DEV+ response (close to an omission potential), we computed the differential wave between the response to the DEV+ in the MMN block and to CTRL+ in the control block. We performed a spatio-temporal cluster analysis and were expecting to find a cluster at the expected offset of the STD.

We found no significant difference at the expected latency. Instead, we found two clusters at the onset of the duration in the rhythmic condition (cluster 1: number of electrodes = 13, time window = 75-114 ms,  $p = 0.024$ ; cluster 2: number of electrodes = 21, time window = 148-227 ms,  $p = 0.001$ ). These effects could be explained by the difference in refractoriness of the N1-P2 auditory evoked responses since the rhythmic DEV+ followed a fixed 600 ms time interval and the CTRL+ followed a jittered 1500 ms (Fig. 2.3B).

The fact that no brain response was observed at the omission of the standard offset for DEV+ questioned the interpretation of a violation of expectation at all. Moreover, the fact that no significant cluster was found even after the offset of the DEV+ suggests that the significant clusters from the DEV-STD contrast are specific to this contrast, and not from the deviance in duration. One major specificity from this contrast, with empty time intervals, is that we compare the responses of stimuli following different objective durations. Hence, this contrast is fully subject to refractoriness. The amplitude of the auditory N1 or P2 will be different because they follow different objective empty time intervals. This difference in amplitude between DEV and STD could result in ERPs that could be misinterpreted as an MMN when the differential wave is computed (Fig. 2.S3). The visual inspection of the auditory evoked responses suggested indeed a change in P2 amplitude according to the preceding empty time interval length (Fig. 2.S4).



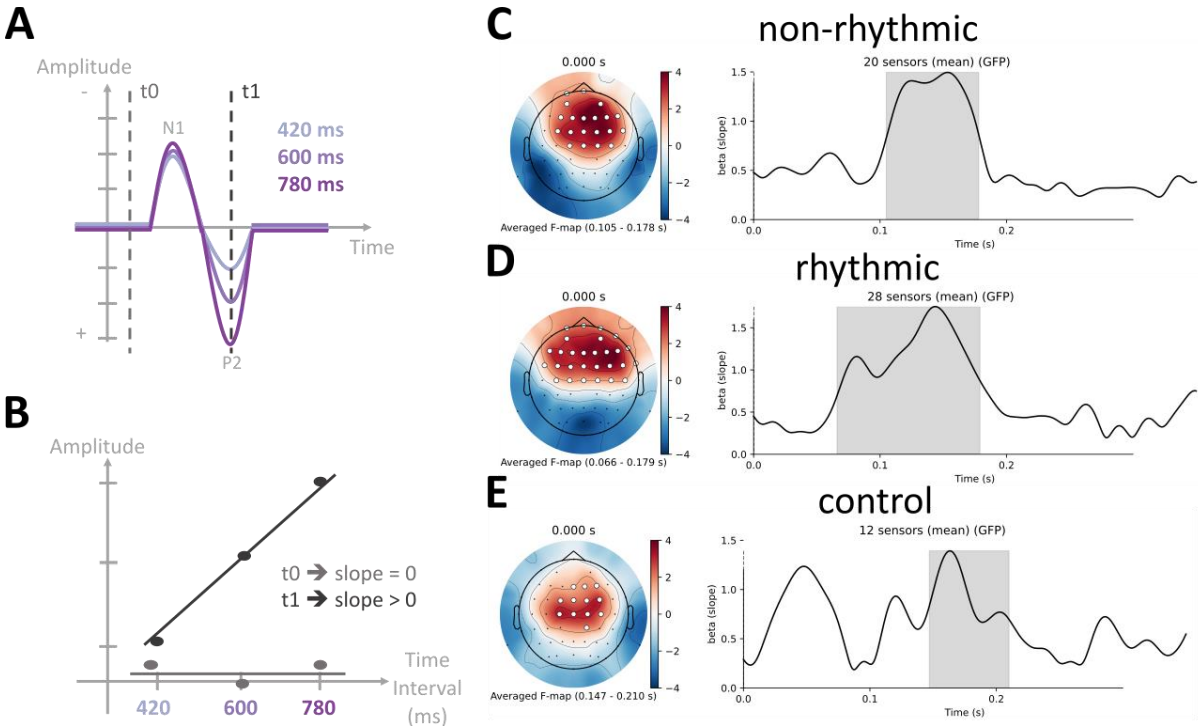
**Fig. 2.3: No omission MMN response when the deviant (DEV+) is longer than the standard at the long duration scale.** A: Non-rhythmic condition. B: Rhythmic condition. In each panel, the upper plot is the evoked responses of the longer deviant (DEV+, red curve) and the same duration in the control block (CTRL+, black curve), and the lower plot is the differential wave across the whole epoch. The grey-shaded areas delimit the significant time windows in the spatio-temporal cluster analysis.

### 2.3.3. Long duration scale: The MMN-like potential of the contrast DEV-STD can be explained by the N1-P2 refractory period

The refractoriness effect posits a parametric effect of the preceding empty time interval on the amplitude of auditory ERPs. So, we can expect a proportional increase in the amplitude according to our empty time interval length. As detailed in the methods section, we computed the linear relationship between the amplitudes of the auditory evoked response as a function of the empty time interval length (Gauthier et al., 2019). If we perform, for each participant, this linear fit at each time point and for each electrode, we can look at the slope of the regression to check whether there is a positive, negative, or null relationship between the amplitudes of each ERPs (Fig. 2.4A-B). To quantify whether this pattern is significant, we performed a spatio-temporal cluster to identify where and when the slope was different from zero. Importantly, this refractoriness pattern should also be found in the control blocks. We found significant frontocentral clusters between 100 and 200 ms for each condition corresponding to the pattern observed at Fz in the differential waves DEV-STD (non-rhythmic: number of electrodes = 20, time window = 105-178 ms,  $p = 0.001$ , Fig. 2.4C; rhythmic: number of electrodes = 28, time window = 66-179 ms,  $p = 0.001$ , Fig. 2.4D; control: number of electrodes = 14,

time window = 147-210 ms,  $p = 0.022$ , Fig. 2.4E). The fact that we observed such pattern for both non-rhythmic and rhythmic but also for the control block aligns well with the explanation of the DEV-STD clusters by an effect of refractoriness.

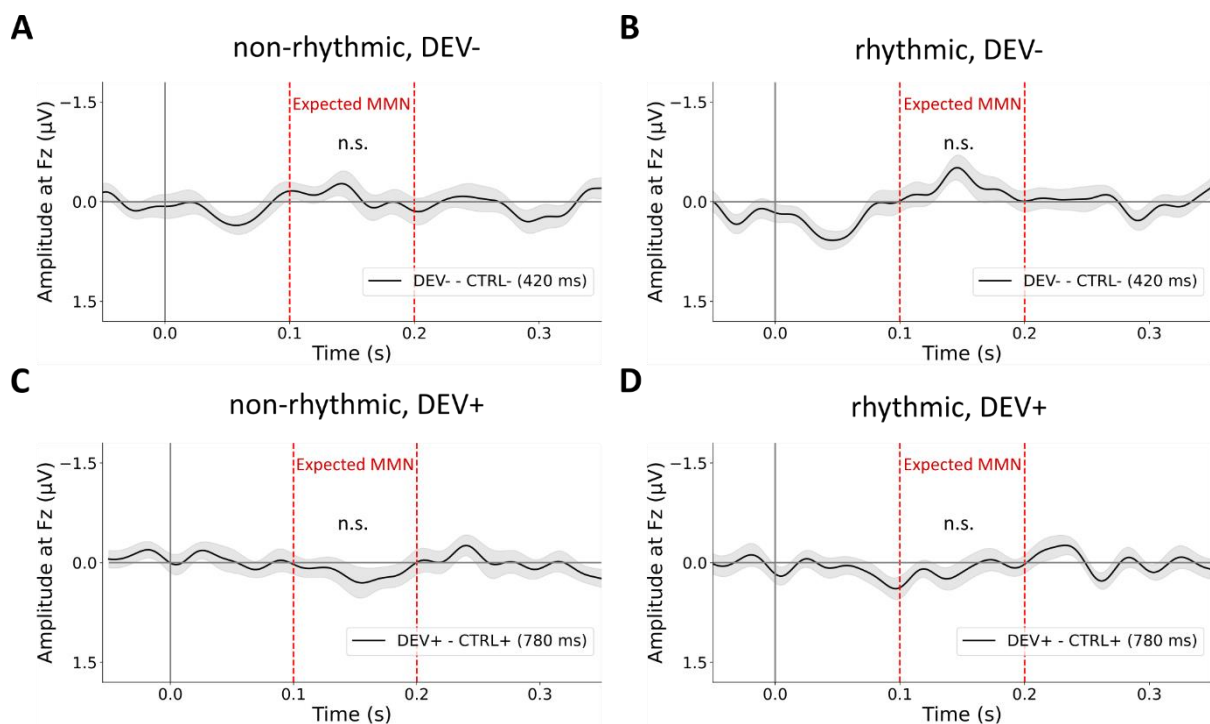
To overcome the effect of refractoriness with an empty time interval, we can compare the responses from the deviant to the responses from the same objective empty time interval in a control block, i.e. the contrast DEV-CTRL (Jacobsen & Schröger, 2003). We will thus compare responses that have the same effect of refractoriness, and the only distinction between the two will be that one is a deviant in its block, and the other will be just an empty time interval among others.



**Fig. 2.4: Linear regression between the amplitude level and the empty time interval length to quantify the refractoriness pattern at the long duration scale.** A: Schematic illustration of a change in the P2 amplitude as observed in the evoked responses (Fig. 2.S4). Vertical dashed lines represent different time points with different amplitude levels. B: Schematic example of the slope of the linear regressions computed at two different time points of the panel A,  $t = 0$  ms for grey and  $t = 100$  ms for dark grey. C: Significant spatio-temporal cluster for the non-rhythmic. D: Significant spatio-temporal cluster for the rhythmic condition. E: Significant spatio-temporal cluster for the control block. Grey shaded areas corresponds to the significant time windows of the cluster. Interestingly, they all fall in the MMN time window, overlapping with the significant clusters from the DEV-STD contrast.

### 2.3.4. Long duration scale: no duration MMN with the DEV-CTRL contrast

Testing the contrast DEV-CTRL in the long temporal scale, we found no significant clusters and thus, no evidence for the elicitation of an evoked response by duration change detection in the absence of attention (Fig. 2.5). This result challenges the past interpretation that change in empty time interval is automatically computed by the brain in the MMN process, obtained with the DEV-STD contrast. When the effect of refractoriness is overcome with the DEV-CTRL contrast, we do not observe an MMN potential. The direct interpretation would be that the brain, at the scale of 600 ms does not compute automatically changes in empty time interval. This would align well with the hypothesis that above TWI, it would be too costly to compute any duration between events (when it is not required by behavior) for the brain, since it is already equipped with mechanisms to automatically segment information, such as TWI.

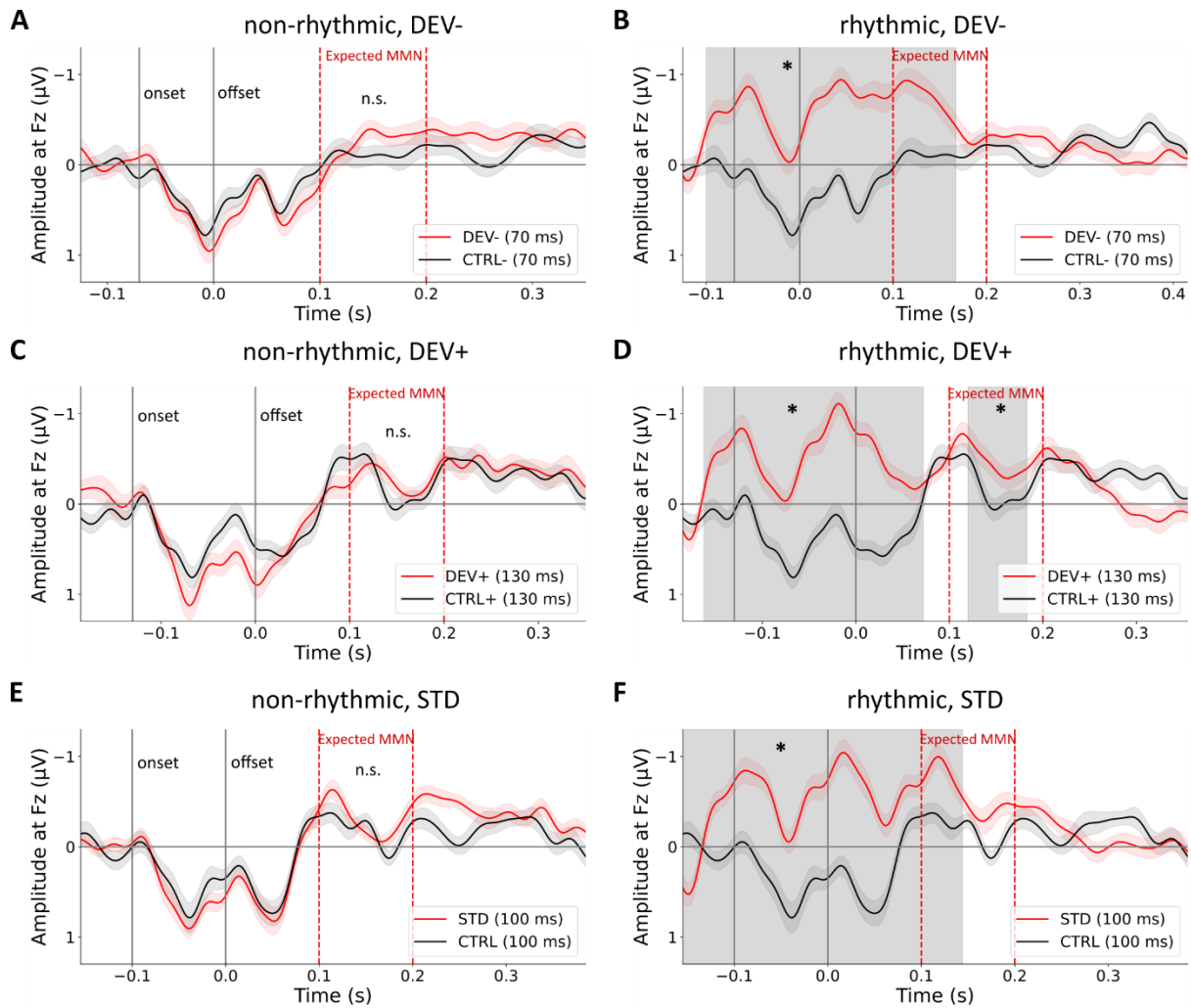


**Fig. 2.5: Differential waves of the contrast DEV-CTRL in the long duration scale condition for each deviant (DEV-, DEV+) in each condition (non-rhythmic, rhythmic).** A: Differential wave DEV-CTRL for DEV- in the non-rhythmic condition. B: Differential wave DEV-CTRL for DEV- in the rhythmic condition. C: Differential wave DEV-CTRL for DEV+ in the non-rhythmic condition. D: Differential wave DEV-CTRL for DEV+ in the rhythmic condition. Black solid lines correspond to differential waves DEV-CTRL at the offset of each empty time interval. Vertical dashed red lines delimit the expected time window of the MMN. Grey shaded areas depict the standard error of the mean of the differential waves.

### 2.3.5. Short duration scale: no duration MMN with the DEV-CTRL contrast in the non-rhythmic stimulation

We showed, with the example of the 600 ms long duration scale, that the contrast DEV-STD is not appropriate to study the empty interval MMN because of the effect of refractoriness. For long conditions, with a standard duration of 600 ms, we found clear auditory responses for each white noise. In the 100 ms short duration scale condition, this contrast seems even less appropriated because the auditory response for the first white noise (onset) overlaps with the response of the second (offset, Fig. 2.S2). This has already been identified as a possible confound in the previous study of Kujala and colleagues (2001) where control blocks have been used to perform the contrast DEV-CTRL at such short duration scale.

We did not replicate Kujala and colleagues (2001) results who reported a clear MMN for shorter deviants with a standard duration of 120 ms. In the non-rhythmic condition, we found no significant clusters for the contrast DEV-CTRL, irrespective of DEV- or DEV+ (Fig. 2.6A-C-E). We can note three distinct parameters in Kujala and colleagues' study and ours. The 1<sup>st</sup> is that they used a fixed SOA between the onset of the pairs, leading to supra-temporal cues. The 2<sup>nd</sup> is that the MMN they observed is for 50% of duration deviance, while ours is of 30% and the MMN amplitude usually increases with the percentage of deviance (Schröger, 1998b). The 3<sup>rd</sup> is that they have three times much more stimuli than us (taking into account the number of participants and the number of stimuli presented) leading to a signal-to-noise ratio ~40% bigger than us (Luck, 2014).



**Fig. 2.6: At short duration scale, the contrast DEV-CTRL shows no specific response for the non-rhythmic condition, and a significant response before the expected MMN time window for the rhythmic condition.** A: ERPs of DEV- (red) in the non-rhythmic condition and CTRL- (black). B: ERPs of DEV- (red) in the rhythmic condition and CTRL- (black). C: ERPs of DEV+ (red) in the non-rhythmic condition and CTRL+ (black). D: ERPs of DEV+ (red) in the rhythmic condition and CTRL+ (black). E: ERPs of STD (red) in the non-rhythmic condition and CTRL (black). F: ERPs of STD (red) in the non-rhythmic condition and CTRL (black). In each panel, vertical grey bars are the onset and the offset of each empty time interval. Vertical dashed red bars delimit the expected time window of the MMN. Grey shaded areas correspond to significant cluster time windows. Shaded areas around the curve correspond to the standard error of the mean of the ERPs.

### 2.3.6. Short duration scale: rhythmic sequences require specific controls

One possible explanation that we did not replicate previous results (Kujala et al., 2001) might come from the fact that they used a rhythmic stimulation. It has been shown that a constant rhythm facilitates the observation of an MMN response (Lumaca et al., 2019). This suggests that we could find a similar MMN response in our rhythmic condition. However, because of the overlap of the auditory responses at such a short duration scale, the contrast DEV-CTRL requires that the CTRL is also from a rhythmic stimulation.

Indeed, we found significant spatio-temporal clusters even before the offset of the deviant duration, that were sustained after the offset (DEV-: number of electrodes = 27, time window = -0.162-167 ms,  $p = 0.001$ , Fig. 2.6B; DEV+, 2 clusters: number of electrodes = 30 & 15, time window = -0.100-72 & 120-183 ms,  $p = 0.001$  & 0.022, Fig. 2.6D). This is possibly due to the fact that the rhythmic stimulation at 100 ms induced drift in the brain responses, probably because to the overlap of each auditory ERPs. This is even more supported by the fact that a similar cluster was found for the STD-CTRL contrast (STD: number of electrodes = 30, time window = -0.100-144 ms,  $p = 0.001$ , Fig. 2.6F). In the evoked response from the whole sequence of white noise bursts, we can visualize that each noise burst (grey dashed line) is preceded with only a sharp P1 and that there is a slow negative drift across the presentation of the all the white noises (Fig. 2.S5).

## 2.4. General Discussion

Taken together, we found that the classical empty interval MMN observed in the contrast DEV-STD is possibly confounded with an effect of refractoriness, therefore not appropriate to study empty interval MMN. When an appropriate control block is used, no specific response for deviance in duration is found at a relatively long standard duration of 600 ms, for non-rhythmic and rhythmic durations. At a shorter standard duration of 100 ms, we also did not find a specific response for duration deviance in the non-rhythmic condition and emphasized that, for the rhythmic condition, an even more specific control block is required to study empty interval MMN.

It is surprising that while the methodological caveat of the contrast DEV-STD for both filled and empty intervals has been already raised in the MMN research community (Kujala et al., 2007), it was not the case for researcher from the timing literature (Ng & Penney, 2014), and still used in very recent papers (Thibault et al., 2023; Isenstein et al., 2024). Indeed, the observation of an empty interval MMN with the contrast DEV-STD was consistently replicated for the shortening of standard empty time interval from 500 ms (Näätänen, Jiang, et al., 1993), 600 ms (Ford & Hillyard, 1981; Lai et al., 2011; and its magnetic counterpart Hari et al., 1989), 1000 ms (Brannon et al., 2008) and 1500 ms (Brannon et al., 2004). While we showed that in our data, the effect of refractoriness impacted the amplitude of the auditory P2, it is not the case for the simple auditory ERPs

of several previous studies (Brannon et al., 2004; Näätänen, Jiang, et al., 1993). In those studies, the auditory ERPs show a sustained negative activity following the N1, as it is classically observed in the MMN response of other stimulus features. As acknowledged by the authors (Brannon et al., 2008), if the response observed was due to changes linked to the refractoriness effect of the N1, they should find a response less negative for the deviant. One possible explanation could be that they didn't use the same number of stimuli to average the response for the deviant and the standard, with either a ratio deviant/standard of 0.02 (Näätänen, Jiang, et al., 1993) or  $\sim 0.15$  (Brannon et al., 2004, 2008), meaning that the signal-to-noise ratio is different for deviants and standards. In our study, we specifically selected standard presented every two standards to compute the ERP, since deviants were only presented at least every two standards as well. Our ratio deviant/standard was much closer to one ( $\sim 0.53$  for non-rhythmic,  $\sim 1$  for rhythmic), hence the signal-to-noise ratio was closer for deviants and standards compared to previous studies. It would be interesting, and possibly necessary, to fully replicate such result (e.g. Brannon et al., 2004: STD+ = 1500 ms, DEV- = 500ms) with simply an additional block where the deviant and the standard are reversed in role (e.g. STD- = 500 ms, DEV+ = 1500 ms) and perform the differential wave DEV-STD but across blocks, meaning that the two empty time intervals would have the same refractory period (e.g. DEV-diff.wave = DEV- - STD-; DEV+diff.wave = DEV+ - STD+). We would also need to select a number of STD similar to DEV in order to have equal signal-to-noise for each ERP. If an MMN-like response is found in such contrast, it would confirm that the previously observed MMN-like responses from those studies are not resulting from a difference in refractoriness.

To the best of our knowledge, only the study of Kujala and colleagues (Kujala et al., 2001) used an adequate control block to investigate empty interval MMN. They studied the shortening of a standard empty interval of 120 ms delimited by pairs of 30 ms sound. However, the onset of each pair was separated by a constant pair onset asynchrony of 500 ms, resulting in a constant rhythm across the pair onsets. They tested 3 shorter deviants of 100, 60, and 20 ms corresponding to 16, 50, and 80% of deviance. They used a control block in which all the deviant pairs were equiprobably presented. They found a reliable MMN response for the 20, 60 ms deviants and replicable within participants across two different sessions conducted on separate days. This



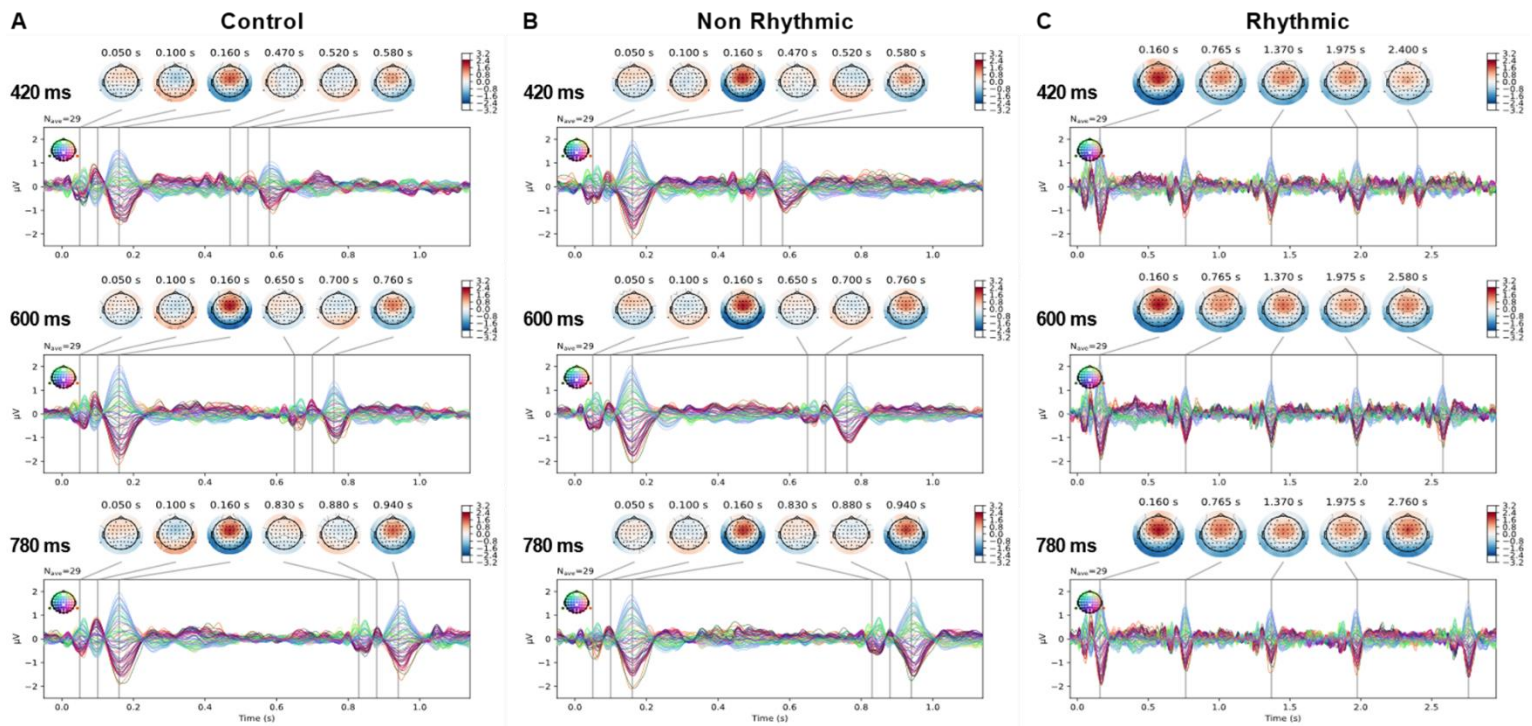
experimental setting is very similar to our DEV- in the short condition. However, we did not replicate their result. We identified at least three main differences between the studies that could explain the non-replication. The first one is the amount of signal/noise ratio. Across participants, they had ~6000 deviant stimuli for the averaging while we have only ~2000, resulting in a difference of ~40% in the signal-to-noise ratio (Luck, 2014). The MMN has been described as a sensitive potential that requires a certain amount of signal-to-noise to be observed (Kujala et al., 2007). The second difference is the percentage of deviance. They found a reliable MMN for deviance of at least 50% and ours was only 30%. However, we can note that a deviance of 30% is already large, especially if we considered other stimulus features and perceptual abilities (Schröger, 1998b). The MMN amplitude have been closely linked to our perceptual abilities (Winkler, 2007), so a change in 30% of duration should easily induce an MMN since it is easily detected (Amenedo & Escera, 2000). The last difference is that, in the study of Kujala and colleagues, the onset of pairs was fully temporally predictable since they used a constant pair onset asynchrony of 500 ms, which constitute supra-temporal cues. Hence, although they used empty time intervals delimited by pairs of sounds, there was a constant rhythm across the stimulation. Previous studies demonstrated that a rhythmic temporal structure can facilitate the elicitation of the MMN, as a clear filled time interval MMN was found when a constant ISI was used (Näätänen et al., 2004) and it was not when a variable ISI was used (Grimm et al., 2004). This suggests that if the temporal structure is highly predictable (e.g. a constant rhythm), the easier the duration change is detected and an MMN is elicited. This is even more important whenever the dimension of interest is the duration (Knight et al., 2020; Lumaca et al., 2019). It was shown that even when a sequence of two empty intervals is used, the shortening of the long empty interval does not elicit an MMN (Nordby et al., 1988b) compared to when only one empty interval is tested (Nordby et al., 1988a).

While we originally wanted to compare non-rhythmic and rhythmic sequences in the short condition, which would have allowed us to possibly reconcile with the study conducted by Kujala and colleagues (2001), we showed that rhythmic sequences at such short duration scale require specific control blocks to take into account the overlap of activity. The presentation of a sequence of five noise bursts induced a slow drift with an oscillatory activity that led to differences in the pre-stimulus period, even between STD

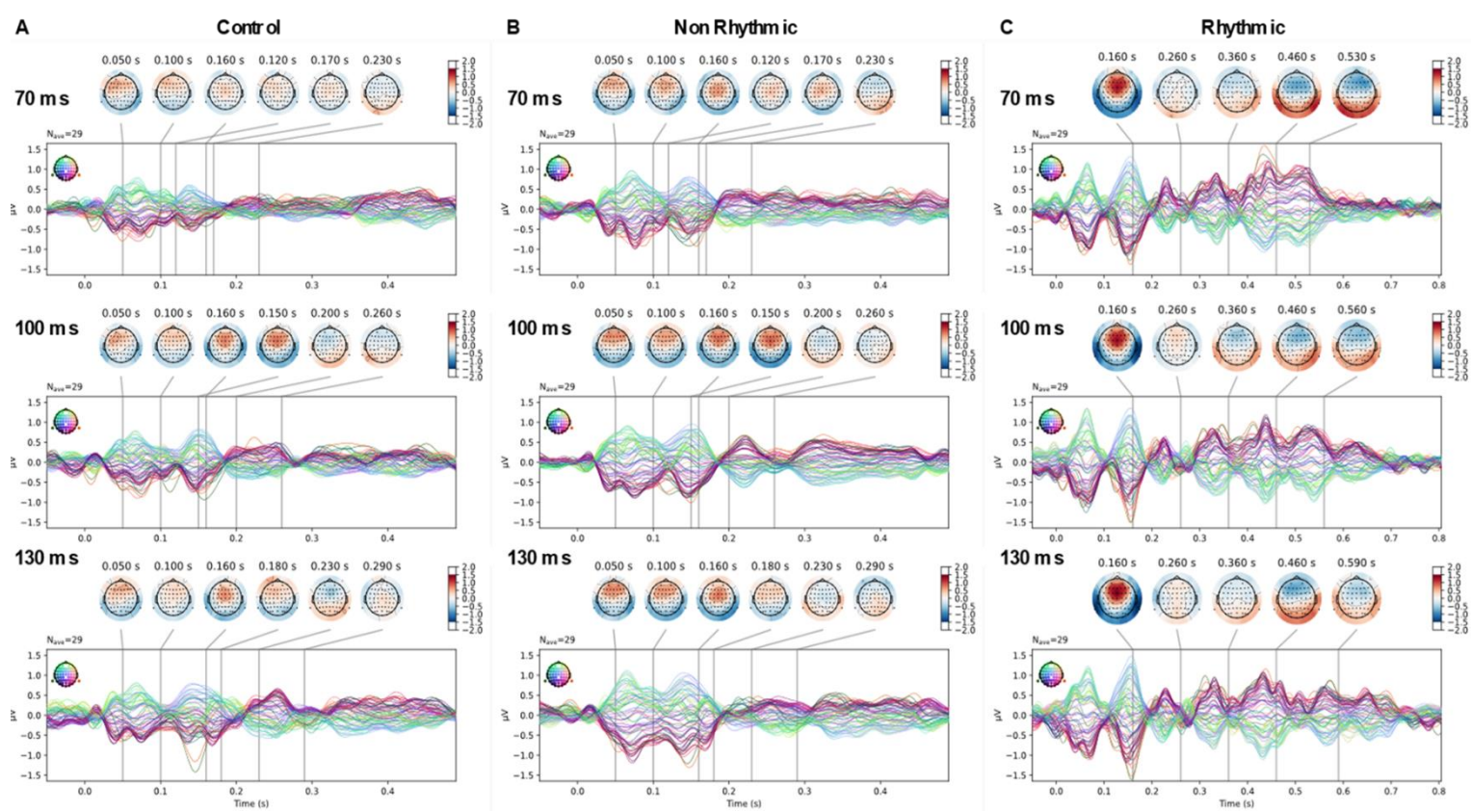
and CTRL (Fig. 2.6B-D-F). The importance of an adequate control block can also be highlighted in a previous study where sequences of four empty time interval have been tested (Sable et al., 2003). In a similar, but larger design than ours, they tested several standard durations (100, 200, 300, and 400 ms) that could either be the first three STD empty interval and/or the last STD/DEV empty time interval. They computed differential waves by subtracting the response from a given time interval preceded by the same first three (e.g. a last time interval of 100 ms preceded by three time intervals of 100 ms, which corresponds to a STD) from the same time interval preceded by a different sequence of empty time interval (e.g. a last time interval of 100 ms preceded by three time intervals of 300 ms, which corresponds to a DEV-). While this allowed them to compare the response from the same time interval, it did not control for the overlap of activity induced by the different rhythmic context in which the time intervals were embedded. It is highly probable that the baseline level before the last time interval was different across the rhythmic contexts, similar to what we observed in the contrast DEV-CTRL for the rhythmic condition (Fig. 2.6B-D-F). An appropriate experimental setting with such stimuli would be to use a paradigm close to the local-global (Bekinschtein et al., 2009). In a test block, STDs would be a sequence of four constant time intervals and DEVs would be a sequence of three constant time intervals followed by a shorter/longer time interval (standard = A A A A; deviant = A A A B, where A and B are distinct time intervals). In a control block, STDs would be the sequence of 3 constant time intervals followed by a shorter/longer time interval and the DEVs would be a sequence of 4 constant time intervals (e.g. standard = A A A B; deviant = A A A A). The contrast DEV-STD across blocks ( $DEV_{A A A B} - STD_{A A A B}$ ) would allow to test for the response of a deviance specific to a change in empty time interval albeit embedded in the same rhythmic context (Bekinschtein et al., 2009). Note that the underlying assumptions might be different than simply testing whether empty time intervals are automatically coded by the brain in a rhythmic sequence. Indeed, in a local-global sequence-like, the question addressed is more whether the specific pattern/rule (A A A B) is automatically detected by the brain, rather than whether the information inside this pattern (the nature of A and B, which is a time interval in our case) is automatically detected. If A and B correspond to time intervals, then the question asked with such design is whether time interval can be used to define specific patterns, as we can do with changes in pitch or sound volume.

Altogether, our results suggest that, in the absence of rhythmic structure, and at the duration scale of 100 and 600 ms, empty time interval is not automatically coded by the brain in the MMN process. To the best of our knowledge, this is the first time that “pure” changes in empty time interval have been tested (with proper control block, and in absence of supra-temporal cues. Hence, it would be very interesting to replicate such results. Additional work is required to conclude whether the previous empty time interval MMN (e.g., Brannon et al., 2004), observed for shortening of a constant rhythm, survives an adequate control. At a standard duration of 100 ms, there is mixed evidence that an MMN is observed (cf. our results compared to Kujala et al., 2001). If a consistent MMN is found at a short duration scale and not at a long one, an interesting hypothesis could be that what is actually coded at the short duration scale is the identity of the stimulus, into which the duration belongs because it falls inside the TWI, while it is not at a long duration scale. The automaticity of TWI and its ability to segment information would make the automatic coding of long duration between events an additional cost to the brain, if the duration is not required by the task. In conclusion, our results call for a battery of studies to be conducted in order to claim that duration is indeed automatically coded, or not, in the MMN process.

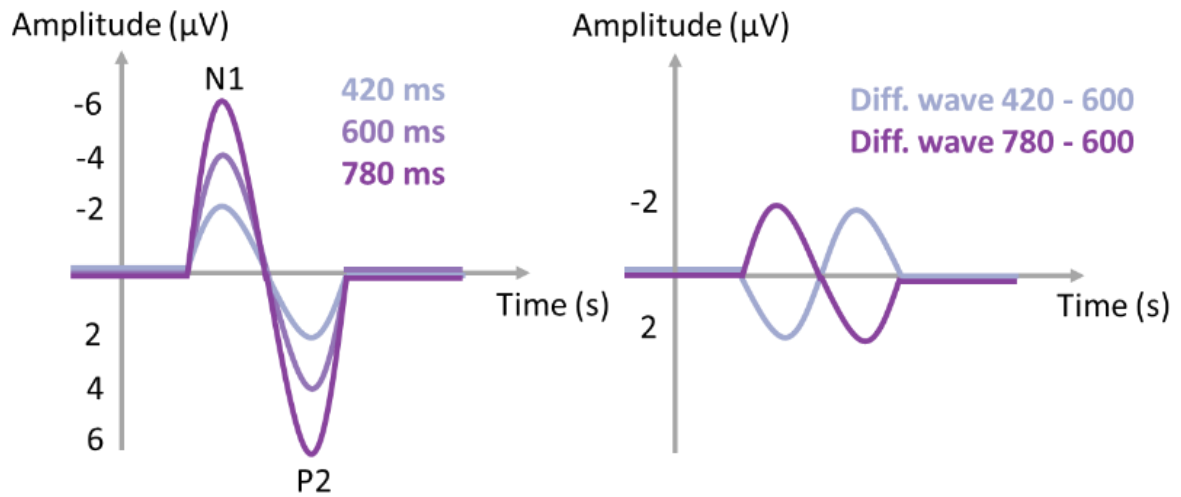
## 2.5. Supplementary Materials



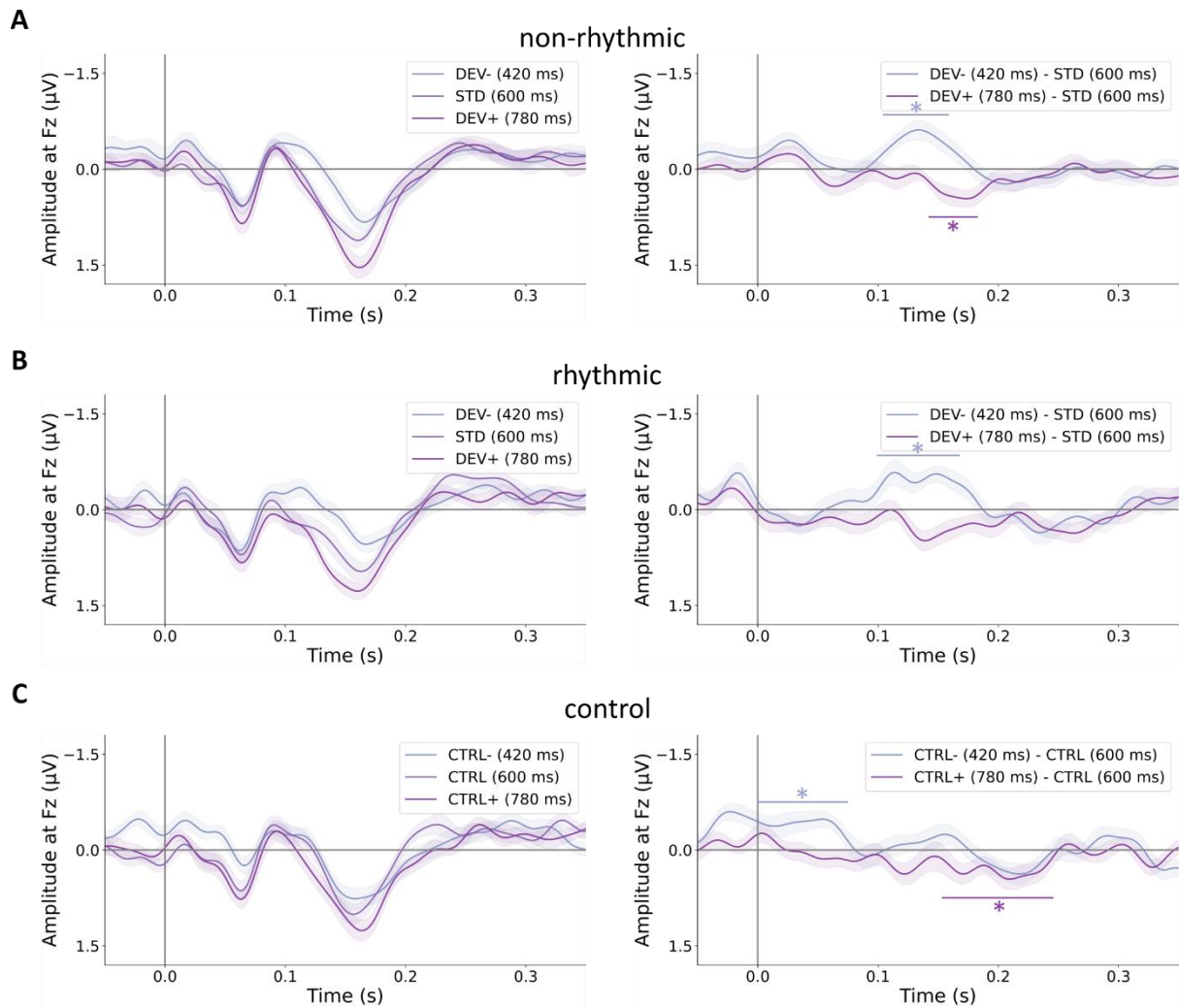
**Fig. 2.S1** Grand-average evoked responses for each stimulus for each sequence type (control, non-rhythmic, rhythmic) at the long duration scale. A: Control condition. B: Non rhythmic condition. C: Rhythmic condition. Color lines are the grand average ERPs (across participants) for each electrode. Vertical grey bars indicate the 50, 100, and 160 ms after the presentation of one auditory click, to emphasize the expected auditory P1, N1, P2 potentials. Those vertical grey bars are associated with the topography displayed above. The important aspect of this figure is to visualize the classic auditory ERPs P1, N1, P2.



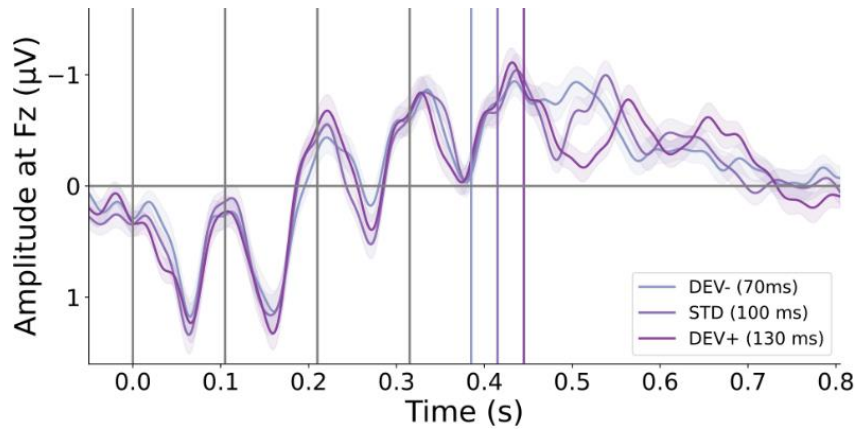
**Fig. 2.S2 Grand-average evoked responses for each stimulus for each sequence type (control, non-rhythmic, rhythmic) at the short duration scale.** A: Control condition. B: Non rhythmic condition. C: Rhythmic condition. Color lines are the grand average ERPs (across participants) for each electrode. Vertical grey bars indicate the 50, 100, and 160 ms after the presentation of one auditory click, to emphasize the expected auditory P1, N1, P2 potentials. Those vertical grey bars are associated with the topography displayed above. The important aspect of this figure is to visualize that the classic auditory P1, N1, P2 for the first auditory click (onset) overlap with the P1, N1, P2 of the second click (offset). This is why I first turned to the long duration scale to investigate the differences between DEV-STD and DEV-CTRL.



**Fig. 2.S3 Schematic illustration of the effect of refractoriness that could elicit an MMN-like waveform in the differential wave DEV-STD.** Left: N1-P2 potentials elicited by a sound following different time intervals and presenting the classical effect of refractoriness. Right: Differential waves of the shorter/longer time interval minus the middle time interval, as it would be for a shorter/longer deviant and a standard in a DEV-STD contrast.



**Fig. 2.S4: Effect of the time interval length on the auditory evoked responses for each sequence type.** A: Non-rhythmic. B: Rhythmic. C: control. Left: Auditory evoked responses elicited by STD and DEV. Right: Differential waveforms (DEV-STD). Solid horizontal lines and stars delimit significant time window found in spatio-temporal cluster analysis. Shaded areas correspond to the standard error of the mean. This figure follows the same structure as Fig. 2.S3, to show that the MMN-like responses observed in the DEV-STD contrast could be explained by a difference in refractoriness.



**Fig. 2.S5: Auditory evoked responses of the whole sequence of auditory clicks in the rhythmic sequence, at the short duration scale.** Vertical grey bars correspond to the onset of shared auditory clicks. Vertical colored bars correspond to the timing of the last noise burst for each stimulus type (DEV-, STD, DEV+). Shaded areas around the curves depict the standard error of the mean. This figure shows that the presentation of auditory clicks in a rhythmic sequence at a rate of 100 ms induces a rhythmic activity that overlap across each classic auditory ERPs. This overlap results in an activity before the presentation of the duration of interest (the last one), that prevents us from comparing this response to the response of the same duration in a non-rhythmic sequence (such as our control condition).



## Chapter 3 – Duration, distance, and speed estimations across a train journey

After investigating the automaticity of the neurophysiological foundations of duration estimations at the millisecond scale, I investigated a more ecologically valid duration judgment, in a daily-life environment: a train journey. This approach is consistent with the primary goal of the WildTimes project, consisting in quantifying time phenomenology in ecological situations. This chapter<sup>2</sup> aims to study the mechanism used by travelers to estimate minute/hour durations during their train journey. To this end, we asked travelers, recruited on the fly, to estimate the duration elapsed since the start of the journey. We also asked them to estimate the distance and speed of the train, to investigate the interaction between these estimates. We hypothesized that the sensory information available onboard the train (e.g. optic flow, acceleration) could impact duration estimations (as it was observed in laboratory studies) if it emerged from the magnitude system based on sensory processing. After showing that participants were very good at estimating duration and distance and less good at speed, I show that they probably do not rely on their speed estimates to estimate duration and distance in relation to each other. Participants' metacognitive judgments and knowledge suggest that distances were estimated based on duration estimates, rather than vice versa. Then, I found that the sensory information available onboard the train did not influence participants' estimates of duration (but also distance and speed). A strong interpretation is that participants used a strategy based on a cognitive map of time, involving their prior knowledge, rather than a strategy based on sensory and perceptual measurement of duration. This interpretation is in line with the duration MMN result, in that it runs against the idea of representing time by a "simple" measure of duration. If measuring duration is not the primary goal of behavior, it is unlikely that the brain uses a measurement mechanism such as interval timing (i.e. internal clock), but rather a cognitive map mechanism (event timing or Gallistel's phase sense).

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<sup>2</sup>This chapter is a scientific article close to be published. This version was adapted to the thesis format.

# A journey into a traveler's mental map: duration, distance, and speed experienced in high-speed trains.

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## 3.1. Introduction

Time perception is the branch of experimental psychology dedicated to the study of how the mind copes with the temporal dynamics of the world (Michon, 1998). Its most studied aspect is how we perceive duration. Laboratory results describe perceived duration as extremely malleable and influenced by a wide range of factors such as attention (Matthews & Meck, 2016), emotional state (Droit-Volet, 2013), and task demands (Polti et al., 2018). However, the processes for operationalizing and measuring time perception as perceived duration, developed in the laboratory, call into question the generalization of results of this natural behavior. This trade-off, between scientific rigor and the naturalness of behavior, is called the "real-world vs lab" dilemma (Holleman et al., 2020). It is therefore crucial to test whether laboratory results generalize to ecological context. In this study, we investigated how durations are perceived in the ecological context of a train journey.

For quantification purposes, duration perception has been mostly studied in a prospective manner (participants know that they have to estimate/classify/judge the time interval that we present to them), but, arguably, its most natural form is when participants have to estimate how much duration has elapsed, without knowing they

would have to do it, a process referred to as retrospective duration estimation (Hicks, 1992). In this study, to get closer to an ecological situation, we used a retrospective duration estimation task. In studies using retrospective duration estimation designs, the focus has predominantly been on time intervals shorter than 10 minutes (see Tobin et al., 2010 for a list of articles). Herein, we tested a wider range of time intervals, ranging from 2 to 130 min.

It has been hypothesized that duration estimation belongs to a magnitude system allowing to represent physical quantities in the mind (Gallistel, 2011). Along with space and numbers, duration has been proposed to be part of a common magnitude system (Walsh, 2003). As a result, duration and distance estimates should bear a specific relationship because they could share common neuronal networks and consequently interfere with each other. At the scale of our perception, duration and distance are physically linked by speed. To investigate the link between perceived duration, distance, and speed, we asked participants to estimate distance, and speed along with duration. While the system of magnitude is thought to be tightly linked to our path integration and sensory-motor system, new theories propose that prior knowledge, therefore cognitive strategy, highly biases our magnitude estimation (Petzschner et al., 2015). In the train, the sensory-motor inputs are reduced and far from our biological system capacities, so it provides an opportunity to investigate whether our magnitude estimation of duration and distance would be impacted by the sensory inputs still available across a train journey. We identified and measured two possible sources of sensory information onboard the train, namely: 1) the acceleration, which was either positive (i.e., during the acceleration phase of the journey), null (i.e., when the train runs at constant speed), or negative (i.e. during the deceleration episode of the journey), and 2) the optic flow orientation, which was forward (i.e. when participants were facing the direction of motion) or backward (i.e. when participants were against the direction of motion).

In the lab, the duration of a moving stimulus is overestimated compared to a static one (Brown, 1995). Specifically, overestimation increases as the speed of the stimulus increases, mostly because of the temporal frequency of the stimulus (Kanai & Watanabe, 2006). Interestingly, this effect disappears when participants are walking, suggesting that our system is able to disentangle retinal motion generated by self-motion from the one generated by the motion of the environment (Verde et al., 2019). In the train, the optic flow is not generated by self-motion and could therefore interfere

with duration estimation. Thus, we hypothesized that the acceleration of the train should impact in a systematic way the magnitude estimations of passengers.

In the present study, we used an experience sampling method (ESM) (Christensen et al., 2003) to ask participants (N=263) to estimate the duration and distance traveled since the departure of their train journey, as well as to estimate the instantaneous and average speed of the train. Before the questionnaire, participants were also queried about their priors of the journey's length (duration, distance) and the maximum train speed. Journeys' objective data were retrieved from the French railway company (SNCF). The first aim of this study was to investigate the profile and relationship of participants' estimations with one another. The second aim was to investigate whether sensory information could impact participants' estimations in a systematic way. Additionally, at the end of the questionnaire, we asked participants to provide a speed of the passage of time judgment (Droit-Volet & Wearden, 2015), as well as to report their emotional states (happiness, sadness, boredom) using Likert scales, which are usually covariates of time estimates in ESM studies (Droit-Volet et al., 2018).

We hypothesized that duration and distance should follow a classical magnitude profile (Petzschner et al., 2015), and therefore present classical a pattern such as the subjective estimate. Their variance should increase with their objective value (Weber's law profile), and short magnitude should be overestimated, while large magnitude should be underestimated (Vierordt's law profile). It is important to note that the observation of Vierordt's law profile, in a between-participants design, can be interpreted as a shared indifference point among the population studied (Woodrow, 1934), therefore a common reference shard across individuals of a population. The speed, in mechanical physics, is the derivative of the position (space) over time. Speed can be viewed as a magnitude per temporal unit. It is therefore unclear whether speed estimation will also follow a magnitude profile. Its absolute value could be represented in the brain by a number (like a magnitude), but its direction is an important aspect as well and could be represented. We wondered to which extent speed can be verbally expressed by participants.

If participants can compute (in any way) the average speed of the train, then duration and distance estimation should be linked by the average speed estimation of participants. We hypothesized that if average speed is coded by the brain, then we should be able to model the duration estimation by the combination of distance and

average speed estimation, and vice versa. If participant cannot compute the average speed, we hypothesized that participant could rely on cognitive computations, based on their prior knowledge, to estimate duration and distance.

Concerning the impact of sensory information (Acceleration and Orientation factors), we hypothesized that facing the optic flow forward (congruent with the direction of motion) would increase the impact of movement on duration estimation, therefore leading to an overestimation compared to facing backward. For the impact of acceleration, we had two competing hypotheses. The first was that it is simply the absolute value of speed that leads to an overestimation of duration, and we expected participants to overestimate in the constant speed episode (null acceleration, but fastest speed of the journey) compared to the acceleration and deceleration episodes, which should be similar. The second was that the overestimation scales with the actual rate of change (acceleration) in the environment, such that estimation from acceleration and deceleration episode (positive and negative acceleration) should be similar but overestimated compared to constant speed (null acceleration). It is important to note that we formulated our working hypotheses solely on the accuracy of estimations, and not the precision since it is a between-participants design.

Very few studies investigated the link between duration estimation and speed of the passage of time judgment (PoTJ) in ecological settings (Wearden, 2005, 2008; Droit-Volet & Wearden, 2015, 2016; Droit-Volet et al., 2017), and even fewer when the speed of the passage of time judgment concerns exactly the same time interval as the duration estimation (Droit-Volet et al., 2018; Martinelli & Droit-Volet, 2022a). Only one study investigated the link between retrospective duration estimation and PoTJ (Martinelli & Droit-Volet, 2022), and showed that PoTJ was judged slower for longer duration. This link is the same whether the duration estimation is made prospectively or retrospectively. Thus, we expected to find slower PoTJ for longer duration as well and hypothesized that longer duration estimation should be correlated to even slower PoTJ (Droit-Volet et al., 2018). Moreover, those ESM studies revealed that long duration estimations are positively and negatively correlated to happiness and boredom, respectively, when self-reported by the participant on a Likert scale (Martinelli & Droit-Volet, 2022b). We therefore expected to find such patterns in our data as well.

As participants can self-report not only the magnitude (how far) but also the direction (under/overestimation) of their timing errors on a trial basis at the scale of

seconds (Akdoğan & Balci, 2017; Kononowicz & van Wassenhove, 2019; Öztel et al., 2021), we tested whether participants can also perform such metacognitive judgment on a single trial, but at a much larger duration scale (minutes to hours) and retrospectively (instead of prospectively). Interestingly, it has been suggested that temporal error monitoring belongs to a wider mechanism, namely metric error monitoring, that is a shared mechanism across magnitude estimation of time, space, and numbers (Yallak & Balci, 2022). Therefore, we tested whether participants could also perform metacognitive judgments (confidence ratings) for distance and speed estimations performed across the train journey. Finally, concerning our hypothesis on the effect of available sensory information onboard, we investigated whether those self-reported metacognitive judgments would correlate with actual changes in magnitude errors due to sensory information processing. This could inform us about whether magnitude distortions from sensory information are accessible to an introspective metacognitive judgment.

## 3.2. Materials & Methods

### 3.2.1. Participants

279 participants were recruited on the fly among the passengers of Paris-Lyon or Lyon-Paris train journeys. Travelers were informed about the general goals of our study and told about their rights, and the use of their data would they agree to take part in the study. When they agreed to contribute to the study, we asked them to read and to sign a written informed consent form in accordance with the declaration of Helsinki (2013). The study was validated by the Ethics Committee for Research (CER) of Paris-Saclay University (CER-Paris-Saclay-2018-034-A2).

Due to their lack of compliance with the goals of the study, 16 out of the 279 recruited participants were discarded from the dataset prior to the analysis: two participants answered only one question; one participant's responses were not timed; nine participants got on or off board at an intermediary stop in the journey; four participants answered the questionnaire during an acceleration or deceleration episode of an intermediary stop. An additional 16 participants were removed because their knowledge about the total duration or distance of the journey was inaccurate according to the following criterion: their responses were below or above the first or the third

quartile, respectively, yet participants answered “yes, I know exactly the duration or distance of the journey” (see Procedure relative to the beginning of the questionnaire). Hence, a total of 247 participants (104 females; 111 males; 32 undeclared; 35.2 +/- 14.1 y.o.) were included for analysis in the study. Additional outliers’ removal was conducted as a function of the different analyses, as explained later in text when needed.

### 3.2.2. Experimental factors: Orientation and Acceleration

Seating orientation was counter-balanced across participants: 133 participants faced the direction of the train (“forward”) and 112 faced in the opposite direction (“backward”). The seating orientation manipulated the direction of the optic flow. This factor is referred to as Orientation throughout text.

Participants were grouped as a function of the acceleration episode during the journey, which was identified manually (see section 3.2.5). This resulted in 34 participants tested during a positive acceleration (start of the journey), 166 tested during a null acceleration (constant speed), and 33 participants tested during negative acceleration i.e. deceleration (end of the journey). These numbers were proportional to the duration of each episode, so that the whole train journey was sampled equally with respect to time in the journey. This factor is referred to as Acceleration throughout text.

### 3.2.3. Procedure

Questionnaires were delivered in paper format and started by inquiring participants about their basic knowledge of the journey. In the first series of yes/no questions, participants were asked to report whether they knew the total duration and the total distance of the journey. Irrespective of their answer, they were asked to provide their best numerical estimate for each (e.g. 2 hours and 47 minutes or 257 km, respectively). They were also asked to provide their best estimate of the maximal speed the train could travel (in km/h). These initial estimates are participants’ prior knowledge of the duration, distance and speed.

In a second series of questions, participants were asked to estimate the elapsed duration, traveled distance, and average speed since departure, as well as the instantaneous speed of the train at the moment they answered the question. The order of the questions was pseudo-randomized across participants. Each magnitude

estimation (duration, distance) was tested on a separate page. The estimations of average and instantaneous speeds were tested on the same page.

Estimates had to be given both graphically (Fig. 3.1A-B-C) and numerically. In the graphical estimation, participants were given a clock, a map of France and a speedometer for duration, distance, and speed estimations, respectively (Fig. 3.1A-B-C). They were instructed to indicate their subjective estimation of duration, distance, and instantaneous and average speed with a pencil mark as represented by the blue crosses in Fig. 3.1A-B-C. For their numerical estimation, participants reported the durations in hours and minutes, the traveled distances in kilometers, and the instantaneous and average speeds in kilometers per hour.

After each estimation, participants rated their confidence level using a 4-point Likert scale ranging from “not confident” to “very confident”. Additionally, following their estimation of duration, participants were also asked to provide a signed metacognitive rating of their estimate using a 4-point Likert-scale with the ranked options “underestimated”, “rather underestimated”, “rather overestimated” and “overestimated” (Chaumon et al., 2022; Kononowicz et al., 2019).

The moments at which participants provided their estimation were collected and written down by the experimenters - e.g. “at 12h33, the participant estimated the distance; at 12h34, the participant estimated the instantaneous speed”. This time-stamping procedure was accurate to the minute. It allowed extracting the objective duration, distance or speed at the moment of data collection and identifying the acceleration episode during which participants performed their estimation (Fig. 3.1D).

At the end of the questionnaire, participants rated their subjective feeling about the speed of the passage of time ranging from “very slow” to “very fast” (Wyrick & Wyrick, 1977) from the departure to the moment of their rating - i.e. the same period as their magnitude estimation. Participants were also asked to rate their emotional states over that time-period including their level of happiness, sadness, and boredom ranging from “not at all” to “very” (Droit-Volet & Wearden, 2016).

Last, participants were asked to freely describe the strategies they used for each estimation. Strategies were clustered into six categories : (1) no strategy or guess (19 participants); (2) strategies using perception, such as visual or auditory cues (e.g., observing the landscape by the window and comparing it with the speed of car passing by; 105 participants); (3) logical or mathematical strategies (e.g. reporting using “ $v=d/t$ ”



or “1/3 of the time means 1/3 of the distance”; 13 participants); (4) strategies using measurement tools despite being explicitly instructed not to do so (e.g. watches, phones or computers; 45 participants, which were not considered outliers; Fig. 3.S2); (5) strategies using knowledge (e.g., high familiarity with the journey, or the train driver giving speed or duration information at the beginning of the journey (39 participants); (6) no answer to the question (12 participants).

### 3.2.4. Data digitization, normalization, and scoring

Participants’ responses were digitized for analysis.

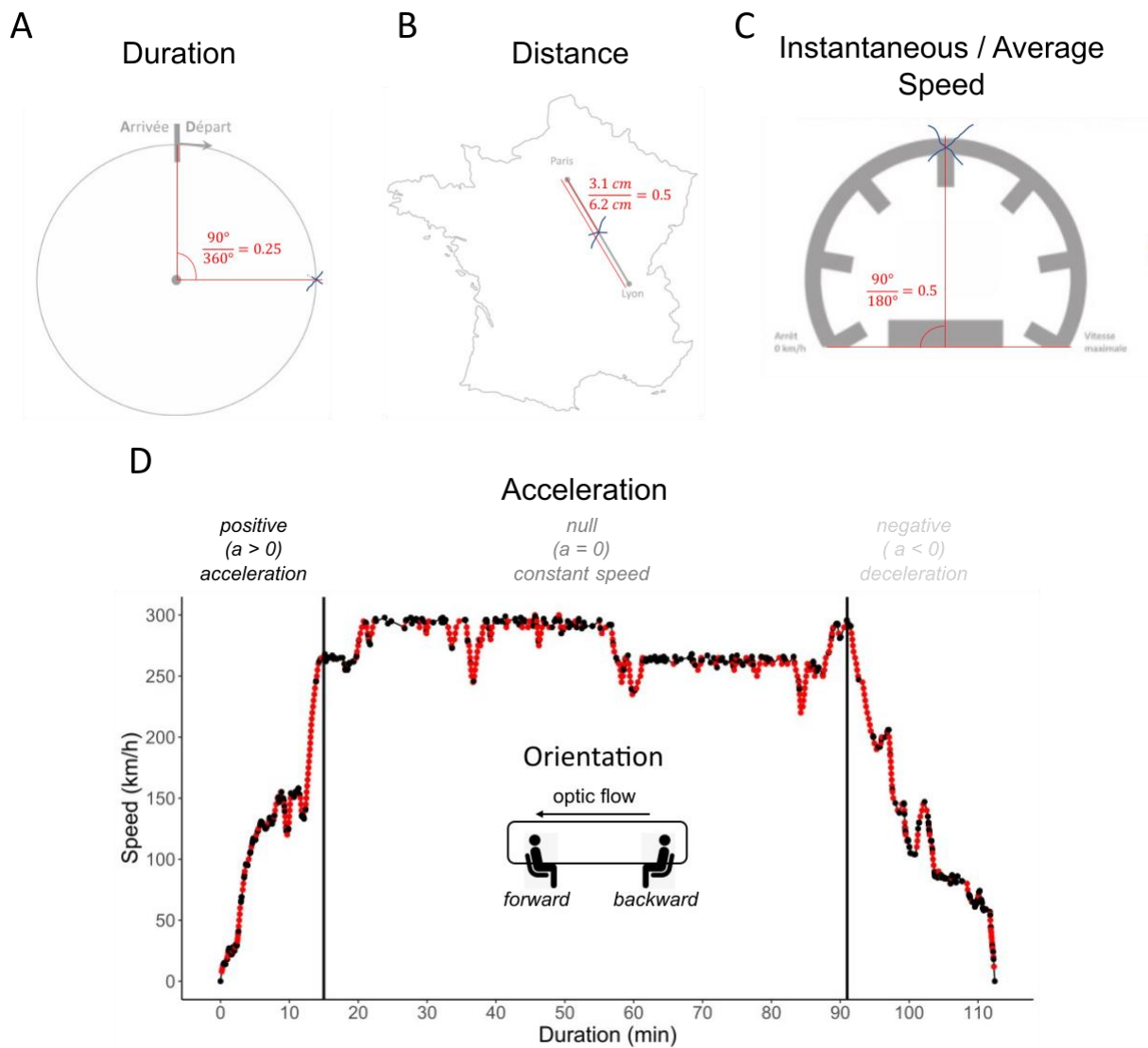
Numerical estimations were manually transcribed from paper format (hour.min) to digital format (min). Graphical estimations were digitized using Angle Meter 360 (Kozlov, 2021). For duration and speed estimates, we measured the angle (in °) between the pencil mark and the vertical line demarcating the departure on the clock (Fig. 3.1A) or the base of the odometer (Fig. 3.1C), respectively. The measured angle was rounded up to the nearest degree and converted into a ratio (measured angle divided by 360° for duration or by 180° for speed, respectively). To convert distance estimations, we used a ruler (Fig. 3.1B). The length (in centimeters) was rounded up to the nearest millimeter and converted into a ratio by dividing by the total length of 6.2 cm demarcating the Paris-Lyon distance on the map of France. The digitized graphical estimations were unitless. To assign them units and compare numerical estimations, we normalized the graphical estimates by participants’ prior knowledge of the total duration, distance, and maximum speed of the train journey. For example, if a participant declared the journey to be two hours and placed a pencil mark at 90° on the graphical estimate (e.g. Fig. 3.1A), the estimated graphical duration was 25% (90/360) of their total journey, which corresponded to 30 min (0.25 \* 120 min). This quantification strategy enabled to normalize participants’ graphical estimates to their prior knowledge about the journey. The digitized graphical estimations were unitless. To provide them units and compare numerical estimations, we normalized the graphical estimates by participants’ self-reported knowledge of the total duration, distance, and maximum speed of the train journey. For instance, if a participant stated that the journey took 2 hours and placed a pencil mark at 90° on the graphical estimate (e.g. Fig. 3.1A), the estimated graphical duration traveled was 25% (90/360) of their total journey, which corresponded to 30

min ( $0.25 * 120$  min). This quantification strategy enabled to normalize participants' graphical estimates to their prior beliefs about the journey.

Participants' numerical and graphical estimates were compared using Pearson's correlation, which confirmed a linear relation between both datasets (Fig. 3.S1). Considering the high correlation score between the two types of estimates, we averaged them into a single score to reduce the number of missing estimations (especially for the graphical ones) and prevent the rounding effect typically found in numerical estimates (Fig. 3.S1; e.g. Balçı et al., 2023; Chaumon et al., 2022). Hence, our dataset consisted of a single score per participant of duration, distance, instantaneous and average speed estimates.

For specific magnitude analyses, we computed the relative estimates by computing the ratio between the subjective score and the objective value to scale and enable comparisons.

For the analysis of confidence, we computed participants' absolute relative error by taking the absolute value of the ratio between the difference of the subjective estimate and its objective value, divided by the objective value.



**Fig. 3.1: Questionnaire and Experimental protocol.** To perform their graphical estimations, participants were provided with (A) a schematic clock, (B) the map of France highlighting the departure and arrival cities of the journey, and (C) a speedometer. Red lines are the construction lines for digitizing the graphical estimates into a unitless ratio subsequently multiplied by the participant's self-reported knowledge of the total duration, distance, or speed of the journey. (D): The questionnaire was a 3 (Acceleration) x 2 (Orientation) between-participants design. The journey was segmented into three episodes as a function of the acceleration of the train (Positive, Null, Negative), which defined our three-level factor Acceleration. The two-level factor Orientation was defined by participants' orientation in the train, facing forward or backward with respect to the train direction (therefore, changing the optic flow as forward or backward (Vallet & van Wassenhove, 2023)). Black dots are actual measurements of the train speed at different times during the journey which were obtained from the train event recorder. Red dots are reconstructed speeds at missing times (see Procedure). Vertical black bars are acceleration boundaries.

### 3.2.5. Objective speed and magnitudes and Acceleration factor

The objective duration, distance, and instantaneous speed data were retrieved (or reconstructed when missing) from the train journey track recordings, which were supplied by the French railway company (SNCF). We described below the procedure

used to extract and reconstruct these objective values, later also used to manually define the acceleration episode of each estimation.

For performance and security purposes, an event recorder is integrated in all trains (similar to flight recorders in planes)<sup>3</sup> to keep track of all driving actions, security events and behavior of the train. These data enabled the extraction of the speed, distance, and duration of each train journey with an average sampling rate of 13.2s (sd = 22.8s). Each sample is a vector containing the time at which the information was recorded, the traveled distance since departure, and the instantaneous speed of the train. Therefore, the objective values of duration, distance, and speed were simply recovered by taking the value closest to the time at which participants responded. As described above, the experimenters time-stamped the collected data with an accuracy to the minute.

In these track records, ~50% of the samples had missing time information, which needed to be reconstructed (Table 3.1). We reconstructed missing data points by using standard methods from kinematics using the traveled distance between the missing point and the closest known point, and by computing the arithmetic mean speed between the two, see equation (1):

$$(1) t_i = t_{i-1} + \frac{d_i - d_{i-1}}{\left(\frac{v_{i-1} + v_i}{2}\right)}, \text{ with } t \text{ as time sample, } d \text{ as distance and } v \text{ as speed.}$$

When multiple consecutive time samples were missing, the uncertainty of the reconstructed times increased. To reduce this uncertainty, we performed a two-ways reconstruction: one going forward from the first known time sample to the last one, and one going backward from the last known time sample to the beginning of the journey. We computed the mean of the forward and backward reconstructions as follows:

$$(2) t_{i,forward} = t_{i-1} + \frac{d_i - d_{i-1}}{\left(\frac{v_{i-1} + v_i}{2}\right)} \quad \& \quad t_{i,backward} = t_{i+1} + \frac{d_{i+1} - d_i}{\left(\frac{v_{i+1} + v_i}{2}\right)}$$

$$(3) t_i = \frac{t_{i,forward} + t_{i,backward}}{2}$$

If the departure or arrival times were missing, only one or the other reconstructions was used accordingly. The original (black) and reconstructed (red) speed profiles of one journey are illustrated in Fig. 3.1D.

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<sup>3</sup> EPSF (04/07/2014). Recommandation - SAM S 704 : Enregistrements des événements liés à la sécurité des circulations -Dispositions à bord des mobiles.

Variables	Number of train journeys	Mean	sd	min	max
samples	32	912.25	166.08	704	1428
missing time samples (%)	32	50.75	8.55	25.49	65.62
total distance (km)	32	429.13	1.15	426.8	431.74
total duration (min) (116 min journeys)	16	116.44	4.07	106.32	123.82
total duration (min) (124 min journeys)	16	125	4.37	120.35	134.28
maximum speed (km/h)	32	298.5	5.19	272	303

**Table 3.1. Summary of train journey data.** Samples are the number of samples per file. Missing time samples are the percentage of missing times per file. Total distance is the traveled distance in kilometers. Total duration is the objective duration of the inbound and outbound journeys differing in total theoretical objective duration (116 or 124 min). Maximum speed is the fastest speed recorded during the journey in kilometers per hour (the theoretical commercial maximum speed is 320 km/h). Number of train journeys is the number of journeys used for the row, primarily relevant for journey duration because half of the journeys had an intermediary stop and were therefore longer.

### 3.2.6. Outliers' removal

In all between-participants analyses (i.e. all figures but Fig. 3.3), participant showing a relative error above the central 95th percentiles were removed. The relative errors were computed as:  $\frac{(\text{subjective estimate} - \text{objective value})}{\text{objective value}}$ . This procedure removed ~6 % of data points per estimation (duration: 5.7 %; distance: 6.5 %; instantaneous speed: 6.5 %; average speed: 6 %). Using a similar criterion for the within-participants analysis reported in Fig. 3.3, 40 participants out of 207 were discarded from this analysis (i.e. 16.2 %).

### 3.2.7. Statistical analyses

All statistical analyses were performed in the R statistical environment (version 4.1.2 R Core Team, 2023). Prior to any analysis, we verified that the strategy used by the participants had no effect on their relative estimates and showed that strategy as a single

predictor of each estimate in a linear model was not significant (Fig. 3.S2). For each scientific question with dedicated working hypotheses, we computed Ordinary Least Square (OLS) linear regression models between the variable and the factors of interest using the `lm()` function from the base R package “stats” (R Core Team, 2023). The independence, normality, and homogeneity of the residuals were verified for each linear regression using the package performance (Lüdtke et al., 2021). When necessary, the F-values of the main effects and the interactions, standard errors (SEs) and corresponding p-values of each factor from each model were computed with the `anova()` function from the `lmerTest` package (Kuznetsova et al., 2017). For post-hoc pairwise contrasts, we reported unstandardized regression coefficients (beta),  $|t|$  or  $|z|$  values and corresponding p-values computed with the `pairs()` function from the `emmeans` package (Lenth et al., 2021).

In perceptual studies, the log-log function is typically used to analyze the link between the psychological reality of a magnitude and its objective value (Balci et al., 2023). Hence, to investigate the estimation profile of each type of estimation (duration, distance, instantaneous and average speed), we performed OLS linear regressions between the logarithm of the single estimation score and the logarithm of the objective values (continuous variables extracted from the reconstructed train data).

We used Pearson’s correlation to investigate whether participants had a consistent bias in duration and distance estimation. For instance, we used this approach to verify whether a participant who overestimated a duration also overestimated distance.

To understand how participants computed the average speed, and which link existed between their duration and distance estimations, we used a modeling approach. We modeled the average speed estimation using each participant’s distance and duration estimation score. We then looked at the linear relationship between the modeled average speed based on their magnitude estimation, and the estimated average speed effectively reported by participants.

To investigate the link between distance and duration estimation, we compared the variance explained ( $R^2$ ) of OLS linear regression models constructed between the numerical estimated duration (or distance) and the modeled duration (or distance) hypothesizing three possible computations (Fig. 3.3C-D):

(1) *Estimated average speed*: participants used the combination of one magnitude (duration or distance) and their average speed estimate to derive the other magnitude (distance or duration, respectively).

$$est.distance = est.speed * est.duration$$

$$est.duration = est.speed * est.distance$$

(2) *Reported maximum speed*: participants used their estimation of the maximum speed of the train reported at the beginning of the questionnaire to convert one magnitude into another.

$$est.distance = max\ speed * est.duration$$

$$est.duration = max\ speed * est.distance$$

with est. for estimated and max for the self-reported maximum train speed.

(3) *Knowledge strategy*: participants used their prior knowledge of the journey to infer another magnitude. In this scenario, we modeled one magnitude (e.g. duration) as the ratio of the other magnitude (e.g. distance) divided by the reported total magnitude for the journey (e.g. total distance) multiplied by the other total magnitude of the journey (e.g. total duration):

$$est.distance = \frac{est.duration}{total\ duration} * total\ distance$$

$$est.duration = \frac{est.distance}{total\ distance} * total\ duration$$

Considering that the estimation scores were self-reported prior knowledge, we used only the numerical estimates for this analysis (Fig. 3.3C-D). This was realized to prevent circularity in the data as our individual scoring method took into account prior knowledge (see 2.4.), which could inflate the variance explained by our model for this specific analysis (indeed, the same outcome is found when using estimation scores, but the variance explained is higher than when using numerical estimations only).

To investigate the effect of our two factors (Orientation and Acceleration), we computed the relative magnitude and speed estimates by taking the ratio between the subjective estimate and its objective value. We, then, used OLS linear models to investigate the effect of Acceleration (positive, null, negative) and Orientation (forward, backward) on participants' relative estimates. To investigate the link between duration estimation and

the speed of the passage of time, the emotional and the metacognitive ratings, we used OLS linear models. For the metacognitive ratings, very few participants used the extremes of the scale (“underestimate”: 9; “rather underestimate”: 110; “rather overestimate”: 107; “overestimate”: 3). Therefore, we converted the 4-points Likert scale into a two-level factor metacognitive rating (“underestimate”: 119; “overestimate”: 110). We computed OLS linear models of the relative duration estimation with each 4-point Likert scale as a single predictor (or a two-level factor for the metacognitive rating) to prevent collinearity between the Likert scale responses, if any.

To investigate the effect of confidence, we looked at the relationship between the absolute relative error of each estimation, separately, and the self-reported level of confidence with OLS linear models.

To investigate the relationship between the subjective report of the speed of the passage of time and the emotional states while preserving the ordinality in the Likert scale responses, we used an ordinal linear regression with the function `polr()` from the MASS package (Venables & Ripley, 2002). Likelihood ratio (LR Chisq) of the main effects, degrees of freedom (Df), and corresponding p-values (p) of each emotional states from separated model were computed with the `Anova()` function from the car package (Fox & Weisberg, 2019) and the posthoc comparison with the `emmeans` package (Lenth et al., 2021).

### 3.3. Results

#### 3.3.1. Magnitude and speed estimation profiles

We first compared participants’ subjective estimations of distance, duration, and instantaneous speed with objective measurements to characterize the general estimation profiles. For this, we performed linear regressions of the logarithm of participants’ subjective estimates as a function of the logarithm of the objective values (Fig. 3.2).

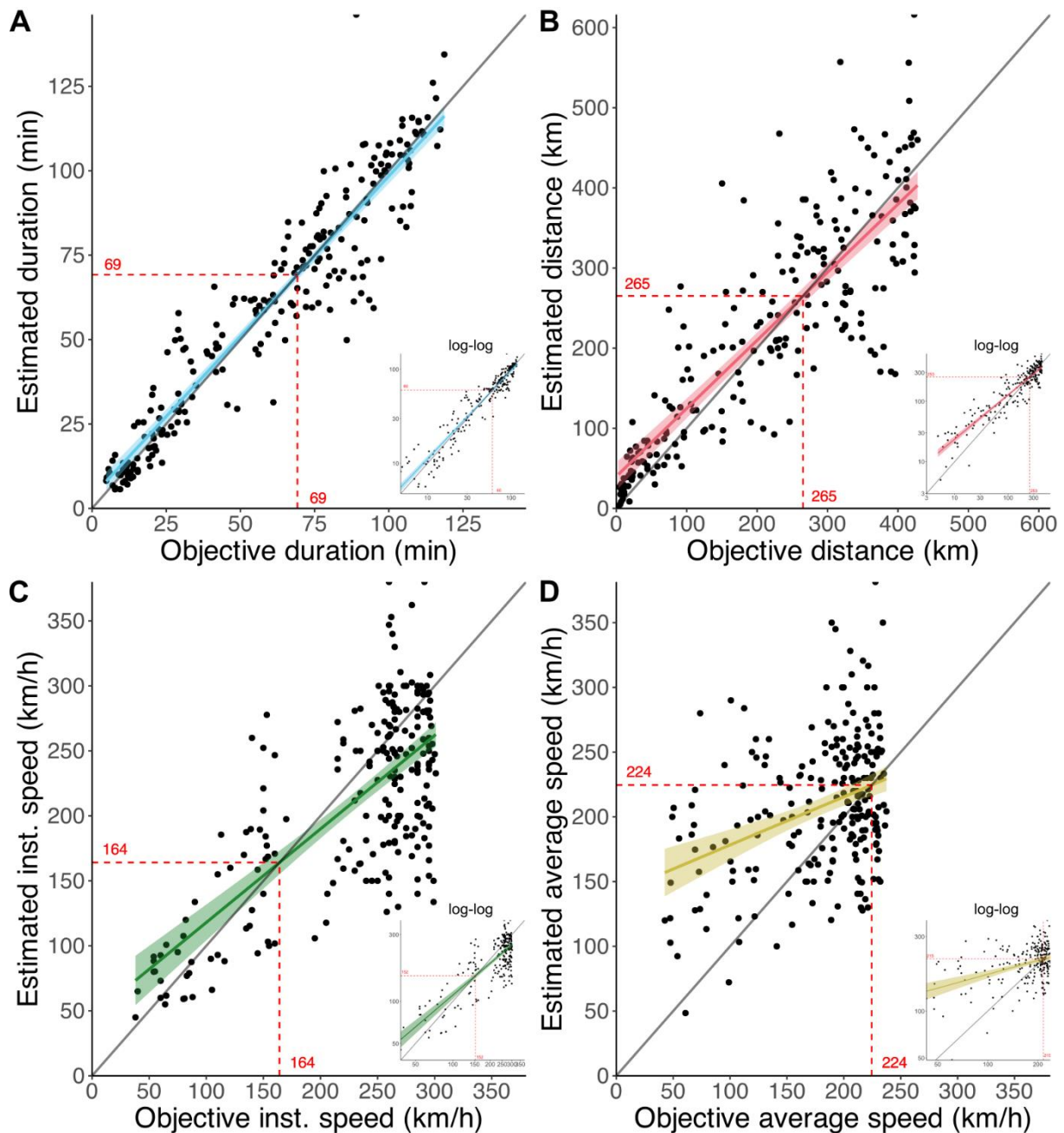
As predicted, we found that a significant part of the variance in duration estimation was explained by the objective duration ( $R^2 = 0.85$ ,  $F(1, 245) = 1343.47$ ,  $p < .001$ , adj.  $R^2 = 0.85$ ) with a significant and positive relationship between the two ( $\beta = 0.94$ , 95% CI [0.89, 0.99],  $t(245) = 36.65$ ,  $p < 0.001$ ; Std.  $\beta = 0.92$ , 95% CI [0.87, 0.97]). We also found that the greater part of the variance in distance estimation was



significantly explained by the objective distance ( $R^2 = 0.85$ ,  $F(1, 229) = 1279.51$ ,  $p < .001$ , adj.  $R^2 = 0.85$ ) with a significant and positive relationship (beta = 0.75, 95% CI [0.71, 0.79],  $t(229) = 35.77$ ,  $p < .001$ ; Std. beta = 0.92, 95% CI [0.87, 0.97]).

The variance explained by the objective instantaneous speed was much lower in instantaneous speed model ( $R^2 = 0.65$ ,  $F(1, 229) = 416.77$ ,  $p < .001$ , adj.  $R^2 = 0.64$ ) and very little variance was significantly explained by the objective average speed ( $R^2 = 0.17$ ,  $F(1, 230) = 46.52$ ,  $p < .001$ , adj.  $R^2 = 0.16$ ). Although the variance explained was lower for instantaneous and average speeds, there was still a significant and positive relationship between their subjective estimates and their objective measurements (instantaneous speed: beta = 0.76, 95% CI [0.68, 0.83],  $t(229) = 20.41$ ,  $p < .001$ ; Std. beta = 0.80, 95% CI [0.73, 0.88]; average speed: beta = 0.29, 95% CI [0.21, 0.38],  $t(230) = 6.82$ ,  $p < .001$ ; Std. beta = 0.41, 95% CI [0.29, 0.53]).

None of the magnitude or speed profiles showed increased variance with increased objective value, commonly expected following Weber's law for within-participants designs (Fig. 3.2). However, we found that small magnitudes tended to be overestimated while large magnitudes tended to be underestimated, which is consistent with Vierordt's law despite the inter-individual design (see Chaumon et al., 2022; Balci et al., 2023). The regression point designating the value at which participants were most accurate are indicated in Fig. 3.2A-B, in red dashed lines. Thus, to exemplify this effect in our data, we found that 5 min was overestimated to 8 min but 120 min was underestimated to 117.4 min; 50 km was overestimated to 81 km whereas a 400 km was underestimated to 375 km. In magnitude estimations, regression points were surprisingly located very close to the middle of the journey (69 min for duration; 265 km for distance).



**Fig. 3.2: Duration, distance, instantaneous and average speed profiles.** Linear regression of the log of subjective estimates as a function of the log of objective measurements for duration (A, blue), distance (B, red), instantaneous and average speed (C-D, green and yellow, respectively). For visualization purposes, we plotted the data without the log. The identity line is indicated in black. Regression lines are colored. Shaded areas indicate the 95% confidence interval of the regression parameters. The intersection between the regression and the identity lines is indicated in red. Small inserts in each plot correspond to the regression at the log-log scale.

### 3.3.2. The role of prior knowledge in distance and duration estimation

Despite participants' accurate estimations of duration and distance, their average speed estimates were not. This was surprising given that the accurate estimation of two magnitudes should suffice to infer an accurate average speed using the simple ratio of

scalars ( $speed = \frac{distance}{duration}$ ). Herein, we thus explored further how participants may have inferred their estimation of duration, distance, and average speed from each other. Specifically, did participants draw their estimations from sensory experience only or did they use their prior knowledge (initial questions about their knowledge of the journey) to estimate duration, distance and average speed?

First, we asked whether participants inferred the average speed with the expected calculation, namely  $est. average speed = \frac{est. distance}{est. duration}$ . For each participant, we computed the expected average speed estimate (modeled average speed) based on the ratio of the estimated distance and duration (Fig. 3.3A). We fitted an OLS linear model to the estimated average speed with the modeled average speed as a single predictor. We found no significant linear relationship between the estimated and the modeled average speeds ( $R^2 = 7.94e-03$ ,  $F(1, 207) = 1.66$ ,  $p = 0.199$ ,  $adj. R^2 = 3.15e-03$ ) and the modeled average speed was not significantly related to the estimated average speed (beta = 0.08, 95% CI [-0.04, 0.19],  $t(207) = 1.29$ ,  $p = 0.199$ ; Std. beta = 0.09, 95% CI [-0.05, 0.23]; Fig. 3.3A). This was partially expected considering the estimation profiles (Fig. 3.2A-B-D).

One possible reason for this result could also be that each individual bias for duration and distance was not consistent within participant. It means that even though participants were accurate, one may have slightly overestimated a duration whilst underestimating the distance, resulting in an inaccurate average speed estimation. To check for these potential individual biases across magnitude estimations, we computed Pearson's correlation between estimated duration and distance across all participants. We found a significant and moderate positive relationship between the two ( $r = 0.46$ , 95% CI [0.34, 0.56],  $t(207) = 7.36$ ,  $p < .001$ ; Fig. 3.3B). This moderate positive correlation appeared to be driven by a large number of participants overestimating both duration and distance. About the same number of participants showed an inverse bias across magnitudes, suggesting that no bias consistency across magnitudes (Fig. 3.3B, red numbers).

In light of this, we compared three possible strategies that participants could have used to link duration and distance estimations. The first model, derived from the reasoning laid out above, posits that participants used their estimation of one magnitude and of average speed to estimate the other magnitude (distance or duration) (Fig. 3.3C-D, grey line). This computation is similar to the one hypothesized in Fig. 3.3A. Based on

our previous analysis (Fig. 3.3A), we expected this model to be the least explanatory of the data.

In the second model, participants assumed that the train was mostly traveling at its maximum speed during the journey. They may have used their knowledge of the train maximum speed reported at the beginning of the questionnaire (max speed; Fig. 3.3C-D, green line) and computed:

$$est. duration = \frac{est. distance}{max speed}$$

$$est. distance = est. duration * max speed$$

In the third model, participants used their prior knowledge of the distance or duration of the journey to infer the other magnitude and the average speed. Hence, we modeled one magnitude (e.g. modeled duration) based on the ratio of the other magnitude estimation (e.g. estimated distance) with participant's reported knowledge of the total magnitude for the journey (e.g. total distance) multiplied by their knowledge of the other total magnitude for the journey (e.g. total duration) (Fig. 3.3C-D, pink line), namely:

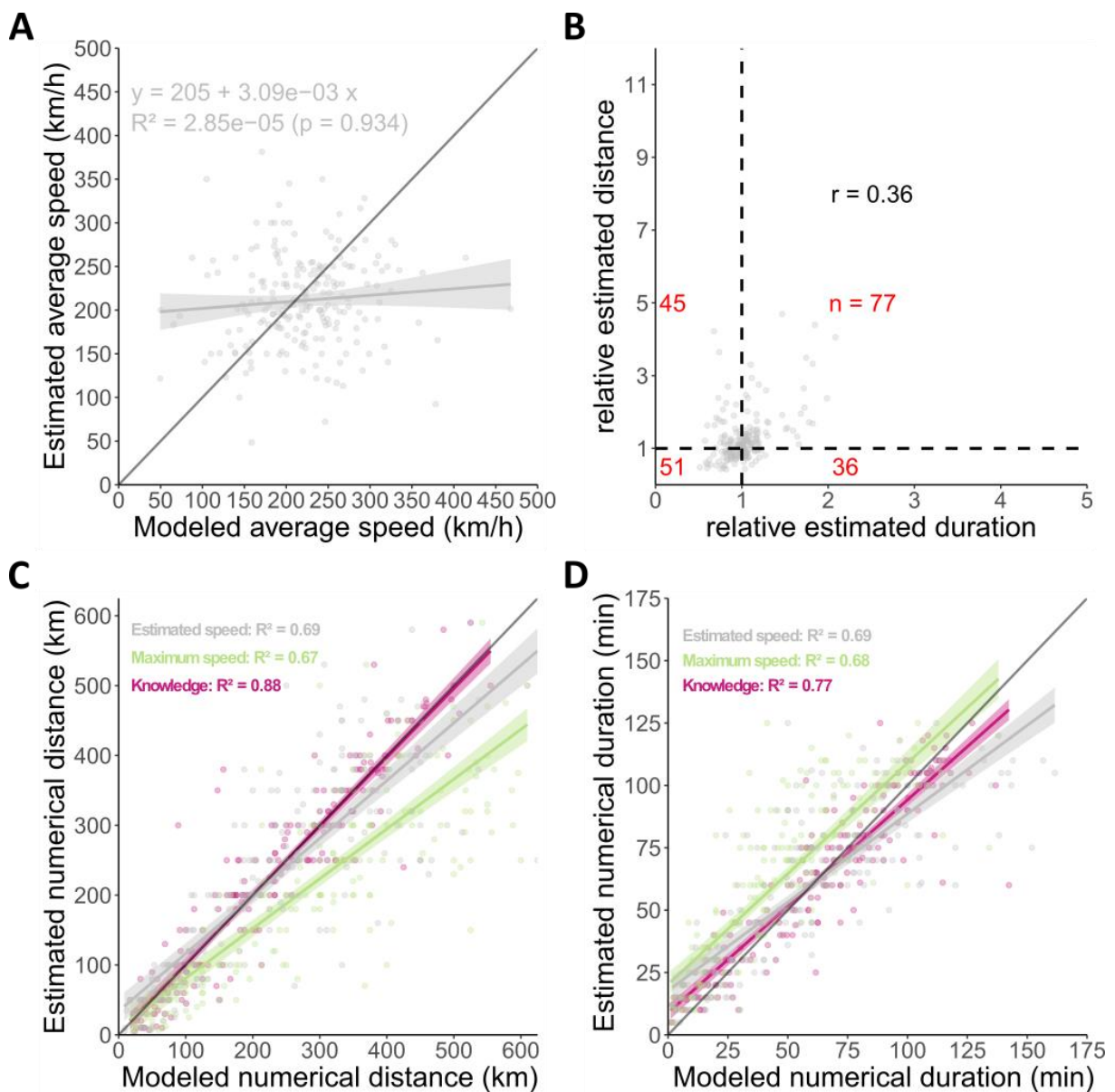
$$est. duration = \frac{est. distance}{total distance} * total duration$$

$$est. distance = \frac{est. duration}{total duration} * total distance$$

Similar to our previous analysis, we fitted OLS linear models to the estimated distance (or duration) with a single predictor of modeled distance (or duration). The best model was chosen based on the largest variance explained ( $R^2$ ). As stated in the statistical analyses section, our analyses used numerical estimations only (as opposed to estimation scores combining graphical and numerical estimations) to prevent circularity.

For distance (Fig. 3.3C), the variance explained ( $R^2$ ) was larger for the third model *knowledge* ( $R^2 = 0.88$ ,  $F(1, 205) = 1564.37$ ,  $p < .001$ , adj.  $R^2 = 0.88$ ) compared to the others, which showed comparable explained variance (*maximum speed*:  $R^2 = 0.67$ ,  $F(1, 203) = 410.47$ ,  $p < .001$ , adj.  $R^2 = 0.67$ ; *estimated average speed*: ( $R^2 = 0.70$ ,  $F(1, 205) = 469.01$ ,  $p < .001$ , adj.  $R^2 = 0.69$ )). For duration (Fig. 3.3D), the pattern was the same although the  $R^2$  was slightly lower (3<sup>rd</sup> model based on *knowledge*:  $R^2 = 0.77$ ,  $F(1, 205) = 668.39$ ,  $p < .001$ , adj.  $R^2 = 0.76$ ; 2<sup>nd</sup> model based on reported *maximum speed*:  $R^2 = 0.69$ ,  $F(1, 203) = 442.47$ ,  $p < .001$ , adj.  $R^2 = 0.68$ ; 1<sup>st</sup> model based on *estimated average speed*:  $R^2 = 0.69$ ,  $F(1, 205) = 449.24$ ,  $p < .001$ , adj.  $R^2 = 0.69$ ).

Therefore, the computation that participants may have used to link duration and distance estimations was likely using the third model, which relied on the prior knowledge of the journey's duration, distance and maximum speed. Additionally, our analysis suggests that distance estimation is better explained by the duration than the duration is explained by the distance. This suggests that participants may have used a time heuristic to estimate traveled distances, and not the other way around. This is also supported by the fact that a majority of participants reported knowing the exact duration of the journey (78% of participants) while a majority reported not knowing the exact distance (82% of participants) as per the initial inquiry of our questionnaire.



**Fig. 3.3: Estimated speed is not predicted by estimated distance and duration.** A: Linear regression between estimated average speed and modeled average speed. The thick grey line corresponds to the regression curve. B: Correlation between relative estimated distance and duration, within participants. Dashed black lines delimit X and Y data below/above 1. Any point below/above the horizontal dashed

black bar corresponds to underestimated/overestimated distance, respectively. Any point before/after the vertical dashed black bar corresponds to underestimated/overestimated duration. Red numbers correspond to the number of observation below/before/above/after the dashed black lines. C: Linear regressions between estimated distance and modeled distance. We tested three different ways of modeling distance. The grey line corresponds to the modeled distance from the estimated average speed and duration estimation from each participant, labeled estimated speed. The green line corresponds to the modeled distance from knowledge of the maximum speed of participants and the estimated duration, labeled maximum speed. The pink line corresponds to the modeled distance from the estimated duration, the knowledge of the total duration, and the knowledge of the total distance reported by each participant, labeled knowledge. D: Same as C but for duration. In each plot, dots correspond to individual participant responses, shaded areas to 95% confidence interval of the regression parameters, and the thin black line corresponds to the unity line.

### 3.3.3. Acceleration, but not Orientation, impacts participants' estimation of magnitude and speed estimation

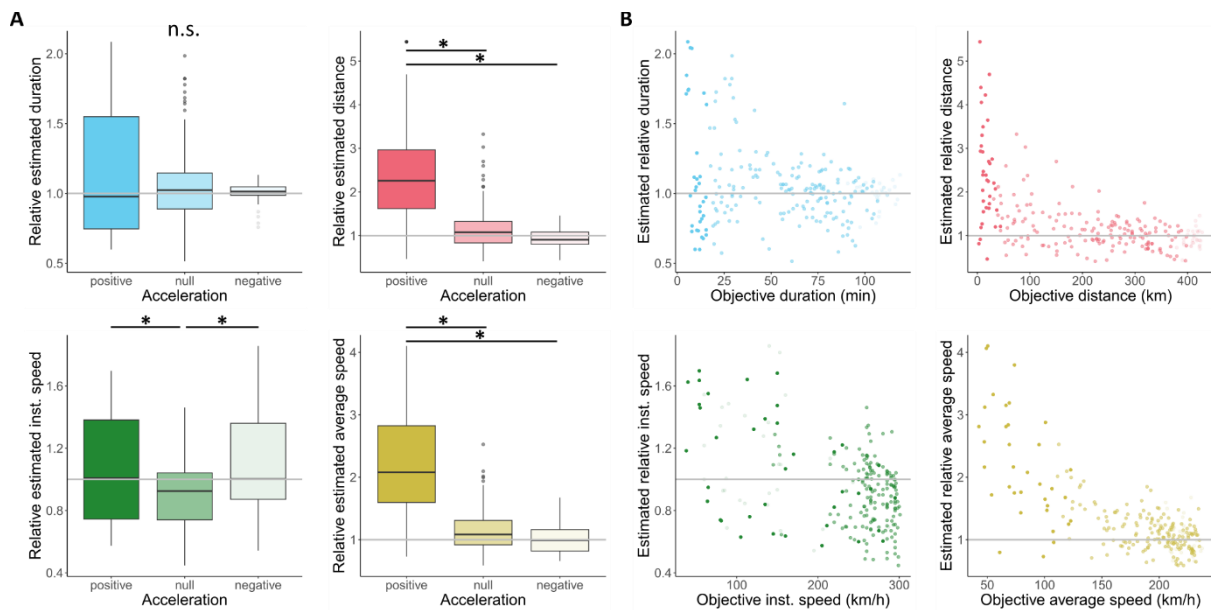
As participants may have used a knowledge heuristic to infer duration, distance, and speed, we expected that Acceleration and Orientation may not massively affect magnitude and speed estimations. To verify this, we fitted a linear model with the two factors Acceleration (3: positive, null, negative) and Orientation (2: forward, backward) to each type of relative estimation (duration, distance, instantaneous, and average speed).

Linear models fits were significant for all except for duration estimation although the variance explained was systematically low: duration ( $R^2 = 0.03$ ,  $F(5, 225) = 1.19$ ,  $p = 0.313$ , adj.  $R^2 = 4.19e-03$ ), distance ( $R^2 = 0.39$ ,  $F(5, 223) = 28.56$ ,  $p < .001$ , adj.  $R^2 = 0.38$ ), instantaneous speed ( $R^2 = 0.11$ ,  $F(5, 224) = 5.37$ ,  $p < .001$ , adj.  $R^2 = 0.09$ ) and average speed ( $R^2 = 0.43$ ,  $F(5, 224) = 33.99$ ,  $p < .001$ , adj.  $R^2 = 0.42$ ).

Specifically, significant effects of the Acceleration factor were found for the distance, instantaneous and average speed estimates but not for duration estimates (Fig. 3.4A). For duration, Acceleration had no effect on the relative estimated duration ( $F(2, 225) = 2.17$ ,  $p = 0.116$ ; Eta2 (partial) = 0.02, 95% CI [0.00, 1.00]). However, acceleration significantly altered distance estimates ( $F(2, 223) = 69.34$ ,  $p < .001$ ; Eta2 (partial) = 0.38, 95% CI [0.30, 1.00]) so that participants overestimated distances during positive acceleration compared to constant speed (beta = 1.332, SE = 0.117,  $t(223) = 11.345$ ,  $p < .001$ ) and deceleration (beta = 1.533, SE = 0.157,  $t(223) = 9.771$ ,  $p < .001$ ). No differences of Acceleration were found between constant speed and deceleration (beta = 0.201, SE = 0.124,  $t(223) = 1.620$ ,  $p = 0.239$ ). The acceleration also significantly altered estimates of instantaneous speed ( $F(2, 224) = 12.17$ ,  $p < .001$ ; Eta2 (partial) = 0.10, 95% CI [0.04, 1.00]) so that participants overestimated instantaneous speed during positive

acceleration compared to constant speed ( $\beta = 0.179$ ,  $SE = 0.0519$ ,  $t(224) = 3.449$ ,  $p = 0.002$ ) but not compared to deceleration ( $\beta = -0.025$ ,  $SE = 0.0672$ ,  $t(224) = -0.377$ ,  $p = 0.925$ ). At constant speed (null acceleration), participants significantly underestimated instantaneous speed compared to deceleration ( $\beta = -0.204$ ,  $SE = 0.0514$ ,  $t(224) = -3.976$ ,  $p < 0.001$ ).

The acceleration altered estimations of average speed ( $F(2, 224) = 84.70$ ,  $p < .001$ ;  $\eta^2$  (partial) = 0.43, 95% CI [0.35, 1.00]) which were overestimated during positive acceleration compared to null ( $\beta = 1.051$ ,  $SE = 0.0949$ ,  $t(224) = 11.074$ ,  $p < .001$ ) and negative ( $\beta = 1.156$ ,  $SE = 0.1195$ ,  $t(224) = 9.673$ ,  $p < .001$ ) accelerations. No differences were found between the null and the negative accelerations ( $\beta = 0.105$ ,  $SE = 0.0882$ ,  $t(224) = 1.187$ ,  $p = 0.462$ ). Interestingly, the overestimation of average speed follows closely the effect of objective magnitudes so that the faster the average speed is, the smaller the overestimation (Fig. 3.4B).



**Fig. 3.4: Main effect of the acceleration episodes (positive, null, negative).** A: Box plots showing the distribution of each relative estimation (blue: duration; red: distance; green: instantaneous speed; yellow: average speed) for each acceleration episode. The median line inside the box indicates the median of the distribution, while the upper and lower boundaries of the box represent the third and first quartiles, respectively. Whiskers extend to the minimum and maximum values not exceeding 1.5 times the interquartile range from the box. Estimations beyond the whiskers are shown as individual points. Significant differences between the distribution are indicated with an asterisk. Non-significant differences between the distribution are indicated with n.s.. B: Scatter plot of the relative estimation (same color code as A) according to their objective values. The acceleration episodes are indicated by a change in transparency. Interestingly, we can see that the patterns captured by acceleration episodes match the patterns observed with the objective value.

Orientation did not affect the estimations of magnitudes or speed (Fig. 3.S3): duration ( $F(1, 225) = 0.91$ ,  $p = 0.342$ ;  $\eta^2$  (partial) = 4.02e-03, 95% CI [0.00, 1.00]),

distance ( $F(1, 223) = 4.53e-03$ ,  $p = 0.946$ ;  $\text{Eta}^2$  (partial) =  $2.03e-05$ , 95% CI [0.00, 1.00]), instantaneous speed ( $F(1, 224) = 0.45$ ,  $p = 0.504$ ;  $\text{Eta}^2$  (partial) =  $1.99e-03$ , 95% CI [0.00, 1.00]), and average speed ( $F(1, 224) = 0.43$ ,  $p = 0.515$ ;  $\text{Eta}^2$  (partial) =  $1.89e-03$ , 95% CI [0.00, 1.00]).

We also found no significant interactions between Acceleration and Orientation for any type of estimation: duration ( $F(2, 225) = 0.36$ ,  $p = 0.701$ ;  $\text{Eta}^2$  (partial) =  $3.15e-03$ , 95% CI [0.00, 1.00]), distance ( $F(2, 223) = 2.06$ ,  $p = 0.129$ ;  $\text{Eta}^2$  (partial) = 0.02, 95% CI [0.00, 1.00]), instantaneous speed ( $F(2, 224) = 1.04$ ,  $p = 0.354$ ;  $\text{Eta}^2$  (partial) =  $9.24e-03$ , 95% CI [0.00, 1.00]) and average speed ( $F(2, 224) = 0.08$ ,  $p = 0.926$ ;  $\text{Eta}^2$  (partial) =  $6.82e-04$ , 95% CI [0.00, 1.00]).

### 3.3.4. No evidence suggesting a link between duration estimation and speed of the passage of time or emotional state in high-speed trains

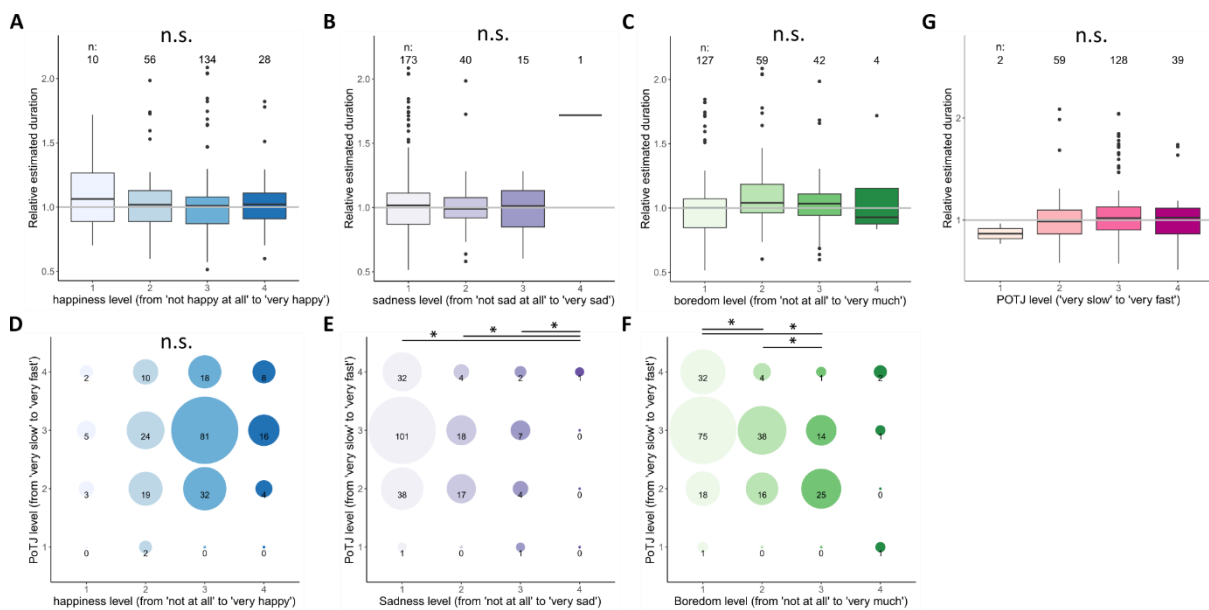
We then explored the relation between the speed of the passage of time, an alternative measure of the subjective time estimation (e.g. Wearden, 2015), and self-reported emotional ratings (e.g. Droit-Volet & Meck, 2007) considering that both measurements have been previously linked to duration estimations.

First, we investigated the link between relative duration estimates and emotional states (happiness, sadness, and boredom) by computing three OLS linear regression models with the relative estimated duration as the dependent variable and one of the emotional states as the explanatory variable. We found no significant relations between the relative duration estimations and the self-reported emotional states: happiness ( $R^2 = 3.61e-03$ ,  $F(3, 224) = 0.27$ ,  $p = .846$ , adj.  $R^2 = -9.73e-03$ ; Fig. 3.5A), sadness ( $R^2 = 0.03$ ,  $F(3, 225) = 2.44$ ,  $p = .065$ , adj.  $R^2 = 0.02$ ; Fig. 3.5B) and boredom ( $R^2 = 0.03$ ,  $F(3, 228) = 2.19$ ,  $p = .089$ , adj.  $R^2 = 0.02$ ; Fig. 3.5C).

Second, we investigated the link between duration and speed of passage of time (PoTJ), we computed an OLS linear regression model with the relative duration estimations as the dependent variable, and the PoTJ level as the explanatory variable. We found no significant relations between duration estimations and PoTJ ( $R^2 = 0.01$ ,  $F(3, 224) = 0.92$ ,  $p = .433$ , adj.  $R^2 = -1.07e-03$ ; Fig. 3.5G).



Finally, we investigated the link between PoTJ and emotional states (happiness, sadness, and boredom) by computing three separated ordinal regression models with the PoTJ as the dependent variable and one of the emotional states as the explanatory variable. We found a significant relationship between PoTJ and sadness (LR chisq = 10.67, Df = 3,  $p = .014$ , Fig. 3.5E), as well as boredom (LR Chisq = 40.05, Df = 3,  $p = 1.04e-08$ , Fig. 3.5F) but not with happiness (LR Chisq = 5.78, DF = 3,  $p = .123$ , Fig. 3.5D). Post-hoc comparisons revealed that the effect of sadness is not interpretable since the significant contrasts always involved the sadness level 4, which contained only one participant (Table 3.2, top row of Fig. 3.5E). Post-hoc comparisons revealed that the boredom level 1 was different from the level 2 and 3, the boredom level 2 was different from the level 3 (Table 3.2, Fig 3.5F).



**Fig. 3.5: No relationship between relative duration estimation and speed of the passage of time judgment or emotional states.** A: Boxplot of the relative duration estimation as a function of the level of happiness self-reported by the participants on a 4-point Likert scale (from “not happy at all” to “very happy”). B: Boxplot of the relative duration estimation as a function of the level of sadness self-reported by the participants on a 4-point Likert scale (from “not sad at all” to “very sad”). C: Boxplot of the relative duration estimation as a function of the level of boredom self-reported by the participants on a 4-point Likert scale (from “not at all” to “very much”). G: Boxplot of the relative duration estimation as a function of the speed of the passage of time feeling self-reported by the participants on a 4-point Likert scale (from “slow” to “fast”). A, B, C, G: The median line inside the box indicates the median of the distribution, while the upper and lower boundaries of the box represent the third and first quartiles, respectively. Whiskers extend to the minimum and maximum values not exceeding 1.5 times the interquartile range from the box. Estimations beyond the whiskers are shown as individual points. D: Scatter plot of the self-reported speed of the passage of time (PoTJ) as a function of the self-reported happiness level. E: Scatter plot of the PoTJ as a function of the self-reported sadness level. F: Scatter plot of the PoTJ as a function of the self-reported boredom level. D, E, F: The size of the dot reflects to the number of participants at each level for both axes. The actual number of participants at each level is indicated by numbers in black. Horizontal black bars and stars indicate significantly different levels of emotional states and n.s. indicate non-significant contrast.

Emotional state	Contrast	Beta	s.e.m.	DoF	z-value	p
<b>Sadness</b>	“1” – “2”	.878	.35	1	3.00	.055
	“1” – “3”	.622	.56	1	1.00	.679
	“1” – “4”	-13.34	.01	1	-132912011.00	< <b>.001*</b>
	“2” – “3”	-.26	.62	1	.00	.976
	“2” – “4”	-14.22	.35	1	-41.00	< <b>.001*</b>
	“3” – “4”	-13.96	.56	1	-25.00	< <b>.001*</b>
<b>Boredom</b>	“1” – “2”	.99	.32	1	3.06	<b>.012</b>
	“1” – “3”	2.27	.39	1	5.87	< <b>.001*</b>
	“1” – “4”	-.57	1.15	1	-.49	.961
	“2” – “3”	1.28	.41	1	3.16	<b>.009*</b>
	“2” – “4”	-1.56	1.18	1	-1.32	.547
	“3” – “4”	-2.84	1.20	1	2.37	.083

**Table 3.2. Statistical results of PoTJ for each contrast of emotional level per type of emotional state.** The emotional state indicates the emotional state for each given contrast. P-values were adjusted using the Tuckey method to take into account multiple-comparisons. Stars and bold p-values indicate significant p-values lower than 0.05.

### 3.3.5. Confidence rating and temporal metacognition onboard

Last, we investigated participants’ confidence ratings on all estimations and their temporal metacognition.

First, we tested whether the self-reported confidence level on a 4-points Likert scale would reflect the absolute relative error of the participants estimations (Yallak & Balci, 2022a). For each estimation type (duration, distance, instantaneous speed, average speed), we computed, an OLS regression model with the absolute relative error as the predicted variable and the confidence level (4-points Likert scale), as the predictor.

For duration estimates, the confidence level significantly affected the absolute relative error ( $F(3, 229) = 12.02, p < .001; \text{Eta}^2 = 0.14, 95\% \text{ CI } [0.07, 1.00]$ , Fig. 3.6A). Post-hoc comparisons between each confidence level revealed that only the contrast “rather confident”-“very confident” was not significant (statistics of each contrast can be found in Table 3.3).

Estimation type	Contrast	beta	Standard Error	Degree of freedom	t-value	p
Duration	"not at all confident" – "not confident"	0.26	0.09	229	2.97	<b>.017*</b>
	"not at all confident" – "rather confident"	0.37	0.08	229	4.53	<b>&lt; .001*</b>
	"not at all confident" – "very confident"	0.45	0.09	229	5.10	<b>&lt; .001*</b>
	"not confident" – "rather confident"	0.11	0.04	229	3.10	<b>.012*</b>
	"not confident" – "very confident"	0.19	0.05	229	3.92	<b>&lt; .001*</b>
	"rather confident" – "very confident"	0.08	0.04	229	1.99	.193
Distance	"not at all confident" – "not confident"	0.11	0.16	227	0.65	.915
	"not at all confident" – "rather confident"	0.14	0.16	227	0.86	.825
	"not at all confident" – "very confident"	-0.43	-0.37	227	-1.15	.658
	"not confident" – "rather confident"	0.03	0.09	227	0.38	.981
	"not confident" – "very confident"	-0.53	0.34	227	-1.55	.410
	"rather confident" – "very confident"	-0.57	0.34	227	-1.65	.353
Instantaneous speed	"not at all confident" – "not confident"	0.04	0.04	224	0.94	.781
	"not at all confident" – "rather confident"	0.11	0.04	224	2.88	<b>.023*</b>
	"not at all confident" – "very confident"	0.16	0.06	224	2.49	.063
	"not confident" – "rather confident"	0.07	0.02	224	3.26	<b>.007*</b>
	"not confident" – "very confident"	0.12	0.06	224	2.20	.126
	"rather confident" – "very confident"	0.05	0.06	224	0.87	.818
Average speed	"not at all confident" – "not confident"	0.05	0.12	227	0.41	.977
	"not at all confident" – "rather confident"	-0.02	0.13	227	-0.20	.997
	"not at all confident" – "very confident"	0.05	0.26	227	0.20	.997
	"not confident" – "rather confident"	-0.08	0.07	227	-1.02	.738
	"not confident" – "very confident"	0.01	0.24	227	0.01	1.0000
	"rather confident" – "very confident"	0.08	0.24	227	0.33	.988

**Table 3.3. Statistical results of absolute relative estimation for each contrast of confidence level per type of estimation.** Estimation type indicate the type of estimation for each given contrast. P-values were adjusted using the Tuckey method to take into account multiple-comparisons. Stars and bold p-values indicate significant p-values lower than 0.05.

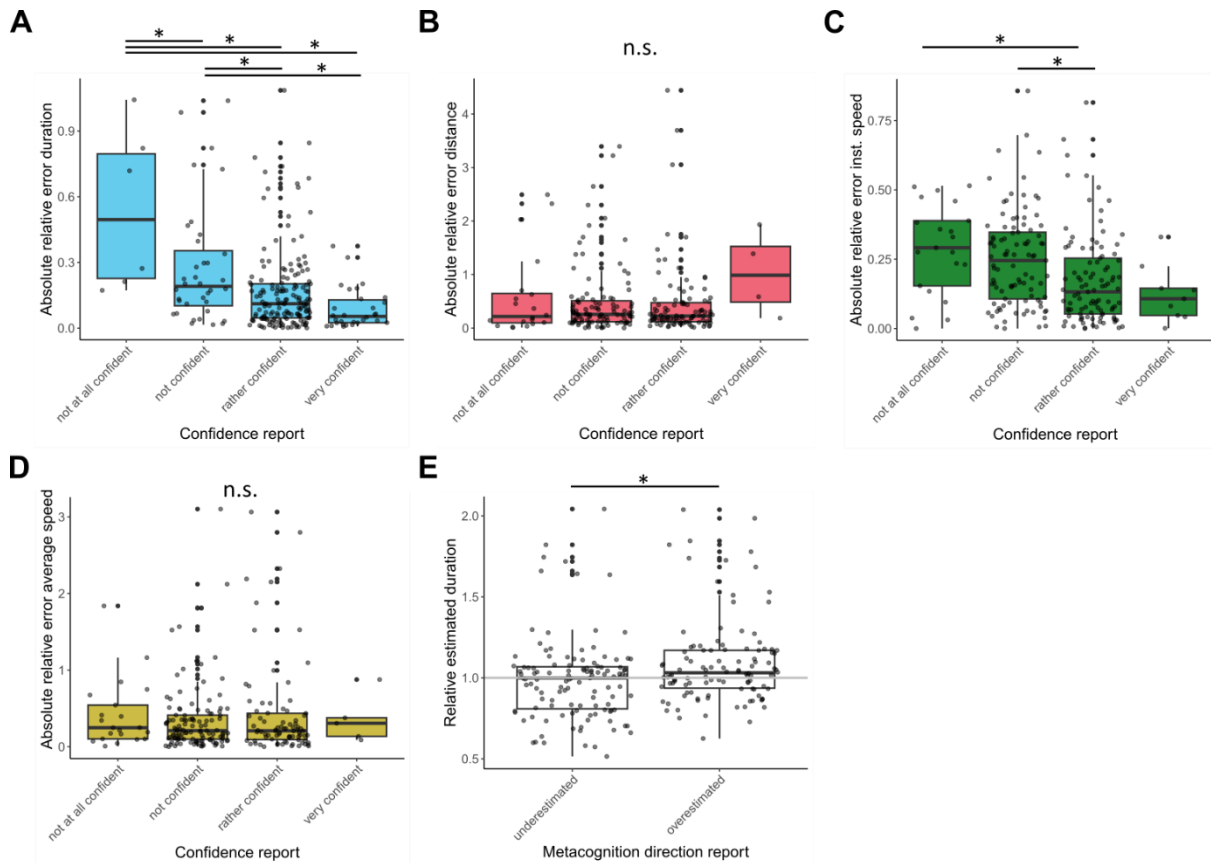
For distance estimates, there was no effect of the confidence level on the absolute relative error ( $F(3, 227) = 1.09, p = 0.355; \text{Eta}^2 = 0.01, 95\% \text{ CI } [0.00, 1.00]$ , Fig. 3.6B). As expected with a non-significant effect, none of the post-hoc contrasts were significant (Table 3.3).

For the instantaneous speed, the confidence level significantly affected the absolute relative error ( $F(3, 224) = 5.85, p < .001; \text{Eta}^2 = 0.07, 95\% \text{ CI } [0.02, 1.00]$ , Fig. 3.6C). Post-hoc contrasts were significant for the "not at all confident"- "rather confident" and "not confident" - "rather confident" (Table 3.3).

For average speed, there was no effect of the confidence level on the absolute relative error ( $F(3, 227) = 0.36, p = 0.779; \eta^2 = 4.78e-03, 95\% \text{ CI } [0.00, 1.00]$ , Fig. 3.6D). As expected with a non-significant effect, none of the post-hoc contrasts were significant (Table 3.3).

Second, we explored participants' temporal metacognition and tested whether they could report the direction of their duration error as in a trial-by-trial design (Kononowicz & van Wassenhove, 2019). We computed an OLS linear model to predict the relative estimated duration by the self-reported direction error (2-level factor: "underestimated"; "overestimated"). When participants reported "underestimated", their relative duration estimates should be below one; when participants reported "overestimated", their relative duration estimates should be above one. Although the variance explained was weak, the model was significant ( $R^2 = 0.04, F(1, 227) = 9.15, p = 0.003, \text{ adj. } R^2 = 0.03$ ). The relative duration estimates were lower when participants reported "underestimated" compared to when they reported "overestimated" ( $\beta = 0.10, 95\% \text{ CI } [0.04, 0.17], t(227) = 3.02, p = 0.003; \text{ Std. } \beta = 0.39, 95\% \text{ CI } [0.14, 0.65]$ ; Fig. 3.6E).

Finally, we tested whether the Acceleration and Orientation factors influenced participants' temporal metacognition. We constructed an ordinal linear model with the self-reported direction error (4-point Likert scale) as the predicted variable, and Acceleration and Orientation as the predictive factors. We found no main effects of Orientation (LR Chisq = 2.780, Df = 1,  $p = 0.095$ ) nor Acceleration (LR Chisq = 2.272, Df = 2,  $p = 0.321$ ) on temporal metacognitive performance. However, their interaction was significant (LR Chisq = 7.178, Df = 2,  $p = 0.028$ ). In the interaction, the difference Backward - Forward was significant only during the positive acceleration episode ( $\beta = 1.649, \text{ SE} = 0.804, z(228) = 2.051, p = 0.040$ ), meaning that during acceleration, participants reported overestimating more when facing backward than when facing forward.



**Fig. 3.6: Participants have access to their duration and instantaneous speed errors via metacognitive judgments.** A-D: Confidence ratings in magnitude and speed estimates. Boxplot of the absolute relative error as a function of the confidence level reported by participants using a 4-point Likert scale (from “not at all confident” to “very confident”) for duration (A, blue), distance (B, red), instantaneous speed (D, green), and average speed (D, yellow). E: Temporal metacognitive judgements. Boxplot of the relative estimated duration as a function of the direction of the duration error. The median line inside the box indicates the median of the distribution, while the upper and lower boundaries of the box represent the third and first quartiles, respectively. Whiskers extend to the minimum and maximum values not exceeding 1.5 times the interquartile range from the box. Individual points are individual estimates. Stars and horizontal black lines correspond to significant post-hoc contrasts.

### 3.4. Discussion

The goal of the present study was two-fold. First, we aimed to investigate magnitude and speed estimation in an ecological setting, such as during a train journey, and to examine its relationship with distance and speed estimation. Second, we tested whether available sensory information onboard would impact the magnitude estimation in a specific way. We found that magnitude estimations presented features of classical magnitude profiles such as the central tendency effect, despite using a between-participants design. Instantaneous and average speed profiles were less reliable. Average speed profiles did not show a scalar magnitude profile and did not result from the simple ratio of distance by duration estimates. Further investigations revealed that the link between distance

and duration estimation was better explained by participants' prior knowledge rather than participants' on-the-fly speed estimates. Congruent with this, the seating Orientation did not affect magnitude or speed estimates, although Acceleration partially did so with a positive acceleration resulting in an overestimation of magnitudes compared to a null (constant high-speed) or a negative acceleration (deceleration). Participants showed accurate confidence levels with duration and instantaneous speed estimation, but not for distance and average speed. Surprisingly, the estimation of duration was not related to the speed of the passage of time or to participants' self-reported emotional states. Below, we discuss the implications of our findings for the representation of mental magnitudes and speed in real-life situations.

### 3.4.1. Mental magnitudes profiles and regression to the mean in between-participants design

A mental magnitude is the representation of a physical quantity in the brain, upon which arithmetic computation can be performed (Gallistel, 2011). This is a fundamental property for any living being to interact with the world around it. Time and space, along with quantity, have been described as part of a common magnitude system (Walsh, 2003). Speed can also be considered as a magnitude, since it can be represented by a number and operations can be performed on it, as psychophysics studies suggest (Schmerler, 1976). However, since speed is, by definition in mechanical physics, a magnitude over a temporal unit, it could also not be reduced to any other magnitude (such as duration and distance). Theoretically and by definition, in mechanical physics, duration, distance, and speed should be completely correlated in a system capable of measuring them separately. In the present data, duration and distance estimation were accurate, while instantaneous and average speeds were not (Fig. 3.2). This suggests that, in high-speed transportation mode, such as a train, participants are still able to encode for the elapsed time and traveled distance even though speed exceeds their biological capacities.

Duration estimations showed a regression effect toward the mean of the journey (Fig. 3.2A). In the lab, regression to the mean is classically accounted for by the set of stimuli tested in a given experimental context (Glasauer & Shi, 2021). In a within-participants design (i.e. multiple samples per participant), the regression point typically lies around the midpoint of the distribution. Here, however, we tested a between-

participants design in which data points were independently sampled (i.e. one sample per participant). When a regression pattern is observed in between-participants designs such as ours, one possible interpretation is that the regression point serves as a reference point shared by the individuals (Woodrow, 1934; Yarmey, 2000; Roy & Christenfeld, 2008). Very recently, Large studies using retrospective duration estimation found a regression point of around 15 min (Chaumon et al., 2022; Balci et al., 2023). In these previous studies and the present experiment, participants were tested once and did not know *a priori* that they would be asked to estimate the duration that had just elapsed. Hence no *a priori* cognitive strategies to count time could be set in place by participants. Thus, we could have expected similar outcomes for the regression point, namely a regression of around a quarter of an hour. In our study, the regression point was located around ~69min. A major difference between the studies is the context in which the duration estimation is done. In previous studies, participants were asked to answer an online questionnaire (Chaumon et al., 2022; Balci et al., 2023), with no information on how long the questionnaire was. In our study, participants knew in advance the duration of the journey, which could have shifted the regression point to the middle of the journey. We suggest that prior knowledge allows anchoring duration estimation by setting prior boundaries from the duration of the journey, in a sort of cognitive mapping process. The assumption that participants build a temporal cognitive map of their journey (or any activity) is directly testable. Pending that participants have an accurate prior belief of the task duration, we predict that a similar regression to the midpoint should be found to scale with the actual task duration. Additionally, blinding participants to the task duration should revert to a sampling heuristic approximating the 15-minute rate, assuming that no implicit priors of duration can be inferred from the nature of the task (Chaumon et al., 2022; Balci et al., 2023). The cognitive mapping influenced by prior knowledge may explain why scalar variability was not observed in our experiment, although it was also observed in previous studies with the absence of prior knowledge about the full task duration and using the same retrospective duration estimation task (Chaumon et al. 2022, Balci et al., 2023). The same rationale could be applied to distance estimations, which also display a pattern of regression to the mean.

The second interesting aspect of this regression pattern is to understand why the shared reference across individuals (aka the regression point) would occur in the middle of the travel, and not at the beginning or the end of the journey for instance. One

plausible explanation could be resulting from the fact that the duration estimation is bounded by zero from one side, and by the knowledge of the total duration of the journey on the other side. If we consider that participants tend to under/overestimate randomly in a single trial because each estimation is the product of the objective temporal interval and a noise (proportional to the objective temporal interval, according to Weber's law). For short durations, the noise cannot lead to underestimation (because the estimation cannot be lower than zero). For long durations, the noise cannot lead to overestimation (because the estimation cannot be higher than the total duration of the journey). It would result in a tendency for participants to overestimate durations close to zero, and underestimate durations close to the end of the journey, as we observe in our data. This could lead to a regression to the mean that would lie around the middle of the journey. It is important to keep in mind that we did not control participants' access to temporal information (throughout the entire journey). It is, therefore, possible that participants watched frequently how much duration elapsed during the train journey, explaining why participants were accurate, even for longer temporal intervals, and that could have facilitated the localization of the regression point at the middle of the journey.

### 3.4.2. Duration, distance and their (non)relationship to speed

Participants displayed accurate estimations of magnitudes suggesting that they should have minimally been able to compute the average speed. Our modeling approach suggested otherwise in that the estimated magnitudes were surprisingly not predictive of participants' average speed accuracy (Fig. 3.2D & Fig. 3.3A). Speed estimates could also not be accounted for by systematic biases between estimated durations and distances (Fig. 3.3B). The fact that participants were imprecise in their average speed estimates, despite accurate magnitude estimations, raises the question of what links these internal representations.

Our modeling approach revealed that the link between duration and distance is best explained when one is inferred from the other along with the prior knowledge about the journey (Fig. 3.3C-D). These findings suggest that in the context of a train journey, participants are more relying on a cognitive strategy involving knowledge (or cognitive maps) rather than sensory evidence, either because sensory signals are beyond biological capacities or not very salient in the context of a train journey. The adoption of this strategy could have been facilitated by the fact that we asked participants to make



these estimates one after the other, implicitly encouraging the direct mapping of one magnitude to the other instead of relying on sensory evidence specifically for one magnitude separately. It would be interesting to confirm this result with separate questionnaires for distance and duration in a between-participants design (one participant is only asked to estimate distance, and another has to estimate duration).

An interesting observation in this result is that the  $R^2$  was larger for the distance explained by the duration and its prior knowledge than the duration explained by the distance and its prior knowledge (Fig. 3.3C-D). Although this is not concrete evidence, it is consistent with the hypothesis that duration was used by participants to infer distance, not the other way around. This is even more plausible given that the distances were well beyond participants' visual capacity, and that they had no access to speed. The fact that participants could provide confidence judgments of their duration accuracy and not for distance supports as well this hypothesis. Even in the absence of external sensory inputs, people can still rely on their internal dynamics to estimate how much duration has elapsed.

Again, we cannot exclude that, since it is a questionnaire and not a fully controlled experiment, participants had often access to temporal information throughout the entire journey, favoring a strategy based on duration rather than distance, and also explaining why duration estimations are so accurate compared to a similar range of duration (Tobin et al., 2010). Nevertheless, the current results are consistent with the setting up of an elaborate internal map of the train journey, in which duration, rather than distance, may be tracked.

### 3.4.3. The absence of available sensory information effects on estimations

Another aim of the study was to investigate whether the sensory information available onboard would impact estimation as it is observed in the laboratory and expected from path integration mechanism. We identified and measured two available sources of sensory information: the seating Orientation (forward or backward optic flow) and the Acceleration (positive, null, or negative).

In the lab, it was found quite early that participants tend to overestimate the duration of a moving stimulus (Brown, 1995) and that the overestimation increases when the speed increases (Kanai & Watanabe, 2006). This effect was also reported when

the environment moved around the stimulus (Mate et al., 2009), suggesting that an optic flow could also result in a similar effect. A more realistic task revealed that the speed of the optic flow of a car simulator led participants to overestimate duration as well (van Rijn, 2014). Therefore, we hypothesized that duration estimation should be impacted in a systematic way by the optic flow that participants can be exposed to. We did not find an effect of the optic flow Orientation (Fig. 3.S3). However, we found a small effect of the Acceleration, where distance, instantaneous, and average speed were overestimated with a positive acceleration compared to a null and negative acceleration (Fig. 3.4). This effect of Acceleration was not significant for duration estimation. We did not predict such a pattern from our two hypotheses, based, either on the maximal speed of the optic flow or on the rate of change of the optic flow. However, this effect might be confounded with the Vierordt law profile that we already observed in our data (Fig. 3.2). Indeed, we found that participants were overestimating small magnitudes, located at the beginning of the journey, and underestimating large magnitudes, located at the end of the journey (Fig. 3.2). The positive acceleration was also always located at the beginning of the journey, and the negative acceleration was always located at the end of the journey (Fig. 3.4A). Therefore, objective small magnitudes were always confounded with the positive acceleration, and objective large magnitudes with the negative acceleration (Fig. 3.4B). We can even note that this effect is not restricted to magnitude (duration and distance) but also to speed estimations. Therefore, the effect of Acceleration cannot be fully interpreted as an effect of sensory information. Such confound could potentially be overcome by performing a similar questionnaire but with several acceleration/deceleration episodes. It would allow us to investigate separately those two effects. It is possible that the exposition of the participant to the optic flow was not fully controlled, either because they were sitting far from the window or because they were engaging in a really demanding task (e.g. reading, working on computers). One way to capture the effect of ecological sensory information could be also to recruit participants who will perform specific tasks, in order to refine our quantification of behavior during the exposure of those sensory signals (Vallet & van Wassenhove, 2023).

#### 3.4.4. Dissociation of duration distortion and changes in the speed of the passage of time

It is, still, unclear how the subjective experience of the speed of time (passing slower or faster) is related to the under/overestimation of duration. Indeed, depressive patients reporting experiencing time as passing slowly, are not affected in their duration estimation performance compared to healthy participants (Thönes & Oberfeld, 2015). It was recently suggested that the speed of the passage of time judgments better capture the phenomenology of time passing and rely on different mechanisms than duration estimation (Wearden, 2015; Droit-Volet & Wearden, 2016). When duration and speed of the passage of time judgment are asked about the same time interval and at the minute scale, longer durations are judged as passing slower than shorter durations (Droit-Volet et al., 2017; Nicolaï et al., 2024). Time error even increases when the speed of the passage of time is judged slower (Martinelli & Droit-Volet, 2022a) suggesting that an underestimation of duration should be perceived as passing faster (and overestimation of duration as passing slower). However, this does not fully demonstrate that there is a specific link between the under/overestimation duration and the faster/slower speed of the passage of time judgment. In a recent study, we even showed the opposite relationship when the density of event was manipulated (Lamprou-Kokolaki et al., 2024), and speed of the passage of time measured with a 2-Alternative Forced Choice task. In this study, when the number of events increases, durations are overestimated, and the speed of the passage of time is rated as going faster, which is opposite to the other observations. Note that it remains unclear whether this new perceptual measure of the speed of time corresponds to our subjective feeling of the time passing slower or faster in everyday life. Therefore, the link between the under/overestimation duration and the faster/slower speed of the passage of time judgment remains to be demonstrated.

In the present study, we did not find a link between the under/overestimation of duration and participants' self-reports of time passing faster or slower (Fig. 3.5). It is possible that the implicit scale at which participants formulated their judgments differed: durations were asked with respect to the departure of the train, whereas speeds of the passage of time estimations may have been answered in a more instantaneous fashion despite our instructions. Given the relationship between duration

scales and the perceived speed of the passage of time (Droit-Volet et al., 2017; Nicolai et al., 2024), this may have affected the outcomes. However, several indicators suggest that our data could lack of granularity to find a relationship between the two variables. First, we used a 4-point Likert scale, while previous studies usually had a 7-point Likert scale, and most of the participants used only the middle level of the Likert scale, reducing our measure to a 2-point Likert scale. This pattern has been reported in other experiments showing the distribution of the data (see Chaumon et al., 2022; Nicolai et al., 2024). Second, our questionnaire was a between-participants design, with only one response per participant, while in other ESM studies usually asked for multiple responses per participant. Third, we did not find other results obtained with Likert scales and duration estimation as in other ESM studies. Indeed, our relative duration estimations were not related to the emotional state of happiness, sadness, and boredom self-reported by participants (Martinelli & Droit-Volet, 2022a). Fourth, we did not find a link between the reported subjective speed of the passage of time feeling and the objective duration (although it was never tested on a between-participants design). All these points question the quality of our Likert scale measures, but still suggest that the subjective experience of the time passing requires more data, operationalization, and methodological clarification.

### 3.4.5. Metacognition in the “wild”

Metric error monitoring is a metacognitive mechanism that has been described in laboratory settings for duration, distance, and numerical judgment (Yallak & Balci, 2022). When participants are asked to make duration, distance, and numerical judgments on the screen of a computer, they can also report how much they were wrong (magnitude), and whether they under/overestimated (direction). We tested, in an exploratory fashion, whether those metacognitive judgments could be made in more complex ecological environments.

In the context of our train journey, we found that participants also had access to the magnitude of their errors, but only for the duration and instantaneous speed judgments as we found that for participants' estimations of duration and the instantaneous speed, participants' confidence reports correlated negatively with the absolute relative errors. The fact that participant had access to their error magnitudes for duration and not for distance is consistent with the idea that they probably relied on

duration estimation to estimate distance. Indeed, unlike in a laboratory setting, the distances they had to estimate far exceeded their visual capabilities, rendering them inaccessible to their sensory-motor systems and path integration mechanisms, especially since the speeds involved surpassed their biological capacities. That distances were above their biological capacities could be reflected in the fact that participants were more confident for distances in the positive acceleration (i.e., short distances) than in the null acceleration episodes. At the beginning of the journey, participants are able to estimate distances, but at some point, distances are no longer available and therefore not well estimated.

Along with the magnitude, our results showed that participants had also access to the direction of their error for duration estimations (we did not measure it for another type of estimation). Participants who had a relative duration estimate lower than one tended to report underestimating, and those with a relative estimate higher than one tended to report overestimating. These findings support the fact that even for such long retrospective duration estimations, participants still have a timing error mechanism (Özcel et al., 2021). We also investigated whether sensory information factors (Acceleration and Orientation) could influence the direction of the errors of duration estimations. We found an interaction between the two factors, suggesting that participants tended to overestimate more when they were seated facing backward rather than forward, and this was specifically observed during episodes of positive acceleration. This finding contradicts our initial hypotheses regarding the impact of sensory information on duration estimation, positing that facing forward would amplify the effect of acceleration. This is also not consistent with the hypothesis that participants would have a metacognitive access to the effect of sensory information on their duration estimations since a significant effect of sensory information was found on participants' duration direction errors, but no effect was observed on duration estimations. It would be interesting to investigate whether, in laboratory settings, a manipulation of a duration estimation by a specific factor (such as working memory, attention, speed) leading to a specific bias, is accessible with a metacognitive assessment of either the magnitude or direction of error.

## 3.5. Conclusion

To the best of our knowledge, this is the first study investigating retrospective duration estimation throughout the specific context of a train journey, along with its relationship with distance and speed estimations. We report several measures suggesting that the temporal dimension of passengers' experience is an essential primitive onto which the perception of distance may be built. This ecological approach provided unexpected results, such as the shift of the regression to the midpoint of the journey. This observation suggests the use of a cognitive map based on landmarks (start and end of the journey) mechanism to track the elapsed duration and distance. The absence of a link between duration/distance and speed estimations led to follow-up questions that could be further investigated in other ecological contexts or in laboratory experiments. However, we noted that this methodology might not be adequate to investigate the effect of ecological sensory inputs, and a more controlled experiment could be better suited.

## 3.6. Supplementary Materials

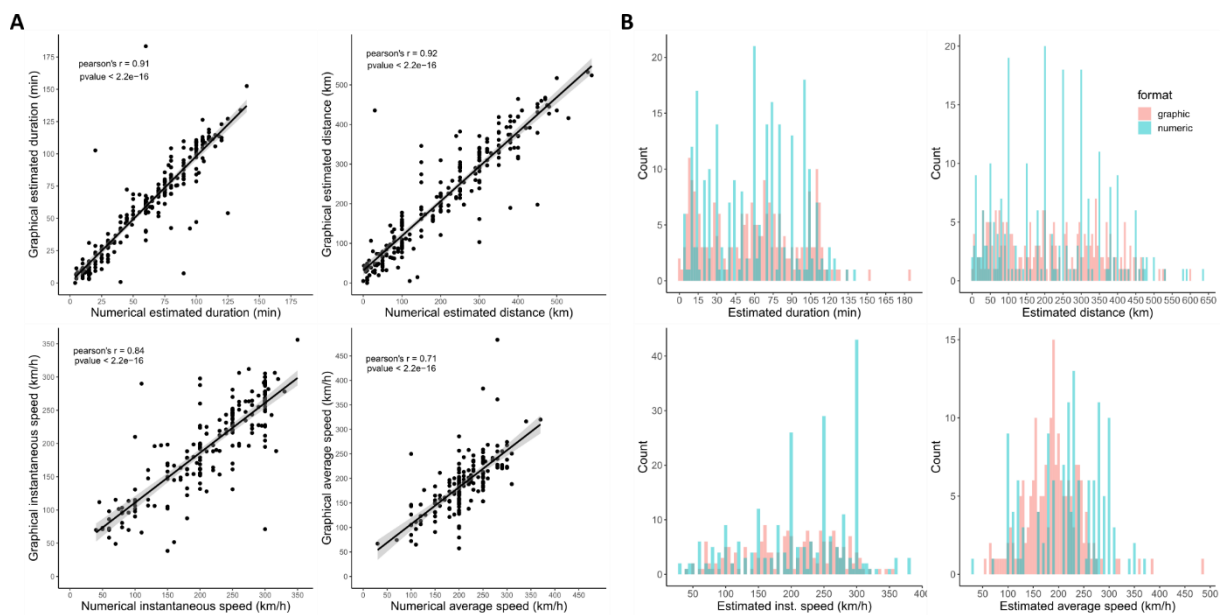
### 3.6.1. Estimation scores combining graphical and numerical estimates

In our experimental design, we asked participants to provide their estimation of magnitudes (duration, distance) and speed (instantaneous, average) in both numerical and graphical formats. Prior to conducting our main analyses, we thus looked at whether the format was a factor or could be disregarded.

To test this, we used Pearson's correlation between the two datasets and found a large, positive, and statistically significant correlation between numerical and graphical estimates for all estimations: in duration estimation ( $r = 0.91$ , 95% CI [0.89, 0.93],  $t(245) = 34.67$ ,  $p < 0.001$ ), in distance estimation ( $r = 0.92$ , 95% CI [0.90, 0.94],  $t(236) = 36.60$ ,  $p < 0.001$ ), for instantaneous speed ( $r = 0.84$ , 95% CI [0.79, 0.88],  $t(196) = 21.72$ ,  $p < .001$ ) and for average speed:  $r = 0.71$ , 95% CI [0.63, 0.78],  $t(183) = 13.75$ ,  $p < .001$ ).

These results suggested that using the "format" as a factor in subsequent analyses would introduce strong collinearities in our statistical models (Fig. 3.S1A). To ease statistical analyses and their interpretations, we merged numerical and graphical estimates into a single score by taking the mean of the two.

Nevertheless, it is noteworthy that histograms of the estimates revealed a slight difference between numerical and graphical estimates. Numerical estimates tended to be rounded to specific values (every 15 minutes for the duration; every 50 km for the distance; and every 50 km.h<sup>-1</sup> for speed, see Fig. 3.S1B). Therefore, computing a score between numeric and graphic estimation also enabled removing the strong rounding effect in numerical estimates and reduce the number of missing estimations (especially for graphical estimates).

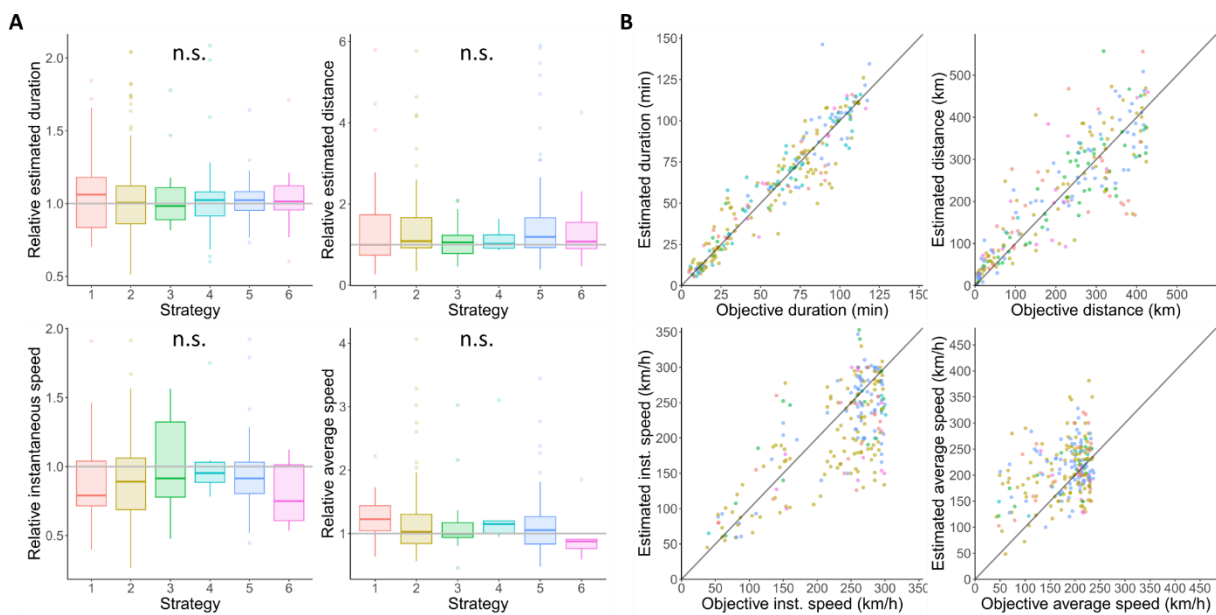


**Fig. 3.S1: Significant correlations between graphical and numerical estimations of duration, distance, instantaneous speed and average speed.** A: Correlation between graphical and numerical estimates of duration (top left), distance (top right), instantaneous and average speed (bottom left and right, respectively). Shaded gray area corresponds to the 95% C.I. Dots are individual data. B: Distributions of estimations grouped by reporting format (blue is numerical; orange is graphical). Distributions are provided for duration (top left), distance (top right), instantaneous and average speed (bottom left and right, respectively).

### 3.6.2. The estimation strategy does not affect relative estimates

Prior to any statistical analysis, we controlled for the effect of the strategy used on the relative estimates. At the very end of the questionnaire, participants explained the strategies they used for each of their estimations; based on their reports, the six possible strategies were: (1) None, (2) Perceptual, (3) Mathematical, (4) Measurement, (5) Knowledge and (6) no answer. Given these strategies, we were concerned that participants who reported using a measurement device (e.g. smartphone, computer) would be too accurate notably compared to other strategies. To test whether the estimation strategy significantly affected participants' estimations, we fitted a linear

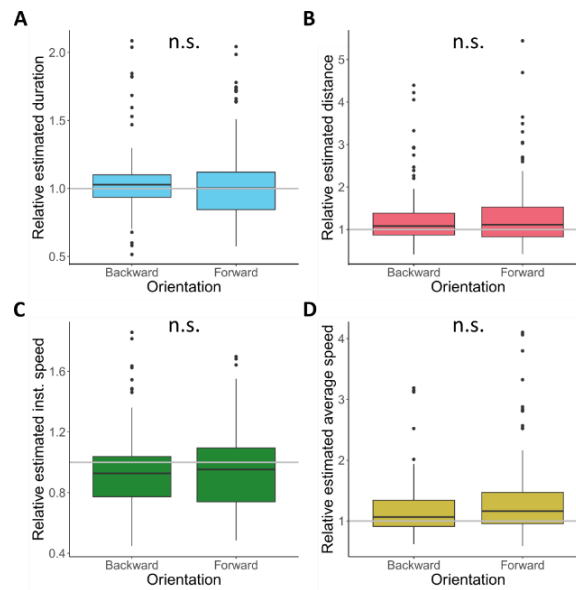
model (estimated using OLS) using the strategy (categorical factor with 6 levels) as predictor of the four possible estimations (Fig. 3.S2A). None of the models indicated a significant effect of strategy on participants' estimation: duration ( $R^2 = 3.80e-03$ ,  $F(5, 227) = 0.17$ ,  $p = 0.972$ , adj.  $R^2 = -0.02$ ), distance ( $R^2 = 0.03$ ,  $F(6, 224) = 1.20$ ,  $p = 0.308$ , adj.  $R^2 = 5.14e-03$ ), instantaneous speed ( $R^2 = 0.04$ ,  $F(5, 225) = 1.72$ ,  $p = 0.130$ , adj.  $R^2 = 0.02$ ) and average speed ( $R^2 = 0.02$ ,  $F(5, 226) = 0.83$ ,  $p = 0.530$ , adj.  $R^2 = -3.72e-03$ ). Thus, different strategies were not a good explanation for the variance in the model. Last, we also ensured that the different strategies were uniformly distributed across the entire journey (Fig. 3.S2B).



**Fig. 3.S2: No effect of participants' reported estimation strategy on relative estimates.** A: Boxplot of the relative estimated duration (top left), distance (top right), instantaneous and average speed (bottom left and right, respectively) as a function of the reported strategy. B: Distribution of the strategies as a function of the different objective estimate values (thus, sample times in the journey). Color code for the points corresponds to the color code of the strategy in panel A.



### 3.6.3. No effect of Orientation on estimation



**Fig. 3.S3: No effect of the seating Orientation (Backward; Forward) on relative magnitude and speed estimates.** Box plot showing the distribution of each relative estimation for each optic flow orientation (A: duration in blue, B: distance in red, C: instantaneous speed in green, D: average speed in yellow). The median line inside the box indicates the median of the distribution, while the upper and lower boundaries of the box represent the third and first quartiles, respectively. Whiskers extend to the minimum and maximum values not exceeding 1.5 times the interquartile range from the box. Estimations beyond the whiskers are shown as individual points.

## Chapter 4 – General Discussion

The main questions of my PhD work were:

- ❖ Are there enough existing data to claim that duration change is detected in the MMN process?
- ❖ When an empty interval change is specifically tested, do we observe an MMN potential?
- ❖ How are durations estimated in an ecological context such as a train journey, and are they influenced by the available sensory information onboard?

And I hope, through its content, to have convinced you (or at least provided enough material to discuss) that:

- ❖ So far, there is not enough data and evidence to assert the existence of duration MMN (Chapter 1)
- ❖ The first study to test properly a change in empty time interval indicates that we do not observe an empty time interval MMN which suggests that the brain does not automatically represent durations between events (Chapter 2).
- ❖ In the context of a train journey, retrospective duration estimation is not simply a measure of elapsed duration reflecting the integration of external or internal sensory information, but also involves notions of knowledge suggesting a cognitive map mechanism (Chapter 3).

This work thus brings new theoretical and empirical tools for studying duration perception. In this Discussion, I start by summarizing, discussing, and offering perspectives on the main results obtained from each chapter. Then, I discuss the “wild” approach more generally, and what it has contributed to the originality and results of my studies and thinkings. Finally, I conclude with some research questions that I would enjoy investigating in a near future.

## 4.1. What it really takes to claim that duration is not automatically coded in the MMN process

Of particular interest to me, about the duration MMN, was to take an old subject and confront it with today's understanding and methodological standards. Surprisingly, while the duration MMN appears established in the literature and already utilized for clinical diagnostic purposes (Fong et al., 2020; Gu & Bi, 2020; Kim et al., 2020; Tseng et al., 2021), a comprehensive analysis of the available literature (see Chapter 1) reveals that the theoretical foundations of such effect were weak. These observations thus necessitate the testing of the robustness of such an effect by attempting to replicate and further analyze the conditions under which it manifests.

My empirical studies (Chapter 2, Annex 5.2) suggest that MMNs are not observed for empty time interval changes in EEG when a careful methodology for duration is used. I had clear hypotheses about the effect of duration scale (in line with the notion temporal window of integration) and its interaction with the direction of deviance (shorter or longer), that I could not investigate because I did not find clear duration MMN responses (in any conditions). First, I replicated the duration MMN that can be found in the literature when the contrast deviant-standard is used. Then, I showed that this contrast deviant-standard does not rule out the effect of refractoriness, hence does not reflect only a duration deviance detection. When the effect of refractoriness is taken into account by the appropriate contrast, namely deviant-control, the differential waves suggest no response specific to the duration deviance detection. Out of intellectual honesty, I must acknowledge that I would like to replicate this result and contrast it with a frequency (or other) MMN in order to fully claim it and defend it. Indeed, non-significant results cannot be used to support this hypothesis. Therefore, this work would necessitate a battery of studies to be conducted in order to clarify this interpretation.

If there were no time, budgetary, or technical constraints, I would conduct a series of small and simple experiments to ensure the accuracy of the results and to extend it to other duration experimental conditions. I would start by replicating the non-observation of the empty time interval MMN at different duration scales and contrasting them with frequency MMNs. To simplify the design, it may even be possible to test only one direction of deviance (shorter or longer) per block. I partially started this work with the latest MMN dataset that I acquired, as mentioned in the introductory paragraph of

Chapter 2, but not analyzed yet. In addition to contrasting duration MMNs with frequency MMNs, this dataset investigates the role of attention in the semi-automatic process of duration measurement. Next, I would test the existence of the empty time interval MMN when it is included in a rhythm to characterize the effect of temporal expectations on the (non-existent?) duration MMN. Subsequently, I would examine the effect of attention on these responses (as attempted in my latest dataset, not presented in this manuscript). Finally, I would conduct the same experiments, but testing filled time intervals to determine whether there is a difference in the processing of these two duration types. Contrary to empty time interval, filled time interval makes duration a feature of stimulus, hence probably probing different mechanism. With a tool of higher spatial resolution such as MEG, we could even consider comparing the neuronal sources of these responses (assuming such responses exist).

## 4.2. One alternative to automatic durations coding is events timestamping

Beyond these theoretical and empirical questions, I can still speculate about the non-existence of the duration MMN and the extrapolation that can be made for the format of the time representation. Since the measurement of a time interval is rarely explicitly required for a behavior, it is questionable whether the format of the time representation should be in the form of the measurement of that time interval (aka duration) if it is not automatically coded (in the MMN process for example). The absence of the empty time interval MMN suggests that the brain does not measure duration information unless explicitly required for the task, in contrast to simple sensory information (e.g., intensity, frequency) or even a repeated abstract rule. One interpretation could be that the duration between two events is an even more abstract information that requires explicit computation.

An embryo of my hypothesis is that the brain does not need to measure all durations at all, because it is already equipped with mechanisms for separating and discretizing information, and events in general. First, it has automatic and structural mechanisms, such as temporal integration window, which allows for rapid analysis (and/or modification according to prediction, recent experience, or coherence with stimuli from another sensory modality) and integration of any sensory information

(Poeppel, 2003; van Wassenhove et al., 2007; Eagleman, 2008; Grabot et al., 2021). Within this window, temporal information (simultaneity, order, duration) plays a crucial role in the formation of a percept associated with these information (van Wassenhove, 2009). Second, beyond this window of temporal integration, the coding of time would involve other types of mechanisms, such as event segmentation (Zacks & Tversky, 2001; Richmond & Zacks, 2017) and temporal timestamping (Gallistel, 1990), especially when duration is not directly necessary to solve the task. When duration is explicitly required for the task, duration measurement mechanisms could take over. Otherwise, duration could be calculated retrospectively from the distance between two temporally marked events (Gallistel, 2011), resulting from the event segmentation mechanism. This mechanism is closer to the elaboration of a temporal cognitive map, rather than measuring time through duration. A promising avenue for the implementation in the brain of such mechanisms relies in the dynamic of neuronal trajectories, as they try to bridge the gap between objective duration, temporal dynamics of brain activity, and subjective duration (Tsao et al., 2022). As a result, the phenomenology of the speed of the passage of time (faster or slower) may have nothing to do with the measurement (if any) of durations, but rather with the (metacognitive?) read-out stage of the neuronal dynamics (van Wassenhove, 2009; Kononowicz & van Wassenhove, 2019).

### 4.3. Estimating duration throughout a train journey involves prior knowledge, not sensory cues

Although the experimental design is relatively simple (albeit the data collection process is tedious), the questionnaire results are diverse and rich. The unexpected observations they have yielded open the door to new questions and experiments, whether on a train journey, in others ecological contexts, or in the laboratory.

The first unexpected result was the replication a regression pattern, with observations from a between-participants design. However, the regression point was not located at ~15 minutes, as reported in two recent and comparable studies (Chaumon et al., 2022; Balcı et al., 2023), but was located at the middle of the journey (~69 minutes) in our study. The main difference between the studies is contextual. In the previous studies, participants estimated the retrospective duration after completing a long questionnaire. Therefore, they had no *a priori* information about the duration of this

questionnaire. In our study, participants had relatively accurate knowledge of the duration of the journey. It is reasonable to assume that this knowledge (implying a boundary) was responsible for the shift in the regression point. Thus, it would suggest that participants may have used a cognitive map mechanism based on their knowledge and influenced by anchor points (landmarks such as the start and end of the journey). To test the effect of knowledge (and boundaries), we could collect the same type of data on journeys of different durations (and thus different anchor points). We could also extend this observation to different contexts of known but different durations (where duration may or may not be of particular importance). Finally, we could test the effect of manipulating the actual duration of a context relative to its expected duration and investigate how it influences (or not) the regression point.

The second unexpected result is that participants were relatively accurate in estimating duration and distance, but not speed. In the context of biological displacement, duration, distance and speed are linked by the mechanism of path integration. However, in the context of a train, speed is much higher than biological speed, and the impoverished sensory cues probably do not allow for its estimation. Our modeling approach revealed that estimates of duration and distance were best explained by each other when used in combination with their prior knowledge. Additionally, the size of the explained variances indicates that participants tend to estimate distance as a function of duration, rather than vice versa. This is further supported by the fact that participants were able to estimate their error for duration via a confidence judgment, but not for distance.

The use of knowledge and the lack of effect of sensory information on estimates suggest once again that, in this particular context of train journey, participants probably used a temporal cognitive map system rather than a sensory magnitude and path integration system. Speculatively, this study further supports the proposal of a temporal cognitive map construction mechanism (based on a non-automatic encoding of sensory duration) that, knowledge-related, landmarks can influence.

Moreover, these data also provide additional evidence for the dissociation between the mechanism of duration measurement and the mechanism of the speed of the passage of time. Indeed, we did not observe any relationship between these two temporal estimations.

#### 4.4. The benefits of being “wild”

I now turn more specifically to the problem of scientific laboratory results generalization and their ecological validity and the beneficial contribution of the "in the wild" approach. The development of experimental psychology opened the path to the scientific study of human cognition and behavior. The scientific criteria required the development of highly controlled environments, parametric manipulation of experimental factors, repetition of tasks for quantification purposes, and sophisticated statistical methods to highlight significant effects (Holleman et al., 2020). Those scientific standards, however, shifted the original goal of psychology – explaining natural human behaviors – to explaining human behavior in very restricted tasks within, non-natural, controlled environments (Vallet & van Wassenhove, 2023). It has long been argued that the scientific rigor in the lab questions the ecological validity of the stimuli and behavior tested (Brunswik, 1952). Thus, if stimuli and behavior in the lab are too far from any natural behavior, it questions the generalization of those results to natural behavior. This “Real-world or the lab” - dilemma (Holleman et al., 2020) is at the heart of the “wild” approach developed in the WildTimes project (for a dedicated review and argumentation, see Vallet & van Wassenhove, 2023). It is therefore required to develop an adequate scientific methodology to resolve this dilemma. Accordingly, Vallet and van Wassenhove recently proposed a set of 8 guiding principles to directly conduct experiments in the “wild” (Vallet & van Wassenhove, 2023).

To overcome this dilemma, I think it would also be beneficial to take a more sequential approach, validating the influence of a factor step by step, starting from the laboratory and working up to the ecological environment. The first step would be to identify a laboratory result of interest. We would start by replicating it with more concrete stimuli inspired by our environment. Then we would have to extend that result to a virtual reality (VR) simulation, simulating the behavior of interest in a real-life situation (note that we would have to consider the possible effect of VR itself, which is often related to the notion of the degree of immersion in the environment). This VR step would allow the parametric manipulation of the factor, and the repetition required to the scientific quantification. Finally, we could replicate this result in an experiment in a real situation. I started to investigate this approach during my master 2 internship by using temporal bisection (a classical task of duration perception) at different episodes of a

train journey. The inconclusive results of this explicit timing task oriented me toward implicit timing, that further led to the MMN studies.

The ecological approach of my work does not follow this sequential proposition. Nevertheless, it has largely contributed to the originality of this work. Concerning duration MMN, my attempt to use it outside the laboratory allowed me to get over the shortcuts and overgeneralization in the existing literature. At the start of the examination of the duration MMN literature, the number of studies as well as reviews conducted by researchers interested in duration perception (Macar & Vidal, 2004; Ng & Penney, 2014; van Wassenhove & Lecoutre, 2015; van Wassenhove et al., 2019) support its existence. Following a surprising preliminary result, the closer examination of the methods used in the studies led to questioning its taken-for-granted characteristics. Therefore, the desire to use the duration MMN as a tool, initially to measure the implicit duration perception outside the lab, led me to question its very own existence. Concerning the questionnaires, unexpected results led me to consider new hypotheses, resulting in new analyses, and thus to propose new experiments.

In addition to studying natural behaviors, conducting experiments in contexts with less control can lead to serendipitous discoveries. Many great discoveries have been made due to errors or randomness in experimental conditions, combined with the vigilance and observational skills of scientists. The “wild” approach inevitably involves a degree of non-control. This can lead to unexpected observations that open up new avenues of research. However, it requires a great understanding of what you are testing and a keen sense of observation. Of course, the principle of serendipity is not exclusive to the “wild” approach and is also present in laboratory settings, but I do think it tends to favor it.

## 4.5. Appealing avenues of future research work

In this section, I briefly develop research works and questions that I could conduct in the near future.

At the largest scale, I think it is necessary to further develop and refine the operationalization of time for the brain (as stated in Chapter 1). It could be done through a literature review, that would re-classify existing results under the categories defined by the operationalization process (see Issa et al., 2020; Tsao et al., 2022 for recent concrete attempts). Essentially, the goal would be to investigate whether this new classification



would lead to the emergence of consistent patterns of results across studies, and therefore validate the necessity and benefit of this approach.

At a narrowest scale, I would be interested in investigating the effect of temporal expectation at the minute scale and its difference for duration and speed of the passage of time judgment. The effect of temporal expectation (via alleged task durations) on minute-scale speed of the passage of time judgments has been investigated by Tanaka and colleagues (Tanaka & Yotsumoto, 2017). In this study, the researchers hypothesized that alleged duration influence perceived duration when the former does not match the objective duration. Thus, the discrepancy between alleged and objective duration should create a feeling of the speed (faster or slower) of the passage of time. However, the researchers did not characterize the effect of alleged duration on perceived duration. In this case, the distinction between duration judgment and the speed of the passage of time cannot be examined. Therefore, I would be interested in testing the same type of manipulation (discrepancy between alleged and objective duration) on duration judgments and speed of the passage of time judgments to disentangle (or not) these two notions.

We recently showed that the speed of the passage of time, measured in a psychophysical way, could be manipulated by the density of events in a time interval (Lamprou-Kokolaki et al., 2024). One hypothesis is that the speed of passage of time could be intrinsically linked to the event segmentation mechanism (see 4.2, Annex 5.3). In event segmentation theory, the number of different events lead to higher number of boundaries that lead to a faster speed of the passage of time (Richmond & Zacks, 2017). However, the predictability of events (and violation of expectation) also lead to higher number of boundaries (Shin & DuBrow, 2021). Therefore, investigating whether events predictability would also impact the speed of the passage of time could provide additional evidence for a link between event segmentation and the speed of the passage of time judgment. Then, we could try to disentangle the effect of event density and event predictability on the speed of the passage of time to refine our understanding of it.

Speed of the passage of time judgments have also been linked to metacognitive judgments (Sackett et al., 2010). It could be worth investigating more concretely their relationship and whether they rely on similar mechanisms. For instance, is there an associated direction between metacognitive duration judgment (under/overestimation) and the speed of the passage of time (faster/slower)?

More specifically on duration metacognitive judgment, testing whether duration distortions, caused by a specific factor (e.g. working memory load, Polt et al., 2018), are accessible through metacognitive judgment could provide information on whether duration distortions directly reflect an associated and accessible feeling of time.

Duration metacognitive judgments have been described as being part of a common metric error of magnitude estimation (Yallak & Balci, 2022). A key point in comparing magnitude estimations is to take into account the rate of sensory evidence (Martin et al., 2017). If not, an obvious distinction between duration magnitude and others (such as distance or numerosity) is the moment and the length of sensory evidence accumulation. Hence, to investigate a common metric error monitoring across magnitudes, we should consider the rate of sensory evidence as well. This could be done with a replication of Yallack & Balci, 2022, combined with the manipulation of sensory rate evidence from Martin et al., 2017.

Last, the interplay between implicit and explicit timing, is of particular importance in understanding how the former can constitute a basis for the representation of the latter (Herbst et al., 2022). Specifically on this topic, it could be interesting to test how our priors of explicit timing (that can be measured with duration production) can be manipulated by the repetitive exposure to feedback, from an implicit timing task performed in between blocks of duration production. A key point would be to measure how much participants are sensitive to this manipulation, which could provide information on the strength of the duration priors that we develop through the course of our lives.

## 4.6. Conclusion

Throughout my PhD, I conducted several studies on duration perception in various contexts and at different temporal scales. In EEG laboratory studies (Chapter 2, Annex 5.2), my data suggests that changes in empty time interval below one second are not automatically computed by the brain. It challenges the hypothesis that the quantification of duration between events is the basic format to represent time in the brain. An alternative (but not mutually exclusive either) to duration quantification is to code the events' timestamp, in a cognitive map kind of way. In such a temporal map, duration could be computed by the distance between timestamps. In a questionnaire study onboard trains, my data suggests that participants rely more on a strategy involving

prior knowledge to estimate duration than a strategy based on sensory cues. This is again close to the idea of constructing a temporal map, with landmarks that can be placed based on knowledge. I discussed the implications and future experimental works that can be conducted to confirm those results. Finally, I introduced other avenues in temporal cognition that could be investigated in the near future.

## References

- Abel, S. M. (1972). Duration discrimination of noise and tone bursts. *The Journal of the Acoustical Society of America*, 51(4B), 1219-1223.
- Akdoğan, B., & Balcı, F. (2017). Are you early or late? : Temporal error monitoring. *Journal of Experimental Psychology: General*, 146(3), 347.
- Allen, J. F. (1983). Maintaining knowledge about temporal intervals. *Communications of the ACM*, 26(11), 832-843. <https://doi.org/10.1145/182.358434>
- Allman, M. J., Teki, S., Griffiths, T. D., & Meck, W. H. (2014). Properties of the Internal Clock : First- and Second-Order Principles of Subjective Time. *Annual Review of Psychology*, 65(1), Article 1. <https://doi.org/10.1146/annurev-psych-010213-115117>
- Amenedo, E., & Escera, C. (2000). The accuracy of sound duration representation in the human brain determines the accuracy of behavioural perception : Mismatch negativity predicts the accuracy of perception. *European Journal of Neuroscience*, 12(7), Article 7. <https://doi.org/10.1046/j.1460-9568.2000.00114.x>
- Atienza, M., & Cantero, J. L. (2001). Complex sound processing during human REM sleep by recovering information from long-term memory as revealed by the mismatch negativity (MMN). *Brain research*, 901(1-2), 151-160.
- Azizi, L., Polti, I., & van Wassenhove, V. (2023). Spontaneous  $\alpha$  Brain Dynamics Track the Episodic “When”. *Journal of Neuroscience*, 43(43), 7186-7197.
- Balcı, F., Ünübol, H., Grondin, S., Sayar, G. H., van Wassenhove, V., & Wittmann, M. (2023). Dynamics of retrospective timing : A big data approach. *Psychonomic Bulletin & Review*. <https://doi.org/10.3758/s13423-023-02277-3>
- Bekinschtein, T. A., Dehaene, S., Rohaut, B., Tadel, F., Cohen, L., & Naccache, L. (2009). Neural signature of the conscious processing of auditory regularities. *Proceedings of the National Academy of Sciences*, 106(5), 1672-1677. <https://doi.org/10.1073/pnas.0809667106>
- Berglund, B., Berglund, U., Ekman, G., & Frankehaeuser, M. (1969). THE INFLUENCE OF AUDITORY STIMULUS INTENSITY ON APPARENT DURATION. *Scandinavian Journal of Psychology*, 10(1), 21-26. <https://doi.org/10.1111/j.1467-9450.1969.tb00003.x>
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, 10(4), 433-436. <https://doi.org/10.1163/156856897X00357>
- Brannon, E. M., Libertus, M. E., Meck, W. H., & Woldorff, M. G. (2008). Electrophysiological Measures of Time Processing in Infant and Adult Brains : Weber's Law Holds. *Journal of cognitive neuroscience*, 20(2), 193-203. <https://doi.org/10.1162/jocn.2008.20016>
- Brannon, E. M., Roussel, L. W., Meck, W. H., & Woldorff, M. (2004). Timing in the baby brain. *Cognitive Brain Research*, 21(2), 227-233. <https://doi.org/10.1016/j.cogbrainres.2004.04.007>
- brown, S. W. (1995). Time, change, and motion : The effects of stimulus movement on temporal perception. *Perception & Psychophysics*, 57(1), 105-116. <https://doi.org/10.3758/BF03211853>
- Brunswik, E. (1952). *The conceptual framework of psychology*. (*Int. Encycl. Unified Sci.*, v. 1, no. 10.) (p. iv, 102). Univ. Chicago Press.
- Budd, T. W., & Michie, P. T. (1994). Facilitation of the N1 peak of the auditory ERP at short stimulus intervals. *Neuroreport: An International Journal for the Rapid Communication of Research in Neuroscience*.
- Buhusi, C. V., & Meck, W. H. (2005). What makes us tick? Functional and neural mechanisms of interval timing. *Nature Reviews Neuroscience*, 6(10), Article 10. <https://doi.org/10.1038/nrn1764>
- Buonomano, D. (2017). *Your brain is a time machine : The neuroscience and physics of time*. WW Norton & Company. [https://books.google.fr/books?hl=fr&lr=&id=0Ep8DAAAQBAJ&oi=fnd&pg=PT6&dq=your+brain+is+a+time+machine&ots=kc2Umk5bNX&sig=HipI\\_U6gYgmAIdj\\_M5wY8RK7Uzg](https://books.google.fr/books?hl=fr&lr=&id=0Ep8DAAAQBAJ&oi=fnd&pg=PT6&dq=your+brain+is+a+time+machine&ots=kc2Umk5bNX&sig=HipI_U6gYgmAIdj_M5wY8RK7Uzg)
- Buonomano, D., & Rovelli, C. (2023). *BRIDGING THE NEUROSCIENCE AND PHYSICS OF TIME* (p. 267-282). [https://doi.org/10.1142/9781800613751\\_0010](https://doi.org/10.1142/9781800613751_0010)

- Cai, M. B., Eagleman, D. M., & Ma, W. J. (2015). Perceived duration is reduced by repetition but not by high-level expectation. *Journal of Vision*, *15*(13), 19. <https://doi.org/10.1167/15.13.19>
- Carlo, R. (2017). *L'ordre du temps*. Paris, Flammarion.
- Catts, S. V., Shelley, A.-M., Ward, P. B., Liebert, B., McConaghy, N., Andrews, S., & Michie, P. T. (1995). Brain potential evidence for an auditory sensory memory deficit in schizophrenia. *The American journal of psychiatry*, *152*(2), 213-219.
- Chaumon, M., Rioux, P.-A., Herbst, S. K., Spiousas, I., Kübel, S. L., Gallego Hiroyasu, E. M., Runyun, S. L., Micillo, L., Thanopoulos, V., & Mendoza-Duran, E. (2022). The Blursday database as a resource to study subjective temporalities during COVID-19. *Nature Human Behaviour*, *6*(11), 1587-1599.
- Christensen : A practical guide to experience-sampling... - Google Scholar. (s. d.). Consulté 12 janvier 2024, à l'adresse [https://scholar.google.com/scholar\\_lookup?title=A%20practical%20guide%20to%20experience-sampling%20procedures&publication\\_year=2003&author=C.T.%20Conner&author=F.L.%20Barrett&author=E.%20Bliss-Moreau&author=K.%20Lebo&author=C.%20Kaschub](https://scholar.google.com/scholar_lookup?title=A%20practical%20guide%20to%20experience-sampling%20procedures&publication_year=2003&author=C.T.%20Conner&author=F.L.%20Barrett&author=E.%20Bliss-Moreau&author=K.%20Lebo&author=C.%20Kaschub)
- Colin, C., Hoonhorst, I., Markessis, E., Radeau, M., de Tourtchaninoff, M., Foucher, A., Collet, G., & Deltenre, P. (2009). Mismatch Negativity (MMN) evoked by sound duration contrasts : An unexpected major effect of deviance direction on amplitudes. *Clinical Neurophysiology*, *120*(1), 51-59. <https://doi.org/10.1016/j.clinph.2008.10.002>
- Creelman, C. D. (1962). Human discrimination of auditory duration. *The Journal of the Acoustical Society of America*, *34*(5), 582-593.
- Cummins, D. D. (2000). *Minds, Brains, and Computers : An Historical Introduction to the Foundations of Cognitive Science*. <https://philpapers.org/rec/CUMMBA-3>
- Davis, H., Mast, T., Yoshie, N., & Zerlin, S. (1966). The slow response of the human cortex to auditory stimuli : Recovery process. *Electroencephalography and Clinical Neurophysiology*, *21*(2), 105-113. [https://doi.org/10.1016/0013-4694\(66\)90118-0](https://doi.org/10.1016/0013-4694(66)90118-0)
- Deacon, D., Nousak, J. M., Pilotti, M., Ritter, W., & Yang, C.-M. (1998). Automatic change detection : Does the auditory system use representations of individual stimulus features or gestalts? *Psychophysiology*, *35*(4), 413-419. <https://doi.org/10.1111/1469-8986.3540413>
- Droit-Volet, S. (2013). Time perception, emotions and mood disorders. *Journal of Physiology-Paris*, *107*(4), Article 4. <https://doi.org/10.1016/j.jphysparis.2013.03.005>
- Droit-Volet, S. (2018). Intertwined Facets of Subjective Time. *Current Directions in Psychological Science*, *27*(6), 422-428. <https://doi.org/10.1177/0963721418779978>
- Droit-Volet, S., Monceau, S., Berthon, M., Trahanias, P., & Maniadakis, M. (2018). The explicit judgment of long durations of several minutes in everyday life : Conscious retrospective memory judgment and the role of affects? *PloS One*, *13*(4), e0195397. <https://doi.org/10.1371/journal.pone.0195397>
- Droit-Volet, S., Trahanias, P., & Maniadakis, M. (2017). Passage of time judgments in everyday life are not related to duration judgments except for long durations of several minutes. *Acta psychologica*, *173*, 116-121.
- Droit-Volet, S., & Wearden, J. (2003). Les modèles d'horloge interne en psychologie du temps. *L'année psychologique*, *103*(4), 617-654. <https://doi.org/10.3406/psy.2003.29656>
- Droit-Volet, S., & Wearden, J. (2016). Passage of Time Judgments Are Not Duration Judgments : Evidence from a Study Using Experience Sampling Methodology. *Frontiers in Psychology*, *7*, 176. <https://doi.org/10.3389/fpsyg.2016.00176>
- Droit-Volet, S., & Wearden, J. H. (2015). Experience Sampling Methodology reveals similarities in the experience of passage of time in young and elderly adults. *Acta Psychologica*, *156*, 77-82. <https://doi.org/10.1016/j.actpsy.2015.01.006>
- Duysens, J., Schaafsma, S. J., & Orban, G. A. (1996). Cortical off response tuning for stimulus duration. *Vision research*, *36*(20), 3243-3251.
- Eagleman, D. M. (2008). Human time perception and its illusions. *Current Opinion in Neurobiology*, *18*(2), Article 2. <https://doi.org/10.1016/j.conb.2008.06.002>

- Fallon, F. T., Ryan, T. J., Krakauer, J. W., & The Rppf Group. (2023). What are we talking about? Clarifying the fuzzy concept of representation in neuroscience and beyond. *The Transmitter*.  
<https://doi.org/10.53053/PFBH5329>
- Fechner, G. T. (1860). *Elemente der psychophysik* (Vol. 2). Breitkopf u. Härtel.  
[https://books.google.com/books?hl=fr&lr=&id=I5ui0NKWXYAC&oi=fnd&pg=PA1&dq=Gustav+Theodor+Fechner+\(1860\).+Elemente+der+Psychophysik+\(Elements+of+Psychophysics\).&ots=47MB0ezLPm&sig=HjhQm\\_a1li0mAGAWfsUE2gfPY5w](https://books.google.com/books?hl=fr&lr=&id=I5ui0NKWXYAC&oi=fnd&pg=PA1&dq=Gustav+Theodor+Fechner+(1860).+Elemente+der+Psychophysik+(Elements+of+Psychophysics).&ots=47MB0ezLPm&sig=HjhQm_a1li0mAGAWfsUE2gfPY5w)
- Fischer, C., Morlet, D., Bouchet, P., Luaute, J., Jourdan, C., & Salord, F. (1999). Mismatch negativity and late auditory evoked potentials in comatose patients. *Clinical neurophysiology*, *110*(9), 1601-1610.
- Fong, C. Y., Law, W. H. C., Uka, T., & Koike, S. (2020). Auditory Mismatch Negativity Under Predictive Coding Framework and Its Role in Psychotic Disorders. *Frontiers in Psychiatry*, *11*, 557932.  
<https://doi.org/10.3389/fpsyt.2020.557932>
- Ford, J. M., & Hillyard, S. A. (1981). Event-Related Potentials (ERPs) to Interruptions of a Steady Rhythm. *Psychophysiology*, *18*(3), 322-330. <https://doi.org/10.1111/j.1469-8986.1981.tb03043.x>
- Ford, J. M., Pfefferbaum, A., & Kopell, B. S. (1982). Event-Related Potentials to a Change of Pace in a Visual Sequence. *Psychophysiology*, *19*(2), Article 2. <https://doi.org/10.1111/j.1469-8986.1982.tb02541.x>
- Fraisse, P. (1984). Perception and Estimation of Time. *Annual Review of Psychology*, *35*(1), 1-37.  
<https://doi.org/10.1146/annurev.ps.35.020184.000245>
- Gallistel, C. R. (1990). *The organization of learning*. MIT Press.
- Gallistel, C. R. (2011). Mental Magnitudes. In *Space, Time and Number in the Brain* (p. 3-12). Elsevier.  
<https://doi.org/10.1016/B978-0-12-385948-8.00001-3>
- Garrido, M. I., Kilner, J. M., Stephan, K. E., & Friston, K. J. (2009). The mismatch negativity : A review of underlying mechanisms. *Clinical Neurophysiology*, *120*(3), Article 3.  
<https://doi.org/10.1016/j.clinph.2008.11.029>
- Gauthier, B., Pestke, K., & van Wassenhove, V. (2019). Building the arrow of time... over time : A sequence of brain activity mapping imagined events in time and space. *Cerebral Cortex*, *29*(10), 4398-4414.
- Gazzaniga, M. S., Ivry, R. B., & Mangun, G. R. (2006). *Cognitive Neuroscience. The biology of the mind*, (2014). Norton: New York. [http://aub.edu/fas/psychology/PublishingImages/Pages/Bachelor-of-Arts-in-Psychology/PSYC%20229%20Cognitive%20Neuroscience%20Fall%202018%20\(Besle\).pdf](http://aub.edu/fas/psychology/PublishingImages/Pages/Bachelor-of-Arts-in-Psychology/PSYC%20229%20Cognitive%20Neuroscience%20Fall%202018%20(Besle).pdf)
- Giard, M., Perrin, F., Pernier, J., & Bouchet, P. (1990). Brain Generators Implicated in the Processing of Auditory Stimulus Deviance : A Topographic Event-Related Potential Study. *Psychophysiology*, *27*(6), 627-640. <https://doi.org/10.1111/j.1469-8986.1990.tb03184.x>
- Gibbon, J. (1977). Scalar expectancy theory and Weber's law in animal timing. *Psychological review*, *84*(3), 279.
- Gibbon, J., Church, R. M., & Meck, W. H. (1984). Scalar timing in memory. *Annals of the New York Academy of sciences*, *423*(1), 52-77.
- Glasauer, S., & Shi, Z. (2021). The origin of Vierordt's law : The experimental protocol matters. *PsyCh Journal*, *10*(5), 732-741. <https://doi.org/10.1002/pchj.464>
- Grabot, L., Kayser, C., & van Wassenhove, V. (2021). Postdiction : When temporal regularity drives space perception through prestimulus alpha oscillations. *eneuro*, *8*(5).  
<https://www.eneuro.org/content/8/5/ENEURO.0030-21.2021.abstract>
- Gramfort, A. (2013). MEG and EEG data analysis with MNE-Python. *Frontiers in Neuroscience*, *7*.  
<https://doi.org/10.3389/fnins.2013.00267>
- Grimm, S., Roeber, U., Trujillo-Barreto, N. J., & Schröger, E. (2006). Mechanisms for detecting auditory temporal and spectral deviations operate over similar time windows but are divided differently between the two hemispheres. *NeuroImage*, *32*(1), 275-282.  
<https://doi.org/10.1016/j.neuroimage.2006.03.032>
- Grimm, S., Widmann, A., & Schröger, E. (2004). Differential processing of duration changes within short and long sounds in humans. *Neuroscience Letters*, *356*(2), 83-86.  
<https://doi.org/10.1016/j.neulet.2003.11.035>

- Grondin, S. (2010). Timing and time perception : A review of recent behavioral and neuroscience findings and theoretical directions. *Attention, Perception, & Psychophysics*, 72(3), Article 3. <https://doi.org/10.3758/APP.72.3.561>
- Grondin, S. (2012). Violation of the scalar property for time perception between 1 and 2 seconds : Evidence from interval discrimination, reproduction, and categorization. *Journal of Experimental Psychology: Human Perception and Performance*, 38(4), 880.
- Grondin, S. (2014). About the (Non)scalar Property for Time Perception. In H. Merchant & V. de Lafuente (Éds.), *Neurobiology of Interval Timing* (p. 17-32). Springer. [https://doi.org/10.1007/978-1-4939-1782-2\\_2](https://doi.org/10.1007/978-1-4939-1782-2_2)
- Grondin, S. (2017). Chronométrage et perception temporelle. *Canadian Journal of Experimental Psychology/Revue canadienne de psychologie expérimentale*, 71(4), Article 4. <https://doi.org/10.1037/cep0000137>
- Gu, C., & Bi, H.-Y. (2020). Auditory processing deficit in individuals with dyslexia : A meta-analysis of mismatch negativity. *Neuroscience and Biobehavioral Reviews*, 116, 396-405. <https://doi.org/10.1016/j.neubiorev.2020.06.032>
- Hari, R., Hämäläinen, M., Ilmoniemi, R., Kaukoranta, E., Reinikainen, K., Salminen, J., Alho, K., Näätänen, R., & Sams, M. (1984). Responses of the primary auditory cortex to pitch changes in a sequence of tone pips : Neuromagnetic recordings in man. *Neuroscience letters*, 50(1-3), 127-132.
- Hari, R., Joutsiniemi, S. L., Hämäläinen, M., & Vilkmann, V. (1989). Neuromagnetic responses of human auditory cortex to interruptions in a steady rhythm. *Neuroscience Letters*, 99(1-2), 164-168. [https://doi.org/10.1016/0304-3940\(89\)90283-8](https://doi.org/10.1016/0304-3940(89)90283-8)
- Hari, R., Pelizzone, M., Mäkelä, J. P., Hällström, J., & Leinonen, L. (1987). Neuromagnetic responses of the human auditory cortex to on-and offsets of noise bursts. *Audiology*, 26, 31-43.
- Hayashi, M. J., Ditye, T., Harada, T., Hashiguchi, M., Sadato, N., Carlson, S., Walsh, V., & Kanai, R. (2015). Time Adaptation Shows Duration Selectivity in the Human Parietal Cortex. *PLOS Biology*, 13(9), Article 9. <https://doi.org/10.1371/journal.pbio.1002262>
- Hayashi, M. J., & Ivry, R. B. (2020). Duration Selectivity in Right Parietal Cortex Reflects the Subjective Experience of Time. *The Journal of Neuroscience*, 40(40), 7749-7758. <https://doi.org/10.1523/JNEUROSCI.0078-20.2020>
- Herbst, S. K., Obleser, J., & van Wassenhove, V. (2022). Implicit Versus Explicit Timing—Separate or Shared Mechanisms? *Journal of Cognitive Neuroscience*, 34(8), 1447-1466.
- Hicks, R. E. (1992). Prospective and Retrospective Judgments of Time : A Neurobehavioral Analysis. In F. Macar, V. Pouthas, & W. J. Friedman (Éds.), *Time, Action and Cognition : Towards Bridging the Gap* (p. 97-108). Springer Netherlands. [https://doi.org/10.1007/978-94-017-3536-0\\_12](https://doi.org/10.1007/978-94-017-3536-0_12)
- Hippo, S. A. (Bishop of. (1841). *Les confessions de Saint Augustin*. Charpentier, Libraire-Éditeur.
- Holleman, G. A., Hooge, I. T. C., Kemner, C., & Hessels, R. S. (2020). The ‘Real-World Approach’ and Its Problems : A Critique of the Term Ecological Validity. *Frontiers in Psychology*, 11. <https://www.frontiersin.org/articles/10.3389/fpsyg.2020.00721>
- Hughes, H. C., Darcey, T. M., Barkan, H. I., Williamson, P. D., Roberts, D. W., & Aslin, C. H. (2001). Responses of Human Auditory Association Cortex to the Omission of an Expected Acoustic Event. *NeuroImage*, 13(6), 1073-1089. <https://doi.org/10.1006/nimg.2001.0766>
- Introducing Time – Icon Books*. (s. d.). Consulté 1 avril 2024, à l’adresse <https://www.iconbooks.com/ib-title/introducing-time-2/>
- Isenstein, E. L., Freedman, E. G., Xu, J., DeAndrea-Lazarus, I. A., & Foxe, J. J. (2024). Probing the Neurophysiology of Temporal Sensitivity in the Somatosensory System Using the Mismatch Negativity (MMN) Sensory Memory Paradigm. *Neuroscience*, 536, 47-56. <https://doi.org/10.1016/j.neuroscience.2023.11.013>
- Issa, J. B., Tocker, G., Hasselmo, M. E., Heys, J. G., & Dombeck, D. A. (2020). Navigating Through Time : A Spatial Navigation Perspective on How the Brain May Encode Time. *Annual Review of Neuroscience*, 43(1), 73-93. <https://doi.org/10.1146/annurev-neuro-101419-011117>
- Jääskeläinen, I. P., Ahveninen, J., Bonmassar, G., Dale, A. M., Ilmoniemi, R. J., Levänen, S., Lin, F.-H., May, P., Melcher, J., Stufflebeam, S., Tiitinen, H., & Belliveau, J. W. (2004). Human posterior auditory cortex

- gates novel sounds to consciousness. *Proceedings of the National Academy of Sciences*, *101*(17), 6809-6814. <https://doi.org/10.1073/pnas.0303760101>
- Jacobsen, T., & Schröger, E. (2003). Measuring duration mismatch negativity. *Clinical Neurophysiology*, *114*(6), Article 6. [https://doi.org/10.1016/S1388-2457\(03\)00043-9](https://doi.org/10.1016/S1388-2457(03)00043-9)
- James, W. (1886). The Perception of Time. *The Journal of Speculative Philosophy*, *20*(4), 374-407.
- Jaramillo, M., Alku, P., & Paavilainen, P. (1999). An event-related potential (ERP) study of duration changes in speech and non-speech sounds: *NeuroReport*, *10*(16), 3301-3305. <https://doi.org/10.1097/00001756-199911080-00010>
- Jaramillo, M., Paavilainen, P., & Näätänen, R. (2000). Mismatch negativity and behavioural discrimination in humans as a function of the magnitude of change in sound duration. *Neuroscience Letters*, *290*(2), Article 2. [https://doi.org/10.1016/S0304-3940\(00\)01344-6](https://doi.org/10.1016/S0304-3940(00)01344-6)
- Kanai, R., & Watanabe, M. (2006). Visual onset expands subjective time. *Perception & Psychophysics*, *68*(7), 1113-1123. <https://doi.org/10.3758/BF03193714>
- Kim, H. K., Blumberger, D. M., & Daskalakis, Z. J. (2020). Neurophysiological Biomarkers in Schizophrenia-P50, Mismatch Negativity, and TMS-EMG and TMS-EEG. *Frontiers in Psychiatry*, *11*, 795. <https://doi.org/10.3389/fpsyt.2020.00795>
- Knight, E. J., Oakes, L., Hyman, S. L., Freedman, E. G., & Foxe, J. J. (2020). Individuals With Autism Have No Detectable Deficit in Neural Markers of Prediction Error When Presented With Auditory Rhythms of Varied Temporal Complexity. *Autism Research*, *13*(12), 2058-2072. <https://doi.org/10.1002/aur.2362>
- Kononowicz, T. W., & van Wassenhove, V. (2019). Evaluation of Self-generated behavior : Untangling metacognitive readout and error detection. *Journal of cognitive neuroscience*, *31*(11), 1641-1657.
- Krakauer, J. W., Ghazanfar, A. A., Gomez-Marin, A., MacIver, M. A., & Poeppel, D. (2017). Neuroscience needs behavior : Correcting a reductionist bias. *Neuron*, *93*(3), 480-490.
- Krauel, K., Schott, P., Sojka, B., Pause, B. M., & Ferstl, R. (1999). Is there a mismatch negativity analogue in the olfactory event-related potential? *Journal of Psychophysiology*, *13*(1), 49-55. <https://doi.org/10.1027/0269-8803.13.1.49>
- Kujala, T., Kallio, J., Tervaniemi, M., & Näätänen, R. (2001). The mismatch negativity as an index of temporal processing in audition. *Clinical Neurophysiology*, *112*(9), Article 9. [https://doi.org/10.1016/S1388-2457\(01\)00625-3](https://doi.org/10.1016/S1388-2457(01)00625-3)
- Kujala, T., Tervaniemi, M., & Schröger, E. (2007). The mismatch negativity in cognitive and clinical neuroscience : Theoretical and methodological considerations. *Biological Psychology*, *74*(1), 1-19. <https://doi.org/10.1016/j.biopsycho.2006.06.001>
- Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package : Tests in linear mixed effects models. *Journal of statistical software*, *82*(13). <https://orbit.dtu.dk/en/publications/lmertest-package-tests-in-linear-mixed-effects-models>
- Lai, Y., Tian, Y., & Yao, D. (2011). MMN evidence for asymmetry in detection of IOI shortening and lengthening at behavioral indifference tempo. *Brain Research*, *1367*, 170-180. <https://doi.org/10.1016/j.brainres.2010.10.036>
- Lamprou-Kokolaki, M., Nédélec, Y., Lhuillier, S., & van Wassenhove, V. (2024). Distinctive features of experiential time : Duration, speed and event density. *Consciousness and Cognition*, *118*, 103635.
- Lenth, R., Singmann, H., Love, J., Buerkner, P., & Herve, M. (2021). Emmeans : Estimated marginal means, aka least-squares means. R Package Version 1 (2018). *Preprint at*.
- Leon, M. I., & Shadlen, M. N. (2003). Representation of Time by Neurons in the Posterior Parietal Cortex of the Macaque. *Neuron*, *38*(2), 317-327. [https://doi.org/10.1016/S0896-6273\(03\)00185-5](https://doi.org/10.1016/S0896-6273(03)00185-5)
- Li, H., Wang, J., Liu, G., Xu, J., Huang, W., Song, C., Wang, D., Tao, H. W., Zhang, L. I., & Liang, F. (2021). Phasic Off responses of auditory cortex underlie perception of sound duration. *Cell Reports*, *35*(3), 109003. <https://doi.org/10.1016/j.celrep.2021.109003>
- Loveless, N., Levänen, S., Jousmäki, V., Sams, M., & Hari, R. (1996). Temporal integration in auditory sensory memory : Neuromagnetic evidence. *Electroencephalography and Clinical Neurophysiology/Evoked Potentials Section*, *100*(3), 220-228. [https://doi.org/10.1016/0168-5597\(95\)00271-5](https://doi.org/10.1016/0168-5597(95)00271-5)
- Luck, S. J. (2014). *An Introduction to the Event-Related Potential Technique, second edition*. MIT Press.



- Lüdecke, D., Ben-Shachar, M. S., Patil, I., Waggoner, P., & Makowski, D. (2021). performance : An R package for assessment, comparison and testing of statistical models. *Journal of Open Source Software*, 6(60). [https://pure.mpg.de/rest/items/item\\_3316363/component/file\\_3316364/content](https://pure.mpg.de/rest/items/item_3316363/component/file_3316364/content)
- Lumaca, M., Trusbak Haumann, N., Brattico, E., Grube, M., & Vuust, P. (2019). Weighting of neural prediction error by rhythmic complexity : A predictive coding account using mismatch negativity. *European Journal of Neuroscience*, 49(12), 1597-1609. <https://doi.org/10.1111/ejn.14329>
- Macar, F., & Vidal, F. (2004). Event-Related Potentials as Indices of Time Processing : A Review. *Journal of Psychophysiology*, 18(2/3), Article 2/3. <https://doi.org/10.1027/0269-8803.18.23.89>
- Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG- and MEG-data. *Journal of Neuroscience Methods*, 164(1), 177-190. <https://doi.org/10.1016/j.jneumeth.2007.03.024>
- Marr, D. (2010). *Vision : A Computational Investigation into the Human Representation and Processing of Visual Information*. The MIT Press. <https://doi.org/10.7551/mitpress/9780262514620.001.0001>
- Martin, B., Wiener, M., & Van Wassenhove, V. (2017). A Bayesian Perspective on Accumulation in the Magnitude System. *Scientific Reports*, 7(1), 630. <https://doi.org/10.1038/s41598-017-00680-0>
- Martinelli, N., & Droit-Volet, S. (2022a). Judgment of duration and passage of time in prospective and retrospective conditions and its predictors for short and long durations. *Scientific Reports*, 12(1), 22241. <https://doi.org/10.1038/s41598-022-25913-9>
- Martinelli, N., & Droit-Volet, S. (2022b). What factors underlie our experience of the passage of time? Theoretical consequences. *Psychological Research*, 86(2), 522-530. <https://doi.org/10.1007/s00426-021-01486-6>
- Mate, J., Pires, A. C., Campoy, G., & Estaún, S. (2009). Estimating the duration of visual stimuli in motion environments. *Psicológica*, 30(2), 287-300.
- Matthews, W. J., & Meck, W. H. (2016). Temporal cognition : Connecting subjective time to perception, attention, and memory. *Psychological Bulletin*, 142(8), 865-907. <https://doi.org/10.1037/bul0000045>
- Michon, J. A. (1998). On the modularity of time. *Teorie e Modelli*, 3, 7-32.
- Myers, G. E. (1971). William James on Time Perception. *Philosophy of Science*, 38(3), 353-360. <https://doi.org/10.1086/288376>
- Näätänen, R. (1990). The role of attention in auditory information processing as revealed by event-related potentials and other brain measures of cognitive function. *Behavioral and Brain Sciences*, 13(2), 201-233. <https://doi.org/10.1017/S0140525X00078407>
- Näätänen, R., Astikainen, P., Ruusuvirta, T., & Huotilainen, M. (2010). Automatic auditory intelligence : An expression of the sensory-cognitive core of cognitive processes. *Brain Research Reviews*, 64(1), Article 1. <https://doi.org/10.1016/j.brainresrev.2010.03.001>
- Näätänen, R., Gaillard, A. W. K., & Mäntysalo, S. (1978). Early selective-attention effect on evoked potential reinterpreted. *Acta Psychologica*, 42(4), 313-329. [https://doi.org/10.1016/0001-6918\(78\)90006-9](https://doi.org/10.1016/0001-6918(78)90006-9)
- Näätänen, R., Jiang, D., Lavikainen, J., Reinikainen, K., & Paavilainen, P. (1993). Event-related potentials reveal a memory trace for temporal features. *Neuroreport: An International Journal for the Rapid Communication of Research in Neuroscience*, 5, 310-312. <https://doi.org/10.1097/00001756-199312000-00033>
- Näätänen, R., Kujala, T., Escera, C., Baldeweg, T., Kreegipuu, K., Carlson, S., & Ponton, C. (2012). The mismatch negativity (MMN) – A unique window to disturbed central auditory processing in ageing and different clinical conditions. *Clinical Neurophysiology*, 123(3), Article 3. <https://doi.org/10.1016/j.clinph.2011.09.020>
- Näätänen, R., Paavilainen, P., & Reinikainen, K. (1989). Do event-related potentials to infrequent decrements in duration of auditory stimuli demonstrate a memory trace in man? *Neuroscience Letters*, 107(1-3), 347-352. [https://doi.org/10.1016/0304-3940\(89\)90844-6](https://doi.org/10.1016/0304-3940(89)90844-6)
- Näätänen, R., Paavilainen, P., Titinen, H., Jiang, D., & Alho, K. (1993). Attention and mismatch negativity. *Psychophysiology*, 30(5), 436-450. <https://doi.org/10.1111/j.1469-8986.1993.tb02067.x>
- Näätänen, R., & Picton, T. W. (1986). N2 and automatic versus controlled processes. *Electroencephalography & Clinical Neurophysiology Supplement*, 38, 169-186.

- Naatanen, R., Syssoeva, O., & Takegata, R. (2004). Automatic time perception in the human brain for intervals ranging from milliseconds to seconds. *Psychophysiology*, *41*(4), 660-663. <https://doi.org/10.1111/j.1469-8986.2004.00182.x>
- Näätänen, R., Syssoeva, O., & Takegata, R. (2004). Automatic time perception in the human brain for intervals ranging from milliseconds to seconds. *Psychophysiology*, *41*(4), 660-663. <https://doi.org/10.1111/j.1469-8986.2004.00182.x>
- Näätänen, R., & Winkler, I. (1999). The concept of auditory stimulus representation in cognitive neuroscience. *Psychological bulletin*, *125*(6), 826.
- Ng, K. K., & Penney, T. B. (2014). Probing Interval Timing with Scalp-Recorded Electroencephalography (EEG). In H. Merchant & V. de Lafuente (Éds.), *Neurobiology of Interval Timing* (Vol. 829, p. 187-207). Springer New York. [https://doi.org/10.1007/978-1-4939-1782-2\\_11](https://doi.org/10.1007/978-1-4939-1782-2_11)
- Nicolaï, C., Chaumon, M., & van Wassenhove, V. (2024). Cognitive effects on experienced duration and speed of time, prospectively, retrospectively, in and out of lockdown. *Scientific Reports*, *14*(1), 2006.
- Nieder, A., Diester, I., & Tudusciuc, O. (2006). *Temporal and Spatial Enumeration Processes in the Primate Parietal Cortex*. 313.
- Nobre, A. C., & van Ede, F. (2018). Anticipated moments : Temporal structure in attention. *Nature Reviews Neuroscience*, *19*(1), 34-48. <https://doi.org/10.1038/nrn.2017.141>
- Nobre, A. C., & van Ede, F. (2023). Attention in flux. *Neuron*, *111*(7), 971-986.
- Nordby, H., Roth, W. T., & Pfefferbaum, A. (1988a). Event-related potentials to breaks in sequences of alternating pitches or interstimulus intervals. *Psychophysiology*, *25*(3), 262-268.
- Nordby, H., Roth, W. T., & Pfefferbaum, A. (1988b). Event-related potentials to time-deviant and pitch-deviant tones. *Psychophysiology*, *25*(3), 249-261.
- Núñez, R., Allen, M., Gao, R., Miller Rigoli, C., Relaford-Doyle, J., & Semenuks, A. (2019). What happened to cognitive science? *Nature Human Behaviour*, *3*(8), Article 8. <https://doi.org/10.1038/s41562-019-0626-2>
- Ofir, N., & Landau, A. N. (2022). Neural signatures of evidence accumulation in temporal decisions. *Current Biology*. <https://doi.org/10.1016/j.cub.2022.08.006>
- Öztel, T., Eskenazi, T., & Balci, F. (2021). Temporal error monitoring with directional error magnitude judgements : A robust phenomenon with no effect of being watched. *Psychological Research*, *85*(5), 2069-2078. <https://doi.org/10.1007/s00426-020-01379-0>
- Paavilainen, P., Karlsson, M.-L., Reinikainen, K., & Näätänen, R. (1989). Mismatch negativity to change in spatial location of an auditory stimulus. *Electroencephalography and Clinical Neurophysiology*, *73*(2), 129-141. [https://doi.org/10.1016/0013-4694\(89\)90192-2](https://doi.org/10.1016/0013-4694(89)90192-2)
- Pariyadath, V., & Eagleman, D. (2007). The Effect of Predictability on Subjective Duration. *PLOS ONE*, *2*(11), e1264. <https://doi.org/10.1371/journal.pone.0001264>
- Pazo-Alvarez, P., Cadaveira, F., & Amenedo, E. (2003). MMN in the visual modality : A review. *Biological Psychology*, *63*(3), 199-236. [https://doi.org/10.1016/S0301-0511\(03\)00049-8](https://doi.org/10.1016/S0301-0511(03)00049-8)
- Peter, V., McArthur, G., & Thompson, W. F. (2010). Effect of deviance direction and calculation method on duration and frequency mismatch negativity (MMN). *Neuroscience Letters*, *482*(1), 71-75. <https://doi.org/10.1016/j.neulet.2010.07.010>
- Petzschner, F. H., Glasauer, S., & Stephan, K. E. (2015). A Bayesian perspective on magnitude estimation. *Trends in cognitive sciences*, *19*(5), 285-293.
- Poeppel, D. (2003). The analysis of speech in different temporal integration windows : Cerebral lateralization as 'asymmetric sampling in time'. *Speech Communication*, *41*(1), 245-255. [https://doi.org/10.1016/S0167-6393\(02\)00107-3](https://doi.org/10.1016/S0167-6393(02)00107-3)
- Polti, I. (2018). The effect of attention and working memory on the estimation of elapsed time. *Scientific REPOrts*, 11.
- Polti, I., Martin, B., & van Wassenhove, V. (2018). The effect of attention and working memory on the estimation of elapsed time. *Scientific Reports*, *8*(1), Article 1. <https://doi.org/10.1038/s41598-018-25119-y>

- Posit team (2023). *RStudio : Integrated Development Environment for R*. Posit Software, PBC, Boston, MA. URL <http://www.posit.co/>. (s. d.).
- Protopapa, F., Hayashi, M. J., Kulashekhar, S., Van Der Zwaag, W., Battistella, G., Murray, M. M., Kanai, R., & Buetti, D. (2019). Chronotopic maps in human supplementary motor area. *PLoS Biology*, *17*(3), e3000026. <https://doi.org/10.1371/journal.pbio.3000026>
- Qin, L., Liu, Y., Wang, J., Li, S., & Sato, Y. (2009). Neural and Behavioral Discrimination of Sound Duration by Cats. *The Journal of Neuroscience*, *29*(50), 15650-15659. <https://doi.org/10.1523/JNEUROSCI.2442-09.2009>
- Rammsayer, T. H., & Lima, S. D. (1991). Duration discrimination of filled and empty auditory intervals : Cognitive and perceptual factors. *Perception & Psychophysics*, *50*(6), Article 6. <https://doi.org/10.3758/BF03207541>
- Reinartz, S., Fassihi, A., Ravera, M., Paz, L., Pulecchi, F., Gigante, M., & Diamond, M. E. (2024). Direct contribution of the sensory cortex to the judgment of stimulus duration. *Nature Communications*, *15*(1), 1712. <https://doi.org/10.1038/s41467-024-45970-0>
- Richmond, L. L., & Zacks, J. M. (2017). Constructing Experience : Event Models from Perception to Action. *Trends in Cognitive Sciences*, *21*(12), 962-980. <https://doi.org/10.1016/j.tics.2017.08.005>
- Rosburg, T., Trautner, P., Dietl, T., Korzyukov, O. A., Boutros, N. N., Schaller, C., Elger, C. E., & Kurthen, M. (2005). Subdural recordings of the mismatch negativity (MMN) in patients with focal epilepsy. *Brain*, *128*(4), 819-828. <https://doi.org/10.1093/brain/awh442>
- Roy, M. M., & Christenfeld, N. J. S. (2008). Effect of task length on remembered and predicted duration. *Psychonomic Bulletin & Review*, *15*(1), 202-207. <https://doi.org/10.3758/PBR.15.1.202>
- Sable, J. J., Gratton, G., & Fabiani, M. (2003). Sound presentation rate is represented logarithmically in human cortex : Sound rate representation in human cortex. *European Journal of Neuroscience*, *17*(11), 2492-2496. <https://doi.org/10.1046/j.1460-9568.2003.02690.x>
- Sackett, A. M., Meyvis, T., Nelson, L. D., Converse, B. A., & Sackett, A. L. (2010). You're Having Fun When Time Flies : The Hedonic Consequences of Subjective Time Progression. *Psychological Science*, *21*(1), Article 1. <https://doi.org/10.1177/0956797609354832>
- Salisbury, D. F. (2012). Finding the missing stimulus mismatch negativity (MMN) : Emitted MMN to violations of an auditory gestalt. *Psychophysiology*, *49*(4), 544-548. <https://doi.org/10.1111/j.1469-8986.2011.01336.x>
- Sams, M., Paavilainen, P., Alho, K., & Näätänen, R. (1985). Auditory frequency discrimination and event-related potentials. *Electroencephalography and Clinical Neurophysiology/Evoked Potentials Section*, *62*(6), 437-448.
- Schmerler, J. (1976). The Visual Perception of Accelerated Motion. *Perception*, *5*(2), 167-185. <https://doi.org/10.1068/p050167>
- Schröger, E. (1998a). Measurement and interpretation of the mismatch negativity. *Behavior Research Methods, Instruments, & Computers*, *30*(1), 131-145. <https://doi.org/10.3758/BF03209423>
- Schröger, E. (1998b). Measurement and interpretation of the mismatch negativity. *Behavior Research Methods, Instruments, & Computers*, *30*(1), Article 1. <https://doi.org/10.3758/BF03209423>
- Shin, Y. S., & DuBrow, S. (2021). Structuring Memory Through Inference-Based Event Segmentation. *Topics in Cognitive Science*, *13*(1), 106-127. <https://doi.org/10.1111/tops.12505>
- Spackman, L. A., Towell, A., & Boyd, S. G. (2010). Somatosensory discrimination : An intracranial event-related potential study of children with refractory epilepsy. *Brain research*, *1310*, 68-76.
- Sysoeva, O., Takegata, R., & Näätänen, R. (2006). Pre-attentive representation of sound duration in the human brain. *Psychophysiology*, *43*(3), 272-276. <https://doi.org/10.1111/j.1469-8986.2006.00397.x>
- Takegata, R., Tervaniemi, M., Alku, P., Ylinen, S., & Näätänen, R. (2008). Parameter-specific modulation of the mismatch negativity to duration decrement and increment : Evidence for asymmetric processes. *Clinical Neurophysiology*, *119*(7), Article 7. <https://doi.org/10.1016/j.clinph.2008.03.025>
- Tallot, L., & Doyère, V. (2020). Neural encoding of time in the animal brain. *Neuroscience & Biobehavioral Reviews*, *115*, 146-163. <https://doi.org/10.1016/j.neubiorev.2019.12.033>

- Tanaka, R., & Yotsumoto, Y. (2017). Passage of Time Judgments Is Relative to Temporal Expectation. *Frontiers in Psychology, 8*. <https://doi.org/10.3389/fpsyg.2017.00187>
- Tervaniemi, M., Saarinen, J., Paavilainen, P., Danilova, N., & Näätänen, R. (1994). Temporal integration of auditory information in sensory memory as reflected by the mismatch negativity. *Biological Psychology, 38*(2-3), 157-167. [https://doi.org/10.1016/0301-0511\(94\)90036-1](https://doi.org/10.1016/0301-0511(94)90036-1)
- Thibault, N., Albouy, P., & Grondin, S. (2023). Distinct brain dynamics and networks for processing short and long auditory time intervals. *Scientific Reports, 13*(1), 22018. <https://doi.org/10.1038/s41598-023-49562-8>
- Thönes, S., & Oberfeld, D. (2015). Time perception in depression : A meta-analysis. *Journal of affective disorders, 175*, 359-372.
- TimeWorld Temps – Rencontres scientifiques mondiales.* (s. d.). Consulté 12 mars 2024, à l'adresse <https://timeworldevent.com/1/>
- Tobin, S., Bisson, N., & Grondin, S. (2010). An Ecological Approach to Prospective and Retrospective Timing of Long Durations : A Study Involving Gamers. *PLoS ONE, 5*(2), Article 2. <https://doi.org/10.1371/journal.pone.0009271>
- Todd, J., Michie, P. T., Budd, T. W., Rock, D., & Jablensky, A. V. (2000). Auditory sensory memory in schizophrenia : Inadequate trace formation? *Psychiatry Research, 96*(2), 99-115. [https://doi.org/10.1016/S0165-1781\(00\)00205-5](https://doi.org/10.1016/S0165-1781(00)00205-5)
- Toso, A., Fassihi, A., Paz, L., Pulecchi, F., & Diamond, M. E. (2021). A sensory integration account for time perception. *PLoS Computational Biology, 17*(1), e1008668.
- Toso, A., Reinartz, S., Pulecchi, F., & Diamond, M. E. (2021). Time coding in rat dorsolateral striatum. *Neuron, 109*(22), 3663-3673.
- Treisman, M. (1963). Temporal discrimination and the indifference interval : Implications for a model of the « internal clock ». *Psychological Monographs: General and Applied, 77*(13), Article 13. <https://doi.org/10.1037/h0093864>
- Tsao, A., Yousefzadeh, S. A., Meck, W. H., Moser, M.-B., & Moser, E. I. (2022). The neural bases for timing of durations. *Nature Reviews Neuroscience, 23*(11), 646-665. <https://doi.org/10.1038/s41583-022-00623-3>
- Tseng, Y.-J., Nouchi, R., & Cheng, C.-H. (2021). Mismatch negativity in patients with major depressive disorder : A meta-analysis. *Clinical Neurophysiology: Official Journal of the International Federation of Clinical Neurophysiology, 132*(10), 2654-2665. <https://doi.org/10.1016/j.clinph.2021.06.019>
- Vallet, W., & van Wassenhove, V. (2023). Can cognitive neuroscience solve the lab-dilemma by going wild? *Neuroscience & Biobehavioral Reviews, 155*, 105463. <https://doi.org/10.1016/j.neubiorev.2023.105463>
- van Wassenhove, V. (2023). *COGNITIVE NEUROSCIENCE OF TIME : NOWS, TIMELINES, AND CHRONOLOGIES* (p. 97-129). [https://doi.org/10.1142/9781800613751\\_0005](https://doi.org/10.1142/9781800613751_0005)
- van Wassenhove, V., Buonomano, D. V., Shimojo, S., & Shams, L. (2008). Distortions of Subjective Time Perception Within and Across Senses. *PLoS ONE, 3*(1), e1437. <https://doi.org/10.1371/journal.pone.0001437>
- van Rijn, H. (2014). It's time to take the psychology of biological time into account : Speed of driving affects a trip's subjective duration. In *Frontiers in Psychology* (Vol. 5, p. 1028). Frontiers Media SA. <https://www.frontiersin.org/articles/10.3389/fpsyg.2014.01028/full>
- van Wassenhove, V. (2009). Minding time in an amodal representational space. *Philosophical Transactions of the Royal Society B: Biological Sciences, 364*(1525), 1815-1830. <https://doi.org/10.1098/rstb.2009.0023>
- van Wassenhove, V. (2017). Time consciousness in a computational mind/brain. *Journal of Consciousness Studies, 24*(3-4), 177-202.
- van Wassenhove, V. (2023). Cracking the neural code of how the brain represents time may make the dualistic stance obsolete. *Timing & Time Perception, 1*(aop), 1-9.
- van Wassenhove, V., Grant, K. W., & Poeppel, D. (2007). Temporal window of integration in auditory-visual speech perception. *Neuropsychologia, 45*(3), Article 3. <https://doi.org/10.1016/j.neuropsychologia.2006.01.001>

- van Wassenhove, V., Herbst, S. K., & Kononowicz, T. W. (2019). Timing the Brain to Time the Mind : Critical Contributions of Time-Resolved Neuroimaging for Temporal Cognition. In S. Supek & C. J. Aine (Éds.), *Magnetoencephalography* (p. 1-50). Springer International Publishing.  
[https://doi.org/10.1007/978-3-319-62657-4\\_67-1](https://doi.org/10.1007/978-3-319-62657-4_67-1)
- van Wassenhove, V., & Lecoutre, L. (2015). Duration estimation entails predicting when. *Neuroimage*, *106*, 272-283.
- Verde, L. L., Alais, D., Burr, D. C., Morrone, M. C., MacDougall, H., & Verstraten, F. A. J. (2019). Time dilation effect in an active observer and virtual environment requires apparent motion : No dilation for retinal- or world-motion alone. *Journal of Vision*, *19*(3), 4. <https://doi.org/10.1167/19.3.4>
- Wacongne, C., Changeux, J.-P., & Dehaene, S. (2012). A neuronal model of predictive coding accounting for the mismatch negativity. *Journal of Neuroscience*, *32*(11), 3665-3678.
- Walsh, V. (2003). A theory of magnitude : Common cortical metrics of time, space and quantity. *Trends in Cognitive Sciences*, *7*(11), 483-488. <https://doi.org/10.1016/j.tics.2003.09.002>
- Wearden, J. H. (2005). The wrong tree : Time perception and time experience in the elderly. *Measuring the mind: Speed, age, and control*, 137-158.
- Wearden, J. H. (2008). Slowing down an Internal Clock : Implications for Accounts of Performance on four Timing Tasks. *Quarterly Journal of Experimental Psychology*, *61*(2), Article 2.  
<https://doi.org/10.1080/17470210601154610>
- Wearden, J. H. (2015). Passage of time judgements. *Consciousness and Cognition*, *38*, 165-171.  
<https://doi.org/10.1016/j.concog.2015.06.005>
- Wickens, A. P. (2014). *A history of the brain : From stone age surgery to modern neuroscience*. Psychology Press.  
[https://books.google.fr/books?hl=fr&lr=&id=gSKcBQAAQBAJ&oi=fnd&pg=PP1&dq=history+of+the+brain+from+stone+age+to+modern+neuroscience&ots=YyH9-6sTWE&sig=9ldMXmW0JGfVs\\_R9SksYG826owo](https://books.google.fr/books?hl=fr&lr=&id=gSKcBQAAQBAJ&oi=fnd&pg=PP1&dq=history+of+the+brain+from+stone+age+to+modern+neuroscience&ots=YyH9-6sTWE&sig=9ldMXmW0JGfVs_R9SksYG826owo)
- Winkler, I. (2007). Interpreting the Mismatch Negativity. *Journal of Psychophysiology*, *21*(3-4), 147-163.  
<https://doi.org/10.1027/0269-8803.21.34.147>
- Woodrow, H. (1934). The temporal indifference interval determined by the method of mean error. *Journal of Experimental Psychology*, *17*(2), 167.
- Wyrick, R. A., & Wyrick, L. C. (1977). Time experience during depression. *Archives of General Psychiatry*, *34*(12), 1441-1443.
- Yabe, H., Tervaniemi, M., Reinikainen, K., & Näätänen, R. (1997). Temporal window of integration revealed by MMN to sound omission. *Neuroreport*, *8*(8), 1971-1974.
- Yabe, H., Tervaniemi, M., Sinkkonen, J., Huutilainen, M., Ilmoniemi, R. J., & Näätänen, R. (1998). Temporal window of integration of auditory information in the human brain. *Psychophysiology*, *35*(5), 615-619. <https://doi.org/10.1017/S0048577298000183>
- Yallak, E., & Balci, F. (2022). Metric error monitoring for a cleaner record of timing. *Journal of Experimental Psychology: Human Perception and Performance*, *48*(10), 1130.
- Yarmey, A. D. (2000). Retrospective duration estimations for variant and invariant events in field situations. *Applied Cognitive Psychology*, *14*(1), 45-57. [https://doi.org/10.1002/\(SICI\)1099-0720\(200001\)14:1<45::AID-ACP623>3.0.CO;2-U](https://doi.org/10.1002/(SICI)1099-0720(200001)14:1<45::AID-ACP623>3.0.CO;2-U)
- Zacks, J. M., & Tversky, B. (2001). Event structure in perception and conception. *Psychological Bulletin*, *127*(1), 3-21. <https://doi.org/10.1037/0033-2909.127.1.3>
- Zakay, D., & Block, R. A. (1996). The role of attention in time estimation processes. In M. A. Pastor & J. Artieda (Éds.), *Advances in Psychology* (Vol. 115, p. 143-164). North-Holland.  
[https://doi.org/10.1016/S0166-4115\(96\)80057-4](https://doi.org/10.1016/S0166-4115(96)80057-4)

## Glossary

**Attention:** The cognitive process of selectively prioritizing one aspect of the environment while ignoring others.

**Coding:** Process of representing an information, by the use of symbols. For the brain, coding an information can be achieved with functioning isomorphism, i.e. a code that reflect the entities but also the relationship between the entities.

**Conscious processing:** Mental activities that are within the awareness and control of the individual.

**Deviant (DEV):** Stimulus that is rarely presented in an oddball paradigm, compared to a standard, overly presented

**Ecological (factors/environment):** Adjective to qualify factors/environment that are close to our natural behavior. I use it to contrast with the artificial laboratory setting.

**EEG:** Electroencephalography. An electrophysiological method to measure brain surface potentials generated from the summation of post-synaptic potentials of cortical pyramidal neurons.

**Encoding:** Process of transducing external information in neuronal pattern. An information can be encoded, because sensory signals have reached the brain, but not coded, and therefore represented.

**Empty time interval:** Time interval delimited by two sensory signals.

**ERP:** Event-Related Potential. Electrical brain responses recorded in EEG that are time-locked to the presentation of a stimulus or an event.

**Feature:** The distinctive attribute of an object, event, or phenomenon.

**Filled time interval:** Time interval delimited by a sustained sensory signal.

**Functioning isomorphism:** Process that maps entities, relations, and operations between two systems, the represented and the representing.

**ISI:** Inter-Stimulus Interval. Time interval between the offset of one stimulus and the onset of the next stimulus.

**ITI:** Inter-Trial Interval. Time interval between the end of one trial and the beginning of the next trial. I use it in my Chapter 2 to emphasize that my stimuli are empty time intervals (constituting one trial) and avoid the confusion with ISI (that could describe the empty time intervals tested).

**Mental activity/process:** Any activity of the mind, including perception, cognition, emotion, memory, reasoning, decision making etc.

**Mind:** Set of mental processes that can be described by representations and operations, enabling the cognitive functions such as perception, attention, emotion, memory, reasoning, decision making.

**Mind-brain:** The interdependence between the mind (mental processes) and the brain (neurobiological processes). I use it in my introduction because I believe that one cannot be studied and understood without the other.

**MMN:** An ERP potential that occurs when a deviant stimulus is presented among a sequence of standard stimuli, indicating the brain's detection of a change in the environment.

**Objective time:** Time as measured by external, physical clocks.

**Oddball paradigm:** Experimental paradigm in psychology and neuroscience to study the detection of a rare or unexpected stimulus within a sequence of more frequent stimuli.

**Perception:** Process of constructing a percept. It starts with the transduction of external information from the world to pattern of neuronal activity through sensory organs and receptors. It ends with the resulting mental representation of this external information (that can be accurate or not), called a percept.

**Psyche:** Philosophical concept that correspond to conscious and unconscious processes, thoughts, feelings, and motivations of an individual.

**Psychophysics:** The scientific study of the relationship between physical stimuli and the sensations and perceptions they evoke.

**Representation:** Entity that arise from a functioning isomorphism.

**Scalar variability:** Scalar distributions, where the standard deviation increases linearly with the mean. It is often found in psychophysics studies (Weber-Fechner's law).

**Soul:** The spiritual or immaterial essence of a person, representing their identity, consciousness, and inner being, often associated with religious or philosophical beliefs.

**Spiritual substance:** A metaphysical concept referring to the essence or nature of a spiritual entity or reality.

**Standard (STD):** Stimulus that is overly presented in an oddball paradigm, compared to a deviant, that is rarely presented.

**Supra-temporal cues:** Cues that provide additional temporal information from duration, such as isochronous rhythm or constant sequences.

**Target:** A stimulus to which participants are required to respond in a specific way.

**Time interval:** The quantity of time of an event or between two events

**TWI (Temporal Window of Integration):** The period of time over which sensory information is integrated or combined to form a coherent percept.

**Wild:** I use this term to name the approach of conducting experiments outside the laboratory, in environment of our daily life such as a train journey

## Chapter 5 – Annex

### 5.1. Pilot recordings: Quick investigation of the empty interval MMN

In this first annex, you will find the preliminary data that led me to conduct a full MMN study in the laboratory (Annex 5.2). Originally, I wanted to rapidly investigate the pattern of the MMN amplitude as a function of duration deviance before using the duration MMN as a marker for implicit duration perception. Unexpectedly for myself at that time, I observed a signed pattern suggesting that the MMN amplitude was following the objective duration, irrespective of the deviant/standard relationship. With the benefit of hindsight, this result is easily explained by the refractoriness effect that I described in the Chapter 2.

#### 5.1.1. Introduction

The aim of these pilot recordings was to obtain a Mismatch Negativity (MMN) elicited by infrequent changes in duration to test, later on, whether the implicit index of duration discrimination, reflected by the MMN, would be impacted by acceleration/deceleration phases of a train journey. **We were particularly interested in the effect of deviance direction on the amplitude of the Mismatch Negativity amplitude**, as conflicting and unclear results can be found in the literature. While no effect of deviance direction was found when several deviants were tested in the same block (Jaramillo et al., 2000), a lower amplitude was found for longer deviant than for shorter ones and this difference tended to increase when the standard duration magnitude increased (Colin et al., 2009). Interestingly, it was poorly investigated on empty durations, which are usually preferred in the time perception domain to rule out possible confounding factors arising from the integration of other sensory properties over time (such as sound intensity). To test the effect of deviance direction on MMN amplitude elicited by infrequent changes of empty duration, **we developed an oddball paradigm with infrequent changes in empty durations that could be either shorter or longer than a standard duration.**



## 5.1.2. Materials & Methods

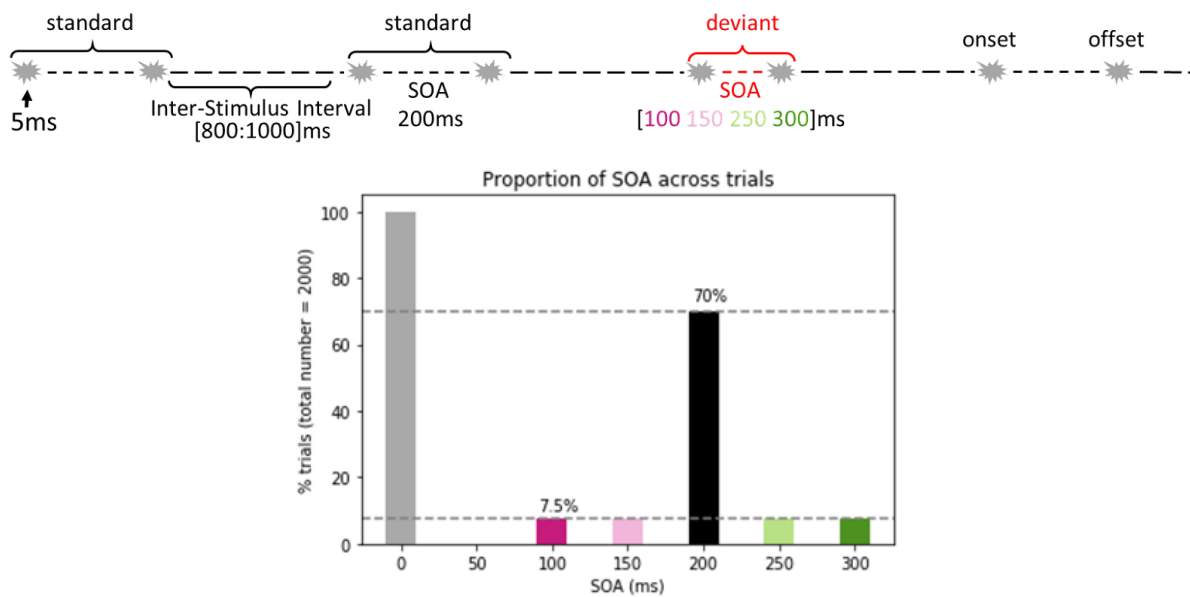
### 5.1.2.1. Participants

Six right-handed volunteers (2 women, mean age = 26,5 years) were recruited *in neurospin corridors* and received *no* monetary compensation for their participation. All declared normal/corrected visual/auditory functions and absence of neurological pathology. Before participating, each participant signed an informed consent validated by the Ethics Committee on Human Research at Neurospin (Gif-sur-Yvette): CPP n° 100049 (Gif-sur-Yvette, France) and the Declaration of Helsinki (2013).

### 5.1.2.2. Stimuli & Procedure

Participants were comfortably seated, 60cm away from the computer screen in a soundproof experimental booth. The experiment consisted of passive listening of an auditory oddball paradigm. To distract participants' attention, they were instructed to watch a silent movie and instructed to ignore sounds. In an oddball paradigm, a stream of standard stimuli is presented to the participant, interspaced by infrequent deviant stimuli.

Stimuli were empty durations characterized by a Stimulus Onset Asynchrony (SOA) delimited between two 5ms white noise bursts with 2,5ms rise and fall ramping intensity, the sound intensity was adjusted individually between 20 to 30 volume levels so that white noises burst were clearly audible but not disturbing. The manipulation in this experiment relied on changes in the length of SOAs. Standard SOAs were set to 200ms. There were 4 types of deviants, two shorter and two longer SOAs, each deviating from 25 and 50% of the standard SOA in one direction or the other (shorter/longer). Shorter deviants SOAs were 100ms (-50%) and 150ms (-25%). Longer SOAs were 250ms (+25%) and 300ms (+50%). SOAs were separated by a random Inter-Stimulus Interval (ISI) ranging from 400 to 600ms. There were at least two standards between each deviant. Standard SOAs represented 70% of the total number of stimuli (2000), and the proportion of each deviant was 7,5% (150 each). The experiment was performed in one single block, lasting 24 min. The task was coded and run on Matlab 2019a, on a Dell Latitude E6530 portable computer.



**Fig. 5.1.1: Experimental design and stimuli.** Standard stimuli were empty time interval of 200 ms delimited by two auditory clicks. Deviants could be shorter (100, 150 ms) or longer (250, 300 ms). Standards were presented with a probability of .7 and each deviants with a probability of .075.

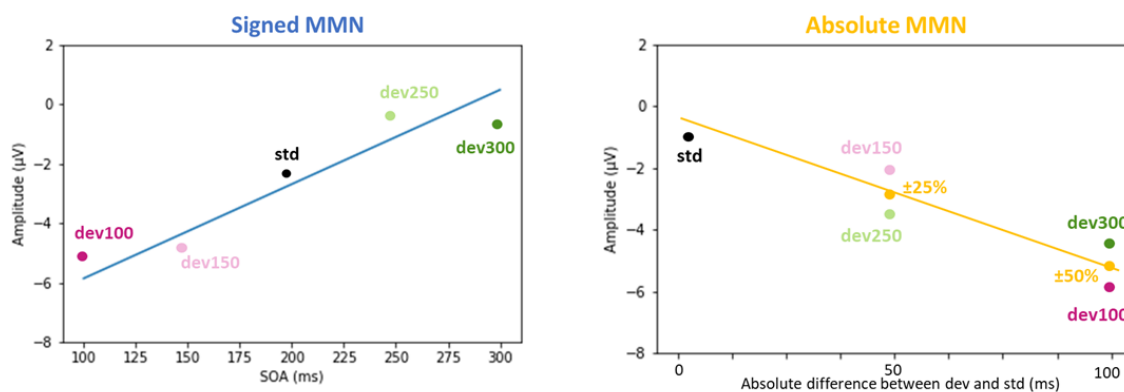
### 5.1.2.3. EEG recordings and Preprocessing

EEG recordings were performed with a high density 64 channel waveguard cap (ANT Neuro, Enschede, Netherlands) and an EEGoPro amplifier (ANT Neuro, Enschede, Netherlands) at a sampling frequency of 512 Hz. Impedances of all channels were set below 20k $\Omega$  before the recording session. The data were pre-processed and analyzed with the MNE-python software. Bad sensors were identified manually and removed from the analysis (interpolated after the pre-processing). A notch filter of 50Hz was applied and Independent Component Analysis was performed to remove blink artefacts.

### 5.1.2.4. EEG data analysis

Data were re-referenced to the average mastoids and band-pass filtered from 0.1 Hz to 40 Hz. For each stimulus, trials were epoched from -200 ms to 800ms locked on the onset of the empty duration. A virtual trigger was added at the offset of the stimulus to perform further analysis at the offset of duration. Epochs were baselined with a 200 ms prestimulus period and discarded if the amplitude exceeded 100  $\mu$ V across the whole epoch. Trials were averaged per condition and per individual. The standard stimulus was used as an auditory localizer to identify a set of channels to quantify the ERPs. A statistical permutation t-test was performed to identify when and where the response to

the standard was significantly different from zero. For each deviant, a differential wave was computed by subtracting the activity after the offset of the standard to the activity after the offset of the deviant. We hypothesized two possible patterns for the effect of direction on the MMN amplitude. Either the response amplitude would follow the absolute amount of difference between the deviant and the standard - independent of the direction - or the amplitude would simply correlate with the duration - dependent of the direction -. To test that, we performed two linear regressions between amplitudes of the responses according to the two hypotheses (see Fig. 5.1.2) at each electrode and each time point after the offset of the durations. The signed MMN hypothesis corresponds to the effect of deviance direction and stimuli amplitudes were sorted according to their durations. The absolute MMN hypothesis corresponds to no effect of deviance direction and stimuli amplitudes were sorted according to their percentage of deviance, so deviants of 150 and 250 ms were merged in the 25% of deviance condition and deviants of 100 and 300 ms were merged in the 50% of deviance condition.



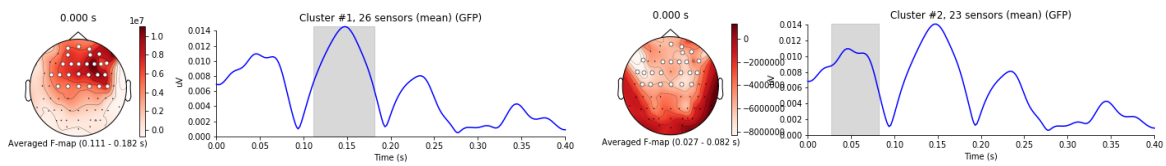
**Fig. 5.1.2: Schematic illustration of the effect of deviance direction on the MMN amplitude.** In the Signed MMN, we expect the MMN amplitude to increase linearly with the objective duration. In the Absolute MMN, we expect the MMN amplitude to increase with the percentage of deviance, such that 150 and 250 ms deviants would yield similar MMN amplitude, and 100 and 300 ms deviants would have similar amplitude levels.

The slope and  $R^2$  of the regression were extracted and statistical permutation t-tests were done to test where and when one of the possible patterns would lead to a significant linear regression.

### 5.1.3. Results

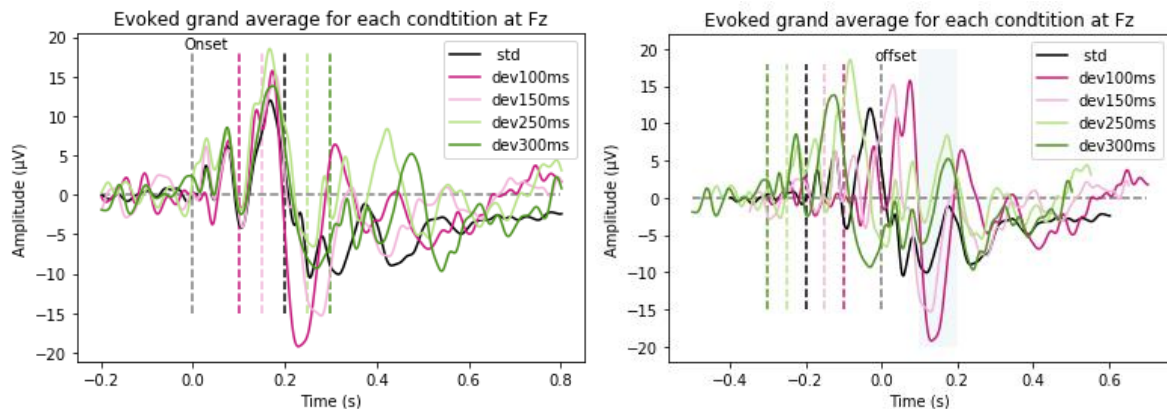
#### 5.1.3.1. Absolute vs Signed pattern:

We found significant clusters only for the signed pattern, where the slope of the regression was significantly different from zero in the first 200 ms after the onset of the duration deviance.



**Fig. 5.1.3: Significant clusters of the slope of regression, for the signed pattern.** Blue line is the global field potential of the slope of regression (similar to Fig. 2.4C-D-E) from the significant cluster of electrodes highlighted in white on the topographies. Grey shaded rectangles delimit significant time windows.

This pattern can be visually observed in the grand average responses of the standard and deviants (Fig. 5.1.4, right blue square)



**Fig. 5.1.4: Grand average evoked response for standard and deviants.** Left: time-locked on the onset of duration. Right: time-locked on the offset of duration. In the blue square, we clearly see the separation of the ERP amplitudes, captured by the regression based on the signed pattern.

## 5.2. 1<sup>st</sup> MMN laboratory study: 1<sup>st</sup> evidence for the absence of the empty time interval MMN

In this second annex, you will find the first duration MMN study that I conducted in the laboratory. In this study, I wanted to investigate the effect of deviance direction on the MMN amplitude (as in the pilot recordings). The non-observation of a clear MMN response for any deviant led me to conduct the specific literature review on the duration MMN and its parameters (Chapter 1), along with another laboratory study to confirm those observations (Chapter 2).

### 5.2.1. Introduction

The goal of this experiment was to investigate the effect of deviance direction (whether the deviant is shorter or longer than the standard) on the MMN amplitude elicited by changes in empty duration.

Predictive coding accounts of the MMN presuppose that the MMN amplitude reflects the residual error between the internalized, and therefore predicted, standard stimulus and the stimulus being processed (Garrido et al., 2009). However, the actual shape of the residual error is still poorly understood. Is it an absolute percentage of deviance ? or a signed difference between the standard and the deviant? This can be investigated using the effect of deviance direction on the MMN amplitude, yet conflicting results are found in the literature. No effect of deviance direction was found when several deviants were tested in the same block (Jaramillo et al., 2000) with a standard duration of 100ms, but when only one shorter and one longer deviant are tested in the same block, at different standard duration magnitude, a lower amplitude was found for longer deviant than for shorter one and this difference tended to increase when the standard duration magnitude increased (Colin et al., 2009). This was mainly investigated for filled durations and therefore durations are confounded with the integration of other sensory signals over time (such as intensity) If one is interested in duration *per se*, it is preferred to work with empty interval (delimited by a sharp sensory stimulus such as an auditory click for example) in the time perception domain. Only one study tested shorter and longer deviants with several standard magnitudes using empty intervals (Sable et al., 2003). Unfortunately, the analysis performed in this study does not allow to reveal a

possible effect of deviance direction. The present study was specifically aimed to investigate the effect of deviance direction on MMN amplitude elicited by changes in empty duration.

In this experiment, two orders of standard duration magnitude were presented repeatedly in separated blocks, occasionally replaced by shorter or longer deviants. There were 2 shorter and two longer deviants along with another deviant corresponding to the standard of the other duration magnitude block. It allowed us to test: (1) whether there is an effect of deviance direction on duration MMN amplitude and (2) whether the overall magnitude of the standard duration can also affect MMN amplitude.

#### 5.2.1.1. Research Question:

What is the effect of deviance direction on MMN amplitude?

- 1- Does the amplitude of the MMN result from a comparison between deviant and standard stimuli? (*centered vs equal probabilistic distribution*)
- 2- Does the amplitude of the MMN elicited by changes in duration result from a signed or an absolute comparison? (*initial design used for the pilot recordings*)
- 3- Does the amplitude of the MMN result from a difference (dev-std) or a ratio (dev/std) between the deviant and the standard stimuli? (*compare the difference in amplitude between the durations shared across FD and LFD blocks*)

#### 5.2.1.2. Working Hypothesis

Based on our pilot study we hypothesized:

- 1- A negative potential in the time window of the MMN would correlate with duration, only in the centered probabilistic distribution block (aka MMN is a comparison process).
- 2- The MMN amplitude would result from a signed comparison and **we will find a positive slope in the linear regression between MMN amplitude and stimulus duration** but not in the linear regression between MMN amplitude and absolute percentage of deviance
- 3- The MMN amplitude results from a ratio between the standard (or the central duration of the block in the equiprobable distribution block), as **we expect to find similar MMN amplitude levels across blocks that have different duration magnitudes but the same ratio between the durations**. Moreover, we expect to find

different MMN amplitudes between durations that have the same difference in magnitude

If what we observed in our pilot results from confound because we used too short durations (<300ms) and no control blocks:

1- **We expect to find a negative potential in the time window of the MMN only for the centered probabilistic distribution block.** Computing differential waves (by using the ERPs from the equiprobable distribution block) will allow us to visually observe the MMN potential. However, it might be difficult to observe a MMN in the differential wave of the shorter duration because MMN-like potentials have been observed for the shortest duration in equiprobable distribution blocks

2- Based on the literature of MMN elicited by empty duration changes, we expect to find at least a clear MMN for deviants shorter than the standard and we might not find MMN for deviants longer than the standard. Therefore, if we compute linear regression according to duration (signed) or percentage of deviance (absolute), we might find a positive relationship for the signed hypothesis (MMN amp. increase (more positive) with duration and with values close to 0 for std and longer deviants) and a negative relationship for the absolute hypothesis (MMN decrease (more negative) with the percentage of deviance). In this specific case, for both regressions, we expect to find poor (or bad)  $r^2$  (closer to 0)

3- (Same as above, if any MMN is found) The MMN amplitude results from a ratio between the standard (or the central duration of the block in the equiprobable distribution block), as **we expect to find similar MMN amplitude levels across blocks that have different duration magnitudes but the same ratio between the durations.** Moreover, we expect to find different MMN amplitudes between durations that have the same difference in magnitude

## 5.2.2. Materials & Methods

### 5.2.2.1. Participants

Twenty-four right-handed volunteers (11 women, mean age = 26.5 years +/- s.d.), took part in the study and received monetary compensation for their participation. All declared normal to corrected vision, normal hearing, and no neurological or psychiatric

pathology. Before participating, each participant signed an informed consent validated by the Ethics Committee on Human Research at Neurospin (Gif-sur-Yvette): CPP n° 100049 (Gif-sur-Yvette, France) and the Declaration of Helsinki (2013). One participant was removed from the analysis due to a poor signal-to-noise ratio in the EEG data, resulting in a final sample size of 23 participants. A sample size of 21 participants was calculated using the software G-Power to find a significant difference ( $\alpha= 0.05$ , effect size = 0.74) between the amplitude of two deviants. It was calculated based on reported values from a previous study (Jaramillo et al., 2000) (see annex).

#### 5.2.2.2. Stimuli & Procedure

Participants were comfortably seated 60 cm away from the computer screen in an experimental room. Due to the covid-19 related sanitary measures, our soundproof experimental booths were not available. The experiment consisted of passive listening to an auditory oddball paradigm. To distract participants' attention, they were instructed to watch a silent movie and to ignore sounds. In an oddball paradigm, a stream of standard stimuli is presented to the participant, interspaced by infrequent deviant stimuli.

The task was coded and run on Matlab 2019a using Psychtoolbox (Brainard, 1997) on a Dell Latitude E6530 portable computer. Stimuli were empty intervals or durations, i.e. silent intervals delimited by two 5 ms white noise bursts (2.5 ms rise and fall ramping intensity) and whose durations were defined by the Stimulus Onset Asynchrony (SOA) between these two noises. The sound intensity was adjusted individually between 20 to 30 volume levels so that auditory clicks were clearly audible but not disturbing.

The experimental manipulation consisted in testing the effects of the length of SOAs and their general distribution. Three types of experimental blocks were tested as a function of the SOAs distribution: a short and a long focal distributions (sFD, lFD, respectively) and an equiprobable (ED) distribution block.

In the sFD and lFD, there were 5 types of deviants ( $\pm 10\%$ ,  $\pm 30\%$ ) of the standard SOA. In the sFD, standard SOA was 550 ms and deviants were 385 ms ( $-30\%$ ), 495 ms ( $-10\%$ ), 605 ms ( $+10\%$ ) and 715 ms ( $+30\%$ ). In the lFD, the standard was 750 ms and deviants were 525 ms ( $-30\%$ ), 675 ms ( $-10\%$ ), 825 ms ( $+10\%$ ) and 925 ms ( $+30\%$ ). Standards were 70% and each deviant was 6% of the total number of stimuli. A

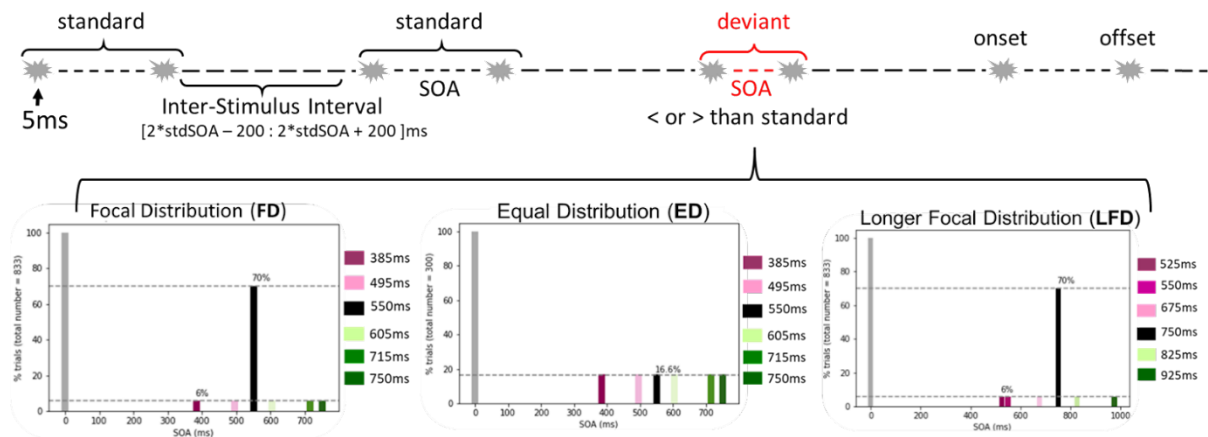


total of 833 stimuli with each deviant presented 50 times (yielding a total of 250 deviants and 583 standards).

Note that the fifth deviant in SFD corresponded to the standard of the LFD.

All stimuli were separated by a random Inter-Stimulus Interval (ISI) with a mean of two times the standard duration, to ensure a perceptual grouping of empty intervals, and jittered by +/-200 ms to avoid a supra-rhythmic sequences. In the sFD and lFD , there were at least two consecutive standards between each deviant.

In the ED block, SOAs were equally presented with a probability of 16.6% for a total number of stimuli of 300 (50 each) lasting 8.25 min. FD and LFD blocks lasted 22.9 and 32.23 min respectively.



**Fig. 5.2.1: Oddball paradigm and SOAs probability distribution used in different blocks.** Standard stimuli were empty time interval delimited by two auditory clicks. Deviants could be shorter or longer. Standards were presented with a probability of .7 and each deviant with a probability of .06. In the Focal Distribution block, the standard was 550 ms and the deviants were 385, 495, 605, 715, 750 ms. In the Equal Distribution block, all the empty duration were presented equally. In the Longer Focal Distribution block, the standard was 750 ms and the deviants were 525, 550, 675, 825, 925 ms.

### 5.2.2.3. EEG recordings and Preprocessing

EEG recordings were performed with a high density 64 channels waveguard cap (ANT Neuro, Enschede, Netherlands) and an EEGoPro amplifier (ANT Neuro, Enschede, Netherlands) with a sampling frequency of 512 Hz. Impedances of all channels were set below 20 kΩ before the recording session. The data were pre-processed and analyzed using the MNE-python software (v0.20). Bad sensors were identified manually and removed from the analysis (mean 1.23 per participant across blocks) and interpolated during pre-processing. A notch filter of 50 Hz was applied to the data, and an Independent Component Analysis was performed to remove the blink artifacts (mean

ICA component identified visually 2.055 per participant across blocks, automatically 1.398).

#### 5.2.2.4. EEG data analysis

Data were re-referenced to the average mastoids and band-pass filtered from 0.1 Hz to 40 Hz. Single-trials were-locked to stimulus onset epoched from -200 ms to 1250 ms (longest duration of the block + 500 ms) in the FD and ED blocks, and from -200 to 1475 ms (longest duration of the block + 500 ms) locked on the onset of the empty durations. Epochs were baselined using a 200 ms prestimulus. Epochs were discarded if the amplitude exceeded 100  $\mu$ V across the whole epoch. Trials were equalized in number across conditions to equate the SNR between standards and deviants. Evoked responses were obtained by averaging epochs per condition on a per individual basis.

All statistical analyses were performed using a statistical permutation t-test to identify where and when brain responses differed from the zero in the contrast of interest. Unless otherwise specified in Results, we used 1000 permutations, a F-threshold adjusted to  $p = 0.05$  and a spatio-temporal cluster threshold of  $p = 0.05$ .

To identify which electrodes were most responsive to auditory stimuli, a localizer was performed by averaging all conditions together and performing a statistical permutation t-test to identify where and when brain responses on the scalp were different from zero ( $n_{\text{permut}} = 1000$ ;  $p_{\text{thres}} = 0.005$ ,  $\text{thres} = 3.11$ ,  $p_{\text{accept}} = 0.05$ ).

To characterize the MMN elicited by deviants, we performed a statistical permutation f-test to identify where and when the evoked responses elicited by empty intervals in Short and Long MMN blocks differed from the evoked responses elicited by the same empty intervals in the non MMN block. The individual-level differences between auditory evoked responses (FD-ED) computed and a statistical permutation t-test was identified the spatio-temporal clusters in which differential waves were significantly different from zero. ( $n_{\text{permut}} = 1000$ ;  $p_{\text{thres}} = 0.001$ ,  $\text{thres} = 3.79$ ,  $p_{\text{accept}} = 0.05$ ).

Traditionally the MMN was computed as a differential wave between the stimulus being a standard in one block, and deviant in the other. Our FD and LFD blocks respectively contained the standard of the other block as a deviant therefore it was possible to test whether a MMN potential could be obtained by comparing the ERPs across blocks. Again a statistical permutation f-test was performed between the 550 ms

stimulus ERP in the FD block and the 550 ms stimulus ERP in the LFD block. The same was done for the 750 ms stimulus ( $n_{\text{permut}} = 1000$ ;  $p_{\text{thres}} = 0.001$ ,  $\text{thres} = 3.79$ ,  $p_{\text{accept}} = 0.05$ ). A statistical permutation f-test was also performed to test differences between stimulus conditions (durations) both at the onset and offset ( $n_{\text{permut}} = 1000$ ;  $p_{\text{thres}} = 0.001$ ,  $\text{thres} = 3.79$ ,  $p_{\text{accept}} = 0.05$ ).

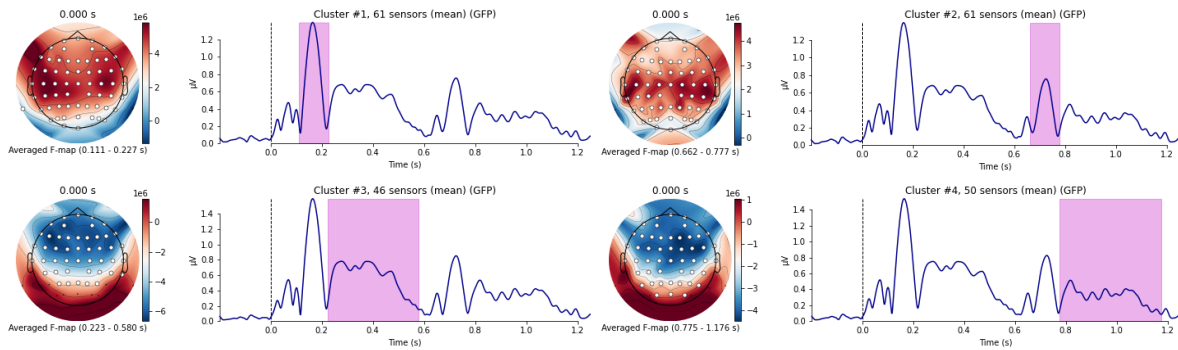
We hypothesized two possible patterns for the effect of direction on the MMN amplitude. Either the response amplitude would follow the absolute amount of difference between the deviant and the standard - independent on the direction - or the amplitude would simply correlate with the duration - dependent on the direction -. To test that, we performed two linear regressions between amplitudes of the responses according to the two hypotheses at each electrode and each time point after the offset of the durations. The signed MMN hypothesis corresponds to the effect of deviance direction and stimuli amplitudes were sorted according to their durations. The absolute MMN hypothesis corresponds to no effect of deviance direction and stimuli amplitudes were sorted according to their percentage of deviance, so deviants of -10 and +10% were merged in the 10% of deviance condition and deviants of -30 and +30% were merged in the 30% of deviance condition. The slope and  $R^2$  of the regression were extracted and statistical permutation t-tests were done to test where and when one of the possible patterns would lead to a significant linear regression ( $n_{\text{permut}} = 1000$ ;  $p_{\text{thres}} = 0.001$ ,  $\text{thres} = 3.79$ ,  $p_{\text{accept}} = 0.05$ ). This test was performed on FD block

Finally, we investigated whether we could find a habituation effect on the ERP amplitude level. To do this, we computed an ERP out of the first 10% stimuli and a second one out of the last 10% stimuli in our FD block, irrespective of stimulus type. We performed a statistical permutation f-test between the two ( $n_{\text{permut}} = 1000$ ;  $p_{\text{thres}} = 0.05$ ,  $\text{thres} = 2.07$ ,  $p_{\text{accept}} = 0.05$ ).

### 5.2.3. Results

#### 5.2.3.1. A too wide localizer

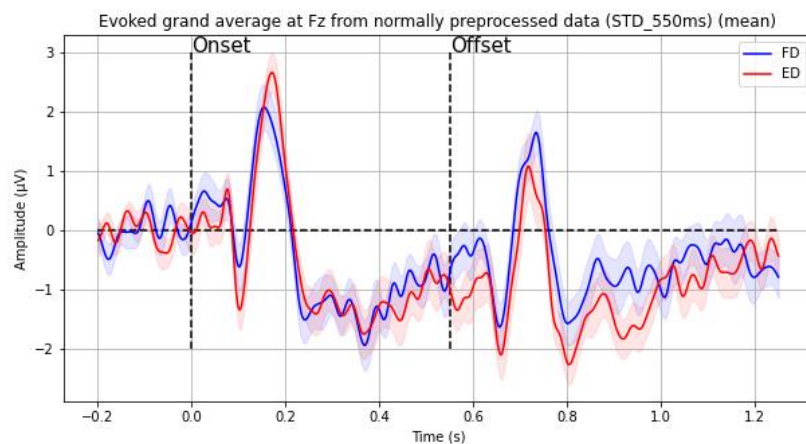
We found 4 clusters covering the whole epoch with 46 to 61 sensitive channels. Because the number of significant channels was too large, we didn't use this localizer in the subsequent analyses.



**Fig. 5.2.2: Significant clusters found when all conditions are mixed in the FD block.**

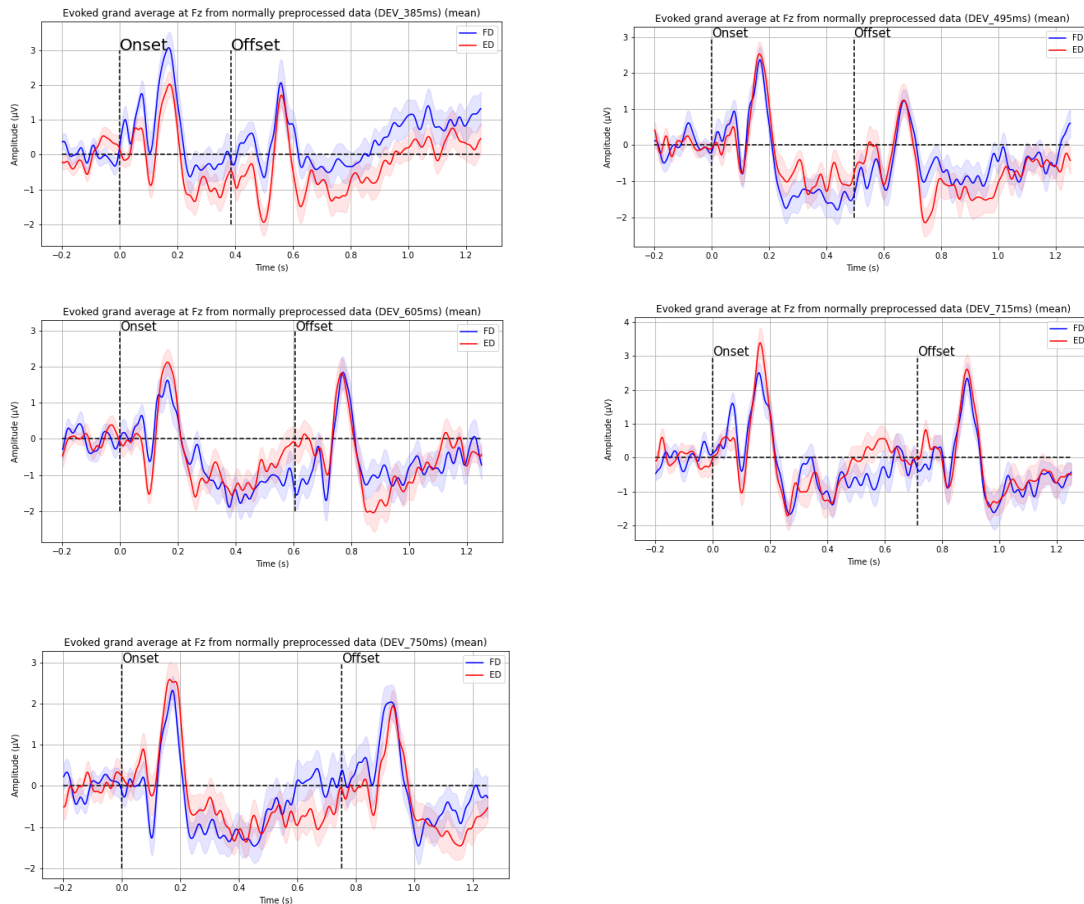
### 5.2.3.2. Deviants did not elicit MMN in the FD block: FD vs ED

Auditory evoked responses elicited by the presentation of a given duration in MMN blocks were compared to those elicited by the same duration in non MMN block. All the ERPs displayed below are at the Fz channel, where the MMN response should be the strongest when EEG signals are re-referenced to the linked mastoids. First, we compared the standard of 550 ms for which we did not expect to find any differences, see Fig. 5.2.3. No statistical cluster was found.



**Fig. 5.2.3: Sanity check of the ERPs elicited by the standard of 550 ms in the FD block (blue) and the 550 ms stimulus in the ED block (red).** Black dashed lines delimit onset and offset of the standard empty time interval. Shaded areas around the curves are the standard error of the mean. As expected from the standard, there was no difference between the ERP of the standard in the FD block, and its corresponding ERP in the ED block.

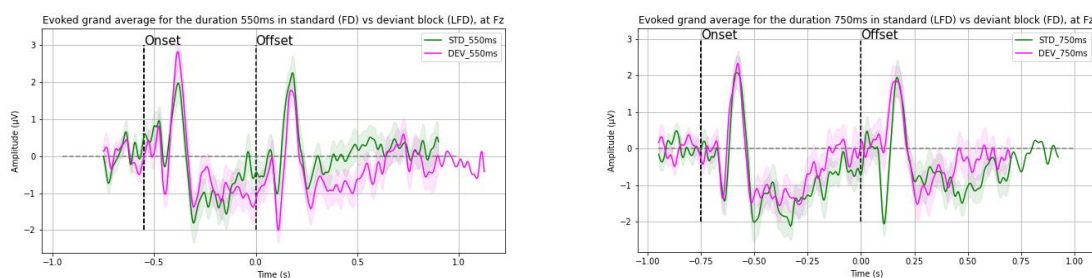
Then, we compared the deviant ERPs in the FD block to their corresponding ERPs in the ED block. No statistical difference was found between any of the durations. Fig. 5.2.4 displays the ERPs from one block and the other. No significant cluster was found either for the differential waves.



**Fig. 5.2.4:** ERPs elicited by the deviants in the FD block (blue) and their corresponding duration in the ED block (red). Black dashed lines delimit onset and offset of the empty time intervals. Shaded areas around the curves are the standard error of the mean. Unexpectedly, we found no differences between the ERPs of the deviants from the FD block, and their corresponding ERPs in the ED block.

### 5.2.3.3. Traditional contrast of the MMN: standard vs deviant in separated blocks; No MMN is found either

Our design allowed us to test another way of observing MMN potential by comparing the ERP of a stimulus when it is standard in one block and deviant in the other. Even with this contrast, we found no statistical difference in the ERPs. Fig. 5.2.5 displays the ERPs obtained for the same duration in different blocks.



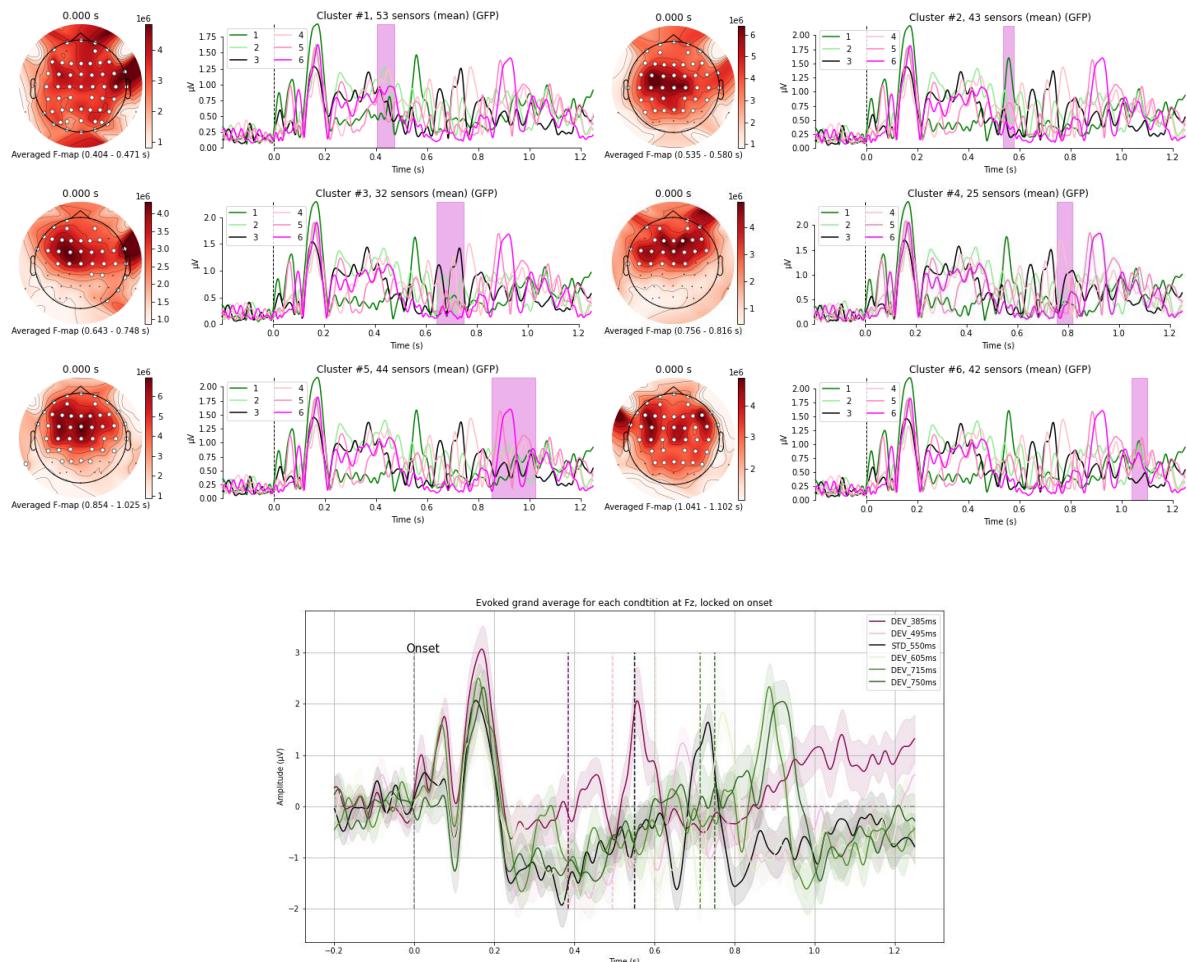
**Fig. 5.2.5:** ERPs elicited by the same duration either being a standard (green) or a deviant (pink). Black dashed lines delimit onset and offset of the empty time intervals. Shaded areas around the curves

are the standard error of the mean. We found no differences between the deviant ERP, and its associated standard ERP form the other MMN block (FD and LFD block)

#### 5.2.3.4. There are differences between our stimulus conditions only at the onset, not the offset

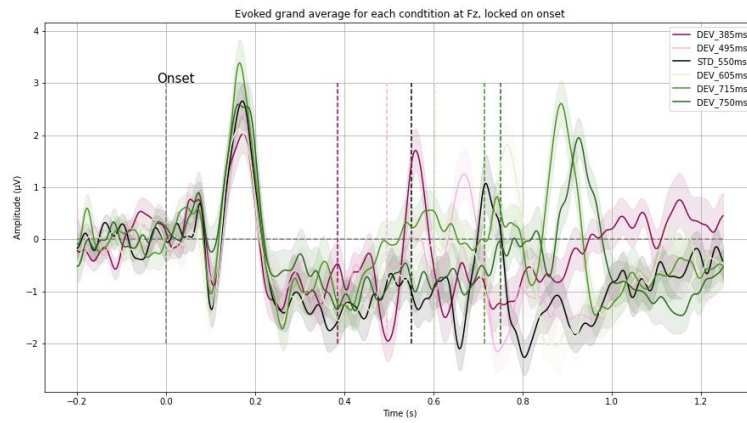
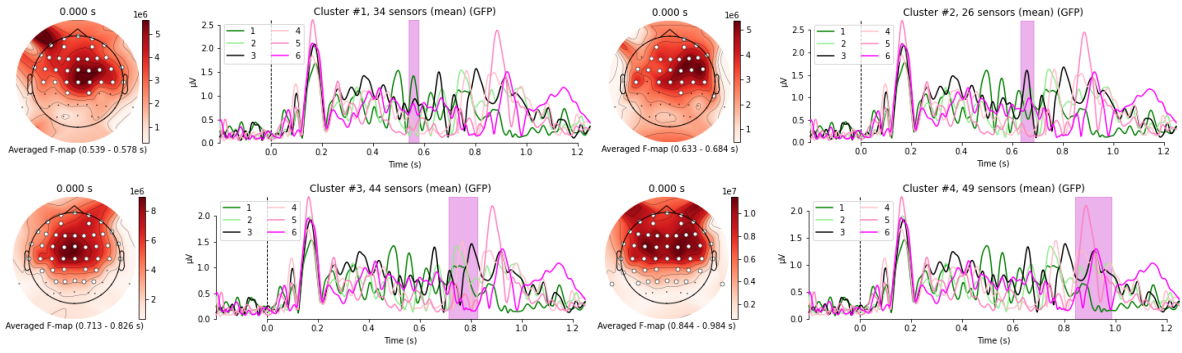
Since we did not find any MMN potentials, we tested, for each block, whether we could find differences between our stimuli of different durations, both after the onset and the offset of durations (i.e. after the first of the two clicks and after the second click, respectively). At the onset, we found statistical differences starting at the offset of each duration in all our blocks. This is a good sanity check as, indeed, we expect to find differences in the latency of the auditory ERPs elicited by the offset (second auditory click) of our durations but not the onset.

FD block onset: 6 clusters found



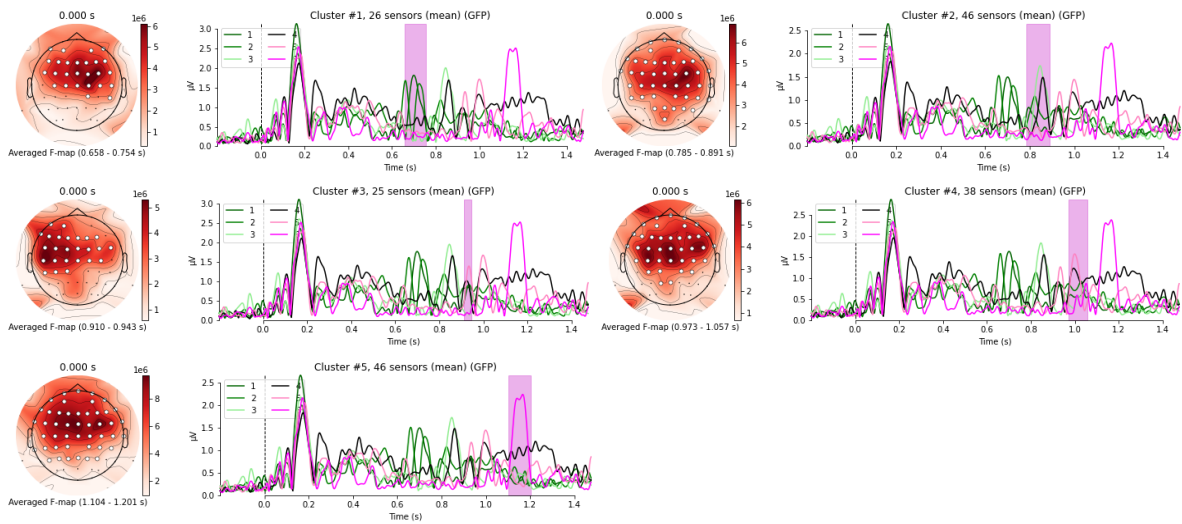
**Fig. 5.2.6: Significant clusters and grand average potential for the FD block at duration onsets. Dotted lines correspond to offsets.**

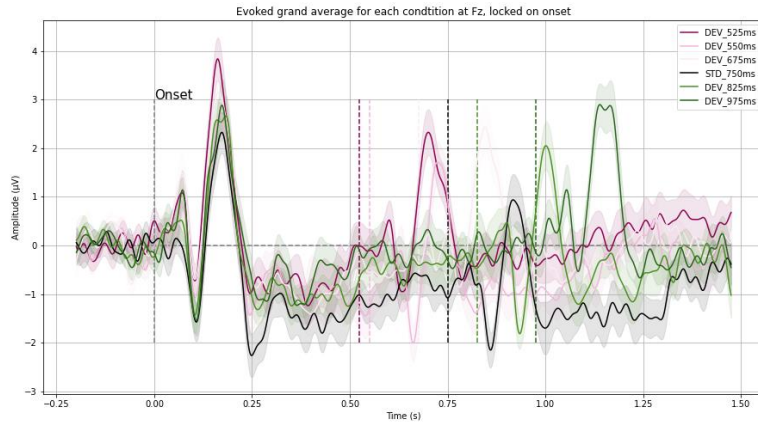
ED block onset: 4 clusters found



**Fig. 5.2.7: Significant clusters and grand average potential for the ED block at duration onsets**

LFD block onset: 5 clusters found

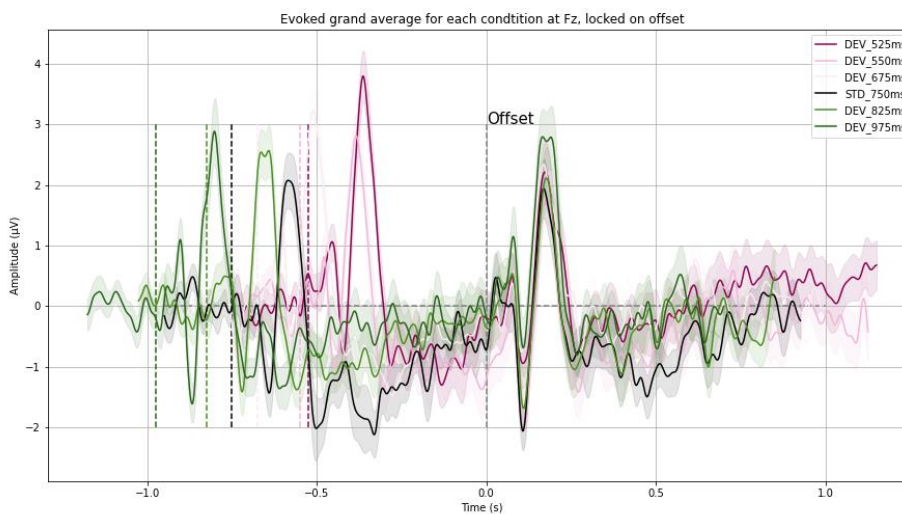
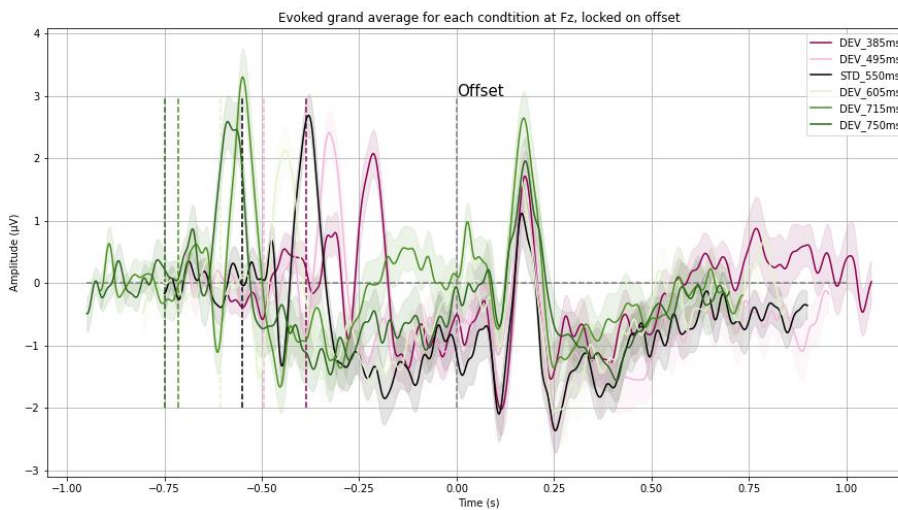
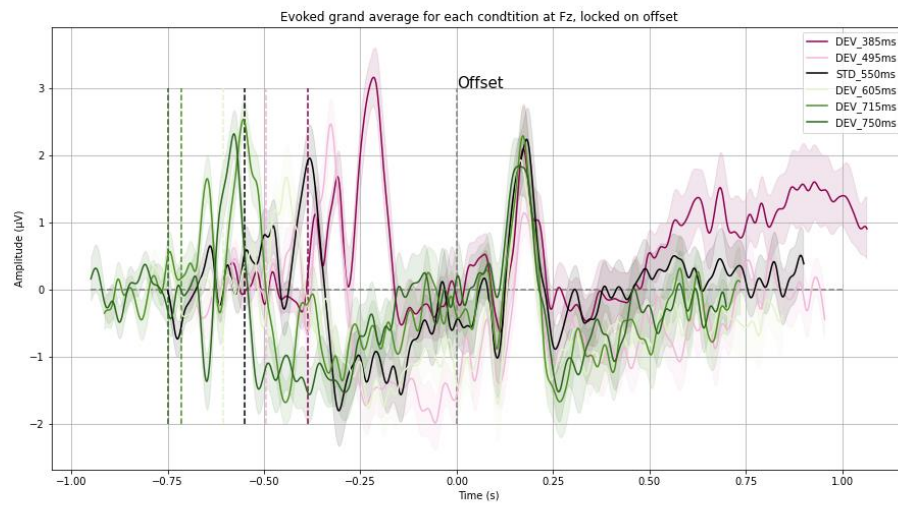




**Fig. 5.2.8: Significant clusters and grand average potential for the LFD block at duration onsets**

On the other hand, when we locked ERPs and analyses at the offset we did not find any statistical cluster, for any block. Fig. 5.2.9 displays the grand average evoked responses at Fz for each stimulus condition for each block.

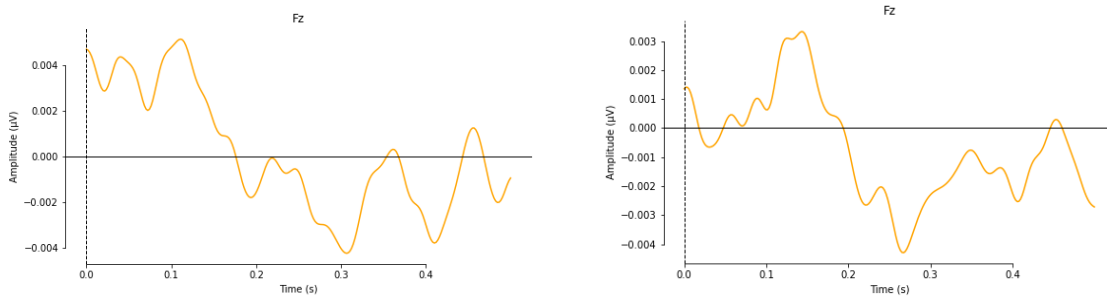




**Fig. 5.2.9: Grand average evoked responses at Fz for each stimulus condition for each block.**

### 5.2.3.5. No signed or absolute MMN

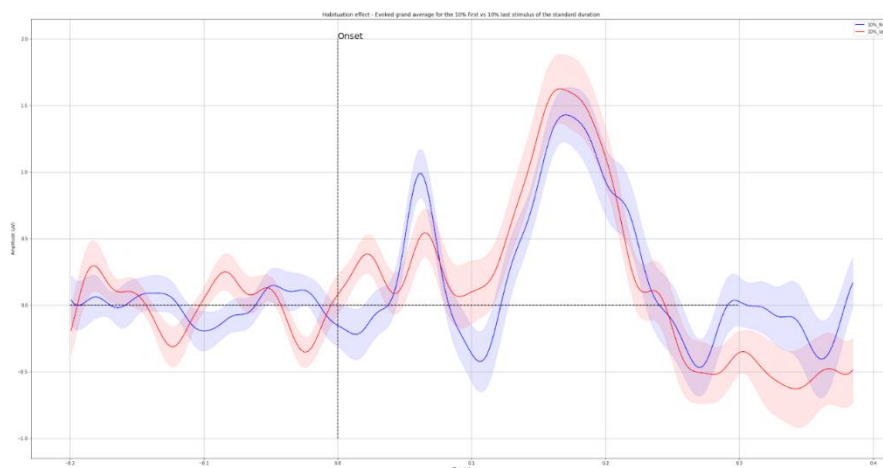
As expected, since no MMN nor differences between our stimulus conditions were observed, slopes of our linear regressions between ERPs amplitude and durations (signed) or percentage of deviance (absolute) did not significantly differ from zero.



**Fig. 5.2.10: Slope of the linear regressions at Fz, absolute on the left and signed on the right.**

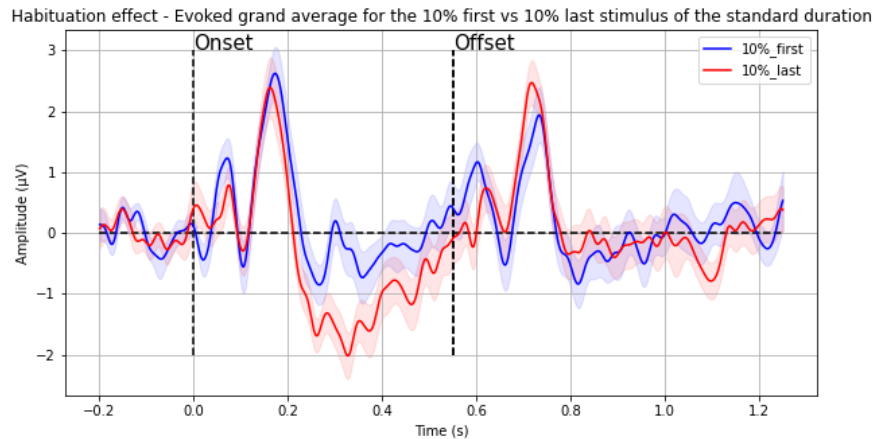
### 5.2.3.6. No statistical habituation effect

No significant difference was found between the first and the last 10% of our stimuli (all conditions merged) although, visually, the P1 in the first 10% has a higher amplitude than the last 10%.



**Fig. 5.2.11: Evoked response of the first (blue) and the last (red) 10% of stimuli in the FD block.**

This habituation effect was also investigated only on the standard stimulus. Similarly, no statistical differences were found although once again the P1 was smaller in the last 10% (but the P2 is larger in the last 10% so this does not say much).



**Fig. 5.2.12: Evoked response of the first (blue) and the last (red) 10% of the standard stimuli in the FD block.**

## 5.2.4. Discussion

### 5.2.4.1. Localizer

This sanity check allowed us to observe that our auditory clicks induced a brain response, but that this response is too widely spread over the scalp so that we could not define a set of channel of interest. This is not a problem *per se*, as the statistical test we are using are spatio-temporal test that will take into account the multiple comparison problem. In all ERPs, we clearly see the traditional auditory ERP complex, N1-P2, see Fig. 5.2.4 for example in the FD and ED block (P50 is apparent but close to the level of noise in the baseline).

### 5.2.4.2. No MMN is to be find for empty interval

The design of this study allowed us to perform several contrasts to observe MMN potentials. The first one is to compare the same duration as being either a deviant or as being part of an equiprobable block. In the present study, this corresponds to compare the ERPs of the same duration from the FD (deviant) and ED (equiprobable) block. We found absolutely no evidence for the elicitation of MMN potentials in the FD block (Fig. 5.2.4). We also computed differential wave by subtracting the ERPs from the ED block to the ERPs from the FD block, and no MMN was found either. The second possible contrast to observe MMN potentials is by comparing the ERPs from duration that were a standard in one block and a deviant in the other block. This was possible for the 550 and 750 ms. As with the first contrast, we did not find evidence for MMN potential either (Fig. 5.2.5).

Those (non)observations are unlikely to arise from wrong parameters in the statistical tests performed since differences in amplitude were found between ERPs locked on the onset. Those differences correspond to the auditory ERPs of the offset (second auditory click) of each duration. When the ERPs are locked at the offset, and statistical differences are searched after the offset, no specific differences is found between ERPs (Fig. 5.2.9).

#### 5.2.4.3. Deviant longer than standard hardly elicit an MMN, specifically for empty interval

The majority of studies investigating the effect of deviance direction used rather short durations and filled intervals (pure tone of FX frequency lasting SX seconds), below 300 ms (Amenedo et al., 2000; Jaramillo et al., 2000). In studies using higher standard duration magnitudes (Colin et al., 2009; Takegata et al., 2008), no clear MMN is found for increment of duration. For empty intervals, the effect of deviance direction was never tested using a non-rhythmic paradigm (variable ISIs between empty durations). When a constant rhythm is used, it was found quite early that an increment of duration (lengthening of the constant ISI) do not elicit a MMN (Ford and Hillyard, 1981) and therefore put aside by the community. It is only years later that a MMN was found for increment of duration, when empty durations were presented in trains of 4 consant SOAs and a 5th deviant SOA (Sable et al., 2003). This was replicated in a later study using even longer empty durations (Lai et al., 2010). The fact that we used a non-rhythmic paradigm in this study could explain why we did not find MMN for deviant longer than standard. Moreover, omission of stimulus do not elicit MMN when the ISI is longer than 175 ms, even if ISIs are constant.

#### 5.2.4.4. Deviant shorter than standard elicit MMN even at long standard magnitude

When a rhythmic paradigm is used, the decrement of ISI (shortening of the constant rhythm) can elicit MMN for standard duration up to 1500 ms (Branon et al., 2008). However in our study we did not find MMN for our deviant shorter than our standard. This could be because we did not used a rhythmic paradigm, but there is also additional factors that could prevent us from observing. First, one of our deviant had a difference of

only -10% from our standard. This amount of difference might be too low to clearly elicit a MMN (Amenedo et al., 2000). Second, we used equiprobable blocks as a control block. However, in equiprobable blocks, the shortest duration can elicit a MMN-like potential (Jacobsen et al., 2003). In our ED block the shortest duration corresponded to our shortest deviant, hence it is possible that no difference is found between the two because there is a MMN-like potential in the ED block.

#### 5.2.4.5. ERPs amplitude do not follow a specific pattern (nor absolute nor signed)

Even in the absence of a clear MMN, we hypothesized, thanks to our pilot recordings, that it could be possible to find a pattern between ERP amplitudes. We tested two possible patterns, either the amplitude at the offset would increase linearly with the duration (signed) or the amplitude would increase with the amount of deviance (absolute). For both patterns, we find that the slope of the linear regression was not different from zero, suggesting that none of these two patterns were present in our data.

#### 5.2.5. Conclusion

Studying the effect of deviance direction with empty intervals in a non-rhythmic paradigm using long standard durations was probably a goal too far from the current available data in the literature. A careful inspection of the literature revealed that while it seems clear that the ratio deviant/standard, rather than the simple difference deviant - standard, is important in the MMN process for empty intervals, the effect of deviance direction along with the existence of a threshold, to process differently short and long durations, remain to be investigated in a non-rhythmic paradigm for a complete understanding of the MMN process for changes in empty duration and the underlying representation of duration. This could be tested in a design with two orders of standard duration, below and above threshold, with at least two deviants, one shorter and one longer. We expect to find clear MMNs in the block with durations below threshold (~200 ms), and no effect of deviance direction. A careful inspection of the latency of the MMN should be done to identify whether duration informations are actually used by the system at such short durations. It is most likely that the above threshold block will not elicit a MMN at all, at least for increment, therefore a third block with either a trial design using trains of constant SOA should be added that could elicit MMN potential for

increment of duration. Of course, control blocks where each deviant is presented alone should be done.

### 5.3. Co-Authored published article on duration and the speed of the passage of time

This annex is a published article from a team member with whom I collaborated. I specifically participated in the conceptualization and the methodology of the article. In this study, we investigated the effect of the number of events on duration and speed of the passage of time judgments. The goal was to investigate the relationship between those two judgments, to test whether they would rely on distinct or similar mechanisms. To do so, we adapted the classical psychometric measure of duration estimation to speed of the passage of time, in order to directly compare those two judgments.

First, we showed that, like duration judgments, we could establish individual psychometric profiles for the speed of the passage of time. Second, we found that both duration and the speed of the passage of time were affected by the manipulation of objective duration, and the number of events. Contrary to the intuitive link between duration and speed of the passage of time (longer duration are perceived passing slower), the number of events tended to lengthen subjective duration and accelerate the speed of the passage of time. Therefore, in conditions where durations were perceived longer, the speed of the passage of time was perceived faster. Interestingly, participants were faster to report speed of the passage of time than duration, going against the idea that duration judgment are needed to estimate the speed of the passage of time. Although we introduced a new methodology to measure the speed of the passage of time, it remains unclear, to me, whether this new type of judgment correspond to the phenomenological experience of time passing faster or slower in daily-life situations. This could be tested by comparing the effect of events density on speed of the passage of time in healthy versus patients reporting time passing faster or slower (such as depressive or schizophrenic patients).

The distinction between duration perception and speed of the passage of time is an interesting topic that was always in my mind during my PhD and that I wanted to investigate since my master 2 internship. Additionally, and in collaboration with the French railway company (SNCF), I developed another online task on the topic, that I was, unfortunately, not able to finalize. The scientific question was close to the effect of temporal expectation on the speed of the passage of time and duration judgments mentioned in section 4.5.

# Distinctive features of experiential time: Duration, speed and event density

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**Author contributions:** M.L.K.: Conceptualization, Formal analysis, Investigation, Methodology, Software, Visualization, Writing – original draft. Y.N.: Conceptualization, Methodology, Writing – review & editing. S.L.: Resources, Software, Writing – review & editing. V.v.W.: Conceptualization, Funding acquisition, Methodology, Project administration, Supervision, Writing – review & editing.

## Abstract:

William James’s use of “time in passing” and “stream of thoughts” may be two sides of the same coin that emerge from the brain segmenting the continuous flow of information into discrete events. Herein, we investigated how the density of events affects two temporal experiences: the felt duration and speed of time. Using a temporal bisection task, participants classified seconds-long videos of naturalistic scenes as short or long (duration), or slow or fast (passage of time). Videos contained a varying number and type of events. We found that a large number of events lengthened subjective duration and accelerated the felt passage of time. Surprisingly, participants were also faster at estimating their felt passage of time compared to duration. The perception of duration scaled with duration and event density, whereas the felt passage of time scaled with the rate of change. Altogether, our results suggest that distinct mechanisms underlie these two experiential times.

### 5.3.1. Introduction

Psychological time is not monolithic and seldom follows physical time (Dennett & Kinsbourne, 1992; van Wassenhove, 2009). The subjective experience of time passing has been argued to be an illusion (Gruber & Block, 2013; Gruber et al., 2018; but see van Wassenhove, 2023), in that what we perceive as the 'flow of time' could better be understood as a 'flow of events' in time (Michon, 1972; Hicks et al., 1977; Fraisse, 1984;



Gruber et al., 2018). In other words, psychology and cognitive sciences tend to attribute the term (psychological) 'time' to phenomena caused by the constant flux of changes, whether they are sensory events in the environment or fluctuations of bodily-clocked signals. Humans and animals can effectively keep track of how long events seem to last (duration perception), feel that time passes (passage of time) and assess the speed with which it seems to pass (Wearden, 2015).

Interestingly, whether estimating a duration and the felt speed of time result from the same timing mechanisms is unclear. At first glance, the length of a time interval and its felt speed seem to be clearly related: short durations are perceived as passing quickly while long durations are experienced as passing slowly (Martinelli & Droit-Volet, 2022b, Nicolai et al., 2023). However, this relation does not always hold and is likely to be more nuanced. For instance, individuals who suffer from depression report a significantly slower passage of time, despite their estimation of duration being comparable to that of healthy individuals (Thönes & Oberfeld, 2015). This observation, along with previous research, suggests that temporal judgments (felt speed and duration) may capture distinct psychological phenomena (Droit-Volet & Wearden, 2015; Droit-Volet et al., 2017; Jording et al., 2022).

Passage of time judgments have been hypothesized to capture the most salient (external or internal) contextual changes experienced in a given time interval (Martinelli & Droit-Volet, 2022b). This proposal is compatible with the contextual change hypothesis (Block & Reed, 1978), in which perceiving the duration of an event results from the number of changes in a context, whether duration is estimated prospectively or retrospectively (Block & Reed, 1978; Zakay & Block, 1997). Although both proposals suggest that contextual changes are the source of temporal experience, they appeal either to duration or to speed. If long durations are linked to slow speed (Martinelli & Droit-Volet, 2022b), one would expect that longer durations would be linked to a slower experience of time passing. However, this contradicts the observation that while fewer events do shorten perceived duration (Jording et al., 2022; Roseboom et al., 2019), fewer events also slow down the experienced speed of time (Jording et al., 2022), raising questions about the underlying mechanisms and their interplay giving rise to these temporal phenomenologies.

Given that our environment is in a constant state of change, it is unsurprising that perceptual changes would relate to our experience of time. Beyond transient perceptual

changes, our brain keeps track of ongoing experiences by segmenting the continuous flow of information into meaningful units or distinct mental “events” (Zacks & Tversky, 2001). Models of event segmentation suggest that the passage of time may be a side effect of constructing and updating event representations (Richmond & Zacks, 2017). In such models, events are functionally defined within a clear temporal framework (Zacks & Tversky, 2001). Contextual changes, perceptual or abstract, affect duration judgments as predicted by the contextual change hypothesis (Hicks et al., 1976; Block & Reed, 1978): the more events, the longer durations are estimated or remembered to be (Brunec et al., 2020; Ezzyat & Davachi, 2014; Roseboom et al., 2019). With respect to speed, a recent study showed that a perceived higher rate of changes in an optical flow display also sped up felt time (Jording et al., 2022). Hence, both duration and speed are influenced by perceptual changes, but whether contextual changes systematically affect them in a similar way is unknown.

In the present study, we investigated how event segmentation influences experiential duration and speed of time. We chose to test realistic contextual changes and events as defined by event segmentation theories in contrast to salient perceptual changes. Stimuli were videos of a train station lasting 17s to 23s, with a varying number of distinguishable events that would naturally occur in such an ecological context. One novel goal was to validate duration and speed measurements for long time scales in the range of seconds. We opted for a bisection task, commonly used for short duration estimations. Bisection tasks (Kopeck & Brody, 2010) are 2-AFC (Alternative Forced Choice) tasks in which participants must select one of two possible options when presented with a stimulus. Herein, participants were provided with a 2-AFC using short or long for the Duration task and slow or fast for the Speed task.. Each stimulus was drawn from a parametrically varied continuum of durations. This psychophysical approach allowed fitting a psychometric curve and deriving the subjective threshold (point of subjective equality [PSE]) and just-noticeable-difference (JND). Reaction times (RTs) were also recorded as participants were instructed to perform as accurately and as fast as possible. This approach allowed going beyond the typical Likert or visual-analog-scale used for passage of time ratings (Wearden, 2015).

Since shorter durations yield faster experienced speed (Martinelli & Droit-Volet, 2022b; Nicolaï et al., 2023), we expected that estimations of the speed of the passage of time would scale with video duration, allowing the use of a psychometric approach.

Additionally, we anticipated scenes with fewer events to result in a slower experience of time passing but in longer duration estimates. Finally, we hypothesized that the presence of a different type of contextual event (in our case, a train) would influence both temporal measurements due to its salience as the most expected event in the context of waiting at a train station, whereas its absence is surprising. Hence, in agreement with event segmentation theories, we predicted that the absence of a train would lead to an overestimation of duration and a deceleration of felt time.

### 5.3.2. Materials & Methods

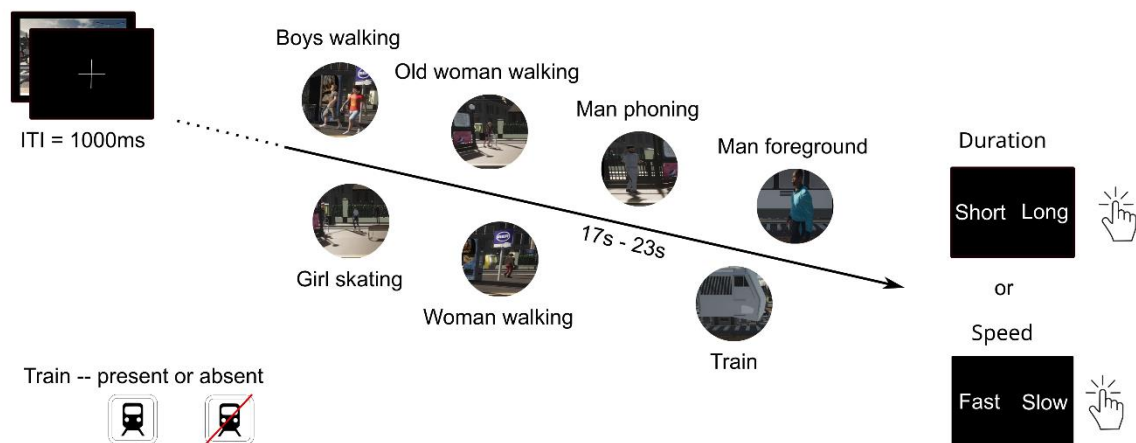
#### 5.3.2.1. Participants

166 adult participants, aged 18 to 51 y.o. (mean = 27.98 y.o., SD = 7.81; 121 females) were recruited in the online study. Participants reported no history of neurological or psychiatric disorders. 143 participants self-declared as right-handed and 23 as left-handed. Participants were recruited online through academic mailing lists and social media. All participants gave their written informed consent for participating before the beginning of the experiment. All participants were compensated for their participation (15€ per hour). The study was approved by the Comité d’Ethique pour la Recherche of Paris-Saclay University (CER-Paris-Saclay-2019-063) and ran in accordance with the declaration of Helsinki (2013). Two participants failed the training and did not advance to the main task. One participant was *a priori* excluded from all psychometric analyses due to poor performance reflected in extreme deviance values and flat curves. Thus, a total of 163 participants were included in the analysis (mean = 27.97 y.o., SD = 7.85; 118 females).

Participants could take part in either one or both tasks (Duration and/or felt Speed). Out of the 163 participants, 52 were tested on the Duration task only, 50 were tested on the Speed task only and 62 contributed to both tasks. This allowed for two kinds of analytical approaches: a between-participants assessment ( $N_{\text{Duration}} = 85$ ;  $N_{\text{Speed}} = 78$ ) and a within-participants analysis ( $N = 62$ ).

### 5.3.2.2. Stimuli

Stimuli were realistic videos of a virtual train station created using the Unity software (Haas, 2014). A total of 40 videos (mp4) were created to manipulate the factors of stimulus duration (5), number of events (Events : 2) and train (Train : 2). Stimulus duration refers to the total duration of the video, which could be 17 s, 19 s, 20 s, 21 s or 23 s (i.e., 20 s +/- 5% or +/- 10%). The number of events in each video could be three or seven. To best simulate the ecological experience of waiting on the dock of a train station, the events added to the environment were the kind expected in such context, and consisted of either human activities (e.g. a person walking while texting) or the passage of a train (refer to Table 5.3.S1 in Supplementary Material for full list). In half of the videos, only human activities were used and no train event occurred (20 videos); in the other half, one of the events was a train passing by, arriving at or leaving the station allowing for a balanced design of two distinct blocks of videos depending on our third factor, the train. Subtle background sounds of a train station were added to each video and the train event was accompanied with the corresponding sound effect.



**Fig. 5.3.1. Task Design.** Videos of a virtual Parisian regional train dock were used as stimuli. Videos could contain 3 or 7 events, one of which could be a train. The experiment was a 5 (durations: 17s, 19s, 20s, 21s, 23s) x 2 (train or no train) x 2 (3 or 7 events) design. Participants were asked to categorize each video as 'long' or 'short' in the Duration bisection task, or as 'slow' or 'fast' in the Speed bisection task. The factor Train was tested in a block design randomized within-participants: one experimental block tested 20 videos without a train, another one tested 20 videos with a train. The order of the Tasks was randomized across participants.

### 5.3.2.3. Task design

The experiment was coded in JavaScript using the jsPsych library (De Leeuw, 2015). The experiment was hosted on a dedicated server for online experiments at Neurospin (CEA, France). It consisted of two 1-IFC 2-AFC bisection tasks, which tested duration estimation and felt speed. The factor Train followed a block-design: the two blocks (Train, No Train) were randomized across participants. Each stimulus duration was presented 4 times in each block. The durations of the video and the number of events were randomized within blocks.

When a participant logged onto the server, the order of the tasks was randomized so that the experiment could start with the Duration or with the Speed bisection task. At the end of the first task, participants could continue to the second task or end their participation in the study. In a given task, participants were presented with one video at a time, which they classified into one of two categories: “Short” or “Long” for the Duration bisection and “Fast” or “Slow” for the Speed bisection (Fig. 5.3.1).

The motor-response mapping was congruent with the Spatial-Numerical and the Spatial-Temporal Association Response Code (SNARC and STARC, respectively) (Fabbri et al., 2012). According to the SNARC and STARC effects, participants’ responses are facilitated by the ranking of the responses (small numbers or durations on the left, large numbers or durations on the right in the SNARC and STARC, respectively) (Hubbard et al., 2005; Ishihara et al., 2008). The Simon effect, according to which responses are facilitated when the position of the response key is congruent with its appearance on the screen, was also taken into account (Hommel, 2011). Hence, in the Duration bisection task, participants were asked to respond with the left arrow key for “Short” presented on the left of their screen and with the right arrow key for “Long” presented on the right of their screen. Keys in Speed bisection followed the same pattern (left for “Fast” and right for “Slow” responses) for consistency.

Both accuracy and speed of responses were emphasized in the instructions. Participants’ responses and reaction times (RTs) were recorded on each trial. RTs were capped to 4 s and skipped trials were rethrown at the end of the block. If an answer was not provided within the available time, a warning message appeared prompting participants to respond faster.

#### 5.3.2.4. Procedure

Before the beginning of the main task, all participants were trained by being presented with the longest and the shortest duration videos. For speed, they were presented with the longest with 3 events and the shortest with 7 events for “slow” and “fast” choices. During the training, participants were provided with feedback. An incorrect response resulted in the rethrow of the training phase (up to three times). Only participants who correctly distinguished the two extreme stimuli could take part in the study.

At the end of the experiment, participants rated three separate emotional states (happiness, sadness and boredom) on a Likert scale ranging from 1 (“not at all”) to 4 (“very much”). Participants also rated and provided their comments on the difficulty of the task and on the strategy they used (if any) to classify the stimuli.). These responses can be found in Fig. 5.3.S1 and Table 5.3.S2 in the Supplementary Material.

#### 5.3.2.5. Psychophysical quantification

Psychometric curves were generated for each individual using the proportion of ‘slow’ responses for Speed and ‘long’ responses for Duration. Four (Duration *or* Speed) or eight (Duration *and* Speed) psychometric curves were fitted by participants for each number of events (3, 7) and Train (present, absent) combination. The mean RT for each combination of duration, number of events and train was computed per participant and a log transformation was performed for further analyses.

Fits were done using the `psignifit` python version 4.0 (Schütt et al., 2016). The Duration and Speed data were fitted using a cumulative Gumbel distribution. The less steep right side of the Gumbel sigmoid function best reflects the scalar properties of timing that is to say, the fact that variability in temporal discrimination increases with mean subjective time i.e, longer durations are associated with greater variance (Allan, 1998; Van Driel et al., 2014; Wiener et al., 2018).

To assess each individual’s goodness of fit, the Deviance was used: Deviance was defined as two times the difference of the model log-likelihood to the log-likelihood of the best fitting model (Schütt et al., 2016; Wichmann & Hill, 2001). A critical Deviance

value was calculated by generating 2000 datasets using the best-fitted function and obtaining the 95% confidence interval of the resulting deviance distribution. A Deviance of the data superior to the criterion indicated a bad fit. Bad fits were excluded from the analysis and accounted for less than 5% and 6% of the total dataset for the Duration and Speed, respectively. Individual examples of good and bad fits are provided in Fig. 5.3.S2A-B. The Deviance distributions for all psychometric fits are provided in Fig. 5.3.S2C. From the psychometric fits, we calculated the Point of Subjective Equality (PSE) and the Just Noticeable Differences (JND). The PSE (50% threshold) is an indication of bias towards one of the two possible responses while the JND (the functions interquartile range) reflects the participant's precision (Vatakis et al., 2018).

To directly compare the effect of the number of events in duration and speed, we calculated the difference in the PSEs between the two event conditions (7 – 3) for all participants, who performed both tasks (henceforth referred to as  $\Delta$ PSE). Seven participants with bad fits were excluded. The  $\Delta$ PSE reflects the bias following the change in the number of events. A negative  $\Delta$ PSE indicates that increasing the concentration of events biases towards 'long' or 'slow' responses; conversely, a positive  $\Delta$ PSE indicates a bias towards 'short' or 'fast' responses.

#### 5.3.2.6. Outliers

Conditions in which the PSE fell outside the range of tested durations were excluded in all statistical analyses. In Duration, ~10% (32 out of 340 conditions) of the PSE fell outside the range of tested durations. In Speed, ~28% (90 out of 316 conditions) of PSE fell outside of the tested range (examples are provided in Fig. 5.3.S1D). In the within-participants analysis, 11% of conditions were excluded in Duration (29 out of 252) and 22% in Speed (55 out of 252).

#### 5.3.2.7. Statistical analyses

All analyses were conducted using the R software (R Core Team, 2022) with Rstudio (RStudio Team, 2020). For RTs and psychometric parameters analysis, we used linear mixed models with a random intercept for participants. Models were fitted using the lme4 package for R (Bates et al., 2015) and p-values and degrees of freedom were

obtained with the lmerTest (Kuznetsova et al., 2017) and car (Fox & Weisberg, 2019) packages. The emmeans package (Lenth, 2017) was used for pairwise comparisons for PSE.

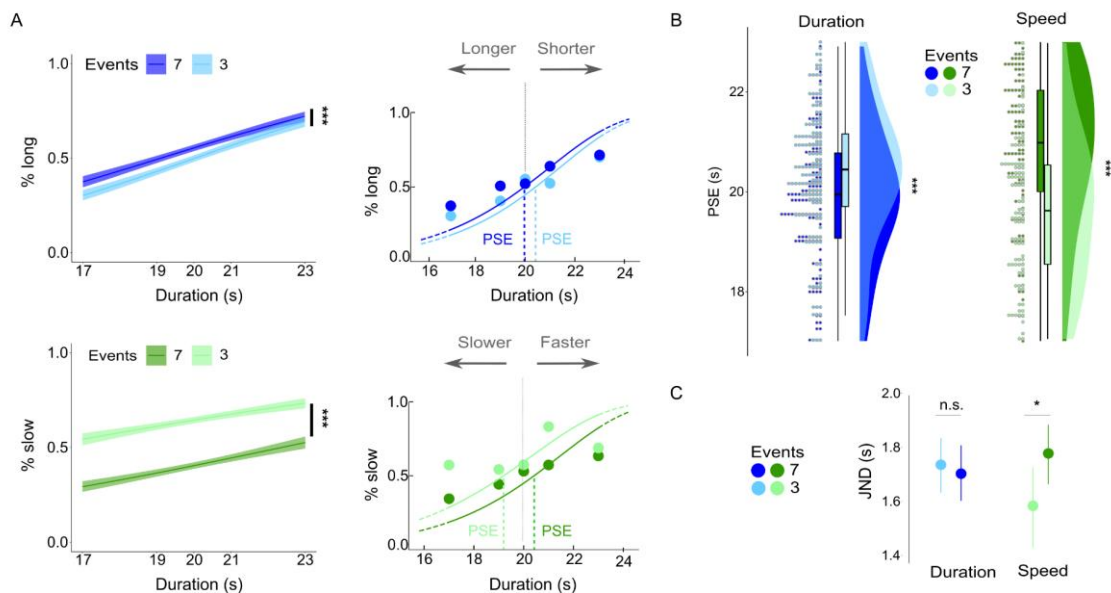
The goodness of fit of the models and the significance of fixed effects was assessed using the Akaike Information Criterion (AIC) and Wald  $\chi^2$  tests. For the JND analysis, the conditions for a parametric statistical approach were not met and so aligned rank transformation (ART) was performed on the data using the ARTTool (Kay et al., 2021) followed by a repeated measures three-ways Anova.

For the analysis of the raw data to assess the feasibility of a psychometric curve, a mixed effect logistic regression model was used with duration and number of events as variables.

All statistical tests were performed against an alpha level of  $p < 0.05$ . All plots were generated with the ggplot2 package for R (Wickham, 2016).

### 5.3.3. Results

#### 5.3.3.1. The experienced duration and speed of passage of time scale with duration



**Fig. 5.3.2. The number of events influences both experiential duration and speed of time.** A. Left: percentage of 'long' and 'slow' responses (Duration, blues in upper panels and Speed, greens in lower panels, respectively) as a function of stimulus duration for 3 (light) and 7 (dark) events. Longer videos significantly increased the odds of responding 'long' and 'slow' in Duration and Speed, respectively. The



number of events increased the odds of responding 'long' in Duration and decreased the odds of responding 'slow' in Speed. Right: percentage of 'long' (left) and 'slow' (right) responses as a function of video duration for 3 (light) and 7 (dark) events. Dots are mean responses across participants (N=85 for Duration; N=79 for Speed). Mean psychometric curves are for illustration purposes. A leftward shift of the curve (lower PSE) indicates a bias towards 'long' or 'slow' responses, respectively. A rightward shift (higher PSE) indicates a bias towards 'short' or 'fast' responses, respectively. B. Distribution of individual PSEs as a function of duration and number of events (light and dark colors for 3 and 7, respectively) in Duration (left, blues) and Speed (right, greens). Dots are individuals. C. Mean JND as a function of the number of events. Error bars are the 95% CI. Significance codes:  $p < 0.001$  '\*\*\*';  $p < 0.01$  '\*\*';  $p < 0.05$  '\*';  $p > 0.05$  'ns'.

Before psychometric modeling of the data collected in each task, we first established whether responses in both tasks scaled with the duration of the video. For this, we used a mixed effect logistic regression model to analyze the effect of the duration and number of events on the probability of 'long' and 'slow' responses for the Duration and Speed bisection tasks, respectively. This approach was realized using all data with no prior assumption on their psychometric profiles (Fig. 5.3.2A) since no fits were realized to perform this analysis (cf. Fig. 5.3.S1). Longer durations increased the probability of 'long' responses in Duration (OR = 1.17, 95% C.I. [1.14, 1.2],  $p < 0.001$ ; Fig. 5.3.2A top) and of 'slow' responses in Speed (OR = 1.3, 95% C.I. [1.27, 1.33],  $p < 0.001$ ; Fig. 5.3.2A bottom). The number of events significantly affected duration and speed estimates: in Duration, the odds of responding 'long' were higher when videos contained 7 events than when they contained 3 events (OR = 0.79, 95% CI [0.71, 0.87],  $p < 0.001$ ). Conversely, the odds of responding 'slow' in Speed were higher with fewer events (OR = 2.77, 96% CI [2.49, 3.08],  $p < 0.001$ ). Thus, a first experimental observation is that for a given time interval, a larger number of events lengthens subjective duration, and accelerates participants' felt passage of time as compared to a smaller number of events.

In both Duration and Speed, a scaling of responses as a function of elapsed time was found. We thus proceeded with individual psychometric fits to extract individuals' PSE and the JND. Fig. 5.3.2A–B, right panels, illustrate the mean responses across participants for Duration and Speed, respectively.

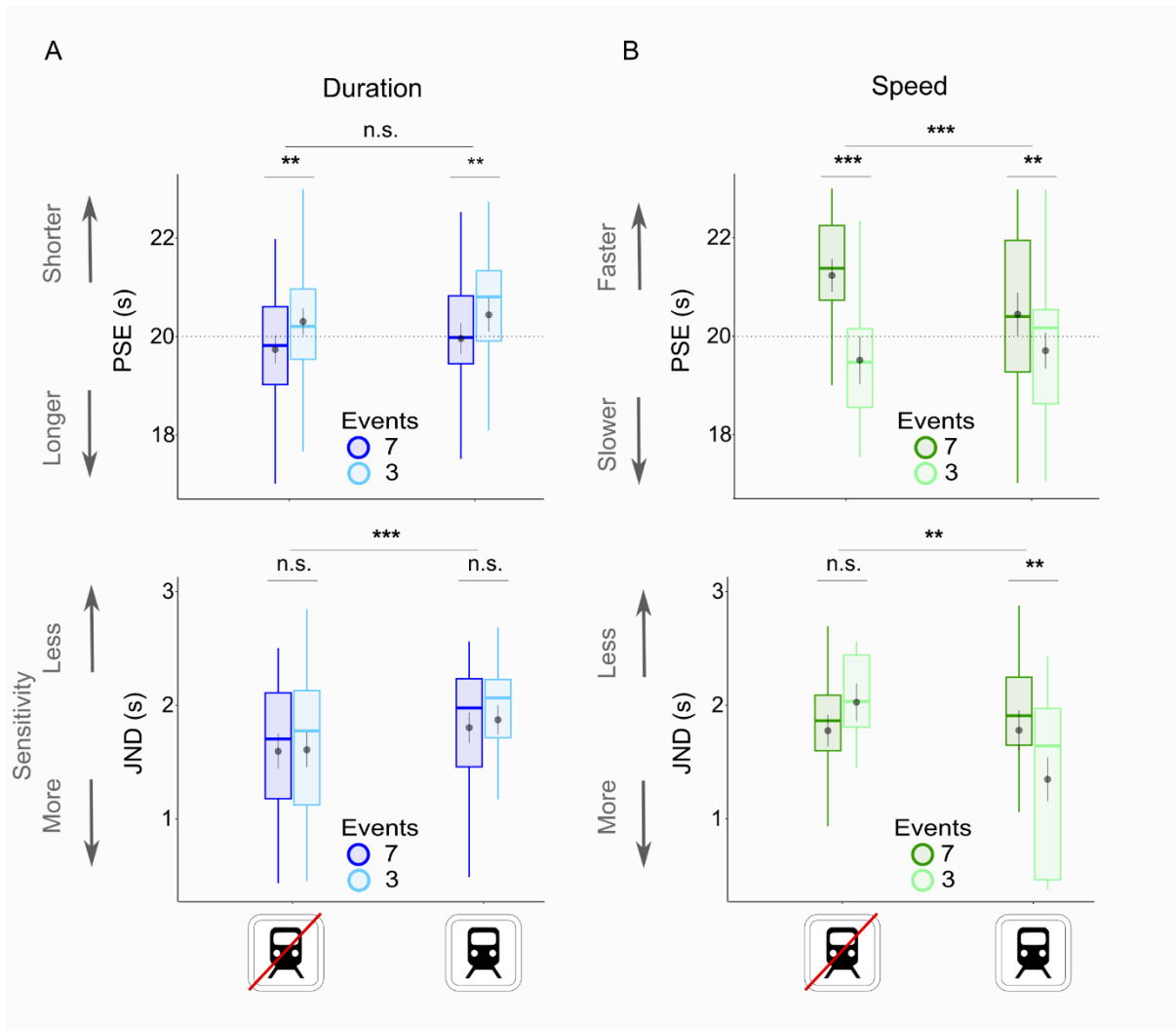
#### 5.3.3.2. More events lengthen duration and increase the speed of the passage of time

As in the previous analysis, we found that the number of events in the videos significantly affected time estimation in both Duration and Speed bisection tasks. In

Duration (Fig. 5.3.2B, blues), consistent with the results of Fig. 5.3.2A, the PSEs were significantly higher in the 3-events videos as compared to the 7-event ones (0.53, 95% CI [0.25, 0.82],  $t(219.5) = 3.69$ ,  $p < 0.001$ ) signifying that participants underestimated the duration of the videos when the number of events was small. We found no significant effects of the number of events on JND ( $F(1, 216.5) = 0.006$ ,  $p = 0.94$ ; Fig. 5.3.2C, left panel) or on RTs ( $\chi^2(1) = 0.78$ ,  $p = 0.38$ ) (Fig. 5.3.S3A and Table 5.3.S3 in Supplementary Material). In Duration, the number of events biased participants' responses without affecting their sensitivity.

In Speed, the number of events significantly affected RTs, PSE and JND. A significant decrease in PSE was found for videos containing 3 events compared to 7 events (-2.41, 96% CI [-3.12, -1.7],  $t(161.35) = -6.59$ ,  $p < 0.001$ ; Fig. 5.3.2B). This indicates that participants favored a 'slow' response in videos containing fewer events. The number of events also significantly affected the JND so that 3-event videos yielded a significantly smaller JND than the 7-event videos ( $F(1, 157) = 31.22$ ,  $p < 0.001$ ; Fig 5.3.2C, right panel). RTs in Speed were also significantly slower for 3-event videos as compared to the 7-event ones (0.44, 95% CI [0.17, 0.7],  $t(1498) = 3.22$ ,  $p < 0.01$ ; Fig 5.3.S3B and Table 5.3.S4 in Supplementary Material). Thus, for a given duration, when a video contained a smaller number of events, participants were slower (RTs), tended to experience time as passing slower (PSE), and were more sensitive to the speed of the passage of time (JND).

### 5.3.3.3. When trains alter the experience of time



**Fig. 5.3.3. The presence of a train influences duration and speed estimates.** A. PSEs and JNDs in the Duration bisection task. Boxplots indicating the mean and 95% C.I. of PSE (top) and JND (bottom) extracted from individual psychometric fits in the train (left) and no train (right) blocks for the 3- and 7-event videos (light and dark blue, respectively). B. PSEs and JNDs in the Speed bisection task. Boxplots indicating the mean and 95% C.I. of PSE (top) and JND (bottom) from individual psychometric fits in the train (left) and no train (right) blocks for 3- and 7-event videos (light and dark, respectively). Mean estimates and 95% C.I. are provided. Significance codes:  $p < 0.001$  '\*\*\*';  $p < 0.01$  '\*\*';  $p < 0.05$  '\*';  $p > 0.05$ ; 'ns'.

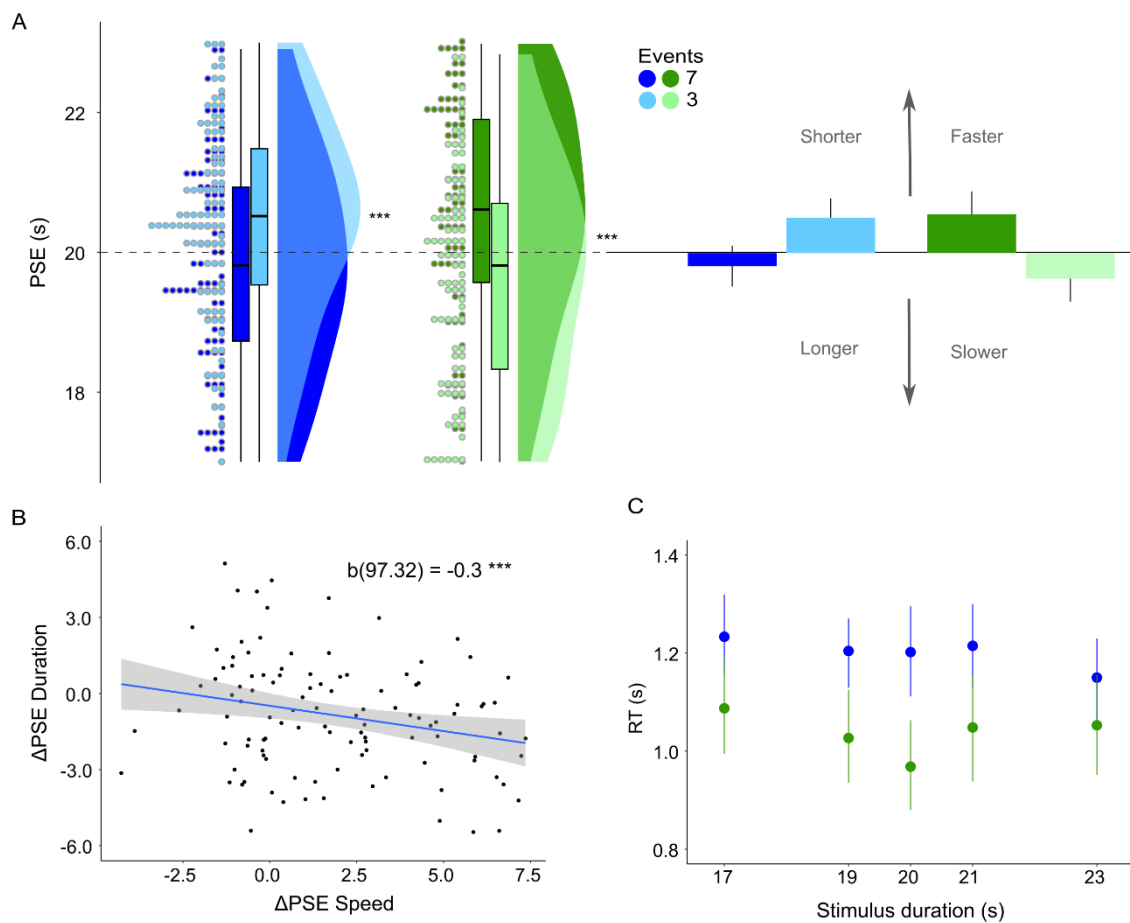
In Duration, the presence of a train did not significantly affect the PSE ( $\chi^2(1) = 2.38$ ,  $p = 0.12$ ) but significantly influenced the JND ( $F(1, 216.5) = 12.9$ ,  $p < 0.001$ ) (Fig. 5.3.3A). Participants showed greater sensitivity to changes in duration when there was no train in the video (Fig 5.3.3A, bottom). We found a significant effect of Train on RTs (0.03, 95% CI [0.01, 0.06],  $t(1613) = 2.78$ ,  $p < 0.01$ ; Fig. 5.3.S3A and Table 5.3.S3 in Supplementary Material) with faster RTs when a train was present in the video. Additionally, we checked if the order of the Train blocks influenced the psychometric parameters. The block order

significantly affected the PSE (-0.62, 95% CI [-0.94, -0.32],  $t(74.72) = -3.94$ ,  $p < 0.001$ ) so that the PSE was smaller when the train was presented in the first block as compared to when it was presented in the second block (Fig 5.3.S4A and Table 5.3.S5 in Supplementary Material for the full model). Hence, participants were biased towards overestimating the duration of the first block when it contained a train event.

In Speed, the presence or absence of a train significantly affected the PSE (-2.41, 95% CI [-3.12, -1.69],  $t(148.97) = -3.09$ ,  $p < 0.001$ ; Fig. 5.3.3B, top) so that the presence of a train sped up felt time. Additionally, we found a two-way interaction between Train and number of events (0.99, 95% CI [0.25, 1.73],  $t(157.97) = 2.6$ ,  $p = 0.01$ ) and Train and block order (1.12, 95% CI [0.38, 1.85],  $t(158.1) = 2.94$ ,  $p = 0.01$ ). These interactions show that the number of events affected the PSE less when one of the events was a 'train' (Fig. 5.3.3B) and when the first block contained a train event (Fig 5.3.S4B and Table 5.3.S6 in Supplementary Material for the full model). The presence of the train also significantly affected the JND ( $F(1, 150.31) = 8.67$ ,  $p < 0.01$ ) with lower JNDs observed when a train event was present in the video (Fig 5.3.3B, bottom). We also found a significant interaction between the number of events and the Train ( $F(1, 158.49) = 16.35$ ,  $p < 0.001$ ; Fig. 5.3.3B) on the JND. Last, the factor Train did not influence RTs ( $\chi^2(1) = 1.93$ ,  $p = 0.16$ ; Fig. 5.3.S3C and Table 5.3.S4 in Supplementary Material). Altogether, these results indicate a major effect of the presence of a train in the estimation of the speed of felt time, highlighting the importance of contextual effects in experiential time.

#### 5.3.3.4. Relation between Duration and Speed judgments

To characterize more precisely the relation between duration and speed of time, we analyzed data collected within-participants ( $N = 62$ ). In the within-participants design, the effect of the number of events on PSE was significant in both tasks (Duration: .69, 95% CI [0.27, 1.08],  $t(197) = 3.43$ ,  $p < .001$ ; Speed: -0.93, 95% CI [-1.35, -0.5],  $t(126.27) = -4.3$ ,  $p < .001$ ; Fig. 5.3.4A). Consistent with our previous analyses, participants favored short durations but slow speed for stimuli with a low number of events as illustrated by an increase and decrease in the PSEs, respectively (Fig. 5.3.4A).



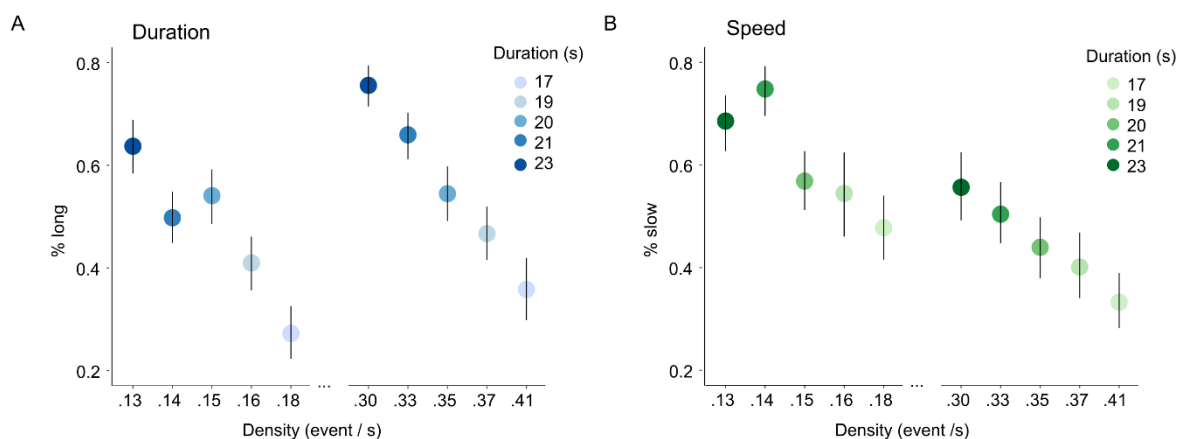
**Fig. 5.3.4. Speed of the passage of time is dissociable from duration estimates (within-participants design).** A. Left: Distribution of individual PSEs for Duration (left, blues) and Speed (right, greens) as a function of the number of events (light for 3 events; dark for 7 events). Dots are individuals. Right: Direction of biases: barplots provide the mean PSE and 95% C.I. for Duration and Speed (blue and green, respectively). The black horizontal line shows the midpoint of the duration distribution used (i.e., 20s). B.  $\Delta$ PSE was computed as the shift of PSE in the psychometric curve from 7 to 3 events in the Duration and in the Speed tasks, separately.  $\Delta$ PSE in Duration as a function of  $\Delta$ PSE in Speed shows a significant negative relation indicating that, given the same time interval, an increase in the number of events lengthens duration and speeds up the felt passage of time. Beta coefficient and degrees of freedom are shown. C. Mean RTs for each stimulus duration in both tasks. RTs in Speed bisection (green) were significantly faster than in the Duration bisection (blue). Error bars indicate 95% C.I..

We then compared the data from the two bisection tasks directly keeping in mind that the speed of the passage of time may be computed as the number of events in a given time interval. This working hypothesis simply indicates that the duration and speed are inversely proportional to each other. First, we investigated whether the impact of the number of events on both temporal experiences was comparable. For this, we computed changes in PSE as a function of the number of events ( $\Delta$ PSE = PSE<sub>7</sub> – PSE<sub>3</sub>) separately for both tasks. Using a linear mixed effects model, we evaluated the relation

between  $\Delta$ PSE in Duration and in Speed and found a statistically significant, albeit small, negative relation between the two (-0.3, 96% CI [-.48, -.12],  $t(97.32) = -3.3$ ,  $p = .001$ ; Fig. 5.3.4B).

Second, given the working hypothesis, we predicted that speed would be computed after a duration had been represented so that the felt passage of time would be a direct outcome of event count in a given time interval. Therefore, we expected participants to be faster at estimating durations than at estimating the speeds of the passage of time. Participants' RTs significantly differed across tasks (-0.83, 95% CI [-1.24, -0.41],  $t(586.58) = -3.93$ ,  $p < 0.001$ ) but participants were surprisingly much faster in answering the Speed task than the Duration task (Fig. 5.3.4C). This suggests that conscious access to estimates of the speed of felt time may be easier and faster than those of durations.

Last, we investigated whether event density (i.e., the number of events in a given duration) was a major driving factor in speed judgments. For this, we calculated the mean percentage of 'long' responses for Duration and the mean percentage of 'slow' responses for Speed as a function of event density. As we did not initially test for the density of events in our experimental design, the data points were not equally spaced, preventing the use of a balanced statistical analysis. Nevertheless, we observed that for Duration, the primary criterion for judgment remained the objective duration of the stimuli so that the density of events rescaled the judgments (Fig. 5.3.5A). However, in Speed, participants' answers scaled almost continuously with density irrespective of the tested duration (Fig. 5.3.5B).



**Fig. 5.3.5. Dissociable effect of event density on Duration and Speed.** A. Mean % of 'long' responses for Duration for each video duration as a function of event density. Event density is defined as the ratio between the number of events and the tested duration. B. Mean % of 'slow' responses for Speed for each

video duration as a function of event density. Speed of the passage of time judgments linearly scale with event density, whereas duration scales with number.

#### 5.3.4. Discussion

Our study explored how contextual changes using real-life events influence experiential duration and speed of time. First, we successfully used bisection tasks to assess seconds-scale duration estimation. Second, we extended this approach to assess the speed of the passage of time judgments, typically assessed using Likert or visual-analog scales. Psychometric assessments provide useful estimates of biases (PSE) and sensitivity (JND) of participants' experiential time. Third, we show that an increasing number of events in a scene lengthens its perceived duration (bias), accelerates felt time and decreases sensitivity to speed. Fourth, the absence of an expected event in a given context (here, a train) lengthens perceived duration, slows down felt time and decreases the sensitivity to experiential speed of time. We discuss below the link between the experience of duration and speed of time, and comment on the observation that speed scales with event density whereas duration increases with the number of events at a given scale.

Herein, we demonstrated the feasibility of a psychometric approach to characterize participants' felt speed of time classification as a function of the duration of videos. The assessment of PSEs indicated that shorter (longer) durations elicited faster (slower) experiential speed. This outcome indicates that speed can be modulated by the duration of external events, even when stimuli are videos of complex realistic scenes captured in a virtual environment. Our observation is consistent with previous research (Jording et al., 2022; Martinelli & Droit-Volet, 2022a, 2022b) in that experiential speed seems to scale with objective duration. Importantly, we report that increasing the number of events significantly accelerated participants' experience of the passage of time, in agreement with a recent visual starfield study assessing perceptual changes (Jording et al., 2022). Interestingly, we found that an increasing number of events decreased participants' sensitivity to speed, suggesting a potential trade-off between speed and the hierarchical level of event boundaries (Zacks et al., 2001; Zacks & Tversky, 2001). Our results converge with perceptual studies, in which sensory changes contribute to duration estimation (Roseboom et al., 2019; Ahrens & Sahani, 2011). However, we deliberately shifted our focus from perceptual changes to event segmentation, so that the granularity of change is an event in a realistic scene. Events

exhibit complex characteristics, often involving animate agents engaged in goal-directed actions (e.g. ‘woman walking’, Fig. 5.3.1). Events are situations with specific spatio-temporal boundaries, formed spontaneously and continuously (Richmond & Zacks, 2017) and they include multiple salient or non-salient perceptual changes (Zacks et al., 2007). From this perspective, in agreement with the event segmentation literature (Ezzyat & Davachi, 2014; Brunec et al., 2020), we found that an increased number of events lengthens and accelerates experiential duration and speed of time, respectively. It is noteworthy that this runs counter-intuitive to the idea that longer duration implies slower times, suggesting that duration and speed reflect distinct psychological phenomena (Brighouse & Levitan, 2014; Droit-Volet & Wearden, 2015; Droit-Volet et al., 2017).

By analogy to canonical speed (i.e. traveled distance by unit of time), the phenomenology of the speed of time could reflect the rate of events per unit of time. One would expect that a time interval (e.g. 20 s) and the number of events in that interval (e.g. 7) need to be estimated before evaluating how fast the passage of time may feel (i.e.,  $7/20$  resulting in .3 events/second). If this were the case, a first prediction would be that RTs in Duration should be faster compared to Speed. Counter to this prediction, our findings reveal instead that participants’ responses were much faster in Speed than in Duration (by as much as ~100 ms). A second prediction would be that the effect of the number of events on Duration would be negatively correlated to the one on Speed. A weak correlation was indeed found. Our findings suggest that representing duration may not be a prerequisite for making a speed assessment and to the contrary, that a speed estimate may be computed earlier than a duration estimate. A consequence of this observation is that units of time must be available endogenously, before the full video has ended. This observation naturally lends itself to the notion of temporal structures (i.e. temporal windows or frames) within which information is integrated at distinct time scales (VanRullen & Koch, 2003; Ghallager & Varela, 2003; Pöppel, 1997, 2009; Wittmann, 2013). This observation is also compatible with recent neurophysiological proposals of time encoding (Issa et al, 2020; Tsao et al., 2022), the known existence of temporal windows of integration in perception (e.g. Yabe et al., 1998; Poeppel, 2003; van Wassenhove et al., 2007; Wutz et al., 2016) and in cortical hierarchies (e.g. Hasson et al., 2008; Lerner et al., 2011; Baldassano et al., 2017).



One explanation of our results is that faster passages of time may result from an increase in sensory information (i.e., noise) over time (Martin et al., 2017; Matthews & Meck, 2016). The speed of time would be influenced by the overall complexity of a scene, rather than relying on accurate estimates of duration. This explanation aligns well with the observed linear relationship between speed and event density across time scales. In an event segmentation framework, the constant updating of event models creates boundaries between the current representation and the previously held one (Richmond & Zacks, 2017; Shin & DuBrow, 2021). Therefore, the more boundaries are formed over time, the faster the experiential passage of time is predicted to be. This is also consistent with the decreased sensitivity to speed observed as the number of events increased. Importantly, duration estimates do not follow this trend. Instead, we observe a rescaling effect and a remarkable dependency on the objective video duration. No linear dependency with event density was found, and the number of events shifted participants' biases as expected (Ezzyat & Davachi, 2014).

The effect of temporal rate (or frequency) on duration has been largely explored in perception. Temporal rate can refer either to a single stimulus moving (e.g. grating) or flickering at a given temporal frequency, or to a series of simple stimuli that are perceived sequentially at a certain rate. The temporal frequency of a given stimulus has been shown to increase the duration of visual stimuli (Herbst et al., 2013) and rate adaptation yield subsequent stimuli to be compressed (Johnston et al., 2006; Eagleman, 2008; Matthews et al., 2014). Comparable distortions emerge when manipulating the predictability of a sequence (Tse et al., 2004; van Wassenhove et al., 2008). However, the simple stimuli used in these studies do not match the more complex dynamics of realistic scenes. Rather, the concept of rate of change goes beyond mere perceptual changes and encompasses dynamic changes in a scene that are parsed into higher cognitive constituents (e.g. a man is walking). Changes are not necessarily confined to a particular sensory modality and they extend beyond strictly perceptual aspects, thereby implicating mnemonic mechanisms and including internal mental states. Nevertheless, there exists a potential interplay between the temporal rate of stimuli in the environment and the rate of change in a scene, or even its segmentation into distinct episodes, that merits investigation (Howard & Kahana, 2002). This interaction holds promise for a more nuanced understanding of how temporal dynamics in a changing context relate to broader cognitive processes in scene segmentation.

Last, the presentation of a train event influenced both duration and speed. The mere presence of a train did not affect duration estimates, but the block in which the train appeared in the experiment did. Participants starting with a ‘train’ block tended to overestimate durations compared to those who started with a ‘no train’ block. One possible explanation is that the first block determines participants’ internal criterion and baseline temporal expectations. Regarding speed, participants were most sensitive to changes in stimuli in the absence of a ‘train’ and in the 3-event condition. The absence of a salient event coupled with fewer events could have increased boredom, decreased vigilance and reduced sensitivity by diverting attention. Indeed, boredom is an important predictor of experiential passage of time (Martinelli & Droit-Volet, 2022a). Alternatively, the salience of an event may affect the speed of time more than duration due to hierarchical event segmentation (Zacks & Tversky, 2001). Just as the sensitivity decreased with the increasing event density following coarser segmentation levels (Zacks, Tversky and Ier, 2001; Zacks & Tversky, 2001), the presence of a train could have yielded a higher-level scene parsing, resulting in a coarser segmentation into a pre-train and post-train episode potentially overshadowing the effect of finer events.

Altogether, we suggest, in agreement with event segmentation theories, that duration estimation (interval timing) derives from speed estimation. This hypothesis implies the stability of an internal updating process relying both on external event boundaries and on internal processes when clear boundaries are absent. The interplay between interval timing and the speed of time would be computationally linked through the rate of change, analogous to what is proposed in the spatial navigation system (Issa et al., 2020). Our current observations are limited in that both duration and speed estimates could result from a common dependency on objective duration. Nevertheless, our results hint at the fact that the temporal measure used in event segmentation studies essentially relies on a speed of time heuristics (i.e. rate of change) rather than interval timing. This observation provides an interesting novel link between time and memory processes.

### **Declaration of competing interests**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data are available upon request from the corresponding author. The stimuli and experimental design code are publicly available at

[https://github.com/mariannLK/design\\_stimuli](https://github.com/mariannLK/design_stimuli).

## Funding

This work was supported by the Agence nationale de la recherche [Project-ANR-18-CE22-0016].

## References

- Ahrens, M. B., & Sahani, M. (2011). Observers Exploit Stochastic Models of Sensory Change to Help Judge the Passage of Time. *Current Biology*, 21(3), 200–206. <https://doi.org/10.1016/j.cub.2010.12.043>
- Allan, L. G. (1998). The influence of the scalar timing model on human timing research. *Behavioural Processes*, 44(2), 101–117. [https://doi.org/10.1016/S0376-6357\(98\)00043-6](https://doi.org/10.1016/S0376-6357(98)00043-6)
- Baldassano, C., Chen, J., Zadbood, A., Pillow, J. W., Hasson, U., & Norman, K. A. (2017). Discovering Event Structure in Continuous Narrative Perception and Memory. *Neuron*, 95(3), 709–721.e5. <https://doi.org/10.1016/j.neuron.2017.06.041>
- Bates D, Mächler M, Bolker B, Walker S (2015). “Fitting Linear Mixed-Effects Models Using lme4.” *Journal of Statistical Software*, 67(1), 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Block, R. A., & Reed, M. A. (1978). Remembered duration: Evidence for a contextual-change hypothesis. *Journal of Experimental Psychology: Human Learning & Memory*, 4(6), 656–665. <https://doi.org/10.1037/0278-7393.4.6.656>
- Brighouse, C., & Levitan, C. (2014). Separate Timing Mechanisms for Duration and Rate Perception: Evidence and Implications. *Procedia - Social and Behavioral Sciences*, 126, 139–140. <https://doi.org/10.1016/j.sbspro.2014.02.346>
- Brunec, I. K., Ozubko, J. D., Ander, T., Guo, R., Moscovitch, M., & Barense, M. D. (2020). Turns during navigation act as boundaries that enhance spatial memory and expand time estimation. *Neuropsychologia*, 141(July 2019), 107437. <https://doi.org/10.1016/j.neuropsychologia.2020.107437>
- de Leeuw, J. R. (2015). jsPsych: A JavaScript library for creating behavioral experiments in a Web browser. *Behavior Research Methods*, 47(1), 1–12. <https://doi.org/10.3758/s13428-014-0458-y>
- Dennett, D. C., & Kinsbourne, M. (1992). Time and the observer: The where and when of consciousness in the brain. *Behavioral and Brain Sciences*, 15(2), 183–247. <https://doi.org/10.1017/S0140525X00068229>
- Droit-Volet, S., Trahanias, P., & Maniadas, M. (2017). Passage of time judgments in everyday life are not related to duration judgments except for long durations of several minutes. *Acta Psychologica*, 173, 116–121. <https://doi.org/10.1016/j.actpsy.2016.12.010>
- Droit-Volet, S., & Wearden, J. (2015). Passage of Time Judgments Are Not Duration Judgments: Evidence from a Study Using Experience Sampling Methodology. *Frontiers in Psychology*, 7. <https://www.frontiersin.org/articles/10.3389/fpsyg.2016.00176>
- Eagleman, D. M. (2008). Human time perception and its illusions. *Current Opinion in Neurobiology*, 18(2), 131–136. <https://doi.org/10.1016/j.conb.2008.06.002>
- Ezzyat, Y., & Davachi, L. (2014). Article Similarity Breeds Proximity : Pattern Similarity within and across Contexts Is Related to Later Mnemonic Judgments of Temporal Proximity. *NEURON*, 81(5), 1179–1189. <https://doi.org/10.1016/j.neuron.2014.01.042>
- Fabbi, M., Cancellieri, J., & Natale, V. (2012). The A Theory Of Magnitude (ATOM) model in temporal perception and reproduction tasks. *Acta Psychologica*, 139(1), 111–123. <https://doi.org/10.1016/j.actpsy.2011.09.006>
- Fox J, Weisberg S (2019). *An R Companion to Applied Regression*, Third edition. Sage, Thousand Oaks CA. <https://socialsciences.mcmaster.ca/ifax/Books/Companion/>.
- Fraisse, P. (1984). Perception and estimation of time. *Annual Review of Psychology*, 35, 1–36. <https://doi.org/10.1146/annurev.ps.35.020184.000245>

Gallagher, S., & Varela, F. J. (2003). Redrawing the Map and Resetting the Time: Phenomenology and the Cognitive Sciences. *Canadian Journal of Philosophy Supplementary Volume*, 29, 93–132. <https://doi.org/10.1080/00455091.2003.10717596>

Gruber, R. P., & Block, R. A. (2013). The Flow of Time as a Perceptual Illusion. *Journal of Mind and Behavior*, 34(1), 91–100.

Gruber, R. P., Smith, R. P., & Block, R. A. (2018). The Illusory Flow and Passage of Time within Consciousness: A Multidisciplinary Analysis. *Timing & Time Perception*, 6(2), 125–153. <https://doi.org/10.1163/22134468-2018e001>

Haas, J. K. (2014). A history of the unity game engine.

Hasson, U., Yang, E., Vallines, I., Heeger, D. J., & Rubin, N. (2008). A Hierarchy of Temporal Receptive Windows in Human Cortex. *Journal of Neuroscience*, 28(10), 2539–2550. <https://doi.org/10.1523/JNEUROSCI.5487-07.2008>

Herbst, S. K., Javadi, A. H., Van Der Meer, E., & Busch, N. A. (2013). How Long Depends on How Fast—Perceived Flicker Dilates Subjective Duration. *PLoS ONE*, 8(10), e76074. <https://doi.org/10.1371/journal.pone.0076074>

Hicks, R. E., Miller, G. W., & Kinsbourne, M. (1976). Prospective and Retrospective Judgments of Time as a Function of Amount of Information Processed. *The American Journal of Psychology*, 89(4), 719–730. <https://doi.org/10.2307/1421469>

Hicks, R. E., Miller, G. W., Gaes, G., & Bierman, K. (1977). Concurrent Processing Demands and the Experience of Time-in-Passing. *The American Journal of Psychology*, 90(3), 431–446. <https://doi.org/10.2307/1421874>

Hommel, B. (2011). The Simon effect as tool and heuristic. *Acta Psychologica*, 136(2), 189–202. <https://doi.org/10.1016/j.actpsy.2010.04.011>

Howard, M. W., & Kahana, M. J. (2002). A Distributed Representation of Temporal Context. *Journal of Mathematical Psychology*, 46(3), 269–299. <https://doi.org/10.1006/jmps.2001.1388>

Hubbard, E. M., Piazza, M., Pinel, P., & Dehaene, S. (2005). Interactions between number and space in parietal cortex. *Nature Reviews Neuroscience*, 6(6), 435–448. <https://doi.org/10.1038/nrn1684>

Ishihara, M., Keller, P. E., Rossetti, Y., & Prinz, W. (2008). Horizontal spatial representations of time: Evidence for the STEARC effect. *Cortex*, 44(4), 454–461. <https://doi.org/10.1016/j.cortex.2007.08.010>

Issa, J. B., Tocker, G., Hasselmo, M. E., Heys, J. G., & Dombeck, D. A. (2020). Navigating Through Time: A Spatial Navigation Perspective on How the Brain May Encode Time. *Annual Review of Neuroscience*, 43(1), 73–93. <https://doi.org/10.1146/annurev-neuro-101419-011117>

Johnston, A., Arnold, D. H., & Nishida, S. (2006). Spatially Localized Distortions of Event Time. *Current Biology*, 16(5), 472–479. <https://doi.org/10.1016/j.cub.2006.01.032>

Jording, M., Vogel, D. H. V., Viswanathan, S., & Vogeley, K. (2022). Dissociating passage and duration of time experiences through the intensity of ongoing visual change. *Scientific Reports*, 12(1), 1–15. <https://doi.org/10.1038/s41598-022-12063-1>

Kay M, Elkin L, Higgins J, Wobbrock J (2021). *ARTool: Aligned Rank Transform for Nonparametric Factorial ANOVAs*. doi:10.5281/zenodo.594511, R package version 0.11.1, <https://github.com/mjskay/ARTool>.

Kopec, C. D., & Brody, C. D. (2010). Human performance on the temporal bisection task. *Brain and Cognition*, 74(3), 262–272. <https://doi.org/10.1016/j.bandc.2010.08.006>

Kuznetsova A, Brockhoff PB, Christensen RHB (2017). “lmerTest Package: Tests in Linear Mixed Effects Models.” *Journal of Statistical Software*, 82(13), 1–26. doi:10.18637/jss.v082.i13.

Lenth R (2022). *\_emmeans: Estimated Marginal Means, aka Least-Squares Means\_*. R package version 1.8.3, <<https://CRAN.R-project.org/package=emmeans>>.

Lerner, Y., Honey, C. J., Silbert, L. J., & Hasson, U. (2011). Topographic Mapping of a Hierarchy of Temporal Receptive Windows Using a Narrated Story. *Journal of Neuroscience*, 31(8), 2906–2915. <https://doi.org/10.1523/JNEUROSCI.3684-10.2011>

Martin, B., Wiener, M., & van Wassenhove, V. (2017). A Bayesian Perspective on Accumulation in the Magnitude System. *Scientific Reports*, 7(1), Article 1. <https://doi.org/10.1038/s41598-017-00680-0>

Martinelli, N., & Droit-Volet, S. (2022a). Judgment of duration and passage of time in prospective and retrospective conditions and its predictors for short and long durations. *Scientific Reports*, 12(1), 22241. <https://doi.org/10.1038/s41598-022-25913-9>

Martinelli, N., & Droit-Volet, S. (2022b). What factors underlie our experience of the passage of time? Theoretical consequences. *Psychological Research*, 86(2), 522–530. <https://doi.org/10.1007/s00426-021-01486-6>

Matthews, W. J., Terhune, D. B., Rijn, H. van, Eagleman, D. M., Sommer, M. A., & Meck, W. H. (2014). Subjective Duration as a Signature of Coding Efficiency: Emerging Links Among Stimulus Repetition,

Predictive Coding, and Cortical GABA Levels. *Timing & Time Perception Reviews*, 1. <https://ugp.rug.nl/ttpr/article/view/15504>

Matthews, W. J., & Meck, W. H. (2016). Temporal cognition: Connecting subjective time to perception, attention, and memory. *Psychological Bulletin*, 142(8), 865–907. <https://doi.org/10.1037/bul0000045>

Michon, J. A. (1972). Processing of Temporal Information and the Cognitive Theory of Time Experience. In J. T. Fraser, F. C. Haber, & G. H. Müller (Eds.), *The Study of Time: Proceedings of the First Conference of the International Society for the Study of Time Oberwolfach (Black Forest)—West Germany* (pp. 242–258). Springer: [https://doi.org/10.1007/978-3-642-65387-2\\_17](https://doi.org/10.1007/978-3-642-65387-2_17)

Nicolai, C., Chaumon, M., & van Wassenhove, V. (2023, May 10). *Cognitive effects on duration estimation and passage of time judgments, prospectively, retrospectively, in and out of lockdown*. <https://doi.org/10.21203/rs.3.rs-2827534/v1>

Poeppel, D. (2003). The analysis of speech in different temporal integration windows: Cerebral lateralization as ‘asymmetric sampling in time.’ *Speech Communication*, 41(1), 245–255. [https://doi.org/10.1016/S0167-6393\(02\)00107-3](https://doi.org/10.1016/S0167-6393(02)00107-3)

Pöppel, E. (1997). A hierarchical model of temporal perception. *Trends in Cognitive Sciences*, 1(2), 56–61. [https://doi.org/10.1016/S1364-6613\(97\)01008-5](https://doi.org/10.1016/S1364-6613(97)01008-5)

Pöppel, E. (2009). Pre-semantically defined temporal windows for cognitive processing. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1525), 1887–1896. <https://doi.org/10.1098/rstb.2009.0015>

R Core Team (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.

Richmond, L. L., & Zacks, J. M. (2017). Constructing experience: Event models from perception to action. *Trends in cognitive sciences*, 21(12), 962-980. <https://doi.org/10.1016/j.tics.2017.08.005>

Roseboom, W., Fountas, Z., Nikiforou, K., Bhowmik, D., Shanahan, M., & Seth, A. K. (2019). Activity in perceptual classification networks as a basis for human subjective time perception. *Nature Communications*, 10(1), 267. <https://doi.org/10.1038/s41467-018-08194-7>

RStudio Team (2020). RStudio: Integrated Development for R. RStudio, PBC, Boston, MA URL <http://www.rstudio.com/>

Schütt, H. H., Harmeling, S., Macke, J. H., & Wichmann, F. A. (2016). Painfree and accurate Bayesian estimation of psychometric functions for (potentially) overdispersed data. *Vision Research*, 122, 105–123. <https://doi.org/10.1016/j.visres.2016.02.002>

Shin, Y. S., & DuBrow, S. (2021). Structuring Memory Through Inference-Based Event Segmentation. *Topics in Cognitive Science*, 13(1), 106–127. <https://doi.org/10.1111/tops.12505>

Thönes, S., & Oberfeld, D. (2015). Time perception in depression: A meta-analysis. *Journal of Affective Disorders*, 175, 359–372. <https://doi.org/10.1016/j.jad.2014.12.057>

Tsao, A., Yousefzadeh, S. A., Meck, W. H., Moser, M.-B., & Moser, E. I. (2022). The neural bases for timing of durations. *Nature Reviews Neuroscience*, 23(11), 646–665. <https://doi.org/10.1038/s41583-022-00623-3>

Tse, P. U., Intriligator, J., Rivest, J., & Cavanagh, P. (2004). Attention and the subjective expansion of time. *Perception & Psychophysics*, 66(7), 1171–1189. <https://doi.org/10.3758/bf03196844>

van Driel, J., Knapen, T., van Es, D. M., & Cohen, M. X. (2014). Interregional alpha-band synchrony supports temporal cross-modal integration. *NeuroImage*, 101, 404–415. <https://doi.org/10.1016/j.neuroimage.2014.07.022>

van Wassenhove, V., Buonomano, D. V., Shimojo, S., & Shams, L. (2008). Distortions of Subjective Time Perception Within and Across Senses. *PLoS ONE*, 3(1), e1437. <https://doi.org/10.1371/journal.pone.0001437>

van Wassenhove, V., Grant, K. W., & Poeppel, D. (2007). Temporal window of integration in auditory-visual speech perception. *Neuropsychologia*, 45(3), 598–607. <https://doi.org/10.1016/j.neuropsychologia.2006.01.001>

van Wassenhove, V. (2009). Minding time in an amodal representational space. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1525), 1815–1830. <https://doi.org/10.1098/rstb.2009.0023>

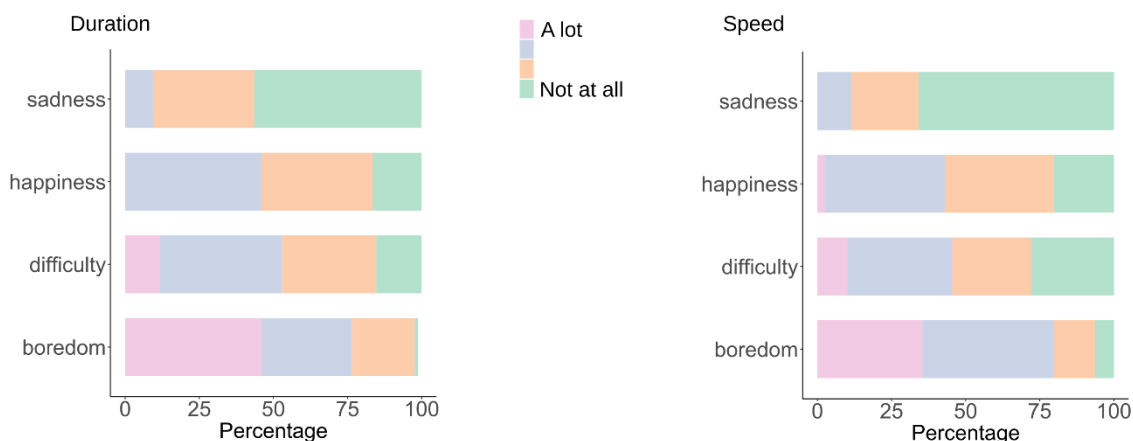
van Wassenhove, V. (2022). Cognitive neuroscience of time: Nows, timelines, and chronologies. In *Time and Science* (1–3, pp. 97–129). WORLD SCIENTIFIC (EUROPE). [https://doi.org/10.1142/9781800613751\\_0005](https://doi.org/10.1142/9781800613751_0005)

van Wassenhove, V. (2023). Cracking the Neural Code of How the Brain Represents Time May Make the Dualistic Stance Obsolete. *Timing & Time Perception*, 1(aop), 1–9. <https://doi.org/10.1163/22134468-bja10099>

VanRullen, R., & Koch, C. (2003). Is perception discrete or continuous? *Trends in Cognitive Sciences*, 7(5), 207–213. [https://doi.org/10.1016/S1364-6613\(03\)00095-0](https://doi.org/10.1016/S1364-6613(03)00095-0)

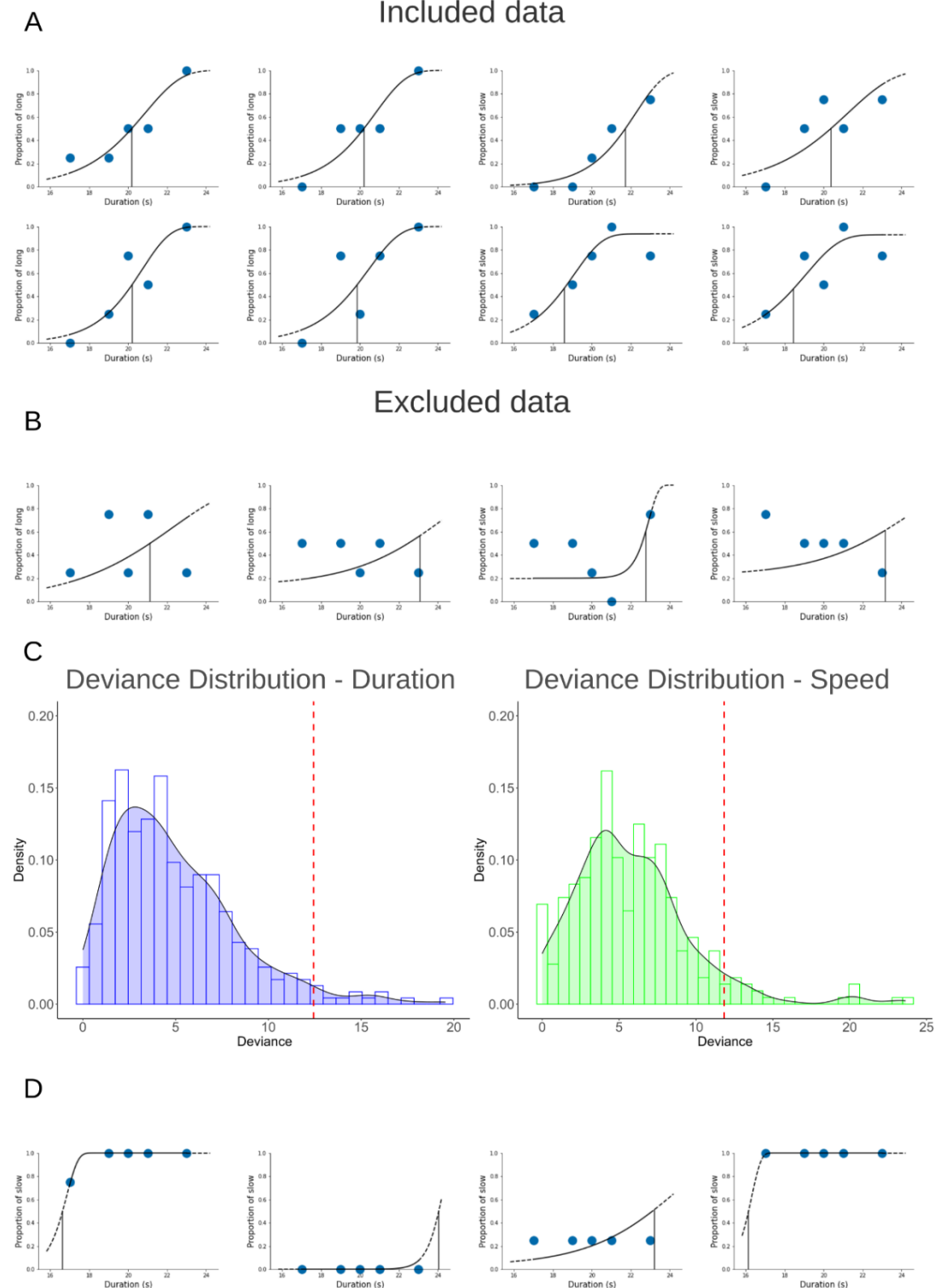
- Vatakis, A., Balci, F., Di Luca, M., & Correa, Á. (2018). Timing and Time Perception: Procedures, Measures, & Applications. *Timing and Time Perception: Procedures, Measures, & Applications*. <https://doi.org/10.1163/9789004280205>
- Wearden, J. H. (2015). Passage of time judgements. *Consciousness and Cognition*, 38(October 2014), 165–171. <https://doi.org/10.1016/j.concog.2015.06.005>
- Wichmann, F. A., & Hill, N. J. (2001). The psychometric function: I. Fitting, sampling, and goodness of fit. *Perception and Psychophysics*, 63(8), 1293–1313. <https://doi.org/10.3758/BF03194544>
- Wickham H (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York. ISBN 978-3-319-24277-4, <https://ggplot2.tidyverse.org>.
- Wiener, M., Parikh, A., Krakow, A., & Coslett, H. B. (2018). An intrinsic role of beta oscillations in memory for time estimation. *Scientific Reports*, 8(1), 1–17. <https://doi.org/10.1038/s41598-018-26385-6>
- Wittmann, M. (2013). The inner sense of time: How the brain creates a representation of duration. *Nature Reviews Neuroscience*, 14(3), Article 3. <https://doi.org/10.1038/nrn3452>
- Wutz, A., Muschter, E., van Koningsbruggen, M. G., Weisz, N., & Melcher, D. (2016). Temporal Integration Windows in Neural Processing and Perception Aligned to Saccadic Eye Movements. *Current Biology*, 26(13), 1659–1668. <https://doi.org/10.1016/j.cub.2016.04.070>
- Yabe, H., Tervaniemi, M., Sinkkonen, J., Huotilainen, M., Ilmoniemi, R. J., & Näätänen, R. (1998). Temporal window of integration of auditory information in the human brain. *Psychophysiology*, 35(5), 615–619. <https://doi.org/10.1017/S0048577298000183>
- Zacks, J. M., & Tversky, B. (2001). Event structure in perception and conception. *Psychological bulletin*, 127(1), 3. <https://doi.org/10.1037/0033-2909.127.1.3>
- Zacks, J. M., Tversky, B., & Iyer, G. (2001). Perceiving, remembering, and communicating structure in events. *Journal of Experimental Psychology: General*, 130(1), 29–58. <https://doi.org/10.1037/0096-3445.130.1.29>
- Zacks, J. M., Speer, N. K., Swallow, K. M., Braver, T. S., & Reynolds, J. R. (2007). Event Perception: A Mind/Brain Perspective. *Psychological Bulletin*, 133(2), 273–293. <https://doi.org/10.1037/0033-2909.133.2.273>
- Zakay, D., & Block, R. A. (1997). Temporal Cognition. *Current Directions in Psychological Science*, 6(1), 12–16. <https://doi.org/10.1111/1467-8721.ep11512604>

## Supplementary Materials



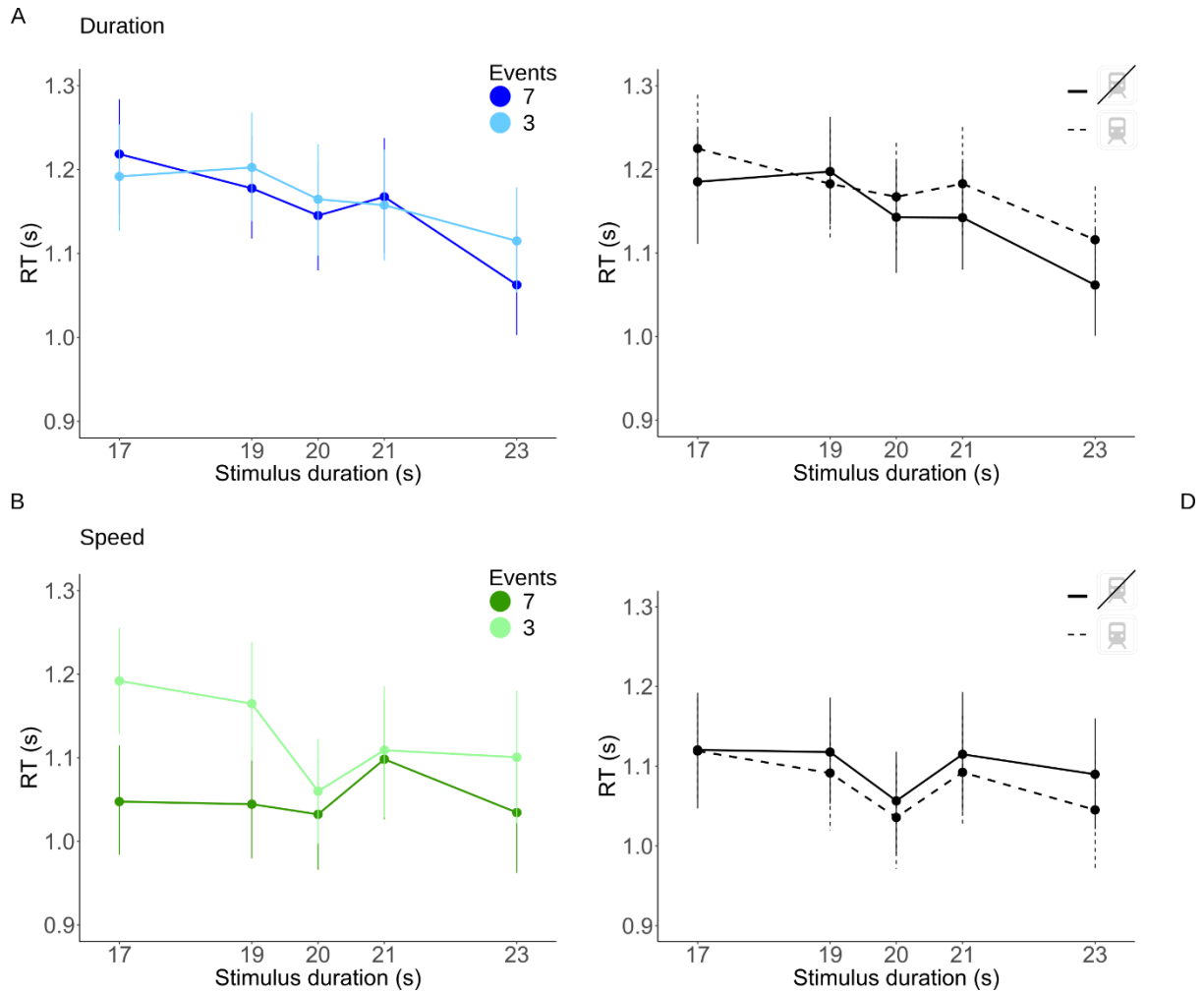
**Figure 5.3.S1. Emotional state and task difficulty ratings do not affect Duration and Speed estimates.** Participants' emotional states and difficulty ratings were collected to test whether they systematically affected their time estimations. After each test, participants rated their sadness, happiness, task difficulty and boredom on a 4 point Likert scale ranging from "not at all" to "a lot". The percentage of choices in each of the four tested categories after the Duration (left) and Speed (right) are reported. Neither participants' rating of emotional state nor of task difficulty significantly accounted for Duration or Speed judgments. Duration:  $\chi^2(4) = 4.82$ ,  $p = 0.3$  for boredom;  $\chi^2(2) = 0.06$ ,  $p = 0.97$  for happiness;  $\chi^2(2) =$

3.8,  $p = 0.15$  for sadness and,  $\chi^2(3) = 0.35$ ,  $p = 0.95$  for difficulty. Speed: ( $\chi^2(3) = 1.04$ ,  $p = 0.8$  for boredom;  $\chi^2(3) = 5.48$ ,  $p = 0.14$  for happiness;  $\chi^2(2) = 1.68$ ,  $p = 0.43$  for sadness;  $\chi^2(3) = 6.61$ ,  $p = 0.08$  for difficulty).



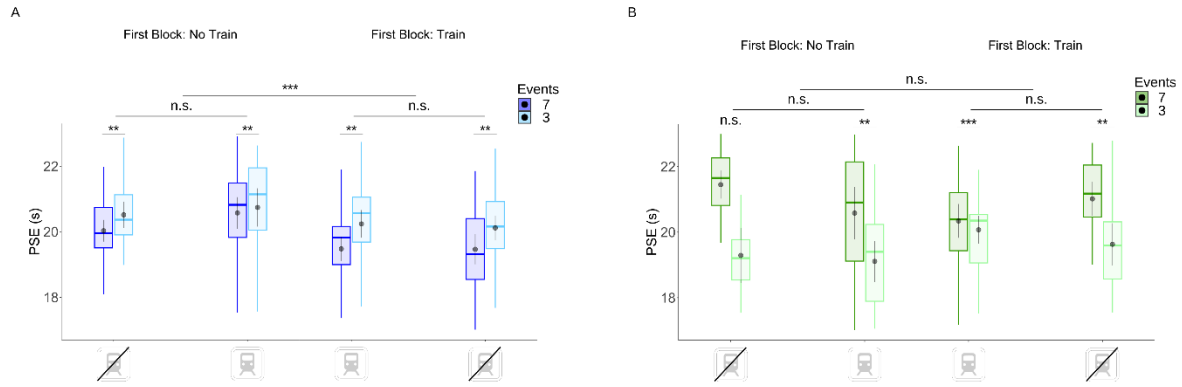
**Figure 5.3.S2. Examples of psychometric fits.** A. Examples of individual psychometric fits, which were included in all statistical analyzes using individuals' PSE for Duration (left) and Speed (right). B. Examples of bad fits that were excluded from all analyses using individuals' PSE due to a high Deviance score (goodness of fit statistic) in Psignifit (see Methods). C. Histogram and density plot of the Deviance distribution for Duration (left) and Speed (right). The red dashed line denotes the mean Critical Deviance value. Fits above the critical Deviance value were excluded from all analyses using psychometric parameters. D. Examples of fits that showed an extreme bias towards one of the two possible responses

(answers below 25% or above 75% for all stimulus durations). These fits were also excluded from all analyses using psychometric parameters. In the Speed bisection task, 42 out of the 90 excluded fits (90 out of 316) were excluded due to extreme biases. However, including or excluding data from these participants did not alter the results reported in the logistic regression of Fig. 2A.



**Figure 5.3.S3. Reaction times did not follow an inverted U shape pattern.** A. Mean reaction times (RTs) for each stimulus duration in the duration bisection task. On the left, 3 and 7 events are in light and dark blue respectively; on the right, with and without train are in dotted and continuous line, respectively. Error bars are 95% CI. B. Mean RTs for each stimulus duration in the Speed bisection task. On the left, 3 and 7 events are light and dark green, respectively; on the right, with and without a train in dotted and continuous line, respectively. Error bars are 95% CI. Contrary to expectations, RTs did not follow an inverted U shape pattern in either task.





**Figure 5.3.S4. The order of the train blocks influenced participants' judgments.** A. Boxplots of the PSE parameters extracted from the duration bisection task. Blocks (train, no train) are separated based on the order with which they appeared. 3 and 7 event conditions are shown with light and dark blue, respectively. The mean and 95% CI are plotted for each event/train combination with dark gray. B. Boxplots of the PSE parameters extracted from the duration bisection task. Blocks (train, no train) are separated based on the order with which they appeared. 3 and 7 event conditions are shown with light and dark green, respectively.

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Event list

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- Human walking
- Human phoning
- Human pacing
- Human running
- Elder walking (walker)
- Human skating
- Human running
- Child dancing/playing/running
- Train passing/arriving

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**Table 5.3.S1.** List of possible events in the stimuli.  
 Human: adult male/female; teenager male/female; elder female/male.  
 Possible items carried: briefcase; bag; walker; phone; headphones.  
 Human actions happen alone or in pairs.  
 Actions for humans end when out of scene; sits on a bench; stands idle.  
 Human events happen either on background or foreground; Train events position is counterbalanced.  
 Duration of each event was constant across videos; two humans were idle in the background in every video.

Duration		Speed	
Strategies used	Participants that used them	Strategies used	Participants that used them

Character movement (speed)	19 (8)	Character movement (speed)	52 (23)
Presence of train (speed)	13 (7)	Presence of train (speed)	23 (14)
Number of characters	9	Number of characters	11
Level of boredom	2	Level of boredom	3
Personal time/ General feeling	8	Duration/ General feeling	25
Sound	1	Sound	5
No strategy	42	General movement	7
		No strategy	22

**Table 5.3.S2.** Strategies reported by participants for the duration and Speed judgments.

<i>Predictors</i>	<b>Logrt - Duration</b>			
	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>df</i>
(Intercept)	7.34	7.20 – 7.47	<b>&lt;0.001</b>	892.15
Stimulus duration	-0.02	-0.02 – -0.01	<b>&lt;0.001</b>	1613.00
Train presence	0.03	0.01 – 0.06	<b>0.005</b>	1613.00
<b>Random Effects</b>				
$\sigma^2$	0.06			
$\tau_{00 \text{ ID}}$	0.10			
ICC	0.63			
$N_{\text{ID}}$	85			
Observations	1700			
Marginal $R^2$ / Conditional $R^2$	0.010 / 0.631			
AIC	366.516			

**Table 5.3.S3.** Model results for logRTs for duration. Significant p-values are bold.

<i>Predictors</i>	<b>Logrt - Speed</b>			
	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>df</i>
(Intercept)	6.91	6.70 – 7.11	<b>&lt;0.001</b>	1314.50
Stimulus duration	-0.00	-0.01 – 0.01	0.668	1498.00
Event number	0.44	0.17 – 0.71	<b>0.001</b>	1498.00
stimulus x event	-0.02	-0.03 – -0.01	<b>0.006</b>	1498.00
<b>Random Effects</b>				
$\sigma^2$	0.07			
$T_{00 \text{ ID}}$	0.12			

ICC	0.63
N <sub>ID</sub>	79
<hr/>	
Observations	1580
Marginal R <sup>2</sup> / Conditional R <sup>2</sup>	0.010 / 0.629
AIC	677.014

**Table 5.3.S4.** Model results for logRTs for Speed. Significant p-values are bold.

<i>Predictors</i>	<i>Estimates</i>	<b>PSE - Duration</b>		
		<i>CI</i>	<i>p</i>	<i>df</i>
(Intercept)	20.19	19.92 – 20.47	<b>&lt;0.001</b>	130.20
Event number	0.53	0.25 – 0.82	<b>&lt;0.001</b>	219.46
Block order	-0.63	-0.95 – -0.31	<b>&lt;0.001</b>	74.72
<b>Random Effects</b>				
$\sigma^2$	1.52			
T <sub>00 ID</sub>	0.09			
ICC	0.06			
N <sub>ID</sub>	85			
<hr/>				
Observations	293			
Marginal R <sup>2</sup> / Conditional R <sup>2</sup>	0.093 / 0.145			
AIC	984.185			

**Table 5.3.S5.** Model results for PSE for duration. Significant p-values are bold.

<i>Predictors</i>	<i>Estimates</i>	<b>PSE - Speed</b>		
		<i>CI</i>	<i>p</i>	<i>df</i>
(Intercept)	21.41	20.95 – 21.87	<b>&lt;0.001</b>	174.84
Event number	-2.41	-3.14 – -1.69	<b>&lt;0.001</b>	161.35
Train presence	-0.77	-1.27 – -0.28	<b>0.002</b>	148.97
Block order	-0.31	-0.87 – 0.24	0.265	137.81
event x train	0.99	0.24 – 1.74	<b>0.010</b>	157.97
event x block	1.12	0.37 – 1.87	<b>0.004</b>	158.11
<b>Random Effects</b>				
$\sigma^2$	1.70			
T <sub>00 ID</sub>	0.27			
ICC	0.14			
N <sub>ID</sub>	75			
<hr/>				
Observations	206			

Marginal R<sup>2</sup> / Conditional R<sup>2</sup> 0.217 / 0.322

AIC 737.280

**Table 5.3.S6.** Model results for PSE for Speed. Significant p-values are bold.