The neural and behavioral basis of serial dependence in time perception

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Contents

Abstract

Sequential bias influences decision-making by leveraging past experiences to shape current perception. This phenomenon has been extensively studied in the visual domain, however, only a handful of recent behavioral studies have explored trial-to-trial sequential effects on timing, and even fewer have linked these effects to specific neural signatures. This leaves a significant gap in our understanding of neural mechanisms underlying temporal sequential effects at play. Moreover, the underlying mechanisms of whether serial dependence arises from perceptual or post-perceptual processes remain debatable. One perspective posits it as a perceptual mechanism aiding perceptual stability and temporal continuity by integrating past and current information to filter out abrupt noises. Alternatively, recent insights link it to decision-related post-perceptual factors, with working memory playing a crucial role in integrating preceding stimuli with current sensory inputs for decision-making and motor plans.

Therefore, this thesis aims to investigate the serial dependence effect in time perception. To begin with, Chapter 2 explores the impact of task measurements and task relevance on temporal sequential biases using a dual-feature random dot kinematogram. Participants encoded both features (duration and direction) and reported one based on a post-cue. The preceding duration-report trials were task-relevant, while the previous direction-report trials were considered task-irrelevant. Two experiments, employing time discrimination task and duration reproduction tasks, were conducted to further explore the influence of task measurements. Chapter 3 addresses sequential dependence in both motion direction and temporal perception concurrently. It utilized a unified experimental paradigm employing coherent motion stimulus for direction and time reproduction tasks. Additionally, two experiments varied the cue setting where participants were informed about the task before (pre-cue setting) or after (post-cue setting) the stimulus to further explore the influence of working memory underlying spatial and temporal serial dependence effect. Chapter 4 investigates the neural mechanisms underlying serial dependence in a duration reproduction task in conjunction with functional Magnetic Resonance Imaging (fMRI) scanning. Participants were required to remember the stimulus duration, and then either reproduce it or passively observe it, as instructed by the cue. This design allowed us to compare how the post-perceptual factors contribute to sequential dependence and further explore the neural representations underlying such bias.

Our studies consistently identify an attractive sequential bias in time perception, where durations are perceived as longer following longer previous durations, and vice versa. In Chapter 2, task measurements significantly influence sequential dependence in time perception. The discrimination task shows consistent sequential effects regardless of whether it follows a timing or direction task. Conversely, the reproduction task exhibits a more pronounced sequential effect following the same timing task compared to the direction task. Findings in Chapter 3 reveal an attraction bias in time reproduction and a repulsion in direction estimation. The temporal attraction was more pronounced when the preceding task

was also time-related, while direction repulsion remains unaffected by the preceding task. Additionally, both attraction and repulsion biases were intensified by the post-cue compared to the pre-cue. These results suggest that opposing sequential effects in spatial and temporal domains may originate from different processing stages linked to sensory adaptation and post-perceptual processes involving working memory. In Chapter 4, at the neural level, our results link striato-thalamo-cortical and performance monitoring networks to time perception and prior tasks, respectively. Notably, we observed that hippocampus activity was directly linked with the sequential bias on both prior tasks and prior duration. This hippocampal activation was particularly evident during the encoding phase following passive viewing trials and led to a decrease in sequential bias. These findings highlight the involvement of post-perceptual stages that link sensory representations to responses and underscore the critical role of active timing-related and memory networks in the temporal sequential dependence.

Deutsche Zusammenfassung

Der sequenzielle Bias beeinflusst die Entscheidungsfindung, indem vergangene Erfahrungen genutzt werden, um die aktuelle Wahrnehmung zu formen. Dieses Phänomen wurde im visuellen Bereich intensiv erforscht. Allerdings haben nur wenige neuere Verhaltensstudien die Versuch-zu-Versuch-sequenziellen Effekte auf das Zeitverhalten untersucht, und noch weniger Arbeiten haben diese Effekte mit spezifischen neuronalen Signaturen in Verbindung gebracht. Dies führt zu einer erheblichen Wissenslücke hinsichtlich der neuronalen Mechanismen, die den zeitlichen sequenziellen Effekten zugrunde liegen. Zudem bleibt die Frage offen, ob die serielle Abhängigkeit aus perzeptuellen oder postperzeptuellen Prozessen resultiert. Ein Ansatz sieht die serielle Abhängigkeit als perzeptuellen Mechanismus, der die Wahrnehmungsstabilität und zeitliche Kontinuität unterstützt, indem frühere und aktuelle Informationen integriert werden, um plötzliche Störungen herauszufiltern. Alternativ wird die serielle Abhängigkeit mit entscheidungsbezogenen postperzeptuellen Prozessen in Verbindung gebracht, wobei das Arbeitsgedächtnis eine entscheidende Rolle bei der Integration früherer Reize mit aktuellen sensorischen Eingaben für die Entscheidungsfindung und Handlungsplanung spielt.

Ziel dieser Arbeit ist es, den Effekt der seriellen Abhängigkeit in der Zeitwahrnehmung zu untersuchen. In Kapitel 2 wird untersucht, wie Aufgabenmessungen und Aufgabenrelevanz zeitliche Verzerrungen beeinflussen. Die Teilnehmenden kodierten sowohl Dauer als auch Richtung und gaben eines dieser Merkmale nach einem Hinweis (Post-Cue) an. Zwei Experimente – eine Zeitdiskriminationsaufgabe und eine Dauerreproduktionsaufgabe – wurden durchgeführt, um den Einfluss dieser Messungen zu erforschen. Kapitel 3 untersucht die serielle Abhängigkeit in der Bewegungsrichtung und Zeitwahrnehmung mit einem kohärenten Bewegungsstimulus. Zwei Experimente variierten, ob die Teilnehmenden vor (Pre-Cue) oder nach (Post-Cue) dem Stimulus über die Aufgabe informiert wurden,

um den Einfluss des Arbeitsgedächtnisses zu testen. Kapitel 4 erforscht die neuronalen Mechanismen der seriellen Abhängigkeit bei einer Dauerreproduktionsaufgabe mittels fMRI. Die Teilnehmenden mussten die Stimulusdauer entweder reproduzieren oder passiv beobachten, was half, den Einfluss postperzeptueller Faktoren und die zugrunde liegenden neuronalen Repräsentationen zu untersuchen.

Unsere Studien zeigen durchgängig einen attraktiven sequenziellen Bias in der Zeitwahrnehmung, bei dem Zeitspannen nach längeren vorherigen Zeitspannen als länger wahrgenommen werden und umgekehrt. In Kapitel 2 wurde festgestellt, dass Aufgabenmessungen einen signifikanten Einfluss auf die serielle Abhängigkeit in der Zeitwahrnehmung haben. Die Diskriminationsaufgabe zeigte konsistente sequenzielle Effekte, unabhängig davon, ob sie auf eine Zeit- oder eine Richtungsaufgabe folgte. Im Gegensatz dazu wies die Reproduktionsaufgabe einen stärkeren sequenziellen Effekt auf, wenn sie auf eine vorherige Zeitaufgabe folgte, im Vergleich zu einer vorherigen Richtungsaufgabe. Kapitel 3 zeigte einen Anziehungsbias in der Zeitreproduktion und einen Abstoßungsbias in der Richtungsschätzung. Der zeitliche Anziehungsbias war stärker ausgeprägt, wenn die vorherige Aufgabe ebenfalls zeitbezogen war, während die Richtungsabstoßung von der vorherigen Aufgabe unbeeinflusst blieb. Darüber hinaus verstärkten sich sowohl der Anziehungs- als auch der Abstoßungsbias durch den Post-Cue im Vergleich zum Pre-Cue. Diese Ergebnisse deuten darauf hin, dass entgegengesetzte sequenzielle Effekte im räumlichen und zeitlichen Bereich auf unterschiedliche Verarbeitungsstufen zurückgeführt werden können, die mit sensorischer Adaption und postperzeptuellen Prozessen zusammenhängen, welche das Arbeitsgedächtnis einbeziehen. In Kapitel 4 konnten wir auf neuronaler Ebene unsere Ergebnisse mit striato-thalamo-kortikalen Netzwerken und Performanzüberwachungsnetzwerken in Verbindung bringen, die jeweils für die Zeitwahrnehmung und die vorherigen Aufgaben verantwortlich sind. Insbesondere beobachteten wir, dass die Aktivität des Hippocampus direkt mit dem sequenziellen Bias sowohl für vorherige Aufgaben als auch für vorherige Zeitspannen verknüpft war. Diese hippocampale Aktivierung war besonders während der Enkodierungsphase nach passiven Beobachtungsdurchgängen ausgeprägt und führte zu einer Verringerung des sequenziellen Bias. Diese Erkenntnisse unterstreichen die Bedeutung postperzeptueller Stufen, die sensorische Repräsentationen mit Reaktionen verknüpfen, und heben die entscheidende Rolle von zeitbezogenen Netzwerken und Gedächtnisnetzwerken in der zeitlichen seriellen Abhängigkeit hervor.

Keywords: Time perception; Serial dependence effect, Attraction; Repulsion; Task relevance; Working memory; Post-perceptual processes

Overview

This dissertation comprises a general introduction, three research chapters, and a general discussion, all centered around the serial dependence effect in time perception, examining both behavioral (Chapter 2 and Chapter 3) and neural (Chapter 4) mechanisms underlying temporal serial dependence.

Chapter 1: General introduction - This chapter provides an overview of research in the field, emphasizing sequential effects in time perception and debates surrounding the underlying mechanisms. It highlights the inconsistency in findings across different measurements and introduces the research gap and aims of the current studies.

Chapter 2: Task types affect serial dependence in time perception - Here, we investigate how task relevance and types influence temporal sequential biases using a dual-feature random dot kinematogram (RDK). Participants encoded duration and direction, with preceding duration-report trials considered task-relevant. We compare temporal sequential biases in time discrimination and duration reproduction tasks. Findings underscore the crucial role of task nature in shaping sequential dependence in time perception, probably modulated by working memory processes that link sensory representation and task-specific decision criterion.

Chapter 3: Distinct sequential effects in space and time - We employ a unified experimental paradigm to examine sequential effects in spatial and temporal domains. Findings reveal an attraction bias in time reproduction and a dominant repulsion in direction estimation, with temporal attraction more pronounced when the preceding task is time-related, indicating distinct sequential effects in spatial and temporal perception. Both biases intensify with the post-cue compared to the pre-cue, highlighting the role of working memory underlying sequential effects in both spatial and temporal tasks.

Chapter 4: Neural mechanisms of sequential dependence in time perception - Using functional Magnetic Resonance Imaging (fMRI), we investigated neural mechanisms underlying temporal sequential dependence. Sequential biases in time perception are evident only when the preceding task involves active duration reproduction. Neurally, activation in timing-related and performance monitoring networks were observed during the task when a duration reproduction trial was anticipated. Importantly, the hippocampus correlates with sequential biases, emphasizing the role of memory networks in shaping time-related sequential biases at post-perceptual stages.

Chapter 5: General discussion - The dissertation systematically explores behavioral and neural mechanisms underlying serial dependence in time perception, emphasizing task types, task relevance, and working memory. Integrating behavioral assessments and fMRI, the studies delineate cognitive processes governing temporal estimates and shed light on underlying mechanisms of temporal serial dependence. The findings enhance our understanding of temporal processing and sequential biases, laying groundwork for further investigations into the underlying cognitive and neural mechanisms.

1 General Introduction

1.1 The serial dependence effect in time perception

Time perception is a crucial element of the human mind, involving a fundamental mental ability that underlies cognitive and perceptual functions. This ability allows organisms to gauge *when* events occur and their *duration*, connecting memories of the past, present sensations and expectations about the future. Usually, our subjective timing is not the exact as the physical time, and is susceptible to various factors, such as attention, memory, sensory modality, psychophysical task, and temporal context (Lapid et al., 2008; Penney et al., 2000; Shi, Church, et al., 2013; Treisman & Williams, 1984; Wittmann, 2009). Research has demonstrated that our time perception was context dependent (Baykan & Shi, 2023; Ofir & Landau, 2022). For example, when we are waiting in line, our perception of waiting time is influenced by the pace of the adjacent queue. Seeing a faster-moving line nearby can make our own wait feel longer, this is because we compare our own waiting time with the progressing time of other queues, creating a subjective experience of time that doesn't necessarily align with the objective passage of time.

Early research on time perception has shown that our subjective duration can be biased toward recent history (Burr et al., 2009; Jazayeri & Shadlen, 2010; Nakajima et al., 1992; Vierordt, 1868), leading to an underestimation of long durations and an overestimation of short durations (Glasauer & Shi, 2021; Hollingworth, 1910). In 1868, Vierordt published *Der Zeitsinn nach Versuchen* and this seminal book was the first quantitative attempt to investigate time perception (Vierordt, 1868). One of his main findings is now known as *Vierordt's Law (Glasauer & Shi, 2021; Wearden, 2023)*, a tendency to overestimate short durations and underestimate long durations. Similar effects are found in magnitude estimation tasks (Lejeune & Wearden, 2009; Penney et al., 2000; Taatgen & van Rijn, 2011). For example, Hollingworth (1910) demonstrated *Vierordt's Law* for a length reproduction task, where small lengths are overestimated, whereas longer lengths are inevitably shortened, showing the *central tendency effect*. An early explanation of the central tendency bias, proposed by Helson (Helson, 1964), is that the percept of the current quantity is assimilated to the past background context - the mean of the sampled magnitudes. In the absence of any information, the mean of all the magnitudes presented may be the best estimate of any individual one in terms of being the smallest absolute deviation from it. Recent quantitative Bayesian approaches suggest that biases come from the integration of the sensory measures and the prior knowledge acquired from the past is optimally integrated with the sensory measures, either static or iteratively (Jazayeri & Shadlen, 2010; Petzschner & Glasauer, 2011).

The central tendency effect in time perception is influenced by various factors, including individual characteristics, sensory modality, and stimulus set properties. For instance, expert musicians, known for their heightened time perception, exhibit fewer central tendency biases in temporal reproduction compared to non-musicians (Vibell et al., 2021). Conversely, individuals with Parkinson's

disease, characterized by dysfunctional dopaminergic regulations in the striatum and disturbances in interval timing, display stronger central tendency biases than healthy controls (Malapani et al., 1998). Previous studies have shown that time estimations across different sensory modalities may be different (Goldstone & Lhamon, 1972), for example, auditory stimuli are more precisely encoded compared to visual stimuli. Additionally, the central tendency is also known to be more pronounced for larger sample intervals as compared to shorter sample intervals, known as the *range effect (Jazayeri & Shadlen, 2010)*.

The other phenomenon in time perception that is frequently studied is the *sequential effect*, which is different from the central tendency effect, for it refers to the influence of recent past trials on the perception of the current stimuli, rather than a tendency to the average or mean value of a set of stimuli. Early in the history of psychological research, most tasks consist of a long sequence of discrete trials differing in the stimuli. Researchers noticed that the response on a particular trial could depend on the previous sequence of trials (Fernberger, 1920; Turner, 1931). For instance, in Hollingworth's length reproduction experiments (1910), he hinted some sort of influence of the preceding trials on judgements of the current one, showing a trial-by-trial assimilation. But he seemed to have a rather ambiguous attitude to this sort of assimilation, arguing that each impression leaves a mental set which tends more or less to assimilate a succeeding impression, apparently suggesting some sort of trial-by-trial assimilative process. One can see intuitively how what one might call "one-back assimilation" or "sequential effect", that is, an effect on the subjective value of the current stimulus by the preceding one, might explain Hollingworth's basic result. Historically, sequential effects have been widely documented in judgments of length, size, number, and duration (Bevan & Turner, 1964; Cicchini et al., 2014; Hollingworth, 1910; Wiener et al., 2014), and people tend to judge a current stimulus as similar to a previous one.

Early researchers have raised an important question about what is driving sequential effects: is it the physical attributes of the stimuli or the judgements made about those same stimuli? Though early psychophysical studies attempted to disentangle this ambiguity and tried to figure out the source of sequential effect, it's hard to distinguish the perception of a stimulus and the judgment on it, because most of the experiments involved the procedure that perception of a stimulus is always followed by a judgment. Sometimes, the distinction between perception and judgment is controversial, especially in nonvisual modalities (Keller, 2016). For example, in a traditional signal detection task, participants are tasked with discerning a series of auditory stimuli and determining the presence or absence of a target sound (e.g., a high-pitched tone) (Kerkhof et al., 1980). In such scenarios, the perception and judgment of the target sound intertwine, especially when the target signal is weak. However, in the current dissertation, we adopt a refined conceptualization of perception and judgment. Perception involves the initial reception of sensory input, whereas judgment encompasses the evaluation and decision-making processes based on that information. This conceptual demarcation plays a pivotal role in elucidating sequential effects.

Sequential effects, also known as carryover effects, manifest as the impact of prior trials on subsequent ones. The carryover effects can be divided into two primary categories: sensory carryover and decisional carryover. Both sensory and decisional carryover effects refer to the influence of the previous trials on the current trials, the key difference between them is that sensory carryover denotes how past stimuli shape current perception, while decisional carryover is contingent upon prior responses.

Decisional carryover highlights the influence of prior responses and has been widely documented in the literature. Early researchers noted that trial-to-trial responses exhibited sequential dependence (also known as "Choice history biases"), leading to an alternation bias and a repetition bias (Urai et al., 2019). The alternation bias refers to the tendency to alternate choices for successive judgements. In an early experiment, Fernberger (1920) instructed participants to compare two different weights in each trial, and he observed such bias when, on a given trial, the reference weight was judged to be "lighter", in the next trial the reference weight would be more likely to be judged "heavier", and vice-versa. This alternation effect was greater the closer the two weights being compared were. Conversely, the repetition bias is the tendency to persistently repeat previous choices. The repetition bias is widely documented in judgments of length, size, number, and duration (Bevan & Turner, 1964; Cicchini et al., 2014; Hollingworth, 1910; Wiener et al., 2014). The decisional carryover effect in temporal judgment has been consistently replicated in recent studies, emphasizing the enduring influence of prior decision (Wehrman et al., 2023; Wehrman, Wearden, et al., 2020; Wiener et al., 2014). For example, Wiener et al. (2014) identified an assimilation between successive judgments, wherein a prior judgment of a duration as "Long" increased the likelihood of judging the current duration as "Long", emphasizing the enduring influence of prior decision (Wehrman et al., 2023; Wehrman, Wearden, et al., 2020). Research attempted to separate the response alternation and repetition biases and has demonstrated that the response repetition tendency is especially common when the choice is difficult to make (Akaishi et al., 2014), and the response alternation is triggered by the changing context (Notebaert & Soetens, 2003). In an early weight lifting task (Turner, 1931), the experimental procedure included two types of situation: one in which judgements were emitted on two consecutive trials and another in which a judgment trial would follow a trial in which a judgment was omitted. It showed that the effect of judgment and stimulus magnitude could influence the response in opposite directions, i.e. the sequence of judgements induces an alternation bias and the stimulus magnitude a repetition bias. In addition, the task performed, the feedback received, the confidence on the response and individual characteristics also have influence on the direction of the response biases (Bosch et al., 2020; Braun et al., 2018; Kelly et al., 1997; Lepora & Pezzulo, 2015; Urai et al., 2019), for example, some subjects tended to alternate judgements but others actually tended to repeat them (Arons & Irwin, 1932).

Sensory carryover, on the other hand, indicates the influence of the prior stimulus. The evidence for the pure influence of the prior stimuli is relatively limited, one reason is that in most of the experiments, presentation of a stimulus is always followed by a judgment. Approximately a decade ago, Fischer & Whitney (2014) introduced a quantitative technique to investigate the impact of temporal contextual information on perception. In their study, participants viewed a series of briefly presented (500 ms) Gabor patches (randomly oriented Gaussian windowed sine wave gratings) and adjusted the perceived orientation of each grating using an adjustment tool. They found that the perceived orientation of the current Gabor patch was strongly and systematically attracted toward the orientation of the previous stimulus, such that the current orientation looked more like the previous one. They termed such phenomena as "*serial dependence effect*", indicating that our perception is not only influenced by the current stimulus but also by what we encountered just before (Cicchini et al., 2014; Fischer & Whitney, 2014; Glasauer & Shi, 2022). Meanwhile, Cicchini (2014) found that the current perception showed assimilation toward prior stimulus in a number estimation task. In their studies, participants (both adults and school children) were required to imagine a line with numbers from 0 to 100, and position specific numbers (e.g., 10, 50, 80) on this mental number-line. The researchers noticed that the way participants placed these numbers was related to the magnitude (size) of the number they had encountered in the previous trial. In other words, if the previous number was large, participants tended to place the current number higher on the number-line, and vice versa. Since then, this serial dependence effect has captured the attention of researchers and has been widely investigated using basic visual features, including orientation, motion direction, color, and numerosity (Barbosa & Compte, 2020; Fornaciai & Park, 2018b; Kristensen et al., 2021; Manassi et al., 2018), as well as complex abstract representations, such as summary statistics, faces and attractiveness (Manassi et al., 2017; Suárez-Pinilla et al., 2018; Taubert & Alais, 2016; Turbett et al., 2021), highlighting the very widespread nature of the serial dependence effect.

Throughout the current dissertation, we adopted the recent name "serial dependence effect" instead of the sensory carryover effect to avoid confusion. The serial dependence effect manifests as attraction or repulsion biases: attraction makes successive stimuli seem more alike than they are, while repulsion occurs when the current percept is biased away from the preceding stimulus. Both sequential attraction and repulsion have been extensively explored in spatial perception (Bae & Luck, 2020; Barbosa & Compte, 2020; Cicchini et al., 2023; Fischer & Whitney, 2014; Manassi et al., 2023; Pascucci et al., 2023). There are many reports of repulsive biases only (Bae & Luck, 2019; Pascucci & Plomp, 2021), attractive biases only (Cicchini et al., 2017; Fischer & Whitney, 2014; Manassi et al., 2018; Pascucci et al., 2019), and a mixture of the two (Bliss et al., 2017; Fritsche & de Lange, 2019b; Rafiei et al., 2021) arising from single stimuli in the immediate past and in the long time scales. For example, a study explored the respective timescales of attractive and repulsive biases and found that perceptual decisions

are concurrently attracted toward short-term perceptual history and repelled from stimuli experienced minutes into the past (Fritsche et al., 2020). The direction of serial dependence is related to many factors, such as the feature similarity between successive stimuli, feature-based attention, temporal-spatial proximity, and stimulus duration. It is generally agreed that in the orientation judgment tasks, the attractive bias occurs when the successive stimuli are similar, and repulsive biases emerge when they differ largely (Fritsche & de Lange, 2019b; Rafiei et al., 2021). For feature-based attention, Fritsche and colleagues (2019b) demonstrated that serial dependence in orientation is drastically reduced when attention is directed to the stimulus's size and not the orientation. Other studies suggest repulsive biases dominate when previous stimuli are not attended (Fischer & Whitney, 2014) or task-irrelevant (Pascucci et al., 2019; Pascucci & Plomp, 2021). Additionally, the stimulus's physical attributes, such as the presentation duration, contrast, spatial frequency, and visibility, can influence the direction of serial dependence. For example, a briefly presented low-contrast stimulus induces an attractive bias while prolonged exposure to a high-contrast stimulus can induce a repulsive bias (Fornaciai & Park, 2019; Hata & Motoyoshi, 2018; McGovern et al., 2017; Moon & Kwon, 2022; Zimmermann, 2023).

The serial dependence effect, where recent stimuli bias our current perception, has been extensively studied in the visual domain. However, only a handful of recent studies have explored trial-to-trial serial dependence effects on time perception (Glasauer & Shi, 2022; Togoli et al., 2021; Wehrman et al., 2023; Wiener et al., 2014), and the mechanism underlying temporal serial dependence effects remains unclear. Several studies have investigated the influence of temporal context on time perception. For example, Wiener (2014) tested whether the perception of temporal intervals (visual and auditory domains) in the temporal judgment task is influenced by the preceding temporal context, and the researchers dissociated response bias from perceptual influence for durations. The results demonstrated that the perception of each interval was biased by the prior response, such that each interval was judged similarly to the preceding trial. Second, the perception of each interval was also influenced by the prior interval, such that perceived durations shifted away from the preceding interval. Additionally, the effect of decision bias was larger for visual intervals, whereas auditory intervals engendered greater perceptual carryover. Similarly, a recent study (Li et al., 2023) also observed the repulsive biases caused by the prior interval (using visual and auditory stimuli) and such sequential bias is modality-specific, that is, the repulsive biases generalize within each modality.

While some studies observed assimilation effects toward prior stimulus (Bilacchi et al., 2021; Chen et al., 2023; Togoli et al., 2021). For example, a study (Togoli et al., 2021) required participants to perform either a duration discrimination or a numerosity discrimination task, and showed attractive biases in both time and numerosity domains, and the serial dependence effect occurred within the task-relevant dimension, that is, stimulus numerosity affected numerosity perception only, and duration affected

duration perception only. Some studies employed the time discrimination tasks showed negligible assimilation toward prior intervals and robust attractive decisional carryover to prior responses (Wehrman et al., 2023; Wehrman, Wearden, et al., 2020). However, studies involving time reproduction tasks observed robust assimilation toward the prior stimulus (Bilacchi et al., 2021; Chen et al., 2023), and these studies found that serial dependence effects in timing perception are enhanced as the delay between stimuli increases, highlighting the role of working memory in modulating serial dependence effects in time perception.

The previous studies observed consistent strong attractive decisional carryover effects, that is, the judgment of the current interval as "longer" when the judgment in the previous trial is also "longer", and vice versa. However, the serial dependence effect (the influence of the prior stimulus) in time perception showed inconsistent findings, some studies employed discrimination tasks observed repulsive serial dependence effects (Li et al., 2023; Wiener et al., 2014), as well as small or negligible attractive serial dependence effect (Togoli et al., 2021; Wehrman et al., 2023), while other studies showed assimilation using reproduction (Bilacchi et al., 2021; Chen et al., 2023). Some recent studies suggested that the serial dependence in timing perception depends on the specific task: repulsive serial dependence effect for synchrony judgments, and attractive serial dependence effect for temporal order judgments and magnitude estimation judgment. A framework is proposed where repulsion occurs at sensory layers, while Bayesian-like assimilation operates at higher decision levels (Roseboom, 2019). Additionally, recent studies suggested that prior information is organized based on how sensory information is acted upon, highlighting the role of action in the temporal serial dependence effect (Roach et al., 2017; Wehrman et al., 2018). Overall, the exact mechanism underlying temporal serial dependence remains elusive and requires more empirical evidence that uses distinct tasks.

At the beginning of this dissertation, we introduced the definition of the serial dependence effect and related concepts, including the decisional carryover effect. Despite the recent prominence of serial biases, we delved into the historical roots dating back approximately a century. Conducting a literature review with a broad scope serves two primary purposes. Firstly, it aids in framing the research question comprehensively, distinguishing sequential effects (such as serial dependence and decisional carryover) from other historical effects like priming, after-effects, and proactive interference. By comparing these effects, we can gain insights into how the brain balances between stability and sensitivity, continuity and contrast, integration and adaptation, in various perceptual domains and tasks. We can also explore how these effects are modulated by various factors, such as stimulus similarity, repetition, temporal proximity, spatial proximity, attention, memory, and expectation. Secondly, delving into early empirical literature clarifies enduring research directions in this field. Considering that different experiments showed different types of sequential effects, a more rigorous approach is necessary, as even seemingly small differences in

design have been found to have a strong impact on sequential effects. Additionally, this historical overview aids in testing and refining theoretical models and frameworks, such as Bayesian inference, predictive coding, and signal detection theory, advancing our understanding of the principles and mechanisms of sequential effects. In the subsequent sections, we will emphasize some topics of particular importance towards understanding this dissertation.

1.2 The methodology in the study of serial dependence effect

Serial dependence has been investigated with a variety of paradigms, involving different types of stimuli, responses, and analysis. Diverse approaches have led to disparate, often seemingly contradictory, findings. Here we focus on work with behavioral methods highlighting common threads and missing links between the findings. The aim of this section is not simply to provide an overview of the methodology but to summarize the results and insights gained by using different methods.

Researchers often employ reproduction or forced-choice tasks to assess the serial dependence effect (for a review, see Pascucci et al., 2023). In reproduction tasks, participants are presented with a stimulus (such as a grating or a number) and have to adjust a response tool to replicate the perceived attribute of the stimulus. Fisher and Whitney (2014) introduced a quantitative technique to investigate the serial dependence effect in the orientation. In their study (also in most orientation and direction study), the orientation was randomly selected from a circular distribution, which effectively neutralized any central tendency. The reproduction errors are calculated by the difference between the adjusted value and the true value of the presented stimulus for the current trial (i.e., estimate - orientation). Negative errors indicated a counter-clockwise deviation from the true orientation, while positive errors suggested a clockwise deviation. Additionally, the orientation difference was also calculated between the current trial and the previous trial (the previous orientation - the current orientation). The magnitude of the serial dependence is computed by fitting the first derivative of a Gaussian function (abbreviated as DoG) to the adjustment errors as a function of the difference between the previous stimulus feature and the current one. This function can provide many useful information about the serial dependence effect: firstly, the most used parameter to determine the magnitude of serial dependence is the amplitude or half-amplitude of the DoG function, which scales the amplitude to the curve peak in y units (e.g., degrees); Secondly, the width of the curve indicates the orientation difference between the current trial and the previous trial when the maximum serial dependence effect occurred. Note that, besides approximating the main sinusoidal pattern, the form of this function also reflects two important aspects of serial dependence, the repulsive bias shows in a reverse pattern, usually with a large width (indicating the maximum repulsion occurred when the successive orientation difference was relatively large.) Many studies measure serial dependence using this DoG function, which is most valid when the stimulus distribution is circular distribution. Given

that the focus of this thesis is on open-scale time duration, the DoG function is not a good candidate for our measures.

Compared with the well-documented serial dependence effect in spatial domains, the empirical evidence from time perception is relatively limited. There is a difference in the measurement of the serial dependence effect between circular distribution (i.e., orientation and direction) and the open-scale distribution (i.e., numerosity, length and duration). One advantage of using orientation stimuli is that it allows for a clear separation of sequential effects from pervasive central tendency and range effects (Glasauer & Shi, 2021; Petzschner et al., 2015; Shi, Church, et al., 2013; Teghtsoonian & Teghtsoonian, 1978; Vierordt, 1868) - phenomena that are commonplace in magnitude estimations, such as duration judgments. For example, perceived durations can skew toward a mean duration derived from recent history or sampled durations (Burr et al., 2009; Jazayeri & Shadlen, 2010; Nakajima et al., 1992), leading to underestimate long durations and overestimate short ones. For the numerosity or duration stimuli, they are from open scale distribution and their judgments are subjective to both central tendency and sequential biases (Glasauer & Shi, 2022; Holland & Lockhead, 1968). Usually, researchers estimated the central tendency and sequential dependence effects separately. The central tendency effect can be estimated through linear regression to approximate the relationship between the current reproduction error and the current duration (Cicchini et al., 2012; Jazayeri & Shadlen, 2010; Shi, Church, et al., 2013). The linear regression of the reproduction on the physical duration deviates the perfect performance (that is, the reproduction equals the physical interval), showing short durations were overestimated and long durations were underestimated. The conventional measures of the serial dependence effect, which correlates the current response error to the difference between the previous and the current stimuli (Bliss et al., 2017; Cicchini et al., 2018; e.g., Fischer & Whitney, 2014; Kiyonaga, Manassi, et al., 2017), are not sufficient to separate sequential dependence from the central tendency bias (for more details, see Glasauer & Shi, 2022). Thus, researchers employed linear regression to the previous trial (Holland & Lockhead, 1968; Jesteadt et al., 1977) to analyze the sequential effect. Researchers usually take the slope of the linear fit to indicate the sequential bias (e.g., Glasauer & Shi, 2022; Jesteadt et al., 1977). A positive slope indicates that the current estimation is attracted towards the previous duration (also referred to as the "assimilation"), while a negative slope indicates that the current time estimation is repulsed from the previous duration.

On the other hand, the forced-choice task involves binary responses, requiring participants to judge the perceived stimulus if it is shorter (larger, clockwise) or longer (smaller, anticlockwise) relative to a standard reference. For example, in Fornaciai and Park (2018b), the "inducer" stimulus (a dot array) was presented before the task-relevant stimuli, and participants indicated whether the target had more or fewer dots than a reference numerosity. Usually, the frequency of choosing with "larger or more

clockwise than the standard stimulus" for each comparison stimulus was calculated, and a psychometric function was fitted to the response probability per comparison stimulus. This function is usually based on the cumulative density function of a normal distribution and was parameterized using the maximum likelihood method (Watson, 1979). Then, the point of subjective equality (PSE) was determined, and the PSE represents the comparison stimulus at which the probability of responding "larger or more clockwise than the standard stimulus" is exactly 0.5. In other words, at the PSE, the likelihood of responding "larger or more clockwise" or "smaller or more anticlockwise" than the standard stimulus is equally probable. Shifts of the PSE away from the standard stimulus may reflect biases and the accuracy of subjects' discrimination performance. Additionally, to visualize the variability of the sequential effect, the difference in PSEs among groups with prior stimuli was computed as the sequential effect index. The perceived numerosity of the target was pulled toward the numerosity of the inducer, and the bias is spatially localized to the position of the inducer stimulus, indicating that the serial bias may occur at early perceptual processes (Fornaciai & Park, 2018b). This finding is consistent with other studies utilizing forced-choice tasks in spatial stimulus. The orientation of the adjusted stimulus altered the perceived orientation of the subsequently presented Gabor at the same location, with a significant shift in the point of subjective equality—a result consistent with an attractive effect of the previous stimulus (Fischer & Whitney, 2014).

The results on sequential bias do not consistently align with each other using different tasks. For example, reproduction tasks have shown serial dependence linked to prior choices and post-perceptual decisions (Bae & Luck, 2020), while others demonstrated that serial dependence can occur even without explicit responses in a forced-choice numerosity task (Fornaciai & Park, 2018a). This discrepancy in evidence raises questions about the consistency of sequential dependence effects across different measurements (Cicchini et al., 2023; Manassi et al., 2023). The reproduction and forced-choice tasks may use working memory differently. Reproduction, for example, may require continuous comparison of the adjusting stimulus to the reference from memory, while the forced-choice task only compares the sensory input to the reference once where the post-stimulus retention is minimized. Additionally, the forced-choice tasks and reproduction tasks may employ distinct strategies, such as decision criteria (Lages & Treisman, 1998; Sumner & Sumner, 2020), therefore the impact of task relevance might be minimal in the forced-choice tasks. To date, how tasks influence sequential effects has not been systematically investigated.

1.3   The theory accounts for the serial dependence effect

Despite the widespread observation of the serial dependence effect, ongoing debate persists regarding the underlying mechanisms of this bias. The study of serial dependence has proposed numerous

conceptual and modeling accounts to explain the behavioral patterns and establish the inherent computational principles. Notably, the continuing questions involve the nature of repulsive and attractive effects, the relation of these biases to perception and working memory, the impact of uncertainty, and the putative functional role in everyday activity. In this section, we provide a brief overview of models and frameworks of serial dependence.

Historical frameworks, inspired by signal detection theory (Sumner & Sumner, 2020; Treisman & Williams, 1984), involve *criterion-setting accounts*. The frameworks operate on the assumption that responses induce a momentary shift in the location of the response criterion along the stimulus continuum (Treisman & Williams, 1984). Criterion shifts are governed by two opposite mechanisms, both operating under adaptive principles based on the nonrandomness of real-world events. The *tracking mechanism* operates on the premise that prior perceptual judgments serve as the best guess about the current state of the world. Consequently, prior responses lead to criteria shifts that facilitate the repetition of prior observations, resulting in assimilation. Conversely, the *stabilization mechanism* recognizes that the nonrandomness of external events is typically short-lived. As the interval increases, the likelihood of the present stimulus being similar to the past one diminishes, giving rise to repulsion (Hsu, 2021).

Recent debates on the underlying mechanisms of serial dependence effect center around the level of processing and representation where these effects occur, giving rise to two main perspectives. The first view posits that serial dependence serves as a perceptual mechanism (Fischer & Whitney, 2014; Liberman et al., 2016; Whitney et al., 2022), aiming to maintain perceptual stability and continuity by integrating past and current information to filter out abrupt noises. In contrast, the second perspective links sequential dependence to prior task and response-related post-perceptual factors (Bae & Luck, 2020; Ceylan et al., 2021; Fritsche et al., 2017; Pascucci et al., 2019).

In the first perspective, Fischer and Whitney (2014) introduced the concept of the "*continuity field*" in the context of orientation judgements. In their studies, participants reported the orientation of a briefly presented grating stimulus, revealing a systematic bias toward recently seen stimuli. This bias, influenced by attention and sensitive to the spatial and temporal proximity of successive stimuli, suggested an active perceptual process. They proposed the existence of a continuity field, a mechanism fostering perceptual stability by linking similar objects across time and space. This viewpoint operates under the assumption that the world remains stable over a short period but exhibits diversity over the long term. The visual system, therefore, capitalizes on the temporal continuity and variability of the physical environment to enhance encoding efficiency and accuracy. As a result, current perception demonstrates a bias toward the recent past for similar features, temporal and spatial proximity, presenting an attractive effect. Conversely, perception is repulsed from the recent past when the successive stimulus is notably distinct, particularly within a relatively long time window.

Several studies investigating serial dependence in orientation, face, and numerosity perception contribute to the continuity field account, demonstrating that this bias can even emerge in the absence of a decision process when participants are not required to report the target feature in the previous trial (Czoschke et al., 2019; Fornaciai et al., 2023; Fornaciai & Park, 2018a) or with a "flipped" response (Cicchini et al., 2017). Previous studies characterized the serial dependence effect through temporal, spatial, feature, and attentional tuning (Bilacchi et al., 2021; Collins, 2022; Fritsche & de Lange, 2019b; Lim & Lee, 2023). Temporal tuning indicates that the strength of attractive serial bias decays over time (Bilacchi et al., 2021), and spatial tuning highlights that attractive serial bias is stronger when successive stimuli are closer in space and weaker when farther apart. Studies showed that serial position affected serial dependence even if these changes were task irrelevant, suggesting that spatial tuning might be more automatically integrated into object representations underlying serial dependence (Fischer et al., 2020). Some research showed that the repulsion occurred from more remote history (e.g., minutes in the past) (Fritsche et al., 2020). Feature tuning underscores that serial dependence occurs between similar features and objects (Collins, 2022; Manassi et al., 2017), and the reported features biased towards the previous stimulus within the same object category, enhancing coherence of object but suppressed (or even repulsed) when objects change abruptly. Attentional tuning demonstrates that serial dependence is modulated by attention, stronger when stimuli are attended and weaker when ignored. Fritsche and de Lange (2019b) showed stronger serial dependence in orientation judgments when participants attended to the previous stimulus's orientation, suggesting that attention may enhance the representation of the previous stimuli and propagate it to the current stimuli. Together, these studies demonstrate that serial dependence is influenced by attention, object similarity, spatial-temporal proximity, and relevance, support the continuity field account and its role in enhancing efficiency (Cicchini et al., 2017), accuracy (Cicchini et al., 2018), speed (Cicchini & Burr, 2018), and stability (Manassi & Whitney, 2022) of perception and decision-making.

While previous researchers viewed serial dependence as a low-level perceptual bias and the amount of evidence supporting the continuity field account has been extensively studied in spatial domains, recent research challenges this perspective. Firstly, it lacks a well-defined theoretical framework or computational model to elucidate how various types of tuning (temporal, spatial, feature, and attentional) modulate serial dependence, whether independently or in conjunction, or if potential interactions among them could influence serial dependence in distinct ways. Additionally, similar evidence from non-spatial domains (i.e., time perception) is less developed, which may not capture the full diversity and complexity of serial dependence across diverse cognitive domains and tasks. Finally, the continuity account overlooks higher-level cognitive factors like expectations, response uncertainty and confidence that may influence serial dependence beyond the perceptual level. For example, studies

indicate that confidence in responses impacts serial dependence bias, with a more attractive bias toward highly confident trials (Glasauer & Shi, 2022; Samaha et al., 2019).

Therefore, an alternative perspective links serial dependence effects to decision-related post-perceptual factors (Bae & Luck, 2020; Ceylan et al., 2021; Ceylan & Pascucci, 2023a; Kiyonaga, Manassi, et al., 2017; Pascucci et al., 2019). Take, for example, a study involving either orientation or color judgments with a post-cue (Bae & Luck, 2020), sequential dependence emerged only when both the preceding and current trials were the orientation task, diminishing when tasks differed. This underlines the necessity of task-related responses from previous trials, not just the encoding of the prior stimulus. Post-perceptual processes after the initial sensory processing are miscellaneous and may involve higher-level cognitive functions such as response execution, memory representations, and response feedback. Recent studies highlight the role of the previous trial's response in serial dependence (Morimoto & Makioka, 2024). In a numerosity estimation task, where participants have to estimate the number of dots in an array, it showed a stronger serial dependence effect when participants responded in the previous trial, and this effect remained unaffected by the accuracy or confidence of the preceding response (Morimoto & Makioka, 2024). These findings suggest that the previous response may increase the weight of the previous stimulus or reduce the uncertainty or noise in the current stimulus perception, aligning it more closely with the previous stimulus. Overall, these studies indicate that response history amplifies the serial dependence effect, emphasizing that information from the previous stimulus must reach higher-level processes associated with perceptual decisions to influence the estimation of the current stimulus.

This view also underscores the critical role of working memory in serial dependence, as it combines preceding stimuli with current sensory inputs for decision-making and motor planning (Bae & Luck, 2020; Bliss et al., 2017; Kiyonaga, Scimeca, et al., 2017). In a spatial estimation task, manipulating the delay between stimulus and response revealed that the serial dependence was absent at the time of perception but increased with prolonged memory periods. This finding suggests that serial dependence involves the integration of past and present information in working memory, potentially enhancing the stability and accuracy of visual representations over time. Markov et al. (2023) delved into the role of visual working memory (VWM) in serial dependence during an orientation judgment task, and they found that higher VWM loads intensified serial dependence, regardless of orientation estimation precision. This implies that serial dependence operates at a post-perceptual process, with VWM serving as a crucial component mediating the interaction between past and present stimuli. In this context, working memory serves to store, manipulate, and integrate visual information with prior knowledge and expectations, potentially reducing noise and uncertainty in the visual input to maintain a coherent and stable environmental representation. However, there exists a delicate balance between stability and sensitivity in

visual cognition, especially when the input changes rapidly or unpredictably. Some studies suggested that working memory may also influence serial dependence by actively discarding irrelevant information. Recent research supports this notion, demonstrating that items removed from working memory as no longer relevant in the current trial exert a repulsion effect on the subsequent trial (Shan & Postle, 2022). Therefore, working memory may function to balance the trade-off between stability and sensitivity in visual cognition.

Besides the main accounts on the debates regarding the mechanism of serial dependence, whether it originates from low-level or high-level processing stages, there are some research proposed computational models (Fritsche et al., 2020; Pascucci et al., 2019). Within the Bayesian framework, observers use probabilistic inference to form optimal beliefs about the world, and serial dependence arises from the efficient encoding and Bayesian decoding of visual information in a stable environment to optimize both the accuracy and the efficiency of perception. Efficient encoding compresses visual input, preserving essential information while discarding redundant details to reduce metabolic cost and storage space, enhancing the signal-to-noise ratio. Bayesian decoding reconstructs visual input by combining the compressed representation with a prior probability distribution based on the relative frequency of events. Fritsche et al. (2020) applied these concepts to serial dependence, revealing that current perception was concurrently attracted towards the short-term perceptual history and repelled from stimuli experienced up to minutes into the past, which were not fully captured by a standard Bayesian observer model but explained well by the model with efficient encoding and Bayesian decoding. The authors concluded that the concurrent attractive and repulsive biases may arise from the need for visual processing to satisfy constraints of efficiency and stability simultaneously. This enables the brain to infer the most likely causes of the sensory measurements and to resolve ambiguities or uncertainties in the visual input. Recent models argue that the attractive and repulsive biases reflect effects at different processing stages (Fritsche et al., 2020; Gekas et al., 2019; Pascucci et al., 2019), broadly described as lower level (repulsion) and higher level (attraction). Some studies observed the current perception repelled from previous stimuli, but attracted toward previous responses (Pascucci et al., 2019). Repulsive biases may reflect low-level visual adaptation, while attractive biases may reflect higher-level processes, such as information integration, decision inertia or working memory interference (Fischer et al., 2020; Fritsche et al., 2017, 2020; Pascucci et al., 2019).

Additionally, a recent study aims to explain individual characteristics in serial dependence biases. The researcher developed a Bayesian model that incorporates sensory precision and individual beliefs about temporal continuity as parameters (Glasauer & Shi, 2022), proposing that perceptual estimates are weighted averages of sensory input and prior information. The prior can either be the previous stimulus (sequential bias) or the mean of the stimulus distribution (central tendency bias). The weights are

determined by individual variations in sensory precision and the beliefs about temporal continuity. The study's significant conclusion is that perceptual biases are not static but contingent on implicit beliefs about how stimuli are generated in the world. Observers who strongly believe temporal continuity show strong serial dependence, while those with an opposite belief - randomness - show less bias.

Overall, while the exact mechanism underlying serial dependence remains elusive, these accounts mentioned above offer different perspectives on the serial dependence, and require validation through empirical evidence from neural and psychophysiological studies. The identification of neural correlates for serial dependence has lagged behind behavioral understanding, necessitating advanced analytical and psychophysiological tools to decipher complex patterns of information processing at the neural level. Crucially, bridging these accounts with a more biologically plausible framework is essential to unravel how sequential bias is implemented and constrained in the human brain.

1.4   The neural mechanisms of serial dependence effect

Compared to the vast amount of behavioral work, only a few studies have been performed on the neural underpinnings of serial dependence. In exploring the neural mechanisms underlying the serial dependence effect, several Electroencephalography (EEG) and Magnetoencephalography (MEG) studies have investigated the electrophysiological correlates and temporal dynamics of prior information on the current perception. Previous research has demonstrated that sequential context induces context-dependent power activity preceding the onset of the current stimulus, and such prestimulus activity primarily manifests at alpha and beta bands (de Lange et al., 2013; Hsu, 2015). Specifically, assimilation is manifested by increased power (8 - 30 Hz, prominent at 20 - 28 Hz) and contrast is manifested by decreased power (10–30 Hz) (de Lange et al., 2013; Hsu, 2015). Both alpha and beta are thought to stabilize/maintain ongoing processing via top-down control (Clayton et al., 2018; Engel & Fries, 2010). In this view, reduction in these power activities reflect a change of ongoing states, facilitating shifts toward alternative states, whereas enhancement leads to intended states. The joint influence of context-dependent prestimulus alpha and beta power is proposed to carry cognitive information from previous to current trials, with power magnitude signaling different states of preserved information. Stronger power indicates the maintenance of such carry-over information, thereby leading to increased likelihood for eventual assimilation effects (i.e., response repetition), whereas reduced power indicates destabilization, leading to increased likelihood for eventual contrast effects (i.e., alternative choices) (Clayton et al., 2018; Samaha et al., 2017). In this section, I further introduce recent studies using the neural oscillation decoding approach to unravel intricate patterns of information processing across trials.

Recent studies have shown that prior stimulus information can be decoded from evoked EEG scalp activity in the current trial. These decoding results were obtained in tasks where the previous

stimulus was either relevant or irrelevant and induced attractive or repulsive biases (Bae & Luck, 2019; Fornaciai et al., 2023; Fornaciai & Park, 2020b; Luo & Collins, 2023; Ranieri et al., 2022; Zhang & Luo, 2023). Some EEG studies decoded the neural signature of stimulus history which may reflect serial dependence, providing insights into early visual processing mechanisms. For example, Bae and Luck (2019) decoded the orientation of the previous-trial stimulus using the EEG data from the current trial, suggesting that the current-trial stimulus reactivated or boosted the representation of the previous-trial orientation. The processing of new input can trigger the reactivation of a previous experience, even when that experience is no longer relevant to the task. In a numerosity task, Fornaciai and colleagues (Fornaciai & Park, 2020b) provided a task-irrelevant inducer preceding the numerosity array and observed serial dependence following the task-irrelevant stimulus. The researchers decoded probability distributions from neural activity and identified an early neural signature of serial dependence that emerged soon after stimulus onset. Importantly, the perturbations (pings) at a later latency successfully reactivated the biased representation of the initial stimulus, carrying the serial dependence signature. These studies suggest that biased neural representations may emerge in early visual processing stages.

Other EEG studies have indicated feature-specific reactivations of prior stimulus influencing the current perception. Zhang and Luo's study (2023) examined the neural representations of multiple features (pitch, category choice, and motor response) in an auditory categorization task, and how they are influenced by the corresponding features in the previous trial. The study finds that both pitch and category choice exhibit serial dependence effects, but in different directions: pitch is repulsed from the previous pitch, while category choice is attracted to the previous choice. Moreover, the study shows that past features are reactivated by the corresponding feature in the current trial, and further confirms that the reactivation of neural representations is not due to early task-relevant events or temporal prediction, but triggered by the feature-specific event. The study demonstrates that serial dependence occurs in a feature-dissociated manner, and reveals the direct neural evidence for the shifting of current information by past reactivation. Luo and Collins (2023) presented participants with prototypical visual objects (such as faces, cars, and houses) and morphs that combined properties of two prototypes, and required them to judge the category of the visual stimulus. The researcher used Representational Similarity Analysis (RSA) (Nili et al., 2014) on the EEG signals to examine if neural signals evoked by visual objects contained information about the previous stimulus. RSA analysis showed that the current object's brain response contained information about the preceding object, with this trace emerging immediately upon object appearance. Notably, the neural pattern associated with the previous stimulus differed from that in the current response. In other words, while past stimulus history influenced current representations, there was no shared neural code between the previous trial (memory) and the current trial (perception). Furthermore, studies focused on the role of silent memory signals identified a memory signal decoded

from EEG potentials, correlated with individual participants' serial biases, providing evidence for a silent memory signal contributing to the serial dependence (Ranieri et al., 2022). Collectively, these findings underscore the feature-dissociated nature of serial dependence, providing direct neural evidence for the modulation of current information by the feature-specific reactivations of prior stimuli.

Recent functional Magnetic Resonance Imaging (fMRI) studies reveal neural underpinnings on how the brain integrates information from past experiences to influence current perceptual judgments. In one of the first, Schwiedrzik and colleagues (2014) used fMRI with multistable orientation stimuli to disentangle the effects of perceptual hysteresis from those of adaptation. They found that these two opposite biases (attraction and repulsion) reflect distinct neural circuits: attraction involves a distributed network of higher visual areas and frontoparietal areas—particularly the right dorsomedial prefrontal cortex, which is involved in predictions and memory—whereas repulsion is restricted to activity changes in early sensory areas. This study contributes to our understanding of how the brain integrates prior experience into perception, by exploiting redundancies and staying sensitive to new information through a hierarchical segregation. In a later study, John-Saaltink (2016) asked participants to perform a binary categorization task on a sequence of oriented grating stimuli presented in the left or right visual field in the fMRI scanner. The study found that the perceptual decisions on the current grating were assimilated towards the previous grating, such that more clockwise tilts in the previous trials increased the likelihood of judging the current grating as clockwise, and vice versa. This bias was also reflected in the neural activity patterns in the early sensory cortex V1, such that the orientation signal in V1 was more similar to the previous grating than the current grating. Both the perceptual and neural effects were spatially specific, meaning that they only occurred when the previous and current gratings were presented at the same location, suggesting that the bias in perception may result from the bias in sensory processing.

However, other neuroimaging studies suggested that high-level processes and working memory modulate the serial dependence effect. Sheehan (2022) asked participants to perform a delayed orientation discrimination task, and demonstrated that the behavioral reports of the current orientation were attracted to the previous stimulus, but response patterns in the visual cortex were repelled. The authors reconciled these opposing neural and behavioral biases using a computational model. It suggested that neural adaptation reduces redundancy during encoding, leading to repulsive biases. Simultaneously, the attractive serial biases are mediated by later readout mechanisms for adaptation in the visual cortex, and several modeling studies additionally suggest that serial biases were due to synaptic changes arising from persistent bump attractor dynamics as opposed to early sensory processing (Barbosa et al., 2020; Bliss & D'Esposito, 2017). In van Bergen and Jehee's study (2019), participants performed a working memory task involving reporting the orientation, and it showed that the behavioral bias reflected optimal cue combination (larger serial dependence when the sensory uncertainty decoded on the previous trial was

lower), and uncertain sensory information received less weight during perceptual decisions. The researchers used fMRI techniques to decode representations of sensory uncertainty within the Bayesian framework, and found the uncertainty decoded from the population-level neural activity in the early visual cortex can be related to the strength of serial dependence, emphasizing the rational decision-making process under uncertain conditions and supporting the role of Bayesian computations in sensory processing.

Studies employing Transcranial Magnetic Stimulation (TMS) have contributed valuable insights. A study utilized TMS to investigate the neural mechanisms underlying serial dependence in visuomotor integration (de Azevedo Neto & Bartels, 2021), and found that TMS applied over the premotor cortex decreased serial dependence, supporting that an implicit short-term memory maintenance in the premotor cortex retains information from one trial to the next, leading to the serial dependence bias. Another important finding comes from the work of Barbosa and colleagues (Barbosa et al., 2020), which showed that the strength of memory reactivations in the prefrontal cortex (PFC) correlated with the strength of serial biases in both monkeys and humans, and further demonstrated that single-pulse TMS applied to the human prefrontal cortex between successive trials enhanced serial biases. Additionally, some pathological research involved healthy controls, patients with schizophrenia, and patients recovering from anti-NMDAR encephalitis and how NMDAR-related changes impact serial dependence and working memory processes (Stein et al., 2020). They found that both patient groups exhibited markedly reduced working memory-related serial dependence, and then simulated this finding with NMDAR-dependent synaptic alterations in a microcircuit model of prefrontal cortex. Changes in cortical excitation destabilized within-trial memory maintenance and could not account for disrupted serial dependence in working memory, suggesting alterations in an NMDAR-dependent memory mechanism operating on longer timescales. These behavioral, neuronal, and modeling studies utilizing visual stimuli in working memory paradigms consistently point to attractive effects emerging in either memory or decision-making circuits and not early sensory areas.

In summary, these studies, employing EEG, MEG, fMRI, and TMS techniques, collectively unravel the intricate neural processes governing the serial dependence effect. They highlight the adaptability of perceptual systems influenced by past experiences, the interplay of neural signatures in various brain regions, and the crucial role of memory mechanisms in shaping serial dependence across diverse cognitive domains. The integration of findings from different methodologies underscores the robustness and complexity of the serial dependence phenomenon in shaping perception and decision-making.

1.5 The purpose of the current thesis

The goal of the current dissertation is to advance our understanding of the cognitive and the neural dynamics underlying serial dependence effects in time perception. While behavioral studies reliably demonstrate serial dependence, much of the existing literature has primarily focused on non-temporal spatial features, such as orientation (e.g., Fischer & Whitney, 2014), only a handful of recent behavioral studies have explored trial-to-trial sequential effects on timing (Glasauer & Shi, 2022; Togoli et al., 2021; Wehrman, Wearden, et al., 2020; Wiener et al., 2014), and even fewer have linked these effects to neural underpinnings (Damsma et al., 2021; Fornaciai et al., 2023). This leaves a significant gap in our understanding of neural mechanisms at play. To tackle these issues, classical behavioral experiments, fMRI techniques are employed.

There is ongoing debate regarding whether sequential effects arise from perceptual or post-perceptual processes. The research findings vary, particularly regarding specific task measurements, and the reasons for this diversity remain poorly understood and largely unexplored. Additionally, many studies on the serial dependence effect have focused on scenarios involving a single feature of stimuli, and it has proven difficult to isolate conceptually and methodologically the contribution of task-relevant responses (e.g., task vs attention, memory vs decision, etc.). Participants report a single target feature in most trials, but sometimes no response is required (Czoschke et al., 2019; Fischer & Whitney, 2014). These studies showed serial dependence even without a response in prior trials, suggesting that a task-relevant response isn't essential for sequential effects. However, focusing on a single feature might blur the lines between perceiving and reporting it. The frequent need to report a target feature might prime participants to prepare responses, even when responses are not needed, potentially skewing the observed sequential dependence. Recently, Bae and Luck (2020) introduced two task-relevant features, requiring participants to engage with them attentively - color and motion direction - during the presentation (encoding) and perform either color or motion adjustment tasks according to post cues. This approach is ecologically consistent with real-world scenarios where we often encounter and remember multiple objects and features simultaneously. Their results showed that sequential dependence on motion direction was mainly evident when the preceding and the current tasks were the same direction adjustments but diminished when tasks changed. Their finding highlights the role of task relevance in sequential effects: both features were attentively encoded, but only the reported one impacts sequential effects.

On this ground, in Chapter 2, we examined how previous task-relevant responses affect temporal sequential effects, exploring if these effects vary with different tasks, specifically the time discrimination and reproduction tasks. We employed a classic post-cueing paradigm used in sequential dependence research (Bae & Luck, 2020; Czoschke et al., 2019). The Random Dot Kinematogram (RDK), incorporating two features: motion direction and timing, was used as the target stimuli, and participants

had to remember its duration and direction, reporting one according to post cues. This post-cueing paradigm required attentive engagement with both features in each trial. Our primary focus is the sequential effects on duration estimates across trials (Shi et al., 2022; Shi, Ganzenmüller, et al., 2013; Zang et al., 2022). We consider trials where participants previously reported duration as task-relevant and those reporting direction as task-irrelevant. To understand how the task types influence carry-over effects in time perception, we employed a time discrimination task in Experiment 1, where participants judged whether the perceived duration was shorter or longer than a standard 1-second reference. In Experiment 2, participants performed a time reproduction task, requiring them to reproduce the perceived duration. We analyzed sequential effects on timing-report trials based on whether the previous trial involved reporting the direction (task-irrelevant) or the time (task-relevant).

Subsequently, in Chapter 3, we employed the post-cue paradigm that prior research used (Bae & Luck, 2020) and extended it to include a pre-cue paradigm to vary memory loads. It is important to note that research exploring the impact of tasks and working memory on sequential dependence has primarily focused on a single modality, be it spatial or temporal perception. These studies often employ high memory loads, achieved either through post-cue paradigms (Bae & Luck, 2020; Cheng et al., 2023) or extended retention intervals (Bliss et al., 2017). Given that working memory is often shared between tasks within the same modality (e.g., orientation and color), its influence on sequential bias might be specific to that modality. The question of whether working memory on sequential bias is a modality-independent phenomenon, applicable across both space and time, remains an open issue. To address this, our study required participants to reproduce either the direction (space task) or duration (time task) of a coherent motion display, and the task depended on a cue shown either before (pre-cue, Experiment 1) or after (post-cue, Experiment 2) stimulus presentation. We hypothesized that the pre-cue task, relative to the post-cue task, by removing the need to remember an alternative task, would lessen the memory load. If memory load is crucial in both spatial and temporal tasks, stronger sequential dependence should occur in the post-cue than in the pre-cue task. Furthermore, if spatial and temporal memories function separately, a preceding trial of a different task does not interfere with the current trial, resulting in minimal impact on the current trial response, regardless of whether it's the spatial or temporal task. Conversely, if spatial and temporal memories have differential roles in the direction and duration tasks (e.g., if the spatial task is predominantly influenced by early perceptual processing rather than post-perceptual memory mixing), we may expect distinct patterns in two tasks when comparing the pre-cue to the post-cue tasks.

Finally, Chapter 4 set out to examine the neural mechanisms underlying serial dependence in time perception. In this study, we employed a classic post-cueing paradigm used in sequential dependence research (Bae & Luck, 2020; Czoschke et al., 2019) to investigate the neural mechanisms underlying sequential dependence in a duration reproduction task (Shi et al., 2022; Shi, Ganzenmüller, et al., 2013;

Zang et al., 2022) in conjunction with MRI scanning. The task consisted of an encoding phase and a subsequent phase that was either for reproduction or passive-viewing, contingent on a post-cue that indicated "Response" or "No-response". During the encoding phase, participants had to remember the stimulus duration, and then either reproduce it or passively observe it, as instructed by the cue. With "Response" and "No-response" trials randomly intermixed, participants had to recall the durations accurately in each case. This design allowed us to compare how passive viewing and active reproduction during preceding trials influenced the processing of the subsequent stimuli, thereby shedding light on the post-perceptual factors contributing to sequential dependence.

2 Task types affect serial dependence in time perception

The impact of task measurements on sequential dependence: A comparison between temporal reproduction and discrimination tasks

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AUTHOR CONTRIBUTIONS

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Abstract

Decisions about a current stimulus are influenced by previously encountered stimuli, leading to sequential bias. However, the specific processing levels at which serial dependence emerges remain unclear. Despite considerable evidence pointing to contributions from perceptual and post-perceptual processes, as well as response carryover effects impacting subsequent judgments, research into how different task measurements affect sequential dependencies is limited. To address this gap, the present study investigated the role of task type in shaping sequential effects in time perception, employing a random-dot kinematogram (RDK) in a post-cue paradigm. Participants had to remember both the duration and the direction of the RDK movement and perform the task based on a post-cue, which was equally likely to be direction or duration. To delineate the task type, we employed the temporal bisection task in Experiment 1 and the duration reproduction task in Experiment 2. Both experiments revealed a significant sequential bias: durations were perceived as longer following longer previous durations, and vice versa. Intriguingly, the sequential effect was enhanced in the reproduction task following the same reproduction task (Experiment 2), but did not show significant variation by the task type in the bisection task (Experiment 1). Moreover, comparable response carryover effects were observed across two experiments. We argue that the differential impacts of task types on sequential dependence lies in the involvement of memory reactivation process in the decision stage, while the post-decision response carryover effect may reflect the assimilation by subjective, rather than objective, durations, potentially linking to the sticky pacemaker rate and/or decisional inertia.

Keywords: Sequential dependence; Time reproduction; Time discrimination; Working memory; Post-perceptual processes

2.1 Introduction

　　Our decisions about a current stimulus are influenced by previously encountered events, resulting in a reliable yet biased estimation known as "serial dependence" or "sequential dependence" (Cicchini, Anobile, & Burr, 2014; Cicchini, Mikellidou, & Burr, 2023; Fischer & Whitney, 2014; Glasauer & Shi, 2022; Pascucci et al., 2023). Extensive research has demonstrated the widespread phenomenon of serial dependence using visual features (Bae & Luck, 2020; Barbosa & Compte, 2020; Fischer & Whitney, 2014). Such history dependence and trial-to-trial influences have also been observed in time perception (Glasauer & Shi, 2022; Shi, Church, & Meck, 2013; Togoli, Fedele, Fornaciai, & Bueti, 2021; Wehrman, Sanders, & Wearden, 2023). For instance, subjective duration can be biased by recent history (Burr, Banks, & Morrone, 2009; Jazayeri & Shadlen, 2010; Nakajima, ten Hoopen, Hilkhuysen, & Sasaki, 1992), leading to the central tendency effect – underestimating long durations and overestimating short ones (Glasauer & Shi, 2021; Hollingworth, 1910). Unlike the central tendency effect, sequential dependence specifically refers to the influence of recent trials on the current trial (Glasauer & Shi, 2022; Wehrman et al., 2023; Wiener, Thompson, & Coslett, 2014). Although serial dependence is generally acknowledged, the processing levels at which it emerges remain unclear. Additionally, research on how different task measurements affect sequential dependencies is limited.

　　There are two main perspectives: the perceptual account and the post-perceptual account. The perceptual account suggests that sequential dependence promotes perceptual stability and temporal continuity by integrating past and current information to filter out abrupt noises, functioning mainly as a perceptual rather than decision-making mechanism (Cicchini, Mikellidou, & Burr, 2017; Fornaciai & Park, 2018a; Glasauer & Shi, 2022; Liberman, Zhang, & Whitney, 2016). For instance, research has identified behavioral or neural signatures of serial dependence that occur independently of any response requirement (Czoschke, Fischer, Beitner, Kaiser, & Bledowski, 2019; Fornaciai & Park, 2018a; Fornaciai, Togoli, & Bueti, 2023; Pascucci et al., 2024). Generally, these studies involve experiments where participants focus on a single type of stimulus and often just report one feature, while not always needing to respond (Czoschke et al., 2019; Fischer & Whitney, 2014). However, focusing on a single feature might blur the lines between perceiving and reporting it, and the frequent need to report a target feature might prime participants toward preparing responses even when none are needed, potentially impacting the logic of the interpretation.

　　Conversely, an alternative perspective attributes sequential effects to decision-related post-perceptual factors (Bae & Luck, 2020; Ceylan, Herzog, & Pascucci, 2021; Ceylan & Pascucci, 2023; Fritsche & de Lange, 2019; Pascucci et al., 2019; Ranieri, Benedetto, Ho, Burr, & Morrone, 2022; Suárez-Pinilla, Seth, & Roseboom, 2018). This perspective gains support from studies investigating how task-relevant responses might influence serial dependence when responses involve multiple target feature

dimensions (Bae & Luck, 2020; Fischer et al., 2020; Houborg, Kristjánsson, Tanrikulu, & Pascucci, 2023; Suárez-Pinilla et al., 2018; Togoli et al., 2021). This approach reflects real-world scenarios where individuals typically encounter and remember various features of objects simultaneously. For example, as you wait at a crossroad for the traffic light to turn green, you monitor not just its color but also how long it remains on each signal. In such contexts, judging color and judging duration impact consequent estimations of each differently. A recent study explored this by having participants engage with two features: duration and motion direction, and perform either duration or motion adjustment tasks according to cues presented either before or after the target stimuli were shown (Cheng, Chen, & Shi, 2024). Their findings indicated that sequential dependence in timing tasks was mainly evident when consecutive tasks involved the same duration tasks but diminished when the task types varied, even when participants attentively encoded both features in a post-cue setup.

The varying impacts of task types on serial dependence may also depend on the specific tasks used to assess sequential biases. For example, Pascucci et al. (2023) reviewed recent studies on serial dependence and revealed that the effect depends on whether the task is a reproduction or a forced-choice task. In reproduction tasks, participants replicate the perceived attribute of a stimulus, whereas forced-choice tasks require participants to make binary decisions, judging if the stimulus differs from a standard reference in predefined ways (e.g., shorter vs. longer, larger vs. smaller, etc.). The effects of task-relevant responses on serial dependence are not consistent between these two types of tasks. For example, studies using reproduction tasks have found serial dependence to be influenced by prior choices and post-perceptual decisions (Bae & Luck, 2020; Cheng, Chen, Glasauer, Keeser, & Shi, 2023). In contrast, other studies using forced-choice tasks show that serial dependence can manifest even without explicit responses (Fornaciai & Park, 2018a).

This variation in findings could be attributed to how each task type interacts with working memory. Reproduction tasks may demand ongoing comparisons between the stimulus being reproduced and a memorized one, whereas forced-choice tasks typically require a single, direct comparison of sensory input against a reference, minimizing the need for post-stimulus retention. Additionally, the decision strategies employed in these tasks could differ significantly (Gokaydin, Ma-Wyatt, Navarro, & Perfors, 2011; Lages & Treisman, 1998; Sumner & Sumner, 2020); reproduction tasks require a thorough encoding of the entire stimulus before it can be accurately reproduced, whereas forced-choice tasks may allow for quicker decision-making based on a decision threshold without full stimulus encoding. For example, in short/long timing tasks, participants need not encode the entire duration of the stimulus that lasts longer than a midpoint of the short and long references, given that the "long" decision can already be made. Therefore, the choice of "task" is a crucial factor for understanding the role of task-relevant

response in sequential effect. Yet, the role of task types in sequential dependence in time perception hasn't been investigated.

While task types may potentially impact sequential dependence and decision-making, post-decision responses may impact the upcoming judgments directly. Recent studies have shown that responses from previous trials could significantly influence outcomes in subsequent trials (Li, Wang, & Zaidel, 2023; Wehrman, Wearden, & Sowman, 2020; Wehrman et al., 2023). For example, the prior judgment of a duration as "Long" (or "Short") is likely carried over to the next trial, regardless of preceding durations (Wehrman et al., 2020, 2023; Wiener et al., 2014). This indicates that subjective durations, rather than physical durations, also impact subsequent decision-making (Wehrman et al., 2023). This response carryover may also reflect the observer's inclination to maintain a self-consistent interpretation of the world (Luu & Stocker, 2018), operating under the assumption that the state of the world tends to remain constant (similar argument is also in Glasauer & Shi, 2022), which leads to the observed post-decision biases. Given the carryover of post-decision responses is primarily determined by the response state rather than task types or memory processes, the sequential response carryover might be independent of task types, presenting a complex issue that remains unresolved.

On this ground, we designed two experiments to investigate how different task types - specifically, the duration reproduction and bisection tasks, randomly intermixed with non-timing direction tasks - affect sequential effect and decision carryover in duration judgments. Specifically, we employed the random-dot kinematogram (RDK), incorporating two features: motion direction and timing, in a post-cue setup. Participants had to remember its duration and direction during the encoding phase, reporting one according to post cues. In Experiment 1, we randomly intermixed temporal bisection trials with non-timing direction-adjustment trials, while in Experiment 2, we intermixed duration reproduction trials with the direction-adjustment trials. We hypothesized that the extent to which working memory is involved plays a critical role in sequential dependence (Cheng et al., 2023; Pascucci et al., 2023). Unlike the forced-choice bisection task (categorizing durations as either "Short" vs. "Long"), the duration reproduction requires reactivation of the encoded duration from working memory (Bae & Luck, 2019; Barbosa & Compte, 2020). Consequently, we expect an enhanced sequential effect if consecutive tasks involve the same duration reproduction, compared to when tasks alternate between timing and non-timing tasks. In contrast, the temporal bisection task requires only maintaining a decisional state (either "Short" or "Long") that is likely made during the encoding stage, without further resorting to the memory reactivation process. Of note, decisions can be made even before the complete presentation in some long-duration trials during the encoding phase. Therefore, we anticipate that the sequential dependence, if any, may be less affected by task switching or repetition. On the response level, we presume that the reproduced duration in the reproduction task implicitly represents subjective durations. By categorizing

these subjective responses into "short" or "long" categories, we expect to observe comparable decision carryover effects across two task types, assuming that decision carryover effects are primarily influenced by response states rather than memory processing.

2.2 Experiment 1

Method

Participant

Twenty-six volunteers participated in Experiment 1 (14 females and 12 males, ranging in age from 18 to 26 years, with a mean of 20.8 years and a standard deviation of 2.17 years). All participants were right-handed, with normal or corrected-to-normal color vision. We excluded two participants for their large response variability (see the section "Data Analysis") and reported the results from the remaining 24 participants. We chose the sample size by referencing prior studies (Bae & Luck, 2020; Fischer & Whitney, 2014), which often identify significant effects (Cohen's d > 0.753). Participants signed the informed consent form before the experiment commenced and received compensation at a rate of 9 Euros/hour. The study was approved by the ethics committees of the Psychology Department at LMU Munich.

Stimuli and procedure

We used PsychoPy (Peirce et al., 2019) to manage stimuli presentation and to collect data. Participants were seated approximately 60 cm from the screen in a soundproof, dimly lit cabin. The stimuli were presented on a 24-inch DELL monitor (refresh rate 60 Hz) against a light grey background (39.3 cd/m^2).

As outlined in Figure 1, each trial began with a fixation dot for half a second ($0.5°$ in diameter with a brightness of 85.7 cd/m^2), which cued the start of the trial and drew participants' attention. Next came the encoding phase, wherein a random dot kinematogram (RDK) featuring 15 white dots (each dot diameter of $0.4°$; the luminance of 85.7 cd/m^2) against a dark disc ($17.8°$, 16.5 cd/m^2) appeared at the center of the screen. Initially, the dots within the RDK moved randomly for 400 to 600 ms, without any pattern (at a speed of 1 °/s and a coherence level of 0%). Subsequently, these dots turned green (45.8 cd/m^2) and began moving together (at 100% coherence) at a speed of $6°$/s in a predetermined direction (randomly selected from $11.25°$ to $348.75°$, in steps of $22.5°$) for a randomly chosen length of [0.4, 0.6, 0.8, 1.2, 1.4, 1.6] s. When a dot exited the dark disc boundary, another dot appeared randomly inside to maintain a constant count of fifteen. These green, coherently moving dots served as the target, which participants were asked to memorize regarding their movement direction and duration. After this, the dots returned to their initial random motion for another 400 to 600 ms. The alternating white dot displays served as visual masks to present any residual visual effects from the previous trial.

Following the encoding phase, a post cue - either the letter 'D' ($0.8° × 1.0°$, 85.7 cd/m^2) for the direction task or 'T' for the time task - appeared at the center of the display for half a second, prompting participants to report either the direction or duration. Participants could respond at their own pace. For the duration discrimination task, a display showing the left and the right arrows ("< or >") prompted participants to assess if the duration of the coherent motion was shorter or longer than one second. They made this two-alternative forced choice (2AFC) judgment by pressing the left arrow for "shorter than one second" or the right arrow for "longer than one second".

In the direction task, a line segment started from the center with an overlaid 'D', pointing to a random direction. Participants rotated this line to match the observed motion's direction using the left (counterclockwise) and right (clockwise) arrow keys. A continuous readjustment updated the pointer's direction, and they finalized their choice by pressing the spacebar. If their estimated direction deviated by more than 60°, a warning message "Direction deviated a lot!" would flash on-screen for half a second. The next trial began after a one-second intertrial interval.

To prepare participants for the main experiment, a practice session with 24 practice trials exposed them to a standard one-second stimulus, represented by yellow dots moving horizontally (at a speed of 6 °/s; coherence of 100%). Following a 500 ms blank interval, a comparison stimulus with a duration randomly chosen of [0.4, 0.6, 0.8, 1.2, 1.4, 1.6] s was presented. The comparison stimulus was the same RDK display used in the main experiment. Participants had to judge which one was longer. After the response, they received feedback on their accuracy. The formal experiment consisted of 480 trials, randomly shuffled, and split evenly between duration and direction tasks. The inter-trial transitional probability (from trial *n-1* to trial *n*) between the duration and direction trials ensured an equal probability of all inter-trial combinations. Participants could take a short break after each block of 30 trials.
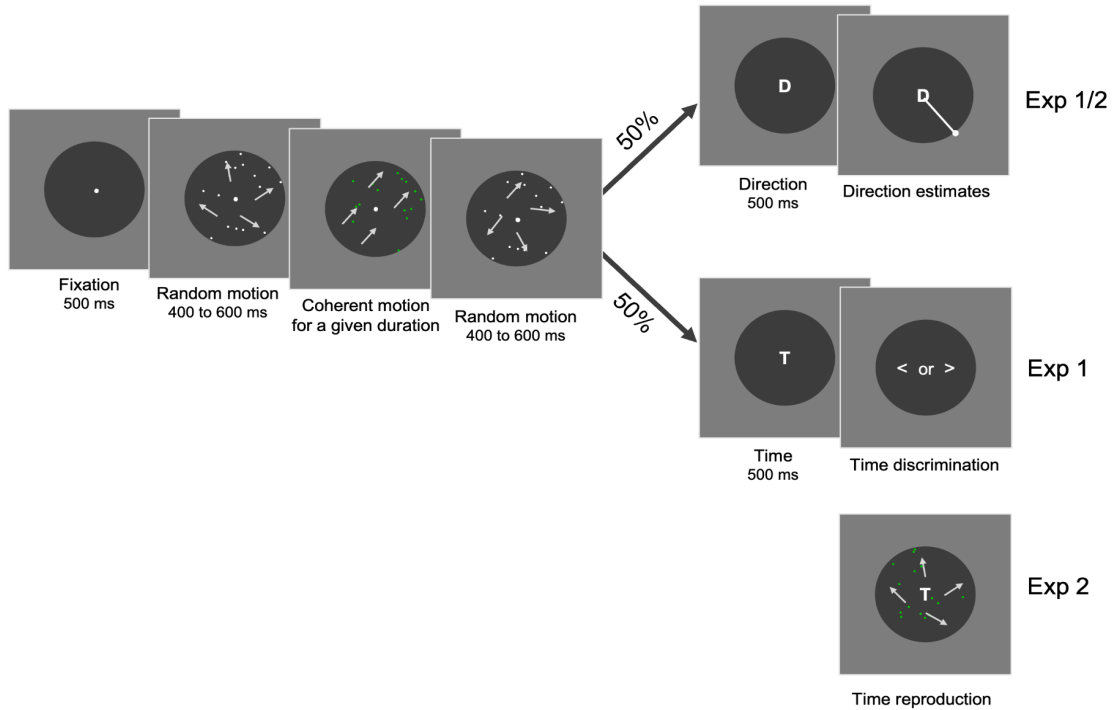
Figure 1. Schematic illustration of the experimental procedure. A trial started with a fixation dot, followed by a white random dot kinematogram. After 400 ms to 600 ms, the dots turned green and moved together in one direction for a given duration; then the display shifted back to the white random dot kinematogram. Next, a cue appeared for half a second, either the letter 'D' for the direction task or the letter 'T' for the timing task. For the direction task, participants adjusted a line pointer with arrow keys and confirmed their report by pressing the spacebar. Experiments 1 and 2 differed in the timing task. In Experiment 1, it was a discrimination task, with a prompt display ("< or >"), while in Experiment 2, the letter 'T' stayed on till the completion of the reproduction task.

Data analysis

In our study, we primarily examined the influence of previous trials on duration judgments within timing tasks. We included the analysis and results for the direction tasks in the supplementary materials for readers interested in exploring this aspect further. For the timing tasks, we categorized trials based on the duration (less than or more than 1 second) and type (Time or Direction) of the previous trial, creating four categories: "Short/Direction", "Long/Direction", "Short/Time", and "Long/Time". We further classified consecutive Time-Time trials according to the preceding timing trials' responses as "Short Response" or "Long Response." Excluding the first trial of each block, we analyzed responses using a psychometric function, a cumulative Gaussian function, including an initial 5% lapse rate for attention errors (Wichmann & Hill, 2001). We then determined each participant's Points of Subjective Equality

(PSE) to identify biases in duration perception and computed the just-noticeable difference (JND) and Weber fraction (WF = JND/PSE) for precision. Two participants with a WF greater than one were excluded for further analysis. Lastly, we used repeated measures ANOVAs and two-sided t-tests to determine the significance of our findings.

Results and discussion

First, we examined whether the difficulty of the two kinds of preceding task (time vs. direction) affected the time discrimination performance in the current trial (Cicchini, Mikellidou, & Burr, 2018), and calculated the just-noticeable difference (JND) for Time and Direction conditions, and it didn't show any significant difference between the two conditions (JND with standard errors for Time: 0.123 ± 0.007, and Direction: 0.129 ± 0.008, $t_{(23)} = 0.589$, $p = .562$, $d = 0.155$), suggesting that the task difficulties for time discrimination following Time and Direction conditions were comparable.

Then, trials were categorized into four groups based on prior task (Time or Direction) and duration (Short or Long), as shown in Figure 2A's psychometric curves. A distinct difference was visible between curves for the preceding "Short" vs. "Long" conditions while preceding "Time" and "Direction" tasks had similar curves. PSEs (with standard errors) were 770 ± 48, 833 ± 51, 775 ± 49, and 820 ± 54 ms for Time/Long, Time/Short, Direction/Long, and Direction/Short, respectively (Figure 2B). A two-way repeated measures ANOVA revealed a significant effect of Prior Duration, $F_{(1,23)} = 6.083$, $p = .022$, $\eta_p^2 = 0.012$, but not of Prior Task ($F_{(1,23)} = 0.045$, $p = .833$, $\eta_p^2 < 0.001$) or their interaction ($F_{(1,23)} = 0.138$, $p = .714$, $\eta_p^2 < 0.001$). These findings indicate that prior duration impacts current duration judgment, with shorter prior durations leading to shorter perceived current durations and vice versa, indicating an assimilation bias. The type of prior task (time or direction), however, had little effect.

Further analysis of the impact of preceding responses revealed a decisional carry-over effect. Figures 2C and 2D show psychometric curves according to prior responses, with a leftward shift for "Long" prior responses. The PSE was significantly lower after "Long" responses (741 ± 44 ms) than "Short" (901 ± 51 ms), $t_{(23)} = 3.795$, $p = .001$, $d = 0.684$, indicating a tendency to judge current durations as longer following the "Long" report.

These findings indicate that duration judgments are influenced by both previous durations and decisions, manifesting as both an assimilation effect and a decisional carry-over effect. Importantly, the type of preceding task (Time or Duration) did not significantly impact these biases, suggesting that temporal bisection task, involving binary decision (either "Short" or "Long"), was likely done already in the encoding phase (when the basis of the subsequent judgment isn't yet known), without needing further involvement of memory reactivation in the reporting stage. In contrast, duration reproduction requires full

presentation of the duration and reactivation of the encoded one from working memory during the reproduction stage. This raises the question of whether these findings from Experiment 1 are applicable to a reproduction task. Therefore, Experiment 2 employed a time reproduction task, asking participants to replicate the duration of a given stimulus.
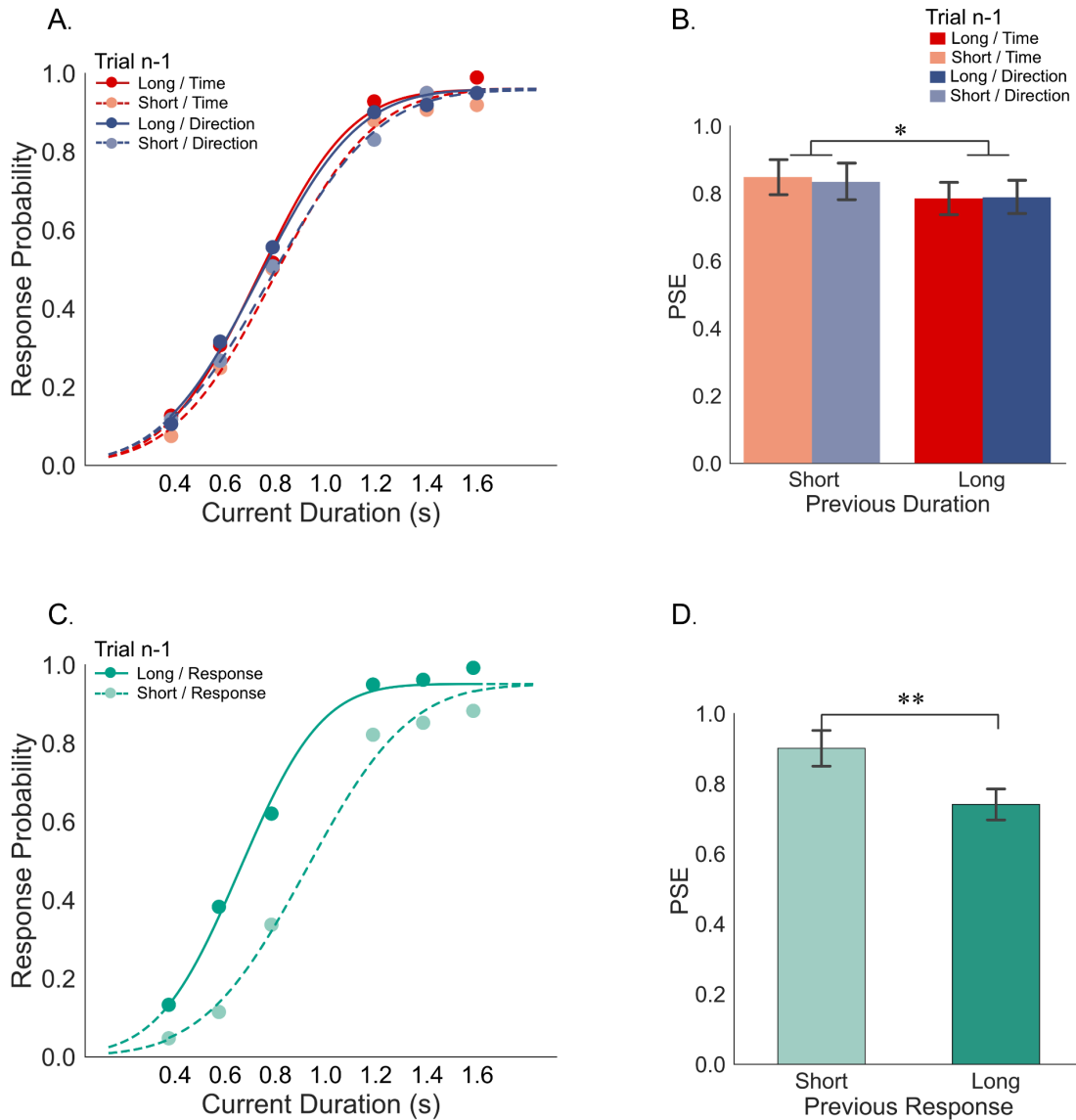
Figure 2. Results of Experiment 1. (**A**). Response probabilities of "Longer than 1 second" on the comparison duration (0.4, 0.6, 0.8, 1.2, 1.4, and 1.6 s) separately for previous time discrimination and direction adjustment tasks when the prior duration was either short (including 0.4, 0.6, and 0.8 s) or long (including 1.2, 1.4, and 1.6 s). The lines show the best-fitting psychometric function. (**B**). Points of subjective equality (PSE) values were plotted for previous time discrimination and direction adjustment

tasks when the previous duration was short or long. (**C**). Response probabilities of "Longer than 1 second" on the comparison duration when participants made "Short Response" or "Long Response" in the previous time discrimination trials. The lines show the best-fitting psychometric function. (**D**). Corresponding PSE values for prior "Short Response" and "Long Response." Error bars represent ± SEM. **p < .01, *p < .05.

2.3 Experiment 2
Method
Participant
Twenty-four participants were recruited in Experiment 2 (13 females; age 18 - 27, mean ± SD: 20.75 ± 2.45 years), all right-handed, with normal or corrected-to-normal vision and color vision. Before the experiment, participants provided written informed consent and received 9 Euros/hour compensation.
Stimuli and procedure
Experiment 2 closely followed the design of Experiment 1, with the following changes for the timing task. This time, participants had to reproduce the duration of the target stimuli, randomly selected from 0.6, 0.8, 1.0, 1.2, 1.4, 1.6, and 1.8 s (see Figure 1). After the post-cue display, participants initiated the task at their own pace by pressing and holding the down arrow key, releasing it when they felt the elapsed duration matched the target duration. Immediately after pressing the down arrow key, a display showing static green random dots (15 dots, each dot diameter of 0.4°; the luminance of 45.8 cd/m^2) turned into a random motion display (velocity of 6 °/s) to minimize inter-trial bias. The key holding duration was recorded as the reproduced duration. If their reproduction error exceeded 30%, they received feedback: "Too short" for relative errors below -30% and "Too long" for errors above 30%. The procedure for the direction adjustment task remained the same as in Experiment 1.
Data analysis
Response errors in duration reproduction trials were calculated as the difference between the reproduced and actual durations. We excluded the first trial of each block and filtered out trials where errors exceeded three standard deviations from the participant's mean error, accounting for accidental presses or attention lapses. These outliers constituted only 0.39% of trials. The remaining trials were categorized into two conditions based on the prior task (Time or Direction).

Previous research has demonstrated that subjective timing is susceptible to contextual factors, such as the "central tendency effect", leading to underestimating long durations and overestimating short durations (Burr et al., 2009; Jazayeri & Shadlen, 2010; Nakajima et al., 1992), and the sequential effect, where reproductions are influenced by preceding durations (Dyjas, Bausenhart, & Ulrich, 2012; Glasauer

& Shi, 2022). We modeled these effects using multiple linear regressions, with current (T_n) and previous (T_{n-1}) durations as predictors:

$$Error_n = a * T_n + b * T_{n-1} + c. \tag{1}$$

The model's slope (*a*) for the current duration indicates the central tendency effect. Following the convention adopted in the literature (Cicchini, Arrighi, Cecchetti, Giusti, & Burr, 2012; Jazayeri & Shadlen, 2010; Shi et al., 2013), we used the positive value (|*a*|) as the central tendency index, with 0 indicating no central tendency. The slope (*b*) for the previous duration reflects the sequential bias (Cicchini et al., 2014; Glasauer & Shi, 2022), and a positive slope indicates that the current estimation is attracted towards the previous duration, denoted as the "assimilation", while a negative slope indicates that the current time estimation is repelled from the previous duration. Lastly, we used repeated measures ANOVAs and two-sided *t*-tests to determine the significance of our findings. The statistical significance of the central tendency effect and the sequential effect was assessed individually using two-sided *t*-tests against a null hypothesis of zero effect, and paired *t*-tests were run for within-subject between-condition comparisons.

Furthermore, we categorized reproduced durations as "Longer" or "Shorter" than the middle duration 1.2 s (omitting 1.2 s) and analyzed sequential effects based on prior stimuli and responses, such that we can compare sequential effects between Experiments 1 and 2. Additionally, to visualize the variability of the sequential effect between experiments, we computed a sequential effect index as the difference in PSEs between groups with prior short and prior long durations for each prior task condition. To assess the decisional carry-over effect between experiments, we calculated a decisional carry-over effect index as the difference in PSEs between prior short and prior long reports separately for each experiment. We used repeated measures ANOVAs and two-sided *t*-tests to determine the significance of our findings.

Results and discussion

The overall mean response error (with SE) for the duration reproduction trials was significantly positive (97 ± 25 ms, $t_{(23)} = 3.911$, $p = .001$, $d = 0.798$), indicating a general overestimation. The mean reproduction error for the prior Time task was 113 ± 24 ms, significantly larger than the mean error for the prior Direction task (78 ± 27 ms), $t_{(23)} = 3.393$, $p = .003$, $d = 0.278$. To examine the variability of duration reproduction for two kinds of preceding task (time vs. direction), we calculated the standard deviation (STD) of reproduction between Time and Direction conditions, and it didn't show any significant difference between the two conditions (STD with standard errors for Time: 0.289 ± 0.016, and Direction: 0.289 ± 0.016, $t_{(23)} = 0.027$, $p = .979$, $d = 0.003$).

Our results showed that both the preceding Time and Direction conditions exhibited central tendency biases and serial dependence effects. As shown in Figures 3A and 3B, the average reproduction error decreases as the current duration increases, indicating that participants tend to overestimate short durations and underestimate long durations. Additionally, reproduction errors increased with longer prior durations, indicating an assimilation effect. To illustrate this bias in more detail, take a current trial where the duration is 1.2 s (middle row of Figure 3A), and it was preceded by a trial with a duration of 1.6 s. In this case, the biased representation of duration takes the value of 1.35 s in the preceding Time condition (the value of 1.31 s in the preceding Direction condition, see Figure 3B), representing an attractive bias towards the previous trial where the current duration being processed and perceived as being more similar to the previous duration than it actually is. This assimilation bias occurs for both preceding Time and Direction conditions but at different levels. To compare the statistical difference, we quantified the central tendency effect and serial dependence effect using the mean slope $|a|$ and b from linear regressions (Eq. 1).

Central tendency effect. The mean central tendency index ($|a|$) was 0.318 ± 0.048 ($t_{(23)} = 6.654$, p <.001, $d = 1.358$) for the Time condition and 0.354 ± 0.048 ($t_{(23)} = 7.329$, p <.001, $d = 1.496$) for the Direction condition. They were comparable ($t_{(23)} = 1.503$, $p = .147$, $d = 0.154$), as depicted by the trends in Figure 3C. This suggests that the task relevance did not influence the central tendency effect. The lack of difference can be attributed to the same distribution and range of durations tested in both tasks, resulting in a stable prior representation of durations across conditions. This finding aligns with previous research that mixing durations leads to generalized prior representation across different conditions (Roach, McGraw, Whitaker, & Heron, 2017).

Serial dependence effect. Figure 3D depicts the assimilation effect of current durations towards prior durations. We quantified this effect using the mean slope b from linear regressions, resulting in slopes of 0.077 for prior Time and 0.031 for prior Direction tasks, as shown in Figure 3D (right panel). Both slopes were significantly greater than zero (Time: $t_{(23)} = 4.370$, $p < .001$, $d = 0.892$; Direction: $t_{(23)} = 2.921$, $p = .008$, $d = 0.596$), confirming a sequential effect in both conditions. Interestingly, the sequential effect was significantly larger in the prior Time relative to the Direction condition ($t_{(23)} = 2.368$, $p = .027$, $d = 0.652$). To rule out statistical artifacts (Cicchini et al., 2014), we also analyzed reproduction errors against durations in future trials, which showed no significance ($ps > .460$). These findings provide clear evidence that, at least in the case of the time reproduction task, task-relevant response in the preceding trials enhanced the sequential effect.
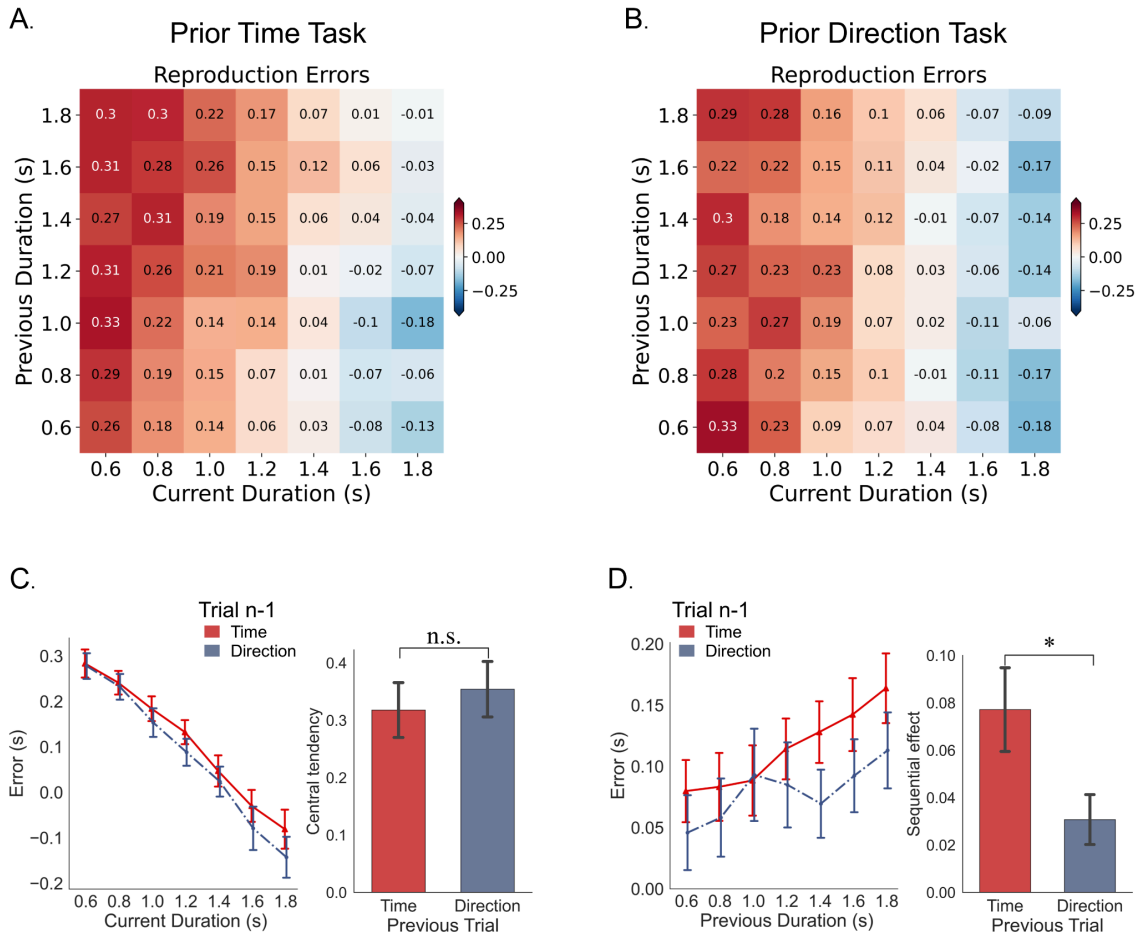
Figure 3. Results of Experiment 2. (**A**) Mean reproduction errors for all participants as a function of current (horizontal axis) and previous (vertical axis) durations for trials preceded by time reproduction task. (**B**) Mean reproduction errors for all participants as a function of current and previous durations for trials preceded by direction adjustment task. The reproduction error decreases as the current duration increases (cells get bluer from left to right, showing central tendency effect), but also becomes more positive as the previous duration increases (cells get redder from bottom to top, indicating sequential dependence effect). (**C**) Central tendency effect. Left panel: mean reproduction errors were plotted on the current sample duration; right panel: index of central tendency effect, plotted separately for trials preceded by time reproduction and direction adjustment tasks. (**D**) Sequential dependence. Left panel: mean reproduction errors were plotted on the previous duration; right panel: index of sequential effect, plotted separately for trials preceded by time reproduction and direction adjustment tasks. Error bars represent ± SEM. *p < .05. n.s. denotes non-significant.
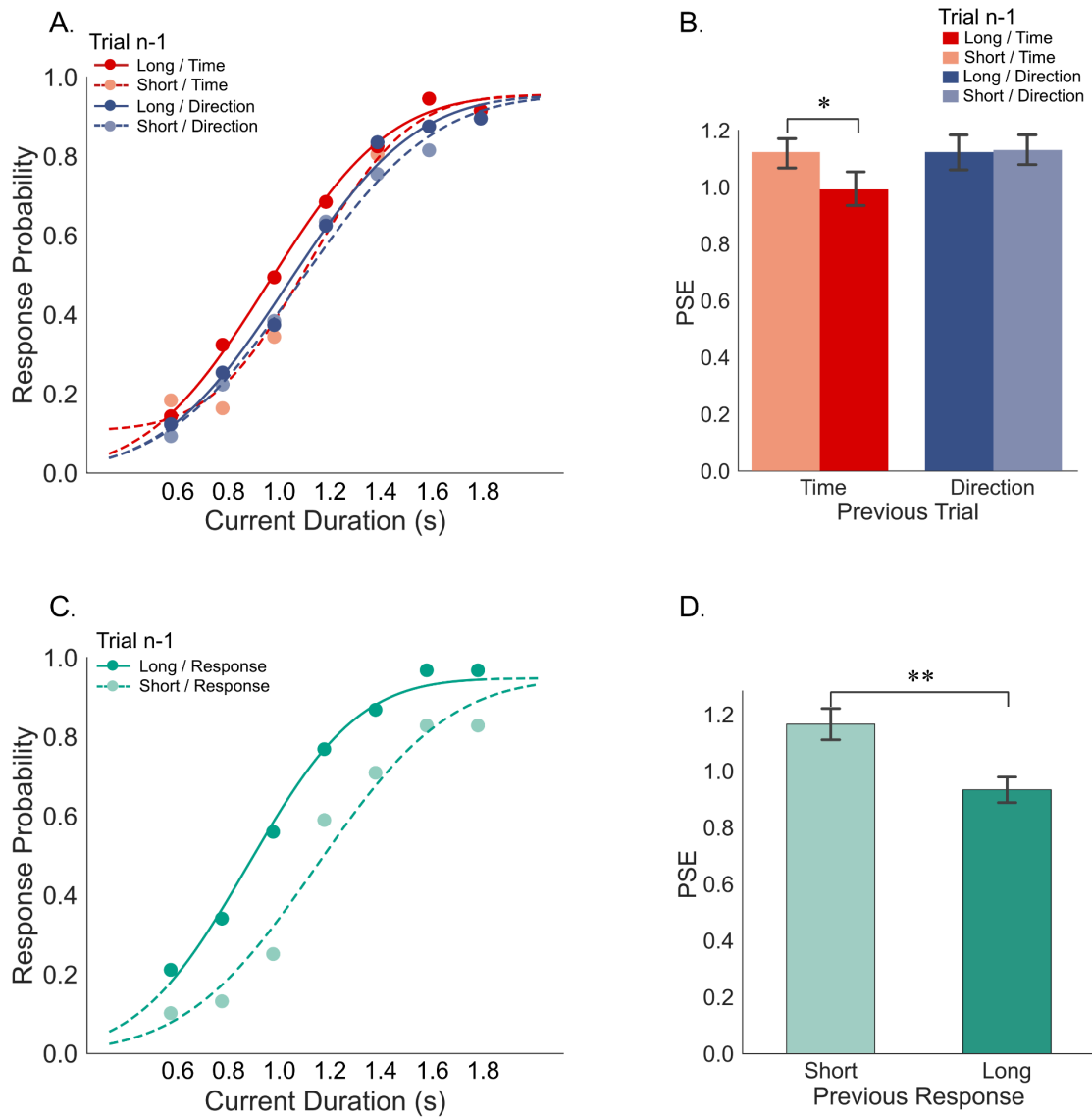
Figure 4. Psychometric function plots of Experiment 2. (**A**) Response probabilities of "Longer than 1.2 second" on the comparison duration (0.6, 0.8, 1.0, 1.2, 1.4, 1.6, and 1.8 s) separately for previous time reproduction and direction adjustment tasks when the prior duration was either short (including 0.6, 0.8, and 1.0 s) or long (including 1.4, 1.6, and 1.8 s). The lines show the best-fitting psychometric function. (**B**) Points of subjective equality (PSE) values were plotted for previous time reproduction and direction adjustment tasks when the previous duration was short or long. (**C**) Response probabilities of "Longer than 1.2 second" on the comparison duration when participants made "Short Response" or "Long Response" in the previous time reproduction trials. The lines show the best-fitting psychometric function. (**D**) Corresponding PSE values for prior "Short Response" or "Long Response". Error bars represent ± SEM. **p < .01, *p < .05.

To compare the findings between Experiments 1 and 2, we categorized reproduced duration as "Short" or "Long" relative to the middle duration 1.2 s. Figure 4A presents psychometric curves that reveal an assimilation bias toward previous durations only in the prior Time condition. In the prior Time condition, the PSE for prior long and short intervals were 987 ± 59 ms and 1111 ± 52 ms, respectively. In the prior Direction condition, these values were 1124 ± 52 ms and 1114 ± 61 ms, respectively (Figure 4B). A two-way repeated measures ANOVA revealed a main effect of the previous Duration, $F_{(1,23)} = 5.407$, $p = .029$, $\eta_p^2 = 0.011$, and a main effect of the prior Task, $F_{(1,23)} = 6.150$, $p = .021$, $\eta_p^2 = 0.017$, and a significant interaction effect between these factors ($F_{(1,23)} = 5.479$, $p = .028$, $\eta_p^2 = 0.015$). Further analysis revealed a significant assimilation effect in the task-relevant (Time) condition ($t_{(23)} = 3.465$, $p = .004$, $BF_{10} = 18.385$) but not in the task-irrelevant (Direction) condition ($t_{(23)} = 0.239$, $p = 1$, $BF_{10} = 0.22$).

Additionally, to assess the decisional carry-over effect, we grouped trials based on the preceding reports ("Short" or "Long" responses). Figure 4C displays psychometric curves for each group, revealing a distinct difference based on prior responses. As indicated in Figure 4D, the PSE values for the prior "Long Response" was 934 ± 45 ms, significantly shorter than the prior "Short Response" (1166 ± 55 ms), revealing a significant decisional carry-over effect ($t_{(23)} = 3.457$, $p = .002$, $d = 0.939$).

2.4 Omnibus analysis

Our study aims to investigate the influence of task relevance on time perception in both time reproduction and time discrimination tasks. In Experiment 1, the preceding task-relevant response was the binary judgment ("shorter" or "longer") in the discrimination task, while the preceding task-relevant response was the duration reproduction task in Experiment 2. Given that the task-relevance in two experiments was qualitatively different, we further conducted a nested ANOVA analysis to compare the sequential effects between the timing discrimination (Experiment 1) and the time reproduction (Experiment 2) tasks. The sequential effect index was calculated as the difference in PSEs between prior short and prior long durations for each prior task condition and for each experiment. A nested ANOVA on the sequential effect index, considering factors of the between-subject factor "Experiment" and the nested within-subject factor "Task Relevance", revealed a significant interaction effect ($F_{(2,92)} = 3.716$, $p = .028$). However, there was no significant main effect of Experiment ($F_{(1,92)} = 0.009$, $p = .927$). Further paired t-tests on the PSE shifts for the difference of sequential effect between task relevance (Time vs. Direction) failed to reveal any significant difference in Experiment 1 ($t_{(23)} = 0.371$, $p = .714$, $d = 0.110$), but a significant difference in Experiment 2 ($t_{(23)} = 2.341$, $p = .028$, $d = 0.723$), indicating a more pronounced sequential dependence in trials with consecutive time reproduction tasks in Experiment 2 (Figure 5A).

The decisional carry-over effect index was calculated as the difference in PSEs between prior short and prior long reports separately for each experiment. A separate *t*-test on the decisional carry-over effect index did not show a significant difference between Experiments 1 and 2 ($t_{(46)} = 0.911$, $p = .367$, $d = 0.263$, see Figure 5B).

Overall, both time discrimination and reproduction tasks demonstrated consistent assimilation toward prior durations, indicating a robust sequential effect in time perception. The comparative analysis revealed that task relevance enhanced sequential biases in the time reproduction task, but not in the time discrimination task. This suggests that the measurement type modulates the mechanism of sequential effect. The difference might stem from the interaction of the timing task with memory retrieval of the encoded duration, with the time reproduction task requiring continuous attention and memory comparison during reproduction.
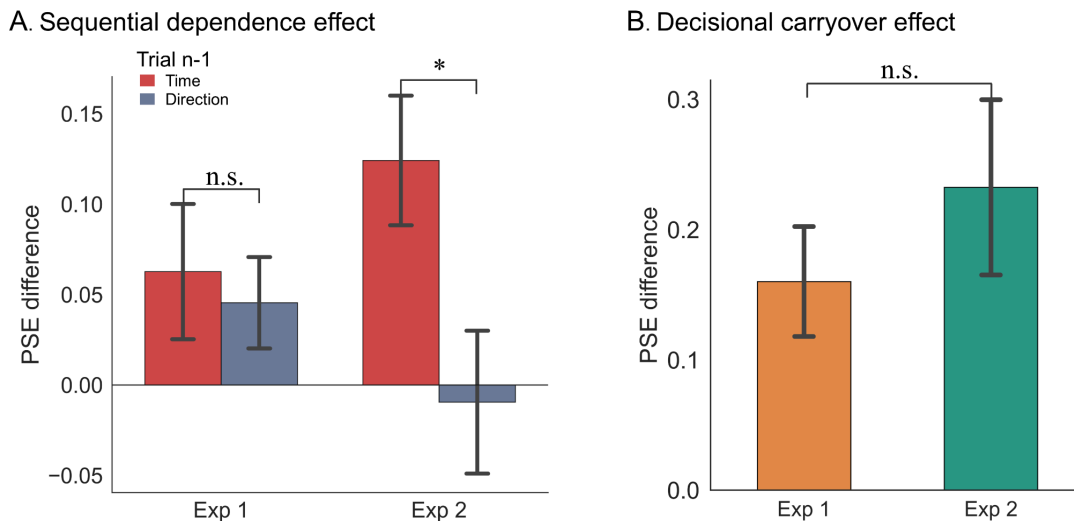
Figure 5. (**A**) The sequential dependence effects, measured by the difference of PSEs between Prior Short and Prior Long durations, are plotted separately for the preceding time-reporting (red) and direction-reporting (blue) trials, and Experiments 1 and 2. (**B**) Decisional carryover effects, measured by the difference of PSEs between Prior Short and Prior Long responses, are plotted separately for Experiments 1 and 2. Error bars represent ± SEM. *p < .05, while n.s. denotes non-significant.

2.5 General Discussion

The present study explored the impact of task relevance on sequential effects in time perception, using discrimination and reproduction tasks (Fornaciai et al., 2023; Togoli et al., 2021; Wehrman et al., 2023; Wiener et al., 2014). Across both timing tasks, we observed a consistent assimilation effect:

participants perceived current durations as longer following long previous stimuli and shorter following short ones. Interestingly, while the assimilation effect with the discrimination task was unaffected by task relevance, it was more pronounced with the time reproduction task following the same task, highlighting distinct impacts of timing tasks on sequential dependence. Furthermore, we observed significant decisional carry-over effects in both timing tasks, where participants were more likely to repeat their responses, regardless of which timing task being used.

Our results indicated a significant sequential dependence effect in both duration discrimination and reproduction tasks, in line with previous findings in time perception (Glasauer & Shi, 2022; Togoli et al., 2021; Wehrman et al., 2023; Wiener et al., 2014). Recent past time intervals, being more accessible in memory, can influence the perception of current durations. In fact, recent studies argue that by integrating noisy sensory inputs with recent past stimuli (sequential effect) could enhance processing efficiency (Cheng et al., 2023; Fornaciai et al., 2023; Tonoyan, Fornaciai, Parsons, & Bueti, 2022), perceptual stability and temporal continuity (Cicchini et al., 2017; Fornaciai & Park, 2018a; Glasauer & Shi, 2022; Liberman et al., 2016). However, this also engenders byproducts, such as the central tendency and sequential biases. In this aspect, mechanisms of sequential dependence in time domain are comparable to those measured in non-temporal domains (Barbosa & Compte, 2020; Cicchini et al., 2014; Fischer & Whitney, 2014; Fornaciai & Park, 2018b; Kristensen, Fracasso, Dumoulin, Almeida, & Harvey, 2021; Manassi, Liberman, Kosovicheva, Zhang, & Whitney, 2018; Suárez-Pinilla et al., 2018; Turbett, Palermo, Bell, Hanran-Smith, & Jeffery, 2021).

Interestingly, though, we found the influence of task relevance in the preceding trial on the current estimate showed distinctive patterns with different types of timing tasks. The task-relevant timing task displayed similar sequential effects to the task-irrelevant direction adjustment tasks, while the impact of the preceding timing task on the current duration reproduction was more pronounced compared with the preceding direction task. One plausible explanation lies in the differential memory processes engaged in reproduction and discrimination tasks. In the reproduction task, participants had to reactivate the encoded duration in working memory through the reproduction phase, as it was used as a reference for stopping the reproduction. This active maintenance was missing for the direction adjustment trials, leading to unequal sequential effects between reproduction-reproduction and direction-reproduction trials. The active memory trace of the target duration through the reproduction phase may thus bias the encoding of the subsequent trial. In contrast, the temporal bisection decision could be already made during the encoding phase, as it only requires the comparison of the target duration to the middle reference duration (here 1 second). Therefore, not much reactivation and memory processes are needed after the cue was presented, leading to comparable sequential effects between the preceding timing and non-timing tasks, as the decision could already be made prior the task cue. The enhanced sequential effect with consecutive

reproduction tasks observed in the present study is inline with a recent fMRI study (Cheng et al., 2023), which also showed that consecutive responses enhanced sequential dependence. Their fMRI results revealed that sequential dependence negatively correlated with hippocampal activity in these consecutive response trials (Cheng et al., 2023), highlighting the crucial role of memory in sequential dependence (Bliss, Sun, & D'Esposito, 2017; de Azevedo Neto & Bartels, 2021).

Early decision criterion-setting accounts (see also Pascucci et al., 2023; Treisman & Williams, 1984) argued that the sequential effect depends on two opposing updating processes involved in setting decision criteria: the tracking and stabilization processes. The tracking process involves tracking recent sensory inputs, which biases decisions toward previous judgments, while the stabilization process reverts decision to a mean criterion set over a long-term process. An attractive sequential effect evolves when the tracking process is dominant. In our Experiment 2, the reproduction task requires more attention in monitoring the passage of time compared to the direction task, which likely strengthens the tracking process rather than the mean-reverted stabilization process for the consecutive reproduction trials. This boosted "internal attention" to the representation of a recently seen stimulus in working memory likely leads to an enhanced sequential effect.

However, this decision criterion-setting account, while explaining the influence of the task type on sequential effects, falls short when attempting to explain the comparable central tendency effects we observed. Recent work with an iterative Bayesian updating model (Glasauer & Shi, 2022) suggests that the short-term sequential effects are influenced by individuals' beliefs in temporal continuity, whereas the long-term central tendency effect relies more on acquired sample distributions. The duration reproduction in our study, which requires ongoing monitoring, likely places more weight on temporal continuity compared to the temporal bisection task. This interpretation also helps to clarify why we observed an enhanced sequential effect in consecutive reproduction trials.

While we found distinct impacts of timing tasks on sequential dependence, strikingly, the decisional carryover effect, when the reproduction response was converted to binary category responses, was comparable between two timing tasks (see Figure 4E). The decisional carryover effect we observed aligns with previous findings of response assimilation in duration judgments (Brown, McCormack, Smith, & Stewart, 2005; Li et al., 2023; Wehrman, Wearden, & Sowman, 2018; Wehrman et al., 2020, 2023; Wiener et al., 2014), particularly under conditions of response uncertainty (Akaishi, Umeda, Nagase, & Sakai, 2014; Wiener et al., 2014). Wehrman et al. (2023) suggest two potential possible explanations for this response assimilation: One is that response assimilation might actually reflect stimulus assimilation based on subjective rather than objective durations. When participants categorize a prior duration as "Short" or "Long", they anchor their judgments of the subsequent stimulus accordingly, leading to judgments being assimilated to previous decisions (Urai, de Gee, Tsetsos, & Donner, 2019; Wehrman et

al., 2023). The second possibility involves the internal pacemaker, described in the classic internal clock model (Gibbon, Church, & Meck, 1984; Wearden, 1991), and assumes that the pacemaker's rate fluctuates slowly and 'sticks' across multiple trials. This consistency, or 'stickiness', could give rise to response assimilation, as trials categorized based on preceding response outcomes ("Short" or "Long") are likely in the same state of pacemaker rate as the preceding trial. Consequently, response assimilation is primarily driven by the 'stickiness' of the fluctuating pacemaker rate, rather than the task type or memory reactivation. While the anchoring account emphasizes that current decision-making is assimilated to an internal reference, the 'sticky' pacemaker account offers a mechanistic interpretation that is not limited to the late post-perceptual stage.

Both the anchoring account and the 'sticky' pacemaker account align with the concept of decisional inertia, proposed for non-temporal serial dependence (Ceylan et al., 2021; Pascucci et al., 2019), although decisional inertia emphasizes serial dependence occurring at the post-perceptual stage. Given that changes in decision states might rather be slow, decisional inertia exerts a stronger influence on decision judgments than the bias from the stimuli. Previous studies have also shown that the impact of decisional inertia can extend across different objects sharing the same decision, such as the orientation task (Ceylan et al., 2021; Fornaciai & Park, 2019; Huffman, Pratt, & Honey, 2018; Tanrikulu, Pascucci, & Kristjánsson, 2023). However, decisional bias seems to operate independently of visual working memory (Pascucci et al., 2019), as also evidenced by the decisional carryover effect observed in the present study (see Figure 5B). In this context, although decisional inertia can explain the decisional carryover effect, but the task relevance effect observed here may be more related to memory reactivation.

In conclusion, our findings highlight distinct impacts of timing tasks on sequential effects but reveal comparable patterns of response assimilation across tasks. While the temporal bisection task showed no changes in sequential effect by preceding task relevance, it was notably stronger in the duration reproduction task when it followed the same reproduction task, compared to a timing-irrelevant direction task. This enhanced sequential effect in consecutive reproduction tasks is likely owing to boosted attention and memory reactivation during the reproduction, absent in both the direction and the temporal bisection tasks. We also found comparable response assimilation across different timing tasks, which can be attributed to the influence of the pacemaker's sticky rate and/or decisional inertia.

Declaration of competing interest
The authors declare no competing interests.
Data and code availability statement

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2.7 Supplementary Materials

Analysis for direction reproduction trials

Outliers due to accidental button presses or inattention were also excluded, specifically those with response errors larger than 45° for direction report trials, before proceeding with further analyses. These outliers were rare, constituting only 1.05% of direction report trials (ranging individually from 0 to 23 outlier trials) for Experiment 1 and 1.07% of direction report trials (ranging individually from 0 to 35 outlier trials) for Experiment 2. Next, we categorized the remaining trials into two categories based on the previous tasks: Time or Direction, to investigate the influence of prior tasks on the sequential effects of current direction estimates.

We focused on two conditions: the prior Direction task representing the prior task-related condition, and the prior Time task representing the prior task-unrelated condition. The direction of motion was randomly selected from a circular distribution, featuring 16 equally spaced angles (from 11.25° to 348.75°, in steps of 22.5°), which effectively neutralized any central tendency. Consequently, we focused solely on the sequential effect and skipped the central tendency analysis. The response error was calculated as the difference between the reported direction and the true motion direction for the current

trial (i.e., estimate - direction). Negative errors indicated a counter-clockwise deviation from the true direction, while positive errors suggested a clockwise deviation. Additionally, the direction difference was also calculated between the current trial and the previous trial (the previous direction - the current direction), following the same method used in previous research (e.g., Fischer & Whitney, 2014). Trials with a direction difference of 0° or ± 180° were excluded, as response errors relative to these direction differences are undefined. Following previous research (Moon et al., 2022) highlighting a significant role of non-directional orientation in the coding of visual motion direction, we reduced the direction difference range from [-180 to 180°] to [-90 to 90°] accordingly. To better reflect the repulsion and attractive biases, we converted the response errors from clockwise or counterclockwise directions to the repulsion (negative) and attractive (positive) biases by collapsing the direction differences to the positive range [0, 90.0°]. This analysis is akin to previous studies (Bae & Luck, 2020).

Prior research has shown that small orientation differences (within 90°) led to a significant attractive bias (Bliss et al., 2017; Fritsche et al., 2017; Fritsche & de Lange, 2019; Samaha et al., 2019). For example, attraction was observed when the orientation difference was around 17° (Fritsche et al., 2017). Thus, we calculated the average response errors for small-orientation-difference trials (22.5°, 45.0° and 67.5°) and compared them to zero for each condition (the prior task being direction reproduction or duration reproduction for the current direction reproduction trials). The statistical significance of the sequential bias was assessed individually using two-sided t-tests against a null hypothesis of zero effect, and paired t-tests were run for within-subject between-condition comparisons.

Results

Direction Estimation in Experiment 1. The mean response errors were plotted against the orientation difference between the previous and the current trials (ranging from -90° to 90°, a positive value representing the difference in the clockwise direction), separated for the prior Direction and Time conditions (Figure S1.A). Then, the direction errors were converted to the attractive (positive) and repulsion (negative) sequential effect and replotted as a function of the absolute orientation difference for each condition (illustrated in Figure S1.B). The average response biases across the orientation differences of 22.5°, 45.0°, and 67.5° were 0.616° ± 0.399° and -0.040° ± 0.311° for the prior Direction and Time conditions. Both response biases did not significantly deviate from zero effect (prior Direction: $t_{(23)} =$ 1.541, $p =$.137, $d =$ 0.315; prior Time: $t_{(23)} =$ -0.128, $p =$.899, $d =$ 0.026) and there was no difference between the two, $t_{(23)} =$ 1.588, $p =$.126, $d =$ 0.374 (Figure S1.C). Experiment 1 didn't reveal a significant attractive bias in the direction reproduction task.
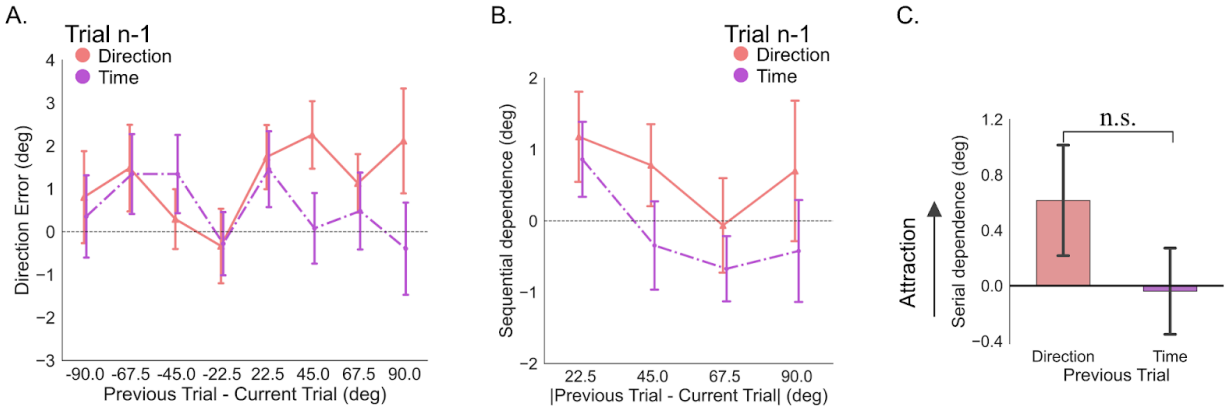
Figure S1. The results of direction reproduction trials for Experiment 1. (**A**) Mean response errors on the orientation difference of [-90°, 90°], plotted separately for trials preceded by Direction report and Time report. The angular difference was realigned to represent the relative motion orientation (plus 180° for the opposite direction) of the previous trial. (**B**) Mean errors on the absolute orientation difference of [0°, 90°], plotted separately for prior Direction and Time conditions. The sign of the response error was coded so that positive values indicate that the current-trial direction report was biased toward the direction of the previous trial, and negative values indicate that the current-trial direction report was biased away from the direction of the previous trial. (**C**) Mean errors averaged across 22.5°, 45.0°, and 67.5°, were plotted separately for prior Direction and Time conditions. Error bars represent ± SEM. n.s. denotes non-significant.

Direction Estimation in Experiment 2. Figure S2.A depicted the response errors against the orientation difference from -90° to 90° for prior direction reproduction and duration reproduction trials separately. The direction errors were translated into the attractive (positive) and repulsion (negative) sequential effect and replotted in Figure S2.B. The average response biases across the orientation differences of 22.5°, 45.0°, and 67.5° were 0.978° ± 0.294° and 0.469° ± 0.303° for the prior Direction and Time conditions. The averaged response biases were significant only for prior Direction task (prior Direction: $t_{(23)}$ = 3.333, p =.003, d = 0.680; prior Time: $t_{(23)}$ = 1.546, p = .136, d = 0.315) and there was no difference between the two, $t_{(23)}$ = 1.167, p =.255, d = 0.348 (Figure S2.C).

To gain a better understanding of the differences between the two experiments, we further conducted an omnibus analysis across both experiments. A two-way mixed ANOVA on the attraction effect (averaged across 22.5°, 45.0°, and 67.5°) yielded neither a significant main effect for Experiment ($F_{(1,46)}$ = 1.495, p = .228, η_p^2 = 0.031), nor for the task relevance ($F_{(1,46)}$ = 3.758, p = .059, η_p^2 = 0.076).

Additionally, there was no significant interaction effect between the two factors ($F_{(1,46)} = 0.059$, $p = .809$, $\eta_p^2 = 0.001$).
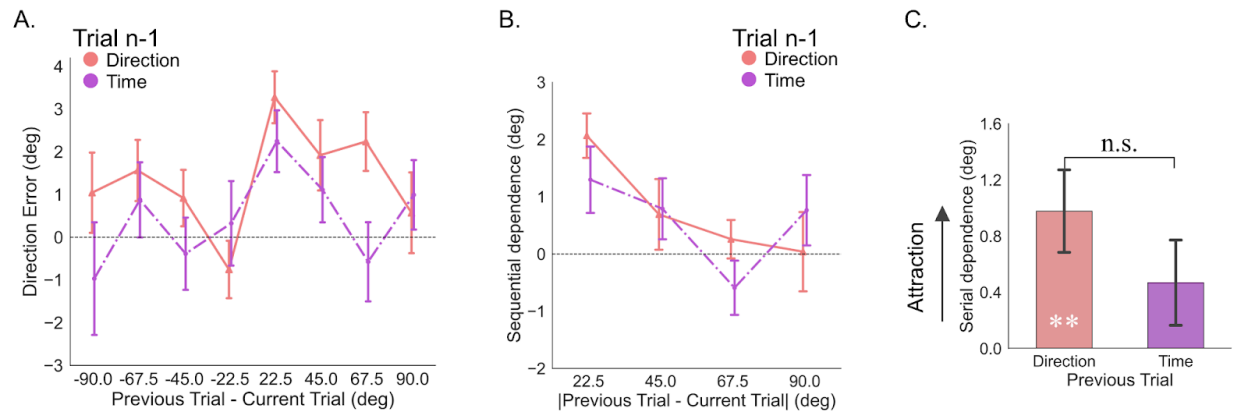

Figure S2. The results of direction reproduction trials for Experiment 2. (**A**) Mean response errors on the orientation difference of [-90°, 90°], plotted separately for trials preceded by Direction report and Time report. The angular difference was realigned to represent the relative motion orientation (plus 180° for the opposite direction) of the previous trial. (**B**) Mean errors on the absolute orientation difference of [0°, 90°], plotted separately for prior Direction and Time conditions. The sign of the response error was coded so that positive values indicate that the current-trial direction report was biased toward the direction of the previous trial, and negative values indicate that the current-trial direction report was biased away from the direction of the previous trial. (**C**) Mean errors averaged across 22.5°, 45.0°, and 67.5°, were plotted separately for prior Direction and Time conditions. Error bars represent ± SEM. n.s. denotes non-significant. ** $p < .01$, and n.s. non-significant.

The results in direction adjustment tasks showed that response biases in Experiment 1 for both preceding direction and time tasks did not significantly deviate from zero, indicating no significant sequential bias in the direction estimation task. However, in Experiment 2, significant attractive biases were observed only for the prior direction task. Considering both Experiments 1 and 2 adopted the adjustment tasks for direction trials, these distinct patterns of response biases in direction estimation tasks across different experiments may be due to the differential memory processes engaged in the encoding phase. For the duration reproduction, participants had to maintain the duration in working memory in the whole encoding phase to process it accurately, while the temporal bisection decision could be made before the end of the encoding display (the decision of "longer" was made after the encoding display passed 1 s, and no need to encode the whole display of 1.8 s). The omnibus analysis across both

experiments revealed a marginally significant main effect for task-relevance ($F_{(1,46)} = 3.758$, $p = .059$, $\eta_p^2 = 0.076$), suggesting that the attractive biases in direction estimates may also be task-relevant. However, there were no significant main effects for Experiment, nor a significant interaction effect between the two factors.

Although previous research has shown strong sequential effects in motion direction estimation, such as attraction (Alais et al., 2017; Fischer et al., 2020; Moon & Kwon, 2022) or repulsion (Bae & Luck, 2017, 2020; Kang & Choi, 2015), the dominance of either effect remain mixed. Recent studies also suggest that attractive and repulsive biases can occur concurrently in motion direction processing (Feigin et al., 2021; Fritsche et al., 2017; Moon & Kwon, 2022; Pascucci et al., 2019; Pascucci & Plomp, 2021; Sadil et al., 2024; Sheehan & Serences, 2023; Zhou et al., 2024). For instance, a recent study showed that the preceding direction response induced an attractive bias, while the preceding motion direction caused a repulsion bias, both contributing to serial dependence (Moon & Kwon, 2022). In our study, we used coherent motion with relatively long exposure times (600 to 1800 ms). The adjustment task for determining motion direction, which required using the left and right arrow keys to modify the direction pointer, might induce significant decisional inertia from the previous response, leading to mixed attraction effects observed in our study.

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3 Distinct sequential effects in space and time

Opposing Sequential Biases in Direction and Time Reproduction:
Influences of Task Relevance and Working Memory

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Abstract

Our current perception and decision-making are shaped by recent experiences, a phenomenon known as serial dependence. While serial dependence is well-documented in visual perception and has been recently explored in time perception, their functional similarities across non-temporal and temporal domains remain elusive, particularly in relation to task relevance and working memory load. To address this, we designed a unified experimental paradigm using coherent motion stimuli to test both direction and time reproduction. The direction and time tasks were randomly mixed across trials. Additionally, we introduced pre-cue versus post-cue settings in separate experiments to manipulate working memory load during the encoding phase. We found attractive biases in time reproduction but repulsive biases in direction estimation. Notably, the temporal attraction was more pronounced when the preceding task was also time-related. In contrast, the direction repulsion remained unaffected by the nature of the preceding task. Additionally, both attractive and repulsive biases were enhanced by the post-cue compared to the pre-cue. Our findings suggest that opposing sequential effects in non-temporal and temporal domains may originate from different processing stages linked to sensory adaptation and post-perceptual processes involving working memory.

Keywords: sequential effect, repulsion, attraction, working memory

3.1 Introduction

Our brain estimates the magnitude of stimuli not only from noisy sensory inputs but also from the recent past. This integration process results in sequential (serial) dependence and central tendency bias (Cicchini et al., 2023; Fischer & Whitney, 2014; Glasauer & Shi, 2022; Manassi et al., 2023; Pascucci et al., 2023). Sequential effects can lead to either attractive or repulsive biases (Ceylan & Pascucci, 2023; Cicchini et al., 2023; Czoschke et al., 2019; Manassi et al., 2023; Moon & Kwon, 2022), depending on the functional roles they serve. Sequential attraction occurs when consecutive stimuli are perceived as more similar than they actually are, believed to promote perceptual stability by integrating similar visual inputs over time (Cicchini et al., 2023; Fischer & Whitney, 2014; Glasauer & Shi, 2022; Liberman et al., 2016). However, there is a debate on whether it represents a purely perceptual phenomenon (Czoschke et al., 2019; Fornaciai & Park, 2018; Murai & Whitney, 2021; Pascucci et al., 2024) or relies more on memory traces of previous stimuli (Bae & Luck, 2020; Ceylan et al., 2021; Ceylan & Pascucci, 2023; Pascucci et al., 2019).

Sequential repulsion, on the other hand, occurs when the current perception is biased away from the preceding or concurrent stimulus. This effect usually appears when multiple stimuli need to be held in working memory (Czoschke et al., 2019) or when stimuli are presented but not reported (Ceylan & Pascucci, 2023; Pascucci et al., 2019; Pascucci & Plomp, 2021). It is thought to amplify small but potentially important differences between stimuli (Burr & Cicchini, 2014), maximizing discriminability (Czoschke et al., 2019; Fritsche et al., 2017) and perceptual accuracy (Ceylan & Pascucci, 2023; Fritsche et al., 2020; Moon & Kwon, 2022).

Sequential effects have been indicated to arise from perceptual or post-perceptual decision stages (Bae & Luck, 2020; Ceylan et al., 2021; Ceylan & Pascucci, 2023; Fischer et al., 2020; Fornaciai & Park, 2019; Fritsche & de Lange, 2019b; Pascucci et al., 2019). The perceptual perspective suggests that sequential attraction helps maintain perceptual stability and temporal continuity by integrating past and current information to filter out abrupt noises (Czoschke et al., 2019; Fornaciai & Park, 2018; Murai & Whitney, 2021; Pascucci et al., 2024). The evidence comes from the fact that this bias can even emerge in the absence of a decision process when participants are not required to report the target feature in the previous trial (Czoschke et al., 2019; Fornaciai & Park, 2018; Murai & Whitney, 2021). Post-perceptual perspective links sequential effects to decision-related factors (Bae & Luck, 2020; Ceylan et al., 2021; Ceylan & Pascucci, 2023; Fischer et al., 2020; Fornaciai & Park, 2019; Fritsche & de Lange, 2019b; Pascucci et al., 2019). For example, in a study involving orientation or color judgments with a post-cue, sequential dependence emerged only when both the preceding and current trials were the same task, diminishing when tasks differed (Bae & Luck, 2020). These findings suggest that task-related responses from previous trials, not just the encoding of the prior stimulus, are necessary for sequential effects.

The two opposing effects, attraction and repulsion, have historically been studied separately, recent research suggests they may co-occur and interact during perceptual processing (Feigin et al., 2021; Fritsche et al., 2017; Moon & Kwon, 2022; Pascucci et al., 2019; Pascucci & Plomp, 2021; Sadil et al., 2024; Sheehan & Serences, 2023; Zhou et al., 2024). For instance, a recent study on motion direction showed that the preceding direction response induced an attractive bias, while the preceding motion direction caused a repulsion bias, both contributing to serial dependence (Moon & Kwon, 2022). The previous response, being the observer's final estimate of the prior stimulus, serves as a predictor for upcoming stimuli, influencing the current perceptual estimate (Burr & Cicchini, 2014; Moon & Kwon, 2022; Sadil et al., 2024). Thus, attraction could also operate at the decision response stage or higher-level processes. Conversely, adaptation in the neural population responsible for encoding specific features, such as orientation or motion direction, plays a crucial role in repulsion (Alais et al., 2017; Fritsche et al., 2017, 2020; Moon & Kwon, 2022; Sheehan & Serences, 2022). This adaptation, often manifested as a reduction in neural response gain to the previously encoded feature, leads to a repulsive shift in the perceived stimulus away from the preceding one or the long-term past (Fritsche et al., 2017, 2020; Moon & Kwon, 2022).

The role of working memory in serial dependence is crucial and multifaceted, as it influences decision-making and motor planning (Bae & Luck, 2020; Bliss et al., 2017; de Azevedo Neto & Bartels, 2021; Kiyonaga, Scimeca, et al., 2017). Research shows that increasing temporal delay between stimulus presentation and response, thereby imposing greater working memory loads, leads to a stronger attractive bias toward the preceding stimulus (Bliss et al., 2017). A recent fMRI study on duration reproduction further demonstrates that consecutive active responses, compared to passive viewing, enhanced attractive biases (Cheng et al., 2023). Crucially, in these consecutive response trials, sequential effects negatively correlated with hippocampus activities (Cheng et al., 2023). While increased working memory demands generally amplify attractive biases, evidence suggests a more complex relationship with repulsive biases. Some findings indicated that repulsive biases might arise from sensory adaptation occurring at an early stage of visual processing, potentially independent of working memory (Fritsche et al., 2017; Kiyonaga, Scimeca, et al., 2017).

It is important to note that the aforementioned studies on sequential effects have predominantly concentrated on non-temporal features within the visual domain, where low-level sensory adaptation and higher-level memory processing may interact. Research on sequential effects in time perception is less developed, with main findings often suggesting attractive rather than repulsive biases (Glasauer & Shi, 2022; Wehrman et al., 2018, 2023; Wiener et al., 2014). The prevalence of attractive biases in time perception remains unclear, but several distinct features in time perception might contribute to this predominance. In contrast to visual processing, time perception is not bound to a specific sensory system

(Wittmann & Paulus, 2008) and may rely more heavily on the representation of stimuli in working memory (B.-M. Gu et al., 2015; Shi et al., 2013; Teki & Griffiths, 2016). Sensory adaptation-induced repulsion biases might be specific to certain modalities, such as vision. Additionally, unlike some visual features that can be simultaneously presented and held in memory, time intervals are monitored and processed sequentially. The natural stimulus distribution also differs between non-temporal visual features (e.g., orientation, motion direction, color) and magnitude stimuli (e.g., time, numerosity, length) (Hahn & Wei, 2024). For example, motion direction follows a circular distribution, ranging from 0 to 360 degrees, potentially mitigating the influence of central tendency biases, whereas temporal stimuli follow an open-scale distribution, mainly influenced by central tendency biases and sequential (serial) dependence biases (Glasauer & Shi, 2022).

Given these distinct processes for non-temporal visual features and time, it remains uncertain if sequential effects share the same mechanisms across temporal and non-temporal domains. Notably, working memory is often shared between tasks across domains, so its influence on sequential effects might have some commonalities. However, the contribution of working memory to sequential effects may differ for temporal and non-temporal processes, which remains an open issue. Studies concurrently addressing sequential effects in both spatial features (such as motion direction) and time are particularly rare. This study aims to address this gap by investigating sequential effects in both temporal and non-temporal domains using coherent motion stimuli, involving both direction and time reproduction tasks.

We hypothesized that sensory adaptation is specific to sensory systems, so adaptation-induced repulsion bias is likely to occur in the non-temporal rather than temporal domain. Early studies suggest that sensory adaptation and perceptual level serial dependence require minimal working memory (Fischer & Whitney, 2014; Fritsche et al., 2017), indicating that sequential effects that emerge at early perceptual processing may be resistant to task changes. In contrast, temporal processing heavily involves memory processing, and its sequential effects may be enhanced by task relevancy and working memory loads. To test these hypotheses, we designed two experiments employing the pre-cue vs. post-cue setting, the latter used in prior research (Bae & Luck, 2020; Cheng et al., 2023). Participants reproduced either the direction (direction task) or duration (time task) of a coherent motion display based on a cue shown either before (pre-cue, Experiment 1) or after (post-cue, Experiment 2) stimulus presentation. By using this unified experimental paradigm involving both direction and time reproduction tasks, we aimed to compare the non-temporal and temporal sequential effects. By randomly interleaving the direction and time tasks, we expected to observe task-relevant modulation for post-perceptual serial dependence. Additionally, comparing the pre-cue and post-cue results, we anticipated an enhancement of sequential effects by memory load.

To foreshadow the results, in two experiments (each N=23), we found that the post-cue, relative to the pre-cue, enhanced sequential effects. For timing tasks, strong attraction was observed only when the task of the preceding trial was the same, indicating that task consistency enhanced the attraction bias. In contrast, we observed repulsion biases for mild inter-trial orientation differences, regardless of the preceding task. These findings highlight the differential mechanisms underlying working memory-based temporal assimilation and adaptation-based spatial repulsion in direction, both of which are reinforced by working memory.

3.2 Experiment 1

Method

Participant

Twenty-three volunteers participated in Experiment 1 (14 females, 9 males; age ranged from 21 to 38, mean ± SD: 26.83 ± 4.18 years). All participants were right-handed and had normal or corrected-to-normal visual acuity and color vision. A meta-analysis of serial dependence in orientation reported in 35 different publications revealed a substantial effect size with a media Fisher z_r of 0.66 (equivalent to Cohen's d of 1.416) (Manassi et al., 2023). The difference in serial dependence between post-cue conditions (action vs. no action) in a recent duration reproduction task with a similar setup (Cheng et al., 2023) yields a large difference (Cohen's *d = 1.367*). To determine the appropriate sample size for our study, we conducted a priori power analysis using G*Power 3 (Faul et al., 2007). Considering our experimental design, which included a pre-cue versus post-cue manipulation and various tasks, we adopted a conservative approach. Based on half of the reported effect size (*d* = 0.7) and a significance level of α = .05, we aimed for a statistical power of 80% (1-β). Our calculations revealed that a minimum of 15 participants would be required to achieve the desired level of statistical power. On the safe side, we increased the sample size to 23. Prior to the experiment, participants gave written informed consent and received compensation of 9 Euro/hour for their involvement. The study was approved by the ethics committees of the Psychology Department at LMU Munich.

Stimuli and procedure

We used PsychoPy3 (Peirce et al., 2019) to control stimulus presentation and data collection. Participants were seated in a soundproof, dimly lit cabin, resting their heads on a chin rest. They kept a viewing distance of 60 cm from a 21-inch CRT monitor (refresh rate at 85 Hz), which presented stimuli on a light grey display background (luminance of 39.3 cd/m^2).
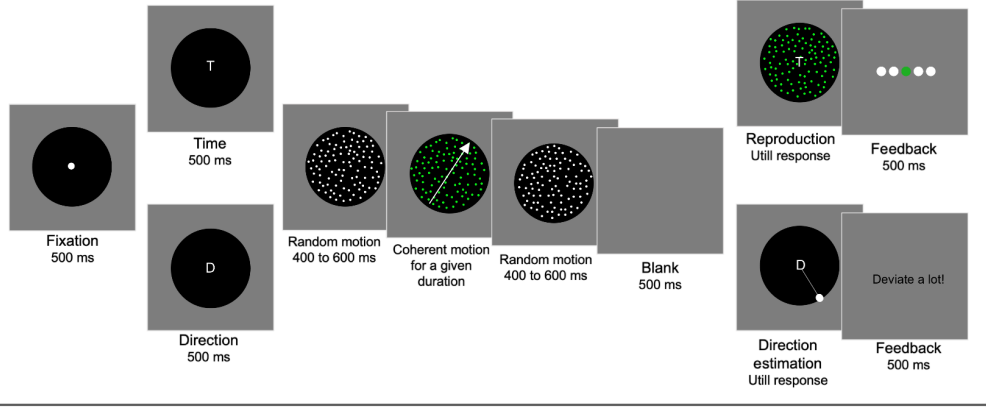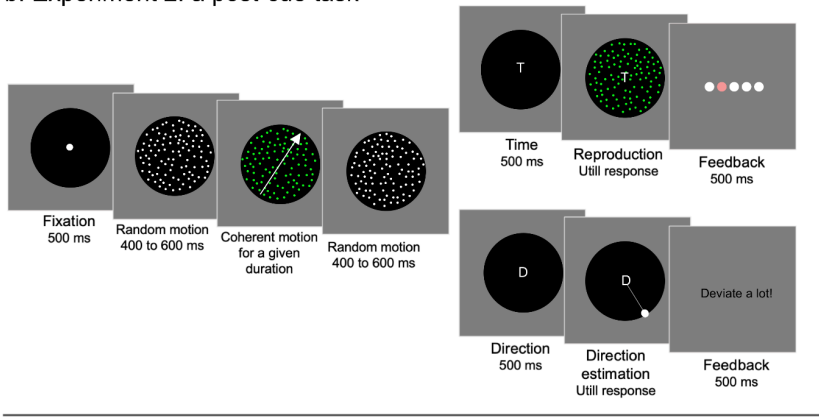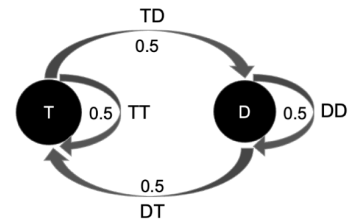
Figure 1. Schematic illustration of the study. (**a**) Procedure of Experiment 1 (the pre-cue task). Each trial began with a fixation dot, followed by a pre-cue letter indicating whether participants should report the direction ("D") or time ("T") of motion. The encoding phase began with a random dot kinematogram (RDK). When the white random-walked dots turned green, they moved in a specific direction for a given duration (indicated by the illustrative white arrow, not shown in the experiment). Then, they reverted to the random-walked white dots motion. The coherent motion was the target stimulus that participants had to remember either its direction or time according to the cue. The reproduction phase began after 500 ms of a blank screen. For the time task, a green RDK display appeared, and participants had to click the left mouse to terminate it when the duration matched to the coherent movement perceived during the encoding phase. For the direction task, a display with an adjustable line point appeared, and participants adjusted its orientation using a mouse, finalizing the direction report by pressing the space key. After their response, a 500-ms feedback display showed their accuracy; (**b**) Procedure of Experiment 2 (the post-cue task). It included the same encoding phase as in Experiment 1 but without a pre-cue. After the encoding phase, a post-cue displays for 500 ms, prompting participants for either time or direction reproduction. The rest of the procedure was the same as in Experiment 1. (**c**) The inter-trial transitional probability (from trial *n-1* to trial *n*) between the time and direction tasks. This transitional structure guarantees equal transitional probability of "Direction to Time (DT)", "Time to Time (TT)", "Direction to Direction (DD)", and "Time to Direction (TD)" trials.

Figure 1 illustrates the study setup. We employed a pre-cue for the time and motion direction reproduction task in Experiment 1. Each trial began with a fixation dot (subtended 0.5°; luminance of 85.7 cd/m^2) for 500 ms, indicating the beginning of the trial and prompting participants to focus their attention. A pre-cue with a letter ("D" or "T", visual angle of 0.8° × 1.0°, luminance of 85.7 cd/m^2) appeared in the display center for 500 ms, indicating whether participants should report the direction (the letter "D") or time (the letter "T") of the coherent motion. The reproduction task consisted of an encoding phase and a reproduction phase. Immediately after the cue display, the encoding phase started with a random dot kinematogram (RDK) display for 400 to 600 ms. The RDK consisted of 100 randomly generated white dots (each dot diameter of 0.2°; luminance of 85.7 cd/m^2) within a dark disk (subtended 17.8°, luminance of 16.5 cd/m^2) at the center of the screen. Those random dots randomly walked at a speed of 1°/s. Subsequently, the white dots turned green (luminance of 45.8 cd/m^2) and moved coherently (100%) with a speed of 6°/s in one direction (randomly selected from 11.25° to 348.75°, in steps of 22.5°) for a randomly sampled duration (0.8, 1.0, 1.2, 1.4, or 1.6 s). Since the primary objective of our research was to investigate the sequential effects in motion direction and time tasks, we selected this stimulus duration range to keep underlying mechanisms of time perception stable (e.g., sub- and supra-second time perception are often assumed to rely on different mechanisms and different brain regions (Hayashi et al., 2014; Lewis & Miall, 2003) as well as balance task difficulty among trials. Additionally, the cardinal motion directions (0°, 90°, 180°, 270°) were also avoided to rule out the cardinal rules (the orientation judgments were more accurate at horizontal and vertical orientation (Bae, 2024; Girshick et al., 2011; Mao & Stocker, 2021).

When a dot moved out of the dark disk, a new dot was randomly regenerated within the disk, keeping 100 dots all the time for the RDK presentation. This coherent motion was the encoding target. According to the pre-cue letter, participants were instructed to remember the direction or duration of the coherent motion for their reproduction task. Then, the dots reverted to random-walked white dot movements for 400 to 600 ms. The RDK displays served as masks before and after the target.

Following the encoding phase, there was a 500 ms blank interval before the participants' response. For the time task, the letter 'T' appeared in the center of the screen along with random-walked green dots (100 dots, each dot diameter of 0.2°; luminance of 45.8 cd/m^2; velocity of 1 °/s). We used a random-walked motion instead of a coherent motion to minimize inter-trial bias caused by the motion from the reproduction phase, given that we were interested in the sequential effects of the motion from the encoding phase. Participants had to terminate the presentation by clicking the left mouse when they perceived the duration to match the duration of the green dots' coherent motion from the encoding phase. After their response, feedback was given for 500 ms using a horizontally arranged display of five disks

(each subtended 1.8°). The accuracy of the response was indicated by one colored disk, from the left to the right, indicating the relative error below -30%, between [-30%,-5%], (-5%, 5%), [5%, 30%] and greater than 30%, respectively. The middle circle appeared in green, representing high accuracy. The middle left and middle right circles are in light red, indicating some deviation from the actual interval. The utmost left and right circles were shown in dark red, indicating a large reproduction error. If it was a direction task, a line pointer with a superimposed letter D appeared. The line started from the center, pointing in a random direction. Participants adjusted the pointer by moving the mouse and confirmed the final orientation by pressing the space key. If the final estimated direction deviated more than 60° from the true direction, a feedback display with the message "Direction deviated a lot!" appeared at the center of the display for 500 ms. Otherwise, a blank display appeared for 500 ms. The next trial began after a second intertrial interval.

Before the formal experiment, participants received 16 practice trials to familiarize themselves with the task. The formal experiment consisted of 480 trials, randomly shuffled with half for time reproduction and half for direction reproduction. The inter-trial transitional probability (from trial *n-1* to trial *n*) between the time and direction trials ensured an equal probability of "Direction to Time (DT)", "Time to Time (TT)", "Direction to Direction (DD)", and "Time to Direction (TD)" trials. Participants could take a short break after each block of 30 trials.

Data analysis

We excluded the first trial of each block, resulting in 16 omitted trials. Outliers due to accidental button presses or inattention were also excluded, specifically those with reproduction errors exceeding three standard deviations from the mean error for time report trials and response errors larger than 45° for direction report trials, before proceeding with further analyses. These outliers were rare, constituting only 0.38% of time reproduction trials (ranging individually from 0 to 6 outlier trials) and 0.24% of direction report trials (ranging individually from 0 to 13 outlier trials). Next, we categorized the remaining trials into four categories based on the inter-trial transition (from trial *n-1* to trial *n*): Direction to Time (DT), Time to Time (TT), Direction to Direction (DD), and Time to Direction (TD). To investigate the influence of prior tasks on the sequential effects of current estimates, we conducted separate analyses for time reproduction and direction reproduction trials.

Time reproduction trials. We focused on two conditions: the "Time to Time (TT)" representing the prior task-related condition and the "Direction to Time (DT)" representing the prior task-unrelated condition. Previous research has shown that subjective timing, on an open scale, is susceptible to both the central tendency bias and the sequential bias (Glasauer & Shi, 2022; Holland & Lockhead, 1968). The central tendency bias leads to an overestimation of shorter durations and an underestimation of longer

durations, while the sequential bias indicates that duration estimations are influenced by preceding durations.

To calculate the central tendency effect, we employed linear regression to approximate the relationship between the current reproduction error ($Error_n$) and the current duration (T_n) (Cicchini et al., 2012; Jazayeri & Shadlen, 2010; Shi et al., 2013).

$$Error_n = a \cdot T_n + b, \qquad (1)$$

where the absolute slope of the linear fit ($|a|$) reflects the central tendency effect. A slope of 0 indicates no central tendency, and 1 represents a strong central tendency.

The conventional measures of the serial dependence effect, which correlates the current response error to the difference between the previous and the current stimuli (Bliss et al., 2017; Cicchini et al., 2018; e.g., Fischer & Whitney, 2014; Kiyonaga, Manassi, et al., 2017), are not sufficient to separate sequential dependence from the central tendency bias (for more details, see Glasauer & Shi, 2022). Thus, we employed linear regression to the previous trial (Holland & Lockhead, 1968; Jesteadt et al., 1977) to analyze the sequential effect. This involved examining the correlation between the current error and the previous duration (T_{n-1}):

$$Error_n = c \cdot T_{n-1} + d, \qquad (2)$$

where the slope of the linear fit (c) indicates the sequential bias (e.g., Glasauer & Shi, 2022; Jesteadt et al., 1977). A positive slope indicates that the current estimation is attracted towards the previous duration (also called the "assimilation"). In contrast, a negative slope indicates that the current time estimation is repulsed from the previous duration. Additionally, as a sanity check and for further verification, we also computed the sequential effect using similar regressions for the durations presented in future trials (n+1).

Direction estimation trials. We focused on two conditions: the "Direction to Direction (DD)" representing the prior task-related condition and the "Time to Direction (TD)" representing the prior task-unrelated condition. The direction of motion was randomly selected from a circular distribution featuring 16 equally spaced angles (from 11.25° to 348.75°, in steps of 22.5°), effectively neutralizing any central tendency. Consequently, we focused solely on the sequential effect and skipped the central tendency analysis. The response error was calculated as the difference between the reported direction and the true motion direction for the current trial (i.e., estimate - direction). Negative errors indicated a counter-clockwise deviation from the true direction, while positive errors suggested a clockwise deviation. Additionally, the direction difference was also calculated between the current trial and the previous trial (the previous direction - the current direction), following the same method used in prior research (e.g., Fischer & Whitney, 2014). Trials with a direction difference of 0° or ± 180° were excluded, as response errors relative to these direction differences are undefined. Following previous research

(Moon et al., 2022) highlighting a significant role of non-directional orientation in the coding of visual motion direction, we reduced the direction difference range from [-180 to 180°] to [-90 to 90°] accordingly. To better reflect the repulsion and attractive biases, we converted the response errors from clockwise or counterclockwise directions to the repulsion (negative) and attractive (positive) biases by collapsing the direction differences to the positive range [0, 90.0°]. This analysis resembles the analysis of previous studies (Bae & Luck, 2020).

Prior research has shown that small orientation differences (within 45°) led to a significant attractive bias, while large orientation differences (greater than 45°) resulted in a repulsive bias (Bae & Luck, 2019; Bliss et al., 2017; Fritsche et al., 2017; Fritsche & de Lange, 2019b; Samaha et al., 2019). For example, attraction was observed when the orientation difference was around 17°, and repulsion was found for orientations more than 60° apart (Fritsche et al., 2017). We hypothesized that the reported orientation for the current trial would be repulsed by the orientation in the previous trial, particularly when orientations differed markedly. Thus, we calculated the average response errors for mild-orientation-difference trials (45.0° and 67.5°) and compared them to zero for each condition (the prior task being direction reproduction or time reproduction for the current direction reproduction trials).

Additionally, we computed the sequential effect in direction estimation, separated for the "short" and "long" stimulus presentation. Durations of 0.8 and 1.0 seconds were categorized as "short", while durations of 1.4 and 1.6 seconds were deemed "long". We excluded the intermediate duration of 1.2 seconds in this analysis. We then analyzed whether the sequential effects in direction estimation were modulated by the durations (short vs. long) of the target stimulus.

The statistical significance of the central tendency effect and the sequential effect was assessed individually using analysis of variances (ANOVAs) and one-sample *t*-tests against a null hypothesis of zero effect. Paired *t*-tests were run for within-subject between-condition comparisons.

Results and discussion
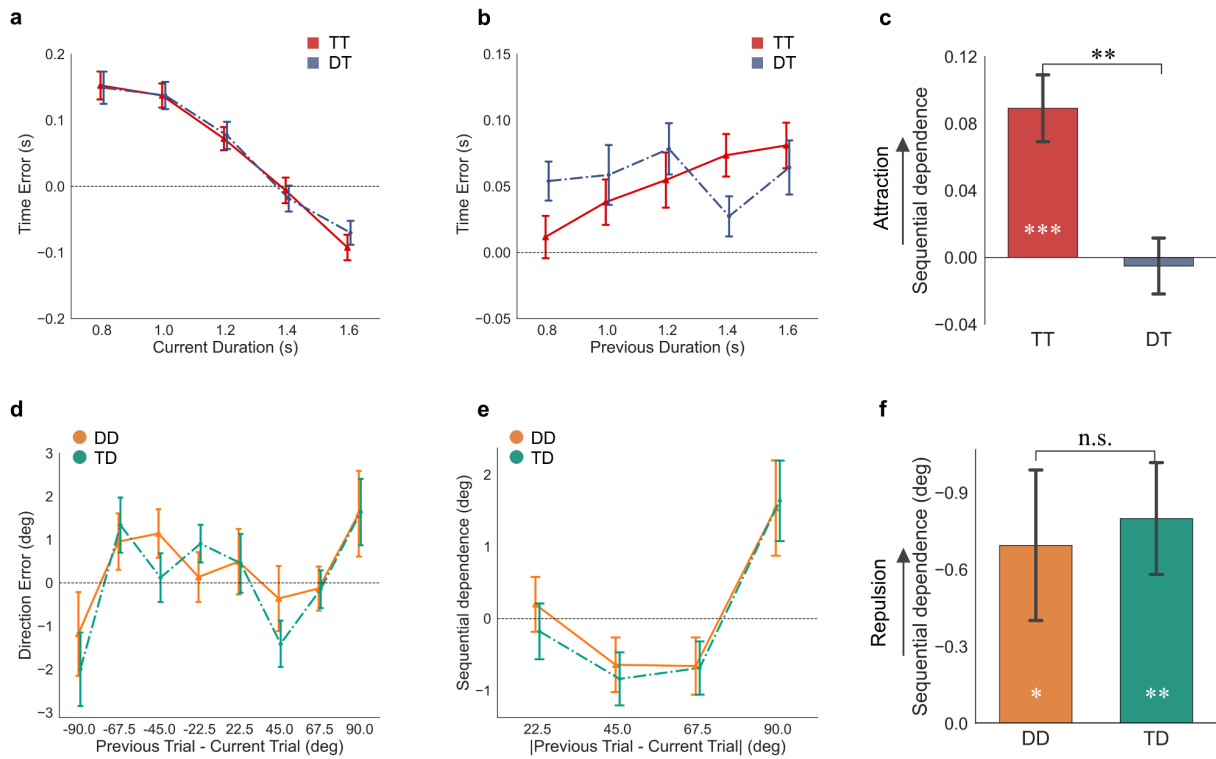
Figure 2. Results of Experiment 1. (**a**), (**b**), and (**c**) were the results of time reproduction trials. (**a**) Central tendency effect. Mean reproduction errors on the current sample duration are plotted separately for trials preceded by time report (TT) and direction report (DT). (**b**) Sequential effect. Mean reproduction errors on the previous duration, plotted separately for TT and DT conditions. (**c**) The mean slope of the linear fit. (**d**), (**e**), and (**f**) were the results of direction reproduction trials. (**d**) Mean response errors on the orientation difference of [-90°, 90°], plotted separately for trials preceded by direction report (DD) and time report (TD). The angular difference was realigned to represent the relative motion orientation (plus 180° for the opposite direction) of the previous trial. (**e**) Mean errors on the absolute orientation difference of [0°, 90°], plotted separately for DD and TD conditions. The sign of the response error was coded so that positive values indicate that the current-trial direction report was biased toward the direction of the previous trial, and negative values indicate that the current-trial direction report was biased away from the direction of the previous trial. Maximum repulsion occurred at 45° and 67.5° orientation differences. (**f**) Mean errors averaged across 45.0° and 67.5° were plotted separately for DD and TD conditions. Error bars represent ± SEM. ** denotes $p < .01$,* $p < .05$, and n.s. non-significant.

Time Reproduction

Overall, the mean reproduction errors (and associated standard errors, SEs) for prior time reproduction trials (task-related: TT) and prior direction estimation trials (task-unrelated: DT) were 51 ± 14 ms and 57 ± 15 ms, respectively. There was no significant difference between the two conditions ($t_{(22)} = -0.647$, $p = .524$, $d = -0.090$). To examine the precision of duration reproduction for two kinds of

preceding task (time vs. direction), we calculated the standard deviation of reproduction between TT and DT conditions, and it didn't show any significant difference between the two conditions ($t_{(22)} = 0.142$, $p = .888$, $d = 0.012$). The central tendency effect (Eq. 1) was evident in both the prior task-related TT and prior task-unrelated DT conditions. The mean central tendency indices (and associated SEs) were 0.317 ± 0.037 ($t_{(22)} = 8.605$, $p < .001$, $d = 1.794$) and 0.297 ± 0.039 ($t_{(22)} = 7.565$, $p < .001$, $d = 1.577$) for the TT and DT conditions, respectively. However, there was no difference between the conditions ($t_{(22)} = 1.364$, $p = .186$, $d = 0.109$, $BF_{10} = 0.479$), as illustrated in Figure 2a.

To quantify the sequential effect, we plotted the reproduction errors on the previous durations separately for the TT and DT conditions (as shown in Figure 2b). The reproduction error increased with increasing prior duration, showing that a longer prior duration attracted bias to a positive direction, manifesting an attractive sequential effect. This effect was quantified using the slope of linear regression (Eq. 2), which showed that the average slope was larger for the prior task-related TT condition ($8.9\% \pm 2.0\%$) than that for the task-unrelated DT condition ($-0.5\% \pm 1.7\%$), with paired t-test $t_{(22)} = 3.813$, $p = .001$, $d = 1.064$. The slope was only significantly positive for the TT condition ($t_{(22)} = 4.457$, $p < .001$, $d = 0.929$), but not for the DT condition ($t_{(22)} = -0.304$, $p = .764$, $d = 0.063$), as illustrated in Figure 2c. To ensure the validity of the findings and avoid statistical artifacts (Cicchini et al., 2014), we also tested and found no sequential effect on the durations presented in future trials ($ps > .417$).

Direction Estimation

The mean response errors were plotted against the direction difference between the previous and the current trials (ranging from -90° to 90°, a positive value representing the difference in the clockwise direction), separated for the prior task-related (DD) and task-unrelated (TD) conditions (Figure 2d). We first examined the precision of response (the standard deviation of direction reproduction) between DD and TD conditions didn't show any significant difference between the two conditions ($t_{(22)} = 0.967$, $p = .344$, $d = 0.061$). Additionally, the direction errors were translated into the repulsion (negative) and attractive (positive) sequential effect and replotted as a function of the absolute orientation difference for each condition (illustrated in Figure 2e). By visual inspection, the maximum repulsion effect is likely between 45.0° and 67.5°, with a large difference between preceding trial types. Indeed, the average repulsive biases across the orientation differences of 45.0° and 67.5° were both significant negative (DD: -0.695° $\pm$ 0.294°, $t_{(22)} = 2.367$, $p = .027$, $d = 0.494$; TD: -0.799° $\pm$ 0.218°, $t_{(22)} = 3.665$, $p = .001$, $d = 0.764$), but no difference between the two, $t_{(22)} = 0.283$, $p = .78$, $d = 0.084$, $BF_{10} = 0.227$ (Figure 2f). To ensure the validity of the findings and avoid statistical artifacts (Cicchini et al., 2014), we also tested and found no repulsion effect across the orientation differences of 45.0° and 67.5° between the future ($n+1$) and current trials ($ps > .635$).

The sequential effect at 90° were significantly positive in both DD (1.537° ± 0.663°, $t_{(22)}$ = 2.320, p =.030, d = 0.484) and TD (1.638° ± 0.599°, $t_{(22)}$ = 2.927, p =.008, d = 0.610) trials, but comparable between the two ($t_{(22)}$ = -0.100, p =.921, d = -0.034, BF_{10} = 0.220). This condition at 90° was a special scenario. If participants' judgments consider only the orientation, the effect can be interpreted as either attraction or repulsion. However, if judgments include both the orientation and direction), the effect is an attraction, assimilating toward the preceding direction. Previous research (Moon et al., 2022) indicated the significant role of non-directional orientation in the coding of visual motion direction. Thus, when the difference between the initial and the subsequent motion directions is 90°, attraction to the initial motion direction may be perceived as repulsion to the opposite direction if the motion direction is encoded in a non-directional orientation framework. The sanity check with the attraction effect for the orientation difference at 90° between the future ($n+1$) and current trials revealed no effects (ps > .372).

To rule out potential impacts of the presentation durations on sequential effects (shown at the direction differences: 45.0°, 67.5°, and 90°), we conducted three-way repeated measures ANOVA on response biases, considering current Stimulus Exposure[1], Prior Task, and inter-trial Direction Difference (45.0°, 67.5°, and 90°) as main factors. The analysis did not reveal any significant effects of Stimulus Exposure or its related interactions (Fs < 0.331, ps > .718, $\eta_p^2 s$ < 0.003). This suggests that variations in stimulus durations in our setup (800 - 1600 ms) did not affect the sequential effect.

Thus, Experiment 1 revealed an attractive bias in time reproduction only when the prior task was also time-related, suggesting that assimilation in temporal perception requires the previous trial to involve the same task. In contrast, the direction task yielded comparable biases unaffected by the prior task type and stimulus exposure. When the difference between two consecutive orientations was large (e.g., 45.0° and 67.5°), a repulsion bias was observed. For orientation differences (90°), an attractive bias emerged. The attractive effects at a 90° orthogonal difference might also be interpreted as a repulsion to the opposite motion direction.

3.3 Experiment 2

In Experiment 1, we employed a pre-cue setting in which participants were aware of the response dimension in advance, and the unattended dimension did not require active working memory maintenance during encoding. This setup might have led to a diminished encoding of the unattended feature dimension, leading to the lack of sequential dependence. To address this, in Experiment 2, we adopted a post-cue setting where both response dimensions, time and direction, had to be memorized during the encoding phase, and a post-cue revealed which dimension was relevant for the response.

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[1] To enhance statistical power given the limited number of trials, we splitted durations into two categories: short (<1.2 s) and long (> 1.2 s).

Methods

Participant

Twenty-three participants were recruited in Experiment 2 (13 females, 10 males; age 19 - 40, mean ± SD: 27.78 ± 5.31 years). All participants provided their written informed consent prior to the experiment and received 9 Euro/hour for their participation. The study was approved by the ethics committees of the Psychology Department at LMU Munich.

Stimuli and procedure

Experiment 2 used the post-cue setting, which was essentially the same as in Experiment 1, with one key difference: the task cue display (500 ms) was shown after the encoding phase (see Figure 1 b). In order to perform the tasks properly, participants had to remember both direction and time in the encoding phase and then report one of them according to the post-cue.

Data analysis

The data analysis for Experiment 2 followed essentially the same approach as that of Experiment 1. The first trial of each block was excluded. The outliers, using the same criteria as in Experiment 1, were rare in Experiment 2, on average only 0.40% of the time reproduction trials (ranging individually from 0 to 4 outlier trials) and 0.96% of the direction reproduction trials (ranging individually from 0 to 37 outlier trials).

Results and discussion

Time Reproduction

The average reproduction errors and their associated SEs for trials with prior time reproduction (task-related: TT) and trials with prior direction reproduction (task-unrelated: DT) were 34 ± 18 ms and 51 ± 16 ms, respectively. The difference between the two conditions was not significant, ($t_{(22)} = -1.755$, $p = .093$, $d = -0.208$, $BF_{10} = 0.818$). The standard deviation of duration reproduction between TT and DT conditions didn't show any significant difference between the two conditions ($t_{(22)} = 0.316$, $p = .755$, $d = 0.020$). Both conditions exhibited significant central tendency biases: 0.471 ± 0.057 and 0.486 ± 0.058 for the TT and DT conditions, respectively ($t s_{(22)} > 8.3$, $p s < .001$, $d s > 1.7$). There was no significant difference between them ($t_{(22)} = -0.581$, $p = .580$, $BF_{10} = 0.255$, Figure 3a).

The sequential effects for each condition were illustrated in Figure 3b, with mean slopes of 15.6% ± 3.2% and 6.0% ± 2.3% for the task-related (TT) and task-unrelated (DT) conditions, respectively (Figure 3c). Both slopes were significantly higher than zero ($t s_{(22)} > 2.6$, $p s < .02$, $d s > 0.55$), indicating a significant attractive bias in both conditions. Moreover, a paired *t*-test showed that the assimilation was significantly larger in the TT than in the DT condition ($t_{(22)} = 2.513$, $p = .020$, $d = 0.728$). Tests of the sequential effect on future trial durations (*n+1*) ruled out any statistical artifacts ($p s > .769$).
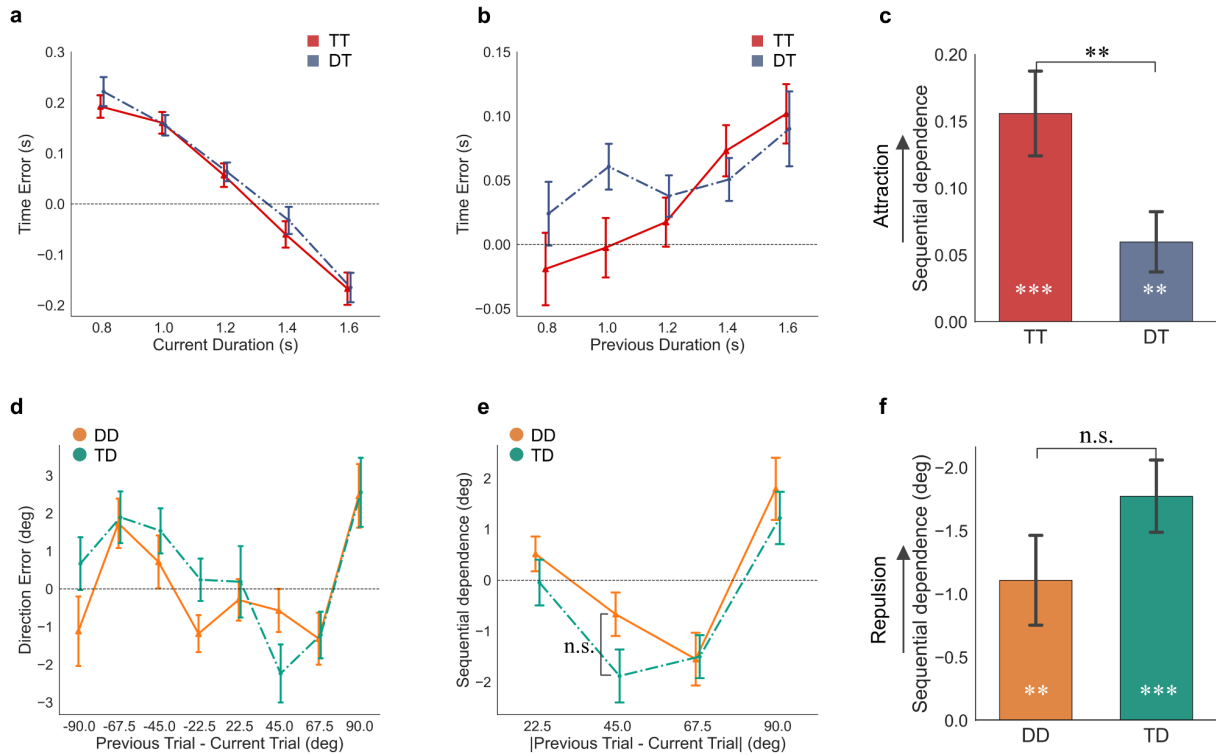
Figure 3. Results of Experiment 2. (**a**), (**b**), and (**c**) were the results of time reproduction trials. (**a**) Central tendency effect. Mean reproduction errors on the current sample duration, plotted separately for trials preceded by time report (TT) and direction report (DT). (**b**) Sequential effect. Mean reproduction errors on the previous duration, plotted separately for TT and DT conditions. (**c**) The slope of the linear fit. (**d**), (**e**), and (**f**) were the results of direction reproduction trials. (**d**) Mean response errors on the orientation difference of [-90°, 90°], plotted separately for trials preceded by direction report (DD) and time report (TD). The angular difference was realigned to represent the relative motion orientation (plus 180° for the opposite direction), rather than the motion direction, of the previous trial. (**e**) Mean errors on the absolute orientation difference of [0°, 90°], plotted separately for DD and TD conditions. The sign of the response error was coded so that positive values indicate that the current-trial direction report was biased toward the direction of the previous trial, and negative values indicate that the current-trial direction report was biased away from the direction of the previous trial. The difference between the DD and TD conditions for the 45° orientation difference didn't reach significance, for the large separation was due to one participant who had large response errors in this type. Maximum repulsion occurred at 45° and 67.5° orientation differences. (**f**) Mean errors averaged across 45.0° and 67.5°, were plotted separately for DD and TD conditions. Error bars represent ± SEM. ** denotes $p < .01$, n.s no significant.

Direction Estimation

Figure 3d depicted the response errors against the direction difference from -90° to 90° for prior direction reproduction and time reproduction trials separately. The standard deviation of direction reproduction between prior direction report and time report trials didn't show any significant difference

between the two conditions ($t_{(22)}$ = 1.091, p = .287, d = 0.103). The direction errors were translated into the repulsion (negative) and attractive (positive) sequential effect and replotted in Figure 3e. Repulsion biases occurred at orientation differences of 45.0° and 67.5°. The averaged repulsion biases from the two orientation differences were significant for both task-related (DD) and task-unrelated (TD) conditions (DD: -1.110° ± 0.355°; TD: -1.775° ± 0.286°, $ts_{(22)}$ > 3.127, ps < .005, ds > 0.65), but did not differ from each other ($t_{(22)}$ = 1.918, p =0.068, d = 0.431, BF_{10} = 1.038), as illustrated in Figure 3f.

We also observed an attractive bias for both TD and DD conditions at an orientation difference of 90° (DD: 1.796° ± 0.610° and TD: 1.224° ± 0.514°, $ts_{(22)}$ > 2.38, p < .026, d > 0.49), and they were comparable ($t_{(22)}$ = 0.937, p =.359, d = 0.211, BF_{10} = 0.324). For sanity check, we tested the repulsion effect (at orientation differences of 45.0° and 67.5°) and attraction effect (at an orientation difference of 90°) across differences between the future ($n+1$) and current trials, and we found no effects (ps > .151).

Similar to Experiment 1, we conducted a further three-way repeated measures ANOVA on the reproduction biases, considering factors of Stimulus Exposure (Short vs. Long), Prior Task (Direction vs. Time), and inter-trial Direction Difference (45.0°, 67.5°, and 90°) failed to reveal any significance (Fs < 2.672, ps > .103, $\eta_p^2 s$ < .010), indicating the sequential bias was unaffected by the variations of stimulus exposure we used (800 to 1600 ms).

3.4 Omnibus analysis

To gain a better understanding of the differences between the pre-cue and post-cue settings in terms of central tendency and sequential effects, we further conducted an omnibus analysis across both experiments. Specifically, we performed a two-way mixed ANOVA, with Prior Task (related task vs. unrelated task) as a within-subject factor and Cue Setting (Exp. 1: pre-cueing vs. Exp. 2: post-cueing) as a between-subject factor, on each effect of interest.
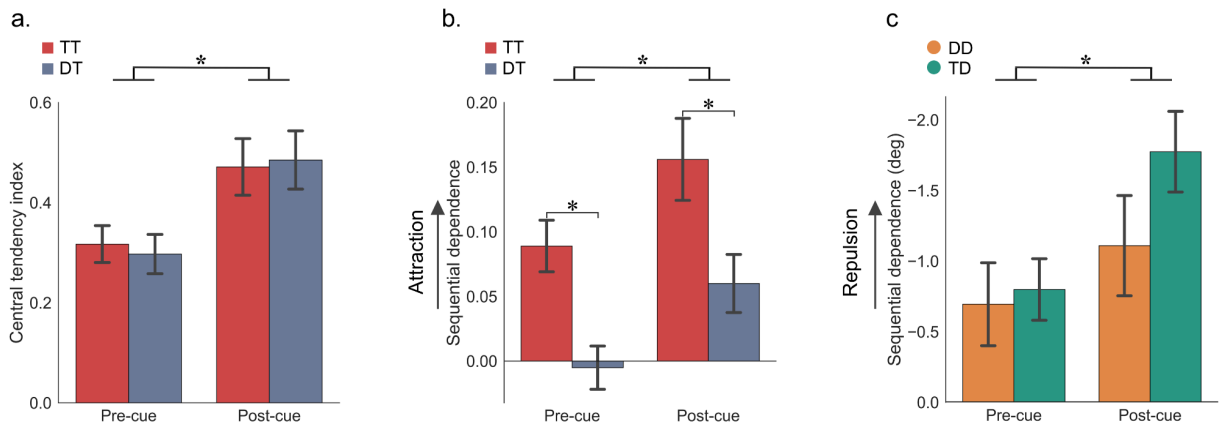
Figure 4. Comparisons between experiments (Exp. 1: pre-cue vs. Exp. 2: post-cue) and prior tasks (task-related vs. task-unrelated). (**a**) Central tendency effect for time reproduction trials. (**b**) Attractive sequential effect for time reproduction trials. TT represents consecutive time tasks, while DT represents a current time task preceded by a direction task. (**c**) Repulsive sequential effect for direction reproduction trials. DD represents consecutive direction tasks, while TD represents a direction task preceded by a time task. Error bars represent ± SEM. $*p < .05$.

For the time reproduction trials, the two-way mixed measurement ANOVA on the central tendency index revealed a significant main effect of Cue Setting ($F_{(1,44)} = 6.448$, $p = .015$, $\eta_p^2 = 0.128$), indicating a larger central tendency with the post-cue (Figure 4a). However, neither the main factor of Prior Task ($F_{(1,44)} = 0.047$, $p = .830$, $\eta_p^2 = 0.001$, $BF_{10} = 0.163$) nor their interaction ($F_{(1,44)} = 1.397$, $p = .244$, $\eta_p^2 = 0.031$) was significant. In contrast, the two-way mixed ANOVA on the sequential effect revealed both main factors were significant: Cue Setting, $F_{(1,44)} = 7.541$, $p = .009$, $\eta_p^2 = 0.146$; Prior Task, $F_{(1,44)} = 17.465$, $p < .001$, $\eta_p^2 = 0.284$. The results revealed that the attraction was significantly larger with the preceding same rather than the different task. Additionally, the attraction was amplified with the post-cue compared to the pre-cue (Figure 4b). However, there was no significant interaction ($F_{(1,44)} = 0.002$, $p = .966$, $\eta_p^2 < 0.001$). Next, we applied the two-way mixed ANOVA on the standard deviation of reproduced duration (i.e., precision), which revealed that neither Prior Task ($F_{(1,44)} = 0.104$, $p = .748$, $\eta_p^2 = 0.002$), nor Cue Setting ($F_{(1,44)} = 1.522$, $p = .224$, $\eta_p^2 = 0.033$), nor their interaction ($F_{(1,44)} = 0.014$, $p = .905$, $\eta_p^2 = 0.000$) was significant. The results suggest that the time task difficulties for the two experiments were comparable.

For the direction reproduction, the two-way mixed ANOVA on the repulsion effect (averaged across 45.0° and 67.5°) revealed a significant main effect of Cue Setting ($F_{(1,44)} = 4.542$, $p = .039$, $\eta_p^2 = 0.146$). The repulsion effect was significantly enhanced with the post-cue relative to the pre-cue (Figure 4c). Neither Prior Task ($F_{(1,44)} = 2.309$, $p = .136$, $\eta_p^2 = 0.050$, $BF_{10} = 0.463$) nor the interaction ($F_{(1,44)} = 1.227$, $p = .274$, $\eta_p^2 = 0.027$) was significant. Another two-way mixed ANOVA for the attractive bias at an orientation difference of 90° revealed neither the main effect Prior Task nor Cue Setting, nor their interaction was significant (all $Fs < 0.329$, all $ps > 0.569$, $\eta_p^2 s < 0.007$). This means that the attractive bias

at the orientation difference of 90° was not influenced by task relevance (task-relevant vs. task-irrelevant) or the cue position (pre-cueing vs. post-cueing).

In summary, comparison across experiments revealed that the post-cue condition enhanced the central tendency and sequential biases in time estimation, suggesting that the sequential attractive bias in time reproduction is influenced by working memory and post-perceptual processing, consistent with prior research (Bliss et al., 2017). In contrast, direction reproduction was unaffected by task relevance in both experiments, indicating that the repulsive bias likely originated from low-level sensory adaptation. The repulsion effects at 45.0° and 67.5° were enhanced by the post-cue (but not at the extreme case of 90°), possibly due to increased working memory load with the post-cue. Our findings contrast with those of Bae and Luck (2020), who reported differential effects of prior tasks with the post-cue setting. The discrepancy may arise from the fact that their experimental setup involved two visual tasks (color and direction) that might interact with each other in working memory, while we employed time and motion direction tasks.

3.5 General Discussion

The present study investigated differential sequential effects in non-temporal and temporal tasks, using task changes and pre-cue vs. post-cue settings to examine the influences of task relevance and working memory load. Intriguingly, we observed only sequential attractive biases in timing tasks, but both repulsion and attraction effects in direction tasks across both experiments. For the time reproduction task, the attractive bias was reliable when the preceding trial involved the same task. However, this attraction was significantly reduced in the post-cue setting and vanished in the pre-cue setting when the preceding trial involved a direction task. In contrast, task relevance had no impact on sequential effects in direction reproduction. Nonetheless, the post-cue setting enhanced both attractive and repulsive biases.

Both sequential attractive and repulsive biases are well-documented in previous studies on orientation and direction judgments. For example, when stimuli such as Gabor orientations or gratings are used, small orientation differences between trials (under 20°) typically yield attraction biases, while larger differences elicit repulsion biases (Ceylan & Pascucci, 2023; Fritsche et al., 2017; Fritsche & de Lange, 2019a). Repulsive bias in orientation may originate from early sensory processing mechanisms, where neurons adapt to prolonged exposure to a specific orientation or direction, decreasing their sensitivity to that feature and subsequently shifting their spatial tuning, which causes negative tilt-aftereffect (Alais et al., 2017; Fritsche et al., 2020). Previous research has demonstrated that attractive and repulsive biases can occur concurrently, such as in motion direction processing (Alais et al., 2017; Ceylan & Pascucci, 2023; Fischer et al., 2020; Moon et al., 2022). For instance, a brief presentation (e.g., 200 ms in Alais et al., 2017 and Fischer et al., 2020) or mostly random motion display (Moon & Kwon, 2022) can make the orientation signal of the motion more dominant, resulting in attractive effects similar to those observed in

static orientation studies (Fischer & Whitney, 2014; Manassi et al., 2018). In contrast, long exposure to a coherent motion signal (e.g., here 800 to 1600 ms) may induce motion adaptation, resulting in repulsive biases, similar to negative tilt-aftereffects (Alais et al., 2017; Moon et al., 2022). Our studies used coherent motion and found repulsion effects, consistent with recent studies on motion direction (Alais et al., 2017; Bae & Luck, 2017, 2020; Kang & Choi, 2015) or orientation (Ceylan & Pascucci, 2023; Su et al., 2023). Repulsive biases dominate when previous stimuli are either unattended or irrelevant to the task, or when visual stimuli have a long duration and high contrast, or a reference (Manassi et al., 2018; Pascucci et al., 2019; Pascucci & Plomp, 2021; Su et al., 2023). The repulsive bias observed here is likely due to dominant low-level motion adaptation with relatively long exposure times (800 to 1600 ms), which may overshadow any minor high-level task modulation, irrespective of the preceding duration or direction tasks.

The fact that repulsive biases can be enhanced by working memory load suggests that both early motion adaptation and late post-perceptual decision-making contribute to the observed sequential repulsion. The latter contribution indicates the involvement of high-level working memory processes, such as maintaining discriminability of multiple items (Czoschke et al., 2019; Fritsche et al., 2017), and active discarding of irrelevant information as well as reduced attention to irrelevant items (Ceylan & Pascucci, 2023). When memory load increases to reach the capacity limit, repulsive representation of multiple items could help maintain discriminability between items being held (Czoschke et al., 2019). This might also explain why repulsive biases occur away from unattended or irrelevant items (Ceylan & Pascucci, 2023; Fischer & Whitney, 2014; Shan & Postle, 2022). For example, irrelevant inducers, while initially attended to, are actively removed from working memory due to limited capacity (Lewis-Peacock et al., 2018; Shan & Postle, 2022). To protect the target item from removal, its representation is repelled away from those irrelevant inducers (Ceylan & Pascucci, 2023; Fritsche & de Lange, 2019b). In our study, the enhancement of the repulsive bias with the post-cue is likely due to the increased memory load, which pushes the current representation of the motion direction away from the preceding one. However, it should be noted that visual working memory load could increase the uncertainty of the target representation, which may result in an enhanced repulsion effect. The increased uncertainty may also potentially lead to an interaction of memory load and task modulation. For example, when the two tasks were in the same visual modality (i.e., orientation and color) and with the post-cue setting, the limited memory capacity may amplify the task relevance effect on repulsive biases (e.g., Bae & Luck, 2020).

Conversely, we observed attractive biases in the timing task. What accounts for the opposing patterns in sequential biases between timing and non-timing (direction) tasks? Time perception, unlike visual perception, lacks dedicated sensory systems (Wittmann & Paulus, 2008). The brain constructs time perception by integrating current sensory estimations with recent history and prior knowledge of the

stimuli to enhance processing efficiency. This integration leads to attractive biases, as recent events serve as predictions (Glasauer & Shi, 2022; Shi et al., 2013). Glasauer and Shi (2022) showed that individual beliefs in temporal continuity impact the magnitudes of the sequential bias, with stronger attractive biases in those with high beliefs in temporal continuity. Unlike visual perception, which involves both early sensory adaptation and post-perceptual processing, time perception relies heavily on post-perceptual processes. In a duration reproduction task, reproducing duration relies on not only the encoded duration in working memory (Cheng et al., 2023) but also prior knowledge of the duration distribution (Jazayeri & Shadlen, 2010; Lejeune & Wearden, 2009; Shi & Burr, 2016). These sources are integrated and mixed in working memory to boost the reliability of estimates (Bausenhart et al., 2016; B. M. Gu & Meck, 2011; Penney et al., 2000). This memory mixing may involve active recall of memory traces from past experiences, contributing to sequential biases (Bliss et al., 2017; Ceylan & Pascucci, 2023; Fornaciai & Park, 2020; Fritsche & de Lange, 2019a; Ranieri et al., 2022).

For non-temporal visual processing, working memory may link sensory representation to responses, enhancing sequential effects. The sensory-level sequential effects can be either attractive or repulsive, depending on their functional roles (Ceylan et al., 2021; Fritsche & de Lange, 2019b; Glasauer & Shi, 2022; Kim et al., 2020; Kim & Alais, 2021; Suárez-Pinilla et al., 2018). For example, increasing the delay between stimulus presentation and response, thereby prolonging the reliance on working memory, leads to a stronger attractive bias toward the preceding stimulus (Bliss et al., 2017). On the other hand, when two visual orientations must be held in the working memory, their representations repel each other (Czoschke et al., 2019). In our study, increasing working memory load by using the post-cue enhanced both the adaptation-induced repulsive bias in direction judgments and attractive biases in time judgments, similar to previous findings that working memory can amplify sequential effects (Bliss et al., 2017).

One might ask about the exact underlying mechanism of this enhancement by working memory load. In our study, with the post-cue, both the non-temporal direction and the time interval had to be simultaneously encoded in working memory before the cue appeared. Shared memory representations likely increase sensory uncertainty (Li et al., 2021; Michail et al., 2021; Simon et al., 2016). According to Bayesian dynamic updating processes (Burr & Cicchini, 2014; Glasauer & Shi, 2022), the weight of prior stimuli increases during the integration, resulting in stronger sequential effects (Ceylan et al., 2021; Cicchini et al., 2018; Markov et al., 2024). Recent research also confirms that uncertainty can modulate the strength of serial dependence (Fulvio et al., 2023; Ozkirli & Pascucci, 2023). Further research is needed to clarify the exact mechanisms through which working memory load influences these sequential biases.

In summary, our study dissected sequential biases in space and time using a unified setting that tested both spatial motion direction and time reproduction. We uncovered distinct sequential biases: time blends through assimilation, while direction skews via dominant repulsion, with time particularly influenced by task relevance. Our findings highlight that sensory adaptation dominates repulsion biases in motion direction judgments, while post-perceptual processes that involve working memory have a greater effect on the bias in time reproduction. Moreover, increasing the working memory load with the post cue enhanced both opposing sequential effects. The distinct pattern of sequential biases between time and space potentially links to the different stages at which sequential effects emerge in processing non-temporal and temporal information.

Conflict of Interest

All the authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Data and code availability statement

The data and analysis code that support the findings of this study will be made available from the author, Si Cheng (chengsi123456@gmail.com), upon reasonable request. All data and code will be made available in online repositories upon acceptance. This study was not preregistered.

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4 Neural mechanisms of sequential dependence in time perception

Neural mechanisms of sequential dependence in time perception:
The impact of prior task and memory processing

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Abstract

Our perception and decision-making are susceptible to prior context. Such sequential dependence has been extensively studied in the visual domain, but less is known about its impact on time perception. Moreover, there are ongoing debates about whether these sequential biases occur at the perceptual stage or during subsequent post-perceptual processing. Using functional Magnetic Resonance Imaging (fMRI), we investigated neural mechanisms underlying temporal sequential dependence and the role of action in time judgments across trials. Participants performed a timing task where they had to remember the duration of green coherent motion and were cued to either actively reproduce its duration or simply view it passively. We found that sequential biases in time perception were only evident when the preceding task involved active duration reproduction. Merely encoding a prior duration without reproduction failed to induce such biases. Neurally, we observed activation in networks associated with timing, such as striato-thalamo-cortical circuits, and performance monitoring networks, particularly when a "Response" trial was anticipated. Importantly, the hippocampus showed sensitivity to these sequential biases, and its activation negatively correlated with the individual's sequential bias following active reproduction trials. These findings highlight the significant role of memory networks in shaping time-related sequential biases at the post-perceptual stages.

Keywords: Sequential dependence; Time perception; Striato-thalamo-cortical networks; Hippocampus; Working memory

Significance Statement

Our study explores the neural mechanisms of sequential dependence in time perception and reveals that active reproduction of time duration in the previous trial can bias subsequent estimates, resulting in a sequential dependence effect. In contrast, passive viewing of a stimulus without reproducing its duration does not produce this effect. At the neural level, we observed increased activity in memory regions like the hippocampus when sequential biases were reduced. Furthermore, we found a negative correlation between hippocampal activation and sequential bias following active reproduction trials, suggesting that the involvement of memory networks mediates how we are influenced by past experiences when judging time.

4.1 Introduction

The world around us is relatively stable and predictable over a short period. A traffic sign at a crossroad will turn periodically into red and green in a predictable way. During rush hour, a traffic jam is likely followed by another. Our experience is thus useful to guide our decisions because the past and the present often correlate. Research has demonstrated that our current perception is biased by recent events, referred to as serial dependence or sequential dependence (Cicchini et al., 2018; Cross, 1973; Fischer & Whitney, 2014; Glasauer & Shi, 2022; Holland & Lockhead, 1968; Pascucci et al., 2023). Such sequential bias has primarily been explored in the context of non-temporal features, such as orientation, color, and motion direction, particularly with a recent paradigm highlighting the influences of the difference between the current and previous stimuli on perceptual biases (Bae & Luck, 2020; Barbosa & Compte, 2020; Cicchini et al., 2017; e.g., Fischer & Whitney, 2014).

There is ongoing debate regarding the underlying mechanisms of sequential dependence. Two main perspectives have emerged. The first view proposes that sequential dependence is thought to maintain perceptual stability and continuity by integrating past and current information to filter out abrupt noises, serving as a perceptual mechanism (Liberman et al., 2016; Whitney et al., 2022). The second view connects sequential dependence to prior task and response-related post-perceptual factors (Bae & Luck, 2020; Ceylan et al., 2021; Fritsche et al., 2017; Pascucci et al., 2019). For instance, sequential dependence is only observed when the current and previous tasks are the orientation judgments (Bae & Luck, 2020), indicating that encoding the previous stimulus was not sufficient but the task-related response in previous trials was essential for sequential effects to occur.

In this latter view, working memory plays a crucial role in sequential dependence, as it involves integrating preceding stimuli with current sensory inputs for decision-making and motor plans (Bae & Luck, 2019; Bliss et al., 2017; Fornaciai & Park, 2020a; Kiyonaga, Scimeca, et al., 2017). Studies have shown the sequential effect increases when the memory retention interval increases (Bliss et al., 2017), and decreases when the short-term memory maintenance in the premotor cortex is interrupted with TMS (de Azevedo Neto & Bartels, 2021). A recent fMRI study showed that neural activity in low-level V1 is opposite to behavioral sequential dependence, which suggests that the effect emerges in high-level memory or decision-making circuits (Sheehan & Serences, 2022). Moreover, a recent electroencephalogram (EEG) study used the auditory pitch categorization task and decoded neural representations of multiple features (i.e., pitch, category choice, motor response) of the current trial as well as the neural response from past-trial features on the current trial, and it found that past-trial features kept their respective identities in memory and were only reactivated by the corresponding features in the current trial, giving rise to sequential biases (Zhang & Luo, 2023).

While behavioral studies reliably demonstrate sequential dependence, much of the existing literature has primarily focused on non-temporal spatial features, such as orientation, that have a circular distribution (e.g., Fischer & Whitney, 2014). One advantage of using this is that it allows for a clear separation of sequential effects from pervasive central tendency and range effects (Vierordt 1868; Teghtsoonian and Teghtsoonian 1978; Shi, Church, et al. 2013; Petzschner et al. 2015; Glasauer and Shi 2021) - phenomena that are commonplace in magnitude estimations, such as duration judgments. For example, perceived durations can skew toward a mean duration derived from recent history or sampled durations (Burr et al., 2009; Jazayeri & Shadlen, 2010; Nakajima et al., 1992), leading to underestimate long durations and overestimate short ones. However, only a handful of recent behavioral studies have explored trial-to-trial sequential effects on timing (Glasauer & Shi, 2022; Togoli et al., 2021; Wehrman, Wearden, et al., 2020; Wiener et al., 2014), and even fewer have linked these effects to specific electroencephalogram (EEG) signatures (Damsma et al., 2021; Fornaciai et al., 2023). This leaves a significant gap in our understanding of neural mechanisms at play.

In this study, we employed a classic post-cueing paradigm used in sequential dependence research (Bae & Luck, 2020; Czoschke et al., 2019) to investigate the neural mechanisms underlying sequential dependence in a duration reproduction task (Shi et al., 2022; Shi, Ganzenmüller, et al., 2013; Zang et al., 2022) in conjunction with MRI scanning. The task consisted of an encoding phase and a subsequent phase that was either for reproduction or passive-viewing, contingent on a post-cue that indicated "Response" or "No-response". During the encoding phase, participants had to remember the stimulus duration, and then either reproduce it or passively observe it, as instructed by the cue. With "Response" and "No-response" trials randomly intermixed, participants had to recall the durations accurately in each case. This design allowed us to compare how passive viewing and active reproduction during preceding trials influenced the processing of the subsequent stimuli, thereby shedding light on the post-perceptual factors contributing to sequential dependence.

To preview our findings, we found behaviorally that the central tendency bias operated independently of the preceding task. However, the sequential dependence was significant only when the preceding task required active reproduction rather than passive viewing. At the neural level, our data link striato-thalamo-cortical and performance monitoring networks to time perception and prior tasks, respectively. Notably, we observed that hippocampus activity was directly linked with the sequential bias on both prior tasks and prior duration. This hippocampal activation was particularly evident during the encoding phase following passive viewing trials and led to a decrease in sequential bias. These findings highlight the involvement of post-perceptual stages that link sensory representations to responses and underscore the critical role of active timing-related and memory networks in the temporal sequential dependence.

4.2 Materials and Methods

Participants

21 participants (9 females; 12 males; age: Mean ± SD = 27.24 ± 3.83, range: 23–33 years) were recruited for the two-session MRI experiment[2]. All of them were right-handed and had normal or corrected-to-normal vision and color vision, no history of neurological, psychiatric, or medical disorders, and no symptoms of COVID-19 in the past two weeks. The sample size was determined based on previous studies (Bae & Luck, 2020; Fischer & Whitney, 2014) that usually found large effect sizes (Cohen's $d > 0.75$), and with a power of 80% ($1 - \beta$), which yielded a minimum of 19 participants according to G*Power (Erdfelder et al., 1996). Participants provided their informed consent prior to the experiment and were compensated for their participation for 15 Euro/hour. The study was approved by the ethics committees of the Psychology Department at LMU Munich.

Experimental design and procedure

We adopted a duration reproduction paradigm (Shi et al., 2022; Shi, Ganzenmüller, et al., 2013; Zang et al., 2022), consisting of an encoding phase and a reproduction phase (see Figure 1). Participants laid down comfortably with their head in the head coil, inside some cushions to fixate the head position and avoid motion. Participants viewed the back projector canvas (diagonal 30 inches) via an adjustable mirror positioned on top of the head coil, with a viewing distance of 110 cm. The task was presented by an MRI-compatible ProPIXX DLP LED projector (Pixx Technologies Inc, Canada).

Each trial began with a black cross (visual angle of 0.5°) at the center of the display on a light gray background for 500 ms, prompting participants to maintain their fixation on the center. Following this, a tunnel view display (subtended 17.8° visual angle) of white randomly moving dots (20 dots with each diameter of 0.4°, moving at a speed of 1°/s) appeared for a randomly selected duration between 400 to 600 ms. The white dots then changed to green and moved 100% coherently with a speed of 6°/s in one direction selected between 0 to 360° for a given duration, chosen from 0.8, 1.0, 1.2, 1.4, and 1.6 secs. Immediately after the given duration, the color of the dots changed back to white and moved randomly again at a speed of 1°/s. When a dot exited the tunnel view, it was regenerated at a random location within the view to maintain dot density. The entire presentation of the tunnel view lasted for 3000 ms. Participants were instructed to remember the duration of the green coherent motion.

Following the encoding phase, a cue was presented in the center for 500 ms that indicates whether participants should perform a reproduction task ("Response") or not ("No-response"). The cue was a color

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[2] During scanning, six participants had large head movements (more than 3 mm of displacement measured by 2nd-degree B-spline interpolation or 3° of rotation in any direction) or distortion in the T1 image. We then replaced with six new participants.

disk (subtended 1.2° visual angle), which could be either green (indicating a Response trial: reproducing the duration) or white (indicating a No-response trial: doing nothing, only passive viewing). For Response trials, immediately following the offset of the cue display, a green random dot motion in a tunnel view (20 green dots with each of 0.4° at a speed of 1°/s) appeared in the center of the screen. Participants had to monitor the elapsed time and press an MRI-compatible ResponsePixx button (Pixx Technologies Inc, Canada) with their right thumb when they perceived the elapsed time as being the same as the duration of coherent movement in the encoding phase. Following the response, a feedback display appeared indicating the response accuracy with a color dot in a horizontal dot array. Each highlighted dot from the left to right five dots corresponded to a range of relative reproduction errors (error/duration): The left most represented below -30%, while the second to fifth dot indicated errors between [-30%, -5%], (-5%, 5%), [5%, 30%], or greater than 30%, respectively. The middle dot was highlighted in green to indicate an accurate reproduction, while the 2nd and 4th dots were highlighted in light red, the utmost 1st and 5th dots in dark red, with the color intensity reflecting the degree of error. The feedback lasted for 500 ms. For the No-response trial, the cue display was followed by a white random dot motion in a tunnel view (20 white dots with each diameter of 0.4°, moving at a speed of 1°/s), lasting the same amount of time as the coherent movement of the green dots in the encoding phase, and participants didn't need to respond and just passively watched the display. Afterwards, a blank feedback display appeared for 500 ms to equate the time with the feedback display in the Response trial. The next trial started after a random interval of 2000 to 3000 ms.

Since we were interested in the impact of the preceding task on the present reproduction, and to ensure equal transitional probability from a "No-response to Response" trial and from a "Response to Response" trial while minimizing the number of trials required for MRI scanning (within one hour), we excluded the possibility of a "No-response to No-response" trial. This yielded a 2:1 ratio of the Response vs. No-response trials while maintaining equal transitional probability (see a similar approach Czoschke et al., 2019).

Prior to the formal scanning, participants received a practice block of 30 trials to familiarize themselves with the task in a sound-reduced and moderately lit chamber, near the scanning room. In the formal MRI study, each participant completed 12 blocks, with each block of 30 trials, among them 20 Response trials and 10 No-response trials. After each block, there was a short 6-second break, and after 6 blocks (comprising a session) a long 7-minute break. During this long break, participants took a rest inside the scanner, and a T1 image was acquired. The whole experiment lasted approximately 60 minutes.
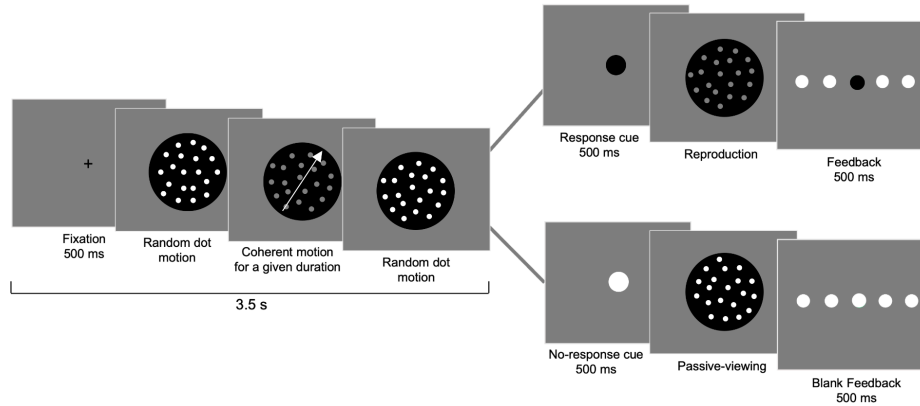
Figure 1. Experimental procedure. Each trial consisted of two phases: the duration encoding phase and the duration reproduction or passive-viewing phase, with the latter being contingent upon the Response / No-response cue. The trial started with a fixation, followed by the display of white random dot motion, which then changed to green dots moving coherently in one direction (e.g., the gray dots in the illustration represented the green coherently moving dots in the direction of the white arrow, not shown in the actual experiment) for a given duration before reverting back to white random dot motion. The entire presentation of the dots display lasted for 3000 ms. Participants were instructed to remember the duration of the green coherent motion. A cue, either a green ("Response" trial, represented as the black disk in the illustration) or a white ("No-response" trial) disk, was then shown on the screen, indicating the beginning of the second phase. In the "Response" trials, the green random dot motion appeared (represented as the gray dots in the illustration), and participants had to press a button when they thought the elapsed duration was the same as the perceived duration in the encoding phase. During "No-response" trials, participants only passively viewed the white random dot motion for the same duration as the coherent movement of the green dots in the encoding phase and were not required to respond. In the end, there was a feedback display featuring five horizontal white disks, with one disk changing color to indicate the accuracy of the reproduction for the "Response" trials.

MRI data acquisition and preprocessing

All MRI data were acquired using a 3-Tesla Siemens Prisma MRI scanner (Siemens, Erlangen, Germany), equipped with a 32-channel head coil. Functional MRI images were obtained using a blood oxygenation level-dependent (BOLD) contrast-sensitive gradient-echo EPI sequence. A total of 3000 to 3300 volumes of fMRI data, depending on the duration of the experiment, were acquired for each participant through two sessions. The following parameters were used: TR = 1000 ms, multi-band factor = 4, TE = 30 ms, flip angle = 45°, FOV = 210 × 210 mm, voxels size = 3 × 3 × 3 mm, slices number = 48, slice thickness = 3 mm. In addition, structural MRI images (T1 weighted) were acquired from the sagittal

plane using a three dimensional magnetization prepared rapid gradient-echo (MPRAGE) pulse sequence with the following scanning parameters: TR = 2500 ms, TE = 2.22 ms, flip angle = 8°, FOV = 256 × 256 mm, voxel size = 0.8 × 0.8 × 0.8 mm, slice thickness = 0.8 mm.

The analyses and visualization of imaging data were performed with SPM12 (Ashburner et al., 2014) and Nilearn - 0.9.2 (Abraham et al., 2014). The functional images were first preprocessed with realignment, reslicing, and slice time correction. Then, the head movement correction was done by using affine transformation in a two-pass procedure and aligning individual functional images to their mean image using 2nd-degree B-spline interpolation. Participants who had head movements more than 3 mm or rotations greater than 3° were excluded from further analysis, which yielded the exclusion of six participants in total, five for large head motion and one for T1 image distortion. We then replaced them with six new participants. The mean image of each participant was then spatially normalized to a 3 mm standard Montreal Neurological Institute (MNI) template using the "unified segmentation" approach, and the resulting deformation field was applied to the individual functional images. The normalized fMRI images were then smoothed with a 6 mm full-width-at-half-maximum (FWHM) Gaussian kernel to improve the signal-to-noise ratio and compensate for residual anatomical variations.

Statistical analyses
Behavioral analysis

The reproduction errors, the difference between the reproduced duration and the physical duration, were calculated for the Response trials. To exclude trials with large reproduction errors due to accidental button presses or inattention, we applied the three-sigma rule to exclude those outliers. Then, we categorized the remaining Response trials into two types depending on the preceding task: (a) Response-Response (RR) trials that were preceded by a reproduction task, and (b) NoResponse-Response (NR) trials that were preceded by a passive viewing task.

Given that time intervals are an open scale and their judgments are subjective to both central tendency and sequential biases, we estimated the central tendency and sequential dependence effects separately. The central tendency effect results from the integration of the prior (D_p) and the current duration (D_n), and can be estimated through linear regression when the prior is considered fixed (Cicchini et al., 2012; Shi, Church, et al., 2013):

$$D_r = wD_n + (1 - w)D_p.$$

Here we applied a linear regression to find the slope (w), and designated $1 - w$ as the index for central tendency. An index of 0 indicates no central tendency, while an index of 1 signals a strong central tendency.

The conventional measures of serial dependence effect, which compare the current response error to the difference between the previous and the current stimuli (Bliss et al., 2017; Cicchini et al., 2018; e.g., Fischer & Whitney, 2014; Kiyonaga, Manassi, et al., 2017), are not sufficient to separate sequential dependence from the central tendency bias (for more details, see Glasauer & Shi, 2022). Instead, we adopted a classical approach to sequential effects (Holland & Lockhead, 1968), which correlates the current error with the previous duration. However, this method could still capture a general bias, such as systematic over- or underestimation, in addition to the sequential trend. Thus, in the analysis, we only focused on the linear trends (i.e., the slopes), rather than the intercepts. Specifically, we applied linear regression to relate the current response errors (E_n) with the previous sample duration (D_{n-1}), and took the slope b of this linear fit as the index of the sequential bias:

$$E_n = a + bD_{n-1},$$

A positive slope indicates that the current error is assimilated towards the previous duration, while the negative slope suggests a repulsion from the previous one. Additionally, as a sanity check and for further verification, we also computed the sequential effect for the durations presented in future trials (n+1).

For statistical analyses, we applied linear regression, simple t-tests and linear mixed models according to the data structure.

fMRI statistical analysis

There were three types of inter-trial transitions: No-response to Response (NR), Response to Response (RR), and Response to No-response (RN). Given that the third type (RN) trials yielded no behavioral response, our analysis focused on the Response trials (i.e., RR and NR). To boost the power of the first-level fMRI analyses, we grouped the preceding durations into two categories: the "Short" and the "Long" categories. The "Short" category included durations of 0.8 and 1.0 s, and the "Long" categories were 1.4 and 1.6 s, with the middle duration of 1.2 s being excluded. Therefore, a combination of the factors of the Prior Task (RR or NR) and the Prior Duration (Short or Long) resulted in four conditions.

At the first-level analysis with individual participants, BOLD responses obtained from the smoothed images were time-locked to the onset of the target duration and modeled using a canonical hemodynamic response function (HRF) with a box-car function to represent the duration of the coherent movement. Our analysis defined four conditions through the combination of the Prior Task and the Prior Duration, each represented by a separate main canonical hemodynamic response function (HRF) regressor. To identify brain regions associated with sequential biases, we incorporated an additional parametric regressor for each main regressor. Parametric modulation serves as an index of the relationship

between neural activity and the normalized response error, helping to pinpoint regions where activity varies based on specific variables (Mumford, 2015; Penny et al., 2011).

Given that the current response error inherited the central tendency biases and the systematic general biases, we can not directly use them as parametric regressors for identifying neural activities associated with the sequential effect. Instead, we employed normalized errors:

$$RE_{n,k} = (D_{n,k} - \overline{R}_k)/\overline{R}_k \, ,$$

where $\overline{R}_k$ is the mean reproduction of the duration D_k, $D_{n,k}$ the reproduced duration at trial n of a given Duration D_k, $RE_{n,k}$ the normalized relative error. The normalized errors retained the trend of sequential dependence associated with the previous duration, yet they were free from the general bias and the central tendency linked to the current duration (see Appendix Figures S1 and S2). This approach allowed us to use it as an additional parametric regressor on the neural activity of the current trial to isolate the impact of sequential dependence. Together, we had four main regressors and four parametric regressors. The beta value of the parametric regressor reveals the strength and linear relationship between brain activity and the relative error. A positive parametric value indicates that brain activity correlated positively with the relative error, while a negative value suggests an inverse correlation between brain activity and the relative error. Importantly, as BOLD activations were analyzed during the encoding phase and sequential biases were assessed during the late reproduction phase, the parametric modulation serves to quantify both the extent and direction of how fluctuations in brain activity influence behavioral sequential bias. Additionally, six head movement parameters were added as nuisance regressors to control head motion artifacts (Lund et al., 2005). The data were high-pass filtered at 1/128 Hz. For each subject, 8 condition-specific contrast images were created (for each trial type and parametric modulator).

The respective contrast images for the main HRF regressors and the parametric regressors were subjected to the second-level analysis with flexible factorial design, separately. In the flexible factorial design, Prior Task and Prior Duration were created as within-subject factors and Participant as a random factor. The 2 (Prior Task: Response (RR) vs. No-response (NR)) × 2 (Prior Duration: Short vs. Long) ANOVAs allowed us to determine the unique contributions of each factor to the brain activity, and how they might interact with each other to affect neural processing. We conducted a whole-brain analysis to determine the candidate brain regions involved in the main effects of Prior Task and Prior Duration, as well as their interaction, by using planned t-contrasts. All contrasts were thresholded at $p < .001$, with FWE cluster correction at $p < .05$. We were interested in brain regions that showed sensitivity to the modulation of brain activity by the normalized relative deviation. Parametric estimates were extracted from the statistically significant clusters and averaged across the voxels in the individual-level analysis.

Once the regions of interest (ROIs) were identified, we proceeded with a comprehensive analysis where all durations were taken into account.

To gain further insight into activation patterns, a separate general linear model (GLM) was applied to the fMRI time series, similar to the model designed above, except all individual durations were included (0.8, 1.0, 1.2, 1.4, and 1.6 s). Thus, we have 2 (Prior Tasks) × 5 (Prior Durations), 10 conditions in total. Each condition had one main HRF regressor and one parametric regressor using the normalized relative error. Beta values of individual main regressor as well as parametric modulator were calculated from the significant voxels detected above (a sphere with a diameter of 10 mm) for individual participants. To assess differences in beta values, we employed a linear mixed model analysis, incorporating Prior Task and Prior Duration as the fixed effect, and Subject as the random factor. Linear mixed models are resilient to violations of sphericity and help mitigate the risk of Type I errors (Singmann & Kellen, 2019). The *p*-values reported for the mixed models were calculated using the maximum likelihood estimation.

We then conducted Spearman's correlation (α = 0.05, two-tailed) to assess the relationship between the magnitude of the sequential dependence effect in behavior and the BOLD activity of interest. The slope of the linear regression with the normalized relative error depending on the previous sample duration was operationalized to indicate the magnitude of the behavioral sequential dependence effect. The BOLD response was measured as the β values of the main regressors in the designated regions detected above.

4.3 Results

Behavioral results

The reproduction errors were calculated for the "Response" trials. Overall, reproduced durations were close to the probe durations, resulting in a mean reproduction error of 35 ms. We excluded trials with large reproduction errors and the outliers were generally rare, on average only 0.89%, ranging individually from 0 to 5 outlier trials. The remaining "Response" trials were categorized into two types depending on the preceding trial: (a) "Response" to "Response" (RR) trials that were preceded by a reproduction trial, and (b) "No-response" to "Response" (NR) trials that were preceded by a passive viewing trial. Given that duration reproduction is affected by both the central tendency effect and the sequential dependence (Glasauer & Shi, 2022), we estimated the central tendency and serial dependence effects separately.

The central tendency effect.

We applied a linear regression of the duration reproduction (D_r) on the current durations (D_n) to obtain the slope (w), and used $1 - w$ as the central tendency index, with 0 indicating no central tendency

and 1 strong central tendency (Cicchini et al., 2012; Shi, Church, et al., 2013). The results, shown in Figure 2a, indicate a strong central tendency effect - participants overestimated short durations and underestimated long durations. The central tendency effect was quantified through linear regression, revealing significant central tendency biases with mean central tendency index $(1 - w)$ of 0.540 ($t_{(20)} =$ 9.13, p <.001, d = 1.99) and 0.594 ($t_{(20)}$ = 9.14, p <.001, d = 1.99) for the NR and RR respectively. But the central tendency biases were comparable between the two conditions ($t_{(20)}$ = 1.748, p = .096, BF_{10} = 0.830). Additionally, there was a minor positive general bias (M ± SE: 35 ± 14 ms, $t_{(20)}$ = 2.452, p = .024, BF_{10} = 2.494), which was comparable between the two conditions ($t_{(20)}$ = 1.298, p = .209, BF_{10} = 0.475). A linear mixed model with Prior Task and Current Duration as the fixed effects and Subject as the random factor also confirmed similar results: no effect of Prior Task (Coef = -0.012, 95% CI [-0.038, 0.014], p = .380), but a significant main effect of Current Duration (Coef = 0.406, 95% CI [0.341, 0.471], p < .001). And their interaction was not significant (Coef = 0.054, 95% CI [-0.038, 0.146], p = .251). That is, the central tendency and the general bias were not influenced by the prior trial task. The lack of a significant difference in the central tendency effect between preceding task types might be primarily due to the same distribution and range of the tested durations for two prior tasks, yielding a consistent long-term representation of the prior durations across tasks. This agrees with previous findings that randomly mixing durations leads to a generalization of the prior across conditions (Roach et al., 2017).

The sequential dependence effect.

Figure 2b shows that the current response errors increased with increasing prior durations, suggesting a sequential dependence effect. This was captured by the slopes of the linear regression, which was only significantly positive for the RR condition (b = 0.103, $t_{(20)}$ = 3.668, p = .002, BF_{10} = 25.043), but not for the NR condition (b = 0.017, $t_{(20)}$ = 0.922, p = .368, BF_{10} = 0.332). Additionally, the slope for the RR condition was significantly larger than that in the NR condition ($t_{(20)}$ = 3.056, p = .006, BF_{10} = 7.510, see Figure 2c). The results were further confirmed by the linear mixed model with Prior Task and Prior Duration as the fixed effects and Subject as the random factor. Neither the main effect of the Prior Task (Coef = 0.012, 95% CI [-0.005, 0.030], p = .174) nor the Prior Duration (Coef = 0.016, 95% CI [-0.027, 0.060], p = .464) were significant. However, their interaction effect (Coef = 0.087, 95% CI [0.025, 0.149], p = .006) was significant, indicating a notable difference in the slopes between the NR and RR conditions. These results suggest that active reproduction in the preceding trial increased the sequential dependence on the current reproduction, whereas passive viewing did not. To avoid statistical artifacts (Cicchini et al., 2014), we also tested the sequential dependence effect on the durations presented in future trials (n+1), which showed no significance (*ps* > .216). Our behavioral results provide clear evidence that merely passively perceiving an interval is not sufficient to bias subsequent duration estimates.
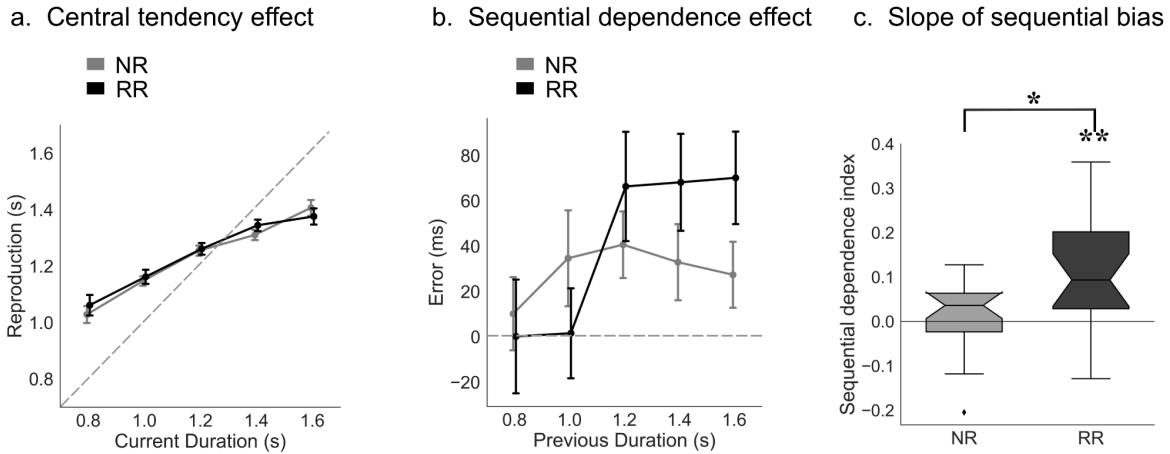
a. Central tendency effect   b. Sequential dependence effect   c. Slope of sequential bias

Figure 2. (**a**) The central tendency effect. The duration reproductions are shown as a function of the actual duration, separated for the inter-trial type: No-response/Response (NR) and Response/Response (RR) trials. Error bars represent ± SEM. (**b**) The sequential dependence effect. The response errors are plotted on the durations from previous trials, separated for NR and RR conditions. Error bars represent ± SEM. (**c**) Notched boxplots of the sequential dependence slope for NR and RR conditions. The box plot depicts the sequential dependence effect, measured by the slope, for each condition. The top and bottom of the notched box represent the interquartile range (between 25% and 75%), and the notch in the box is the 95% confidence interval for the median; whiskers exclude outliers. *p <.05, **p <.01.

fMRI Results

Whole-brain analysis

The main analysis was focused here on the effects of prior tasks on the current duration reproduction (i.e., RR and NR). The combination of the factors of the Prior Task (RR or NR) and the Prior Duration (Short or Long) resulted in four conditions, each represented by a separate main HRF regressor and an accompanying parametric regressor incorporating the normalized relative error $RE_{i,k}$. The results from the main HRF regressors reflect different brain activations across different conditions, while the findings of the parametric regressors reflect the covariate changes of brain activities to the normalized relative errors in duration reproduction. In the following subsections, we report the results separately for the main HRF regressors and parametric regressors.

Table 1. Activations associated with the main HRF regressors defined by the two factors Prior Task and Prior Duration

Contrast	Region label	MNI coordinates			Cluster size	T value
Prior Task						
RR > NR	R inferior frontal gyrus	45,	41,	2	109	5.42
NR > RR	R Posterior medial frontal	6,	-1,	53	8003	6.34
	R Thalamus	9,	-22,	5		6.09
	L Precentral gyrus	-30,	-16,	50		7.46
	L Postcentral gyrus	-51,	-19,	53		6.72
	L Precuneus	-9,	-61,	14	259	3.64
Prior Duration						
Long > Short	R Caudate Nucleus	18,	-22,	26	122	4.42
Prior Task × Prior Duration	n.s.					

Note: Activations were significant at *p* < .001, with FWE cluster correction at *p* < .05, and n.s. denotes non-significant. R Posterior medial frontal, R Thalamus, L Precentral gyrus, and L Postcentral gyrus were in the same cluster.

Table 2. Activations associated with the parametric regressors defined by the two factors Prior Task and Prior Duration

Contrast	Region label	MNI coordinates			Cluster size	T value
Prior Task	n.s.					
Prior Duration						
Long > Short	L Middle frontal gyrus	-21,	38,	32	124	4.46
Prior Task × Prior Duration						
Long (NR > RR)	L Hippocampus	-36	-37,	-7	139	4.09
	R Hippocampus	39,	-31,	-7	305	5.01

Notes: Activations were significant at *p* < .001, with FWE cluster correction at *p* < .05, and n.s. denotes non-significant.

Main HRF regressors

We conducted contrast analyses using 2 (RR vs. NR) × 2 (Prior Short vs. Prior Long) within-subject ANOVAs. Table 1 and Figures 3a and 3b show the significant regions identified through this contrast analysis. The results show that the right inferior frontal gyrus (RIFG), a region associated with response inhibition (Aron et al., 2007; Hampshire et al., 2010), exhibited greater activation during RR trials compared to NR trials. Conversely, the left precuneus and a large cluster comprising the left precentral gyrus, left postcentral gyrus, the right posterior-medial frontal and the right thalamus were more active during NR trials compared to RR trials.

The RIFG is a critical region for response inhibition and detecting important cues (Aron et al., 2007; Hampshire et al., 2010). The activation of the RIFG for the contrast RR vs. NR is likely due to a Response trial (R) can be followed by Response or No-response trials which require response inhibition. In contrast, for the contrast NR vs. RR, we observed high activation in cognitive control and performance monitoring networks, including the right posterior-medial frontal cortex (Debener et al., 2005) and the left precentral gyrus and left postcentral gyrus, as well as the left precuneus (Fitzgerald et al., 2010; Ridderinkhof et al., 2004). Increased activation in the posterior-medial frontal cortex (Fitzgerald et al., 2010; Ridderinkhof et al., 2004) is believed to be engaged in the cognitive control and performance monitoring that leads to response selection and performance adjustments in subsequent trials (Debener et al., 2005), while the precentral gyrus is the site of the primary motor cortex and the postcentral gyrus which constitutes the primary somatosensory cortex also takes part in motor control of the body (Dijkerman & de Haan, 2007; Hari et al., 1998). This was likely due to the activation of the primary motor cortex for those "Response" trials while not for the "No-response" trials, and the sequential structure of the NR, which indicates that the upcoming trial is "Response" before the cue appears. The thalamus plays a key role in the cortico-thalamic-basal ganglia timing circuits (Mole et al., 2018; Yin et al., 2022).

The contrast analysis conducted between the prior short and long durations revealed that the right caudate nucleus, the main component of the dorsal striatum, was more activated when the prior trial was long than short (see Table 1 and Figure 3b). The activity in the dorsal striatum (including the caudate nucleus) is closely related to the representation of temporal information in working memory (Merchant et al., 2013; Teki & Griffiths, 2016; White, 2009; Yin et al., 2022). Thus, our findings suggest preceding long vs. short durations could impact the working memory trace in the following trial, consistent with previous event-related fMRI studies on working memory and time interval demonstrating that activity in the caudate nucleus increased with an increasing number of intervals in the sequence (Coull & Nobre, 2008; Rao et al., 2001; Teki & Griffiths, 2016).
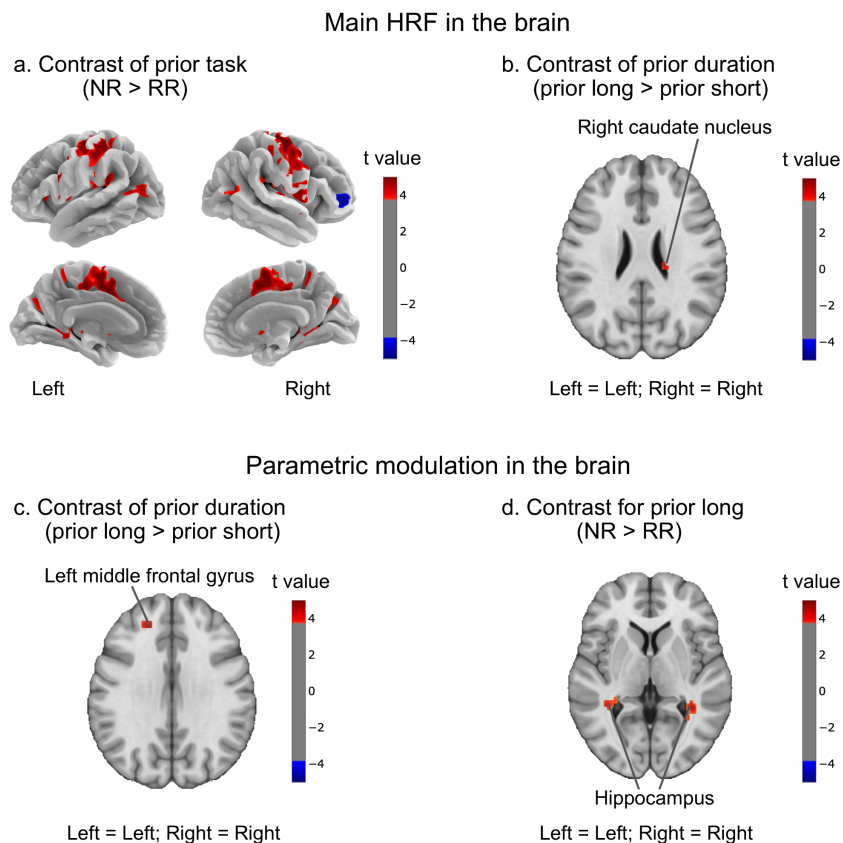
Main HRF in the brain

a. Contrast of prior task
(NR > RR)

b. Contrast of prior duration
(prior long > prior short)

Parametric modulation in the brain

c. Contrast of prior duration
(prior long > prior short)

d. Contrast for prior long
(NR > RR)

Figure 3. Whole-brain activation results. (**a**) and (**b**) are brain regions activated in the main HRF. (**a**) Whole-brain activation patterns colored in red-blue reflected invoked BOLD signals driven mainly by the prior task. The red-marked regions (the left precentral gyrus, the left postcentral gyrus, the left precuneus, the right posterior-medial frontal, and the right thalamus) were activated more for the preceding No-response (NR) task as compared to the preceding Response task (RR), while the blue-marked region (right inferior frontal gyrus) was activated more for the RR than the NR condition. (**b**) Whole-brain activation patterns colored in red-blue reflected invoked BOLD signals that were driven by the prior duration. The red-marked region (right caudate nucleus) was activated more for the long duration as compared to the short duration. (**c**) and (**d**) are brain regions that show sensitivity to normalized relative error in different conditions. (**c**) Main effect of prior duration for the parametric estimates with the normalized error. The red-marked region (left middle frontal gyrus, MNI coordinates: -21, 38, 32) was activated more with a larger normalized relative error for the preceding long duration than the short duration. (**d**) The normalized error-dependent differences between prior tasks (NR vs. RR) in the prior long-duration condition were expressed in the hippocampus (MNI coordinates: -36, -37, -7; MNI coordinates: 39, -31, -7). All thresholding was done at $p < .05$ with FWE-corrected at the clustered level. Neurological convention was used (Left = Left and Right = Right).

Parametric regressors

To investigate the modulation of sequential effects, we employed the normalized error - which is free from the general bias and the central tendency - as a parametric regressor. The results of this analysis are presented in Table 2 and Figures 3c and 3d. These results display the contrasts of the parametric regressors based on a 2 (Prior Task: Response vs. No-response) × 2 (Prior Duration: Short vs. Long) factorial analysis. By examining these contrasts, we can identify which brain regions during the encoding stage correlate with variations in normalized errors based on preceding conditions, which could help pinpoint the brain regions sensitive to sequential bias in time perception.

We observed a significant main effect of Prior Duration. As seen in Table 2 and Figure 3c, the left middle frontal gyrus (LMFG; MNI coordinates: -21, 38, 32, including 124 voxels) was more positively correlated with the normalized error when the duration of the preceding trial was long vs. short. This suggests that influences of the left middle frontal gyrus activation on normalized error depend on the preceding duration. Figure 4a depicts the parametric values extracted from the left middle frontal gyrus. On average, the parametric value was positive (0.412) when the preceding duration was long, but negative (-0.691) when the preceding duration was short. Specifically, activation of the left middle frontal gyrus led to a positive trend of the relative error when the preceding duration was long, but a negative trend of the relative error when the preceding trial was short. Recall the right caudate nucleus was found to activate more strongly in response to a long preceding duration compared to a short one, and the right caudate nucleus is functionally connected to the left middle frontal gyrus (Robinson et al., 2012), which is associated with working memory encoding (Dandolo & Schwabe, 2019; Nee et al., 2013). Given this association, it is possible that these two regions work together to regulate inter-trial dependence in duration judgments.

Additionally, the analysis revealed a significant Prior Duration × Prior Task interaction in the left and right hippocampus (left MNI coordinates: -36, -40, -7, including 16 voxels; right MNI coordinates: 39, -31, -7, including 25 voxels; with small-volume correction at $p < .05$ FWE corrected). Further analyses revealed the most significant contrast results from the left and right hippocampus between RR and NR conditions when the preceding trial was long, which showed different sensitivity to the normalized bias (See Figure 3d, MNI coordinates: -36, -37, -7, including 139 voxels; MNI coordinates: 39, -31, -7, including 305 voxels). As shown in Figure 4b, on average the parametric values were comparable between NR and RR when the preceding duration was short, but exhibited opposite signs for the preceding long durations. In trials preceded by a long/No-response task, the brain activity of the hippocampus was associated with a positive trend in normalized errors. Conversely, in trials preceded by a long/Response task, the hippocampal brain activity was linked to a negative trend in normalized errors.

We then further conducted a correlation analysis to examine the relationship between the hippocampal BOLD signal and the sequential dependence index. To keep the analysis consistent, we used the sequential index obtained from the normalized error. The analysis revealed a negative correlation ($r =$ -.44, p = .044, two-tailed; Figure 4c) for RR trials (for both short and long duration), suggesting more activation in the hippocampus leads to less sequential dependence for RR trials. However, there was no correlation for NR trials (r = -.08, p = .733, two-tailed; Figure 4c), partly because the activation in the hippocampus was generally higher for NR than RR trials (Figure 5a).
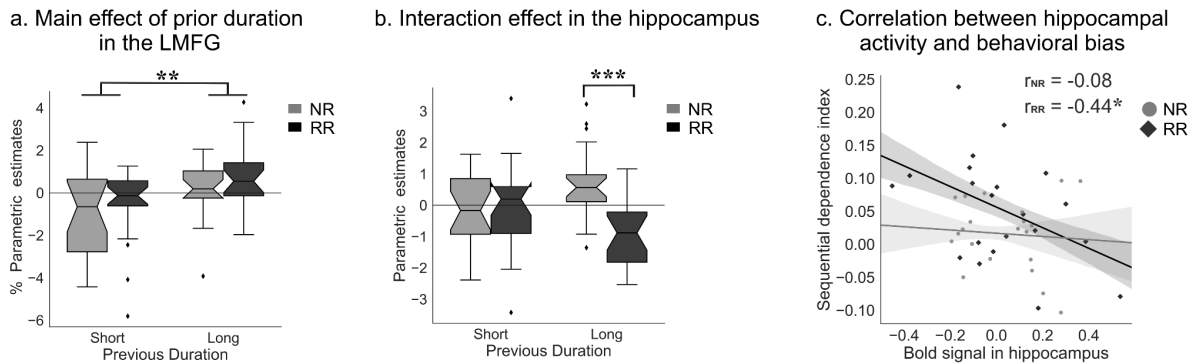

Figure 4. (**a**) Notched boxplots for the mean parameter estimates (β) from the left middle frontal gyrus (LMFG) for the parametric regressor for the prior tasks (NR: No-response; RR: Response), separated for the category of the previous duration (Short vs. Long). The top and bottom of the notched box represent the interquartile range (between 25% and 75%), and the notch in the box is the 95% confidence interval for the median; whiskers exclude outliers. (**b**) Notched boxplots for the mean parameter estimates (β) from the hippocampus for the parametric regressor. (**c**) Correlations between the mean BOLD signal in the bilateral hippocampus (MNI coordinates: -36, -37, -7, including 139 voxels; MNI coordinates: 39, -31, -7, including 305 voxels) and the behavioral bias (slopes of the linear regression with the normalized errors to the previous sample duration) across participants, separated for the RR and NR conditions. The correlation was significantly negative for the RR condition (r_{RR} = -.44, $p < .05$), but not for the NR (r_{NG} = -.08, p = .73). The least-square fit lines are shown. * $p < .05$, ** $p < .01$, and *** $p < .001$.

ROI analysis on the hippocampus

Note that in the whole brain analysis, we observed a large significant activated cluster (consisting of 8003 voxels) in the contrast NR > RR analysis (see Table 1), which included 0.7% (56 voxels) of this cluster that belonged to the hippocampus. To more closely examine the neural activation patterns in the bilateral hippocampus in the cluster we obtained in our ROI analysis (MNI coordinates: -36, -37, -7, including 139 voxels; MNI coordinates: 39, -31, -7, including 305 voxels), we applied a separate GLM on

BOLD signals to model the previous tasks (RR vs. NR) with each of the five previous durations (0.8, 1.0, 1.2, 1.4, and 1.6 s) for the individual subject, and extracted the β values from the main and parametric regressors. The β values of the main HRF regressors are shown in Figure 5a. Further linear mixed model on the β values with the fixed factors of Prior Duration and Prior Task, and a random factor of participants revealed a significant difference between prior tasks ($b = 0.16$, 95% CI [0.08, 0.233], $p < .001$), but not among prior durations and the interaction between Prior Task and Prior Duration (all $ps > .239$). On average, trials with preceding passive viewing (i.e., NR), compared to trials with preceding active reproduction (i.e., RR), had 16% more activations in the hippocampus.

Figure 5b shows that the parametric value decreases with an increase in the previous duration for the RR condition, but increases for the NR condition. A linear mixed model on the parametric values with fixed factors of Prior Duration and Prior Task revealed a significant main effect of Prior Task ($b = 0.64$, 95% *CI* [0.12, 1.17], $p = .016$), and a significant interaction between Prior Task and Prior Duration ($b = 2.32$, 95% *CI* [0.48, 4.17], $p = .014$). The interaction was due to opposite linear trends observed between the parametric values and the previous duration for the NR and RR conditions: a positive trend for the NR ($b = 1.13$, 95% CI [-0.18, 2.43], $p = .091$), but a negative trend for the RR ($b = -1.20$, 95% CI [-2.50, 0.11], $p = .072$). Although the individual trends (the slopes of 1.13 vs. -1.20) were marginally significant from zero, the difference between the two ($b = 2.32$) was significant, particularly for the previous long durations (Figure 5b). Interestingly, for the RR condition, the negative trend of the parametric value with the previous long duration was opposite to the significant positive trend of the sequential dependence effect (Figure 2b). This implies that decreased brain activity in the hippocampus was associated with a high sequential error, possibly due to the recycling of prior information in working memory, which results in strong serial dependence (Sheehan & Serences, 2022; Whitney et al., 2022).
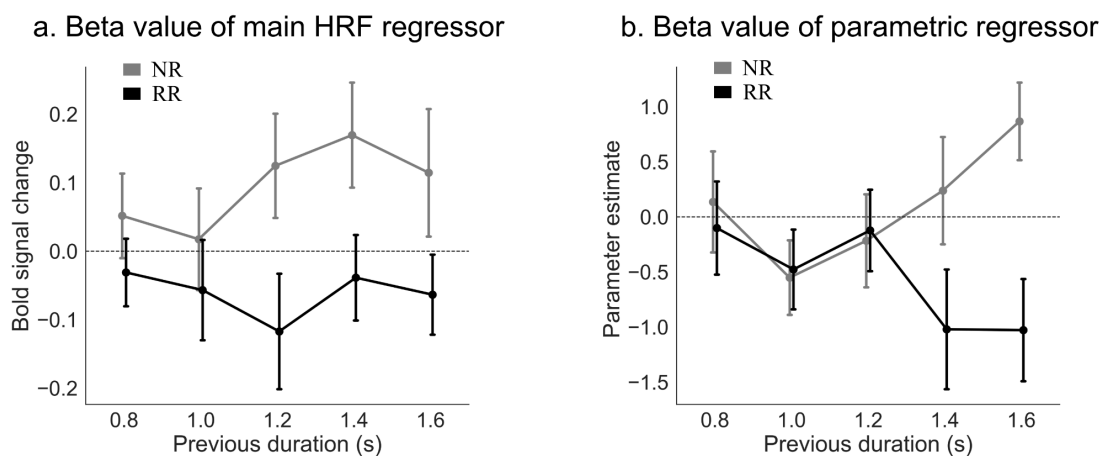

a. Beta value of main HRF regressor   b. Beta value of parametric regressor

Figure 5. (**a**) BOLD signal change estimated from the hippocampus, plotted as a function of previous duration, separated for the previous task (NR: No-response, RR: Response). (**b**) Mean beta value of the parametric regressor extracted from the bilateral hippocampus (MNI coordinates: -36, -37, -7, including 139 voxels; MNI coordinates: 39, -31, -7, including 305 voxels) plotted as a function of previous durations, separated for the previous task (NR: No-response, RR: Response).

4.4 Discussion

This study investigated neural mechanisms that underlie serial dependence in time perception. We conducted a duration reproduction task with a post-cue to manipulate between active reproduction and passive viewing of durations, aiming to determine where the serial dependence originates. We found a strong central tendency effect in duration reproduction, regardless of the preceding task. However, the reproduction errors depended on the preceding task and duration, showing a positive serial dependence effect only for trials with consecutive reproduction (RR), but not for trials preceded by passive viewing (NR).

Our study seeks to extend upon previous research, which has primarily focused on serial dependence in non-temporal domains (e.g., Fischer & Whitney, 2014; Holland & Lockhead, 1968). Previous studies have shown that serial dependence requires active retrieval of a recent past (Bae & Luck, 2020; Fornaciai & Park, 2020b; Ranieri et al., 2022; Suárez-Pinilla et al., 2018). For instance, a study on motion direction judgment (Bae & Luck, 2020) revealed that sequential dependence was only present when the preceding task was identical, as opposed to being different, such as judging the color of the motion stimuli. Our study extends this research by demonstrating that in the temporal domain, simply encoding the previous stimulus was not enough to produce a sequential effect. Employing a post-cueing paradigm offers the advantage of ensuring participants remain attentively engaged with the durations in each trial to perform the task correctly. If merely observing in the prior trials could bias subsequent duration estimates, we would expect to see some serial dependence even after just encoding from the previous trial. By contrast, our results revealed that for sequential dependence in time perception to occur, action component is essential, which suggests that the origin of this temporal sequential dependence is likely rooted in high-level, post-perceptual decisional and integrational processes (Bae & Luck, 2020; Ceylan et al., 2021; Fritsche et al., 2017; Kiyonaga, Scimeca, et al., 2017; Pascucci et al., 2019; Roach et al., 2017).

It should be noted, however, that our findings do not dismiss the potential influences originating from the perceptual stage, as commonly identified in studies involving non-temporal stimuli (Czoschke et al., 2019; Fornaciai & Park, 2018a, 2020b; Togoli et al., 2021). Convergent evidence shows that serial dependence could emerge at different stages. For example, evidence has emerged where irrelevant

stimuli, whether they are response-irrelevant inducers (Fornaciai & Park, 2018a) or simultaneously presented irrelevant (Czoschke et al., 2019), can either attract or repulse estimates in subsequent tasks. Intriguingly, these studies tend to position these task-irrelevant inducers close in time to the target (e.g., within a second in Togoli et al., 2021), which could promote potential perceptual integration. Well-documented phenomena, like ensemble perception (Whitney & Yamanashi Leib, 2018), show a tendency to attract individual items toward the ensemble mean (Baykan, Zhu, Allenmark, et al., 2023; Baykan, Zhu, Zinchenko, et al., 2023; Nakajima et al., 1992; Zhu et al., 2021). A classic manifestation of this is the time-shrinking illusion, where successive intervals seem to blend into one another (Burr et al., 2009; Nakajima et al., 1992). From a Bayesian standpoint, the ensemble prior assimilates the target duration (Shi & Burr, 2016; Zhu et al., 2021). The distinction between action and inaction can impact prior updates in unique ways. For instance, it has been shown that duration judgment exhibits a decisional carryover effect, a tendency to report the current stimulus as being similar to a prior one (Wehrman, Wearden, et al., 2020; Wiener et al., 2014). A study by Roach et al. (2017) highlighted that when participants were tasked with reproducing clearly delineated durations (either short or long) associated with specific spatial locations, the durations from different locations were merged together forming a single prior that significantly influenced their reproductions in all locations. However, merely passive observation of durations from one location left time reproductions from another location largely unaffected. This points to the influential role of responses, suggesting that action may serve as a common cause for temporal assimilation, leading to sequential effects predominantly in consecutive trials that demand a response. Our study using the post-cue paradigm further confirmed that the sequential effect in the time domain relies heavily on late decision stages that engage action. It is essential to highlight that in our study, since both passive no-response trials and response trials covered the same duration range, we cannot conclusively determine if central tendency would differ when passive and active trials span different ranges. Nonetheless, the response-driven common cause hypothesis does suggest a possible variation in central tendency biases. It would be interesting for further studies to validate this prediction.

At the neural level, during the duration encoding phase, BOLD signals were enhanced for NR trials relative to RR trials. This was observed within a network associated with cognitive control and response preparation (Dijkerman & de Haan, 2007; Fitzgerald et al., 2010; Ridderinkhof et al., 2004), which includes regions like the right posterior-medial frontal, the left postcentral gyrus, and the left precuneus. Additionally, the right thalamus, a critical component of cortico-thalamic-basal ganglia timing circuits (Mole et al., 2018; Yin et al., 2022), also showed activation. After a passive-viewing trial with no response demands, the response preparation network and cortico-thalamic-basal ganglia timing circuits were better primed for the upcoming trial. In contrast, the right inferior frontal gyrus (RIFG), essential for response inhibition and cue detection (Aron et al., 2007; Hampshire et al., 2010; Hartwigsen et al., 2019),

displayed increased activity during RR trials compared to NR trials. This enhanced activity occurs because, after an active reproduction trial, the type of next trial (Response or No-response) remains uncertain until the appearance of the post cue.

The contrast between the prior long and short durations revealed greater activation in the right caudate nucleus for the prior long duration. The caudate nucleus, a key part of the dorsal striatum, plays a critical role in the striato-thalamo-cortical network (Coull & Nobre, 2008; Rao et al., 2001; Teki & Griffiths, 2016). Serving as a "core timer" of the timing system (Meck et al., 2008), the caudate nucleus holds temporal "memories" in its GABAergic medium spiny neurons (MSNs) via dopamine-facilitated long-term potentiation and short-term plasticity mechanisms (Allman & Meck, 2012; Kononowicz, 2015). Adjustments to corticostriatal synaptic weights by MSNs in the dorsal striatum could tune them to specific time intervals encoded by coincident oscillatory patterns, increasing the likelihood of them firing upon similar intervals in the future (Kononowicz et al., 2016; Yin et al., 2022). The observed sequential dependence in the present study likely reflects these residual temporal "memories" left in the MSNs of the caudate nucleus from the previous trial.

Using parametric modulation analysis on brain activity, we unveiled compelling patterns reflecting the intricate relationship between sequential bias and BOLD activations. Specifically, the left middle frontal gyrus showed greater sensitivity to sequential bias when previously exposed to long durations as opposed to short ones, resonating with observed activations in the right caudate nucleus. It is widely recognized that the left middle frontal gyrus in concert with the fronto-striatal pathway (Darki & Klingberg, 2015; Teki & Griffiths, 2016) contributes to working memory encoding (Dandolo & Schwabe, 2019; Nee et al., 2013). Past research has solidified this connection, showing that activity in the caudate nucleus and the frontal cortex systematically increased with an increasing number of intervals in the sequence (Coull & Nobre, 2008; Rao et al., 2001; Teki & Griffiths, 2016). This emphasizes the indispensable role of the fronto-striatal pathways in time perception (Matell et al., 2005). Drawing from these insights, our findings thus argue that the strong modulation of sequential bias in the left frontal gyrus can be attributed to the high involvement of working memory encoding and fronto-striatal timing circuits in processing prior long durations.

Furthermore, the hippocampus displayed a higher activity level for NR trials than for RR trials, working together with the preparation network that includes the precuneus - a region known for its crucial role in working memory (Hebscher et al., 2018; Ren et al., 2018). This high activation of the hippocampus during NR trials likely serves to actively preserve the encoded duration, effectively shielding potential sequential biases. In contrast, the subdued hippocampal activation during RR trials suggests a less active maintenance of the current duration, possibly because the information from prior trials is being reused (Sheehan & Serences, 2022; Whitney et al., 2022). Additionally, the parametric

modulation analysis further elucidated the hippocampus's role in shaping sequential bias in both NR and RR conditions. Specifically, as the previous duration lengthened, the parametric value increased for the NR but decreased for the RR condition. Their difference reached significance at long durations (i.e., 1.4 and 1.6 secs). Further supporting this, we found a significant negative correlation between BOLD signals from the hippocampus and the sequential bias, but only in the RR condition. That is, reduced hippocampal activation was linked to a greater likelihood of incorporating the prior duration into the current reproduction. This sequential bias diminished when the hippocampal activation reached a certain threshold, such as the activation level seen in NR trials - nullifying any significant correlation (Figure 4c). These findings underscore the pivotal role of the hippocampus in mitigating or exacerbating sequential bias.

A logical question arises: why does the hippocampal activation remain elevated in NR trials but not in RR ones? One possibility is that after a trial involving no action, both visual attention and motor readiness are more keenly tuned for the next trial. Indeed, our results revealed higher activity in brain networks associated with executive control and performance monitoring during NR trials compared to RR ones. Recent studies suggest that history biases depend largely on the expectation of making a perceptual decision and the subsequent attention state; when individuals pay more attention to the current stimulus, the influence of the preceding one diminishes (Ceylan & Pascucci, 2023b; Pascucci et al., 2023). It is worth noting that this sharpened focus on the current stimulus is likely facilitated by the absence of motor activity in the preceding trial. However, we cannot entirely dismiss other factors, such as the frequency distribution of the "Response" and "No-response" trials, as potential contributors. For instance, stimuli from the less frequent "No-response" trials might be more easily disregarded or even cause an opposite effect (Ceylan & Pascucci, 2023b). Nevertheless, our findings point to more efficient encoding and accurate retention of the current duration during NR trials. This prevents inter-trial memory interference and reduces historical bias. This neural efficiency may reflect a strategic allocation of cognition resources for processing sequential stimuli and optimizing performance (Chanales et al., 2017; Hsieh et al., 2014).

Our findings are broadly consistent with prior studies on non-temporal sequential dependence, corroborating the idea that sequential biases are influenced by the reactivation of the memory trace (de Azevedo Neto & Bartels, 2021; Fornaciai & Park, 2020b; Ranieri et al., 2022; Sheehan & Serences, 2022; Zhang & Luo, 2023). For instance, an EEG study employing an auditory pitch categorization task revealed that past information - be it pitch, category choice, or motor response - stores their respective features in memory. These stored features are only reactivated by the corresponding features in the current trial, thereby shifting current neural encoding and giving rise to sequential biases (Zhang & Luo, 2023). In the present study, we observed similar dynamics: a negative modulation in the hippocampus by prior reproduction on current encoding, as well as a negative correlation between hippocampal BOLD signals

and sequential dependence index. These findings further collectively underscore the crucial role of memory in shaping inter-trial sequential biases.

Turning to future avenues of research, the question of whether hippocampal engagement or associated working memory networks are universally required for sequential dependence in various contexts remains open. Though our study didn't directly tackle working memory tasks, we did reveal the potential role of working memory in shaping sequential effects in time perception. The relatively long durations (e.g., 1.4 and 1.6 seconds) in our study might place greater demands on memory mechanisms, thereby causing significant differences in neural activations between the NR and RR conditions. Previous literature suggests different neural mechanisms for perceiving sub- and supra-second intervals (e.g., Hayashi et al., 2014; Lewis & Miall, 2003; Rammsayer, 1999), though supra-seconds are usually longer (e.g., above 3 seconds) than a simple action task that we adopted here. Nevertheless, our results indicated more pronounced differences between NR and RR trials in the hippocampus when longer durations were present in the preceding trial, consistent with increasing evidence highlighting the hippocampus's central role for longer intervals (Howard & Eichenbaum, 2013; Jacobs et al., 2013; Meck et al., 2013; Palombo et al., 2016; Tsao et al., 2022). This is also consistent with the behavioral study on the non-temporal sequential effect (Bliss et al., 2017), which showed that lengthening retention intervals increased the sequential effect.

While it's clear that the hippocampus plays a key role in sequential-dependent biases in time perception, its role in other types of sequential dependence remains an open question. This complexity mirrors the "sensory recruitment" phenomenon in working memory, where task-specific cortical regions come into play (D'Esposito & Postle, 2015). For instance, a recent study used Transcranial Magnetic Stimulation (TMS) to inhibit the left dorsal premotor cortex - a region critical to short-term memory - and observed a significant reduction in serial dependence for judgments of motion speed (de Azevedo Neto & Bartels, 2021). On the other hand, when focusing on visual features, evidence from fMRI studies points to the early visual cortex as a key region in sequential dependence (Sheehan & Serences, 2022; St. John-Saaltink et al., 2016). Importantly, our findings emphasized that sequential dependence in time perception not only engages specific neural circuits but also relies on the hippocampus's role in fine-tuning these sequential biases.

In summary, our study revealed that action or not in a preceding trial significantly influences sequential dependence in time perception. When a reproduction task follows passive viewing, both memory and striato-thalamo-cortical networks actively engage, effectively nullifying any sequential biases. In contrast, back-to-back reproduction tasks result in subdued hippocampal activity, which in turn gives rise to prominent sequential biases. Intriguingly, these biases show a negative correlation with individual levels of hippocampal activation. Our findings highlight that sequential biases in time

perception do not solely arise at the perceptual stage but also crucially involve the post-perceptual processes. Herr, the hippocampus plays a key role in linking sensory representation to responses.

Data and code availability statement

The data and analysis code that support the findings of this study will be made available from the author, Si Cheng (chengsi123456@gmail.com), upon reasonable request.

4.5 Reference

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4.6 Appendix

Neural mechanisms of sequential dependence in time perception:

The impact of prior task and memory processing

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Normalized relative errors

The current reproduction Error (E_n) inherits the general over-/under-estimation bias and the central tendency bias, as well as the sequential bias. Assume the inter-trial sequential bias is independent from the global general and central tendency biases, we can express the following for the reproduction error:

$$E_n = b + c(D_n - \bar{D}) + sD_{n-1} + \epsilon, \tag{1}$$

where $D_n, D_{n-1}, \bar{D}$ are the current, previous durations, and the mean sample duration, respectively. The coefficients b, c, s are the general bias, the slope of the central tendency, and the slope of the sequential dependence, respectively. And ϵ is the residual.

When the durations are uniformly distributed and randomly sampled, the conditional distribution of the previous duration on the current duration remains uniform. This means the classical measure of the sequential dependence $E_n = b + s'D_{n-1}$ is close to the assumption that the central tendency is linear across the sample durations and averaged out by not considering the current duration. However, this general bias term b remains in the equation. To remove the bias term for further analysis, like in fMRI modeling, one approach is to transform the above equation to:

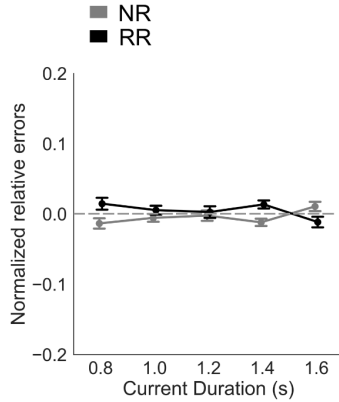$$E_n - [b + c(D_n - \bar{D})] = sD_{n-1} + \epsilon, \tag{2}$$

However, this approach has the assumption that the central tendency trend is linear. To relax this assumption, we used another approach, that is, we subtract the mean reproduction from individual sample durations to obtain the relative errors. To equate potential impact of scalar property (i.e., Weber scaling), we further normalized the relative error ($RE_{n,k}$) as follows:
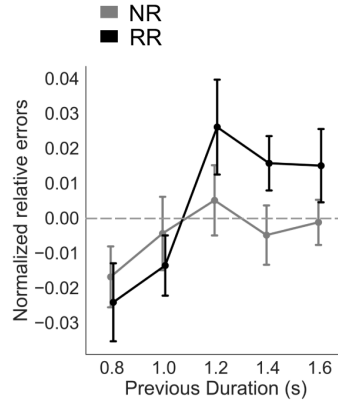
$$RE_{n,k} = (D_{n,k} - \bar{R}_k)/\bar{R}_k,$$

where $\bar{R}_k$ is the mean reproduction of the duration D_k, $D_{n,k}$ the reproduced duration at trial n of a given Duration D_k. When $\bar{R}_k$ is approximately linear $\bar{R}_k = a + bD$, the normalized error is an approximate to Equation (2).

Figure S1 shows the normalized errors were almost flat across all current durations, both for the NR and RR conditions. A repeated-measures ANOVA failed to show any significance ($ps > 0.084$). In contrast, the trends of the normalized error remained similar to the classic measure (Figure 2b), but centered around 0 (see Figure S2). We then calculated the slopes of the linear regression, which was only significantly positive for the RR condition ($b = 0.054$, $t_{(20)} = 3.011$, $p = .007$, $BF_{10} = 6.890$), but not for the NR condition ($b = 0.016$, $t_{(20)} = 1.355$, $p = .190$, $BF_{10} = 0.506$). Additionally, the slope for the RR condition was significantly larger than that in the NR condition ($t_{(20)} = 2.213$, $p = .039$, $BF_{10} = 1.673$, see Figure S3).

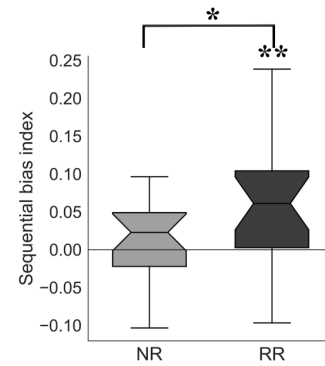Figure S1. The normalized relative response errors are plotted on the current durations, separated for NR and RR conditions. Error bars represent ± SEM. S2. The normalized relative response errors are plotted on the durations from previous trials, separated for NR and RR conditions. Error bars represent ± SEM. S3. Notched boxplots of the sequential bias for NR and RR conditions. The box plot depicts the slope, measured by the normalized relative errors, for each condition. *p <.05, **p <.01.

5 General Discussion

This dissertation systematically investigates the behavioral and neural mechanisms underlying serial dependence in time perception, with a specific emphasis on the impact of response dynamics, task relevance across diverse task paradigms, and the involvement of working memory. Employing a methodological approach integrating behavioral assessments and functional magnetic resonance imaging (fMRI), we conducted three studies to delineate the cognitive and neural processes governing temporal judgments and shed light on the underlying mechanisms of temporal serial dependence. Each study's main results contribute to a nuanced comprehension of how serial dependence manifests in the temporal domain, particularly concerning the influence of response and task-specific factors. In the following sessions, I will briefly synopsis the main results for each quantitative-empirical study and discuss how they contribute to the present dissertation. The next step will be to present a perspective on potential future research directions, followed by a conclusion.

5.1 Summary of results

5.1.1 Behavioral results

The role of response in the previous trial

Initially, we provide a synopsis of the behavioral results in Chapter 4. In this study, we conducted an investigation into the influence of preceding responses on serial dependence in time perception. The study employed a duration reproduction task with a post-cue manipulation, alternating between active reproduction and passive viewing of durations, aiming to determine where the serial dependence originates. Our findings showed a robust central tendency effect in duration reproduction, irrespective of the preceding task condition. However, the reproduction errors were contingent on the preceding task and duration. Specifically, a positive serial dependence effect was observed only for trials involving consecutive reproduction, but not for trials preceded by passive viewing.

Recent temporal intervals, being more accessible in memory, exert an influence on the perception of current intervals. The brain constructs time perception through the integration of noisy sensory inputs with recent past stimuli, resulting in a sequential effect, and the incorporation of general knowledge about stimuli, giving rise to a central tendency effect. These processes facilitate encoding efficiency, leading to an assimilation effect of prior stimuli in time perception. From a Bayesian standpoint, the ensemble prior assimilates the target duration (Shi & Burr, 2016; Zhu et al., 2021). Our findings indicate that for sequential dependence in time perception to occur, action component is essential, which suggests that the origin of this temporal sequential dependence is likely rooted in high-level, post-perceptual decisional and integrational processes (Bae & Luck, 2020; Ceylan et al., 2021; Fritsche et al., 2017; Kiyonaga, Scimeca,

et al., 2017; Pascucci et al., 2019; Roach et al., 2017). The distinction between action and inaction can impact prior updates in distinct ways. For instance, a study by Roach et al. (2017) highlighted that when participants reproduced clearly delineated durations (either short or long) associated with specific spatial locations, the durations from different locations were merged together into a single prior, significantly influencing reproductions across all locations. However, merely passive observation of durations from one location left time reproductions from another location largely unaffected. This points to the pivotal role of responses, suggesting that action may serve as a common determinant for temporal assimilation, leading to sequential effects predominantly in consecutive trials that demand a response.

The behavioral results in Chapter 4 highlight that the sequential effect in the time domain heavily relies on late decision stages that engage action. This extends beyond prior research, which has primarily focused on serial dependence in non-temporal domains (e.g., Fischer & Whitney, 2014; Holland & Lockhead, 1968). Notably, existing studies emphasize the necessity for active retrieval of recent past information for serial dependence to occur (Bae & Luck, 2020; Fornaciai & Park, 2020b; Ranieri et al., 2022; Suárez-Pinilla et al., 2018). For instance, a study on motion direction judgment (Bae & Luck, 2020) revealed that serial dependence was only present when the preceding task was identical, as opposed to being different, such as judging the color of the motion stimuli. Our study contributes to this line of research by demonstrating that in the temporal domain, simply encoding the previous stimulus was not enough to produce a serial dependence effect.

The role of task relevance across diverse task paradigms
In Chapter 2, we examined the impact of task relevance on sequential effects within distinct timing tasks, namely discrimination and reproduction tasks. Across both tasks, a consistent attractive serial dependence effect emerged, where participants perceived current durations as longer following long previous stimuli and shorter following short ones. Notably, while the assimilation effect in the discrimination task remained unaffected by task relevance, it was more pronounced in the time reproduction task when following the same time task, highlighting the importance of task relevance in serial dependence during time reproduction. Furthermore, substantial decisional carry-over effects were observed in both tasks, with participants more likely to repeat their responses, regardless of task type, indicating that decisional carryover is a general phenomenon.

Our findings align with previous investigations into decisional carryover effects in duration judgments (Brown et al., 2005; Wehrman et al., 2018, 2023; Wehrman, Wearden, et al., 2020; Wiener et al., 2014). This tendency for participants to repeat their prior choice, particularly under response uncertainty (Akaishi et al., 2014), is consistent with the concept of response repetition. The response repetition bias might be elucidated by the classical anchor-and-adjust heuristic, where the prior response

serves as a reference point for evaluating the current duration. When rating the prior duration as "Short," participants anchor to this rating and adjust their perception of the next stimulus accordingly, resulting in it being judged as shorter than it would otherwise be. The anchor-and-adjust strategy has been documented in various contexts (Epley & Gilovich, 2006; Sherif et al., 1958).

Importantly, the study in Chapter 2 highlights a significant serial dependence effect in both duration discrimination and reproduction tasks, indicating its general applicability across diverse tasks. However, when comparing sequential effects between discrimination and reproduction tasks, distinctive patterns emerge in how task relevance influences these effects. This dissimilarity is unlikely to arise from task-specific estimations, as the observed difference persists even when reproductions are converted to binary "Short" vs. "Long" categories, similar to the task used in the time discrimination task. One plausible explanation lies in the differential memory processes engaged in reproduction and discrimination tasks. In the reproduction task, active maintenance of the encoded duration in working memory during the reproduction phase was necessary, as it is used as a reference for stopping the reproduction. The active memory trace of the target duration during reproduction may differ from direction estimates trials (recognizing direction may not be needed for the entire presentation), leading to unequal sequential effects between reproduction-reproduction and direction-reproduction trials. This distinct memory maintenance across tasks may thus bias the encoding of the subsequent trial, similar to findings in spatial memory tasks where the increased memory retention interval between the stimulus and response enhances sequential dependence (Bliss et al., 2017). In contrast, the binary discrimination task only requires participants to monitor the target duration until it matches a reference duration (1 second). If the target duration finishes before the reference, a response is made; if it surpasses the reference, a response is made without waiting for the entire duration. This means fully encoding the target duration is unnecessary for the discrimination task, leading to a smaller sequential effect and rendering the preceding task-irrelevant.

Another plausible explanation follows the criterion-setting account (Lages & Treisman, 1998), which assumes that the brain establishes a criterion or reference point for decision-making based on the previous stimulus or response. According to this account, serial dependence effects result from shifting or adjusting the criterion in response to the previous stimulus or response, which influences the current perception. For example, if the previous stimulus had high contrast, the brain may lower the criterion for the current stimulus, making it appear higher in contrast than it actually is. This observation aligns with previous research indicating that in discrimination tasks, the retained information is linked to a pre-established criterion value (Lages & Treisman, 1998). In this context, participants create internal or external criteria and compare incoming sensory input with this response criterion, likely showing less

dependence on the working memory and post-perceptual processes (Bausenhart et al., 2014; Dyjas et al., 2012; Lages & Treisman, 1998).

The role of working memory

Chapter 3 investigated the influence of task relevance and working memory load on direction and timing estimation using pre-cue and post-cue paradigms. Notably, we observed attraction in timing tasks and prominent repulsion effects in direction tasks across both paradigms. The attraction was reliable in duration reproduction when the preceding trial involved the same timing task but significantly reduced when the preceding trial involved a direction task in the post-cue setting and even vanished in the pre-cue setting. However, the preceding task had no effect on sequential repulsion in direction reproduction, regardless of cue type. Nonetheless, the post-cue setting enhanced both attraction and repulsion effects. Our findings thus highlight distinct sequential biases for timing and spatial tasks, suggesting separate underlying processes for temporal and spatial sequential effects.

In previous studies on static orientation judgments, both attraction and repulsion effects have been well documented. For example, small orientation differences (under 20°) typically yield attraction biases, while larger differences elicit repulsion biases (Alais et al., 2017; Bliss et al., 2017; Ceylan & Pascucci, 2023a; Fritsche et al., 2017; Fritsche & de Lange, 2019a). Conversely, studies using coherent motion predominantly report repulsion effects (e.g., Bae & Luck, 2020), consistent with our findings. Motion processing involves the representations of both motion direction and orientation (Alais et al., 2017; Moon et al., 2022). In the case of brief or mostly random motion presentation, the orientation signal of the motion may become more dominant, resulting in attraction effects similar to those observed in static orientation studies (Fischer & Whitney, 2014; Manassi et al., 2018). In contrast, long exposure to a coherent motion signal (e.g., here 800 to 1600 ms) can induce motion adaptation, resulting in repulsive motion aftereffects (Alais et al., 2005; Anstis et al., 1998). These effects tend to overshadow any attraction biases that might occur with small cross-trial differences.

It is worth noting that in our study the preceding task did not show any differential impacts on the repulsion effects, even when the task was known in advance, as in the pre-cue task. This indicates that repulsive biases in motion direction judgments might be attributed to long-lasting visual sensory adaptation, with minimal influence from task-specific attentional orienting. This aligns with the typical pattern of sensory adaptation, where negative biases dominate when previous stimuli are either unattended or irrelevant to the task, or when visual stimuli have a long duration and high contrast, or a reference (Manassi et al., 2018; Pascucci et al., 2019; Pascucci & Plomp, 2021; Su et al., 2023). Although earlier studies have suggested that motion adaptation could be a result of low-level perceptual processing, our findings imply that maintaining both tasks in working memory (as shown in the post-cue settings) can

enhance the repulsion bias. This suggests a potential involvement of high-level working memory interference, particularly the active discarding of irrelevant information, could be pivotal. Recent research supports this, showing that items removed from working memory as no longer relevant in the current trial exert a repulsion effect on the subsequent trial (Shan & Postle, 2022). Moreover, empirical findings suggest that disengaging attention from an item might also involve a mechanism of removing information from working memory (Lewis-Peacock et al., 2018). Furthermore, in our study, the repulsion effect remained unaffected by stimulus duration, likely due to the relatively long stimulus exposure times we employed compared to previous research (e.g., 200 or 500 ms (Bae & Luck, 2020; Fischer et al., 2020)). Interestingly, we observed an attraction effect at a 90° orthogonal difference, which might also be interpreted as a repulsion to the opposite motion direction.

Conversely, we observed an attractive serial dependence effect in timing tasks and such assimilation bias is task-related, prompting an exploration into the distinct sequential bias patterns between timing and spatial tasks. Unlike spatial perception, time perception lacks dedicated sensory systems (Wittmann & Paulus, 2008), and the organism may form time perception by integrating the current sensory estimation with recent history and the prior knowledge of the stimuli. Our study in Chapter 4 has demonstrated that action is essential during these processes, suggesting that the origin of the temporal serial dependence is likely rooted in high-level, post-perceptual decisional and integrational processes (Bae & Luck, 2020; Ceylan et al., 2021; Fritsche et al., 2017; Kiyonaga, Scimeca, et al., 2017; Pascucci et al., 2019; Roach et al., 2017). In line with this, the assimilation effect was more pronounced in duration reproduction following the same timing task, rather than the motion direction task. Moreover, time perception relies on a memory system for monitoring the passage of time and temporal decisions (Gibbon & Church, 1990; Shi, Church, et al., 2013), and it is susceptible to manipulation through working memory tasks, such as pre-cue and post-cue tasks. As a result, buffering two tasks in working memory using the post-cue paradigm amplified the attraction effect in duration reproduction. This suggests that the attractive sequential effect may involve active recall of memory traces (Bliss et al., 2017; Ceylan & Pascucci, 2023a; Fornaciai & Park, 2020b; Fritsche & de Lange, 2019a; Ranieri et al., 2022). The lingering memory trace from a preceding stimulus in working memory likely contributes to sequential biases, as the brain employs recent experiences to shape our perception of the sensory environment in the present moment.

5.1.2 Neural mechanisms

At the neural level, in Chapter 4, we observed that during the duration encoding phase, BOLD signals were enhanced for "No-response to Response (NR)" trials relative to "Response to Response (RR)" trials. This was observed within a network associated with cognitive control and response

preparation (Dijkerman & de Haan, 2007; Fitzgerald et al., 2010; Ridderinkhof et al., 2004), which includes regions like the right posterior-medial frontal, the left postcentral gyrus, and the left precuneus. Additionally, the right thalamus, a critical component of cortico-thalamic-basal ganglia timing circuits (Mole et al., 2018; Yin et al., 2022), also showed activation. After a passive-viewing trial with no response demands, the response preparation network and cortico-thalamic-basal ganglia timing circuits were better primed for the upcoming trial. In contrast, the right inferior frontal gyrus (RIFG), essential for response inhibition and cue detection (Aron et al., 2007; Hampshire et al., 2010; Hartwigsen et al., 2019), displayed increased activity during RR trials compared to NR trials. This enhanced activity occurs because, after an active reproduction trial, the type of next trial (Response or No-response) remains uncertain until the appearance of the post cue.

For the contrast between the prior long and short durations, our results revealed greater activation in the right caudate nucleus for the prior long duration. The caudate nucleus, a key part of the dorsal striatum, plays a critical role in the striato-thalamo-cortical network (Coull & Nobre, 2008; Rao et al., 2001; Teki & Griffiths, 2016). Serving as a "core timer" of the timing system (Meck et al., 2008), the caudate nucleus holds temporal "memories" in its GABAergic medium spiny neurons (MSNs) via dopamine-facilitated long-term potentiation and short-term plasticity mechanisms (Allman & Meck, 2012; Kononowicz, 2015). Adjustments to corticostriatal synaptic weights by MSNs in the dorsal striatum could tune them to specific time intervals encoded by coincident oscillatory patterns, increasing the likelihood of them firing upon similar intervals in the future (Kononowicz et al., 2016; Yin et al., 2022). The observed sequential dependence in the present study likely reflects these residual temporal "memories" left in the MSNs of the caudate nucleus from the previous trial.

Using parametric modulation analysis on brain activity, we unveiled compelling patterns reflecting the intricate relationship between sequential bias and BOLD activations. Specifically, the left middle frontal gyrus showed greater sensitivity to sequential bias when previously exposed to long durations as opposed to short ones, resonating with observed activations in the right caudate nucleus. It is widely recognized that the left middle frontal gyrus in concert with the fronto-striatal pathway (Darki & Klingberg, 2015; Teki & Griffiths, 2016) contributes to working memory encoding (Dandolo & Schwabe, 2019; Nee et al., 2013). Past research has solidified this connection, showing that activity in the caudate nucleus and the frontal cortex systematically increased with an increasing number of intervals in the sequence (Coull & Nobre, 2008; Rao et al., 2001; Teki & Griffiths, 2016). This emphasizes the indispensable role of the fronto-striatal pathways in time perception (Matell et al., 2005). Drawing from these insights, our findings thus argue that the strong modulation of sequential bias in the left frontal gyrus can be attributed to the high involvement of working memory encoding and fronto-striatal timing circuits in processing prior long durations.

Furthermore, the hippocampus displayed a higher activity level for NR trials than for RR trials, working together with the preparation network that includes the precuneus - a region known for its crucial role in working memory (Hebscher et al., 2018; Ren et al., 2018). This high activation of the hippocampus during NR trials likely serves to actively preserve the encoded duration, effectively shielding potential sequential biases. In contrast, the subdued hippocampal activation during RR trials suggests a less active maintenance of the current duration, possibly because the information from prior trials is being reused (Sheehan & Serences, 2022; Whitney et al., 2022). Additionally, the parametric modulation analysis further elucidated the hippocampus's role in shaping sequential bias in both NR and RR conditions. Specifically, as the previous duration lengthened, the parametric value increased for the NR but decreased for the RR condition. Their difference reached significance at long durations (i.e., 1.4 and 1.6 secs). Further supporting this, we found a significant negative correlation between BOLD signals from the hippocampus and the sequential bias, but only in the RR condition. That is, reduced hippocampal activation was linked to a greater likelihood of incorporating the prior duration into the current reproduction. This sequential bias diminished when the hippocampal activation reached a certain threshold, such as the activation level seen in NR trials - nullifying any significant correlation. These findings underscore the pivotal role of the hippocampus in mitigating or exacerbating sequential bias.

A logical question arises: why does the hippocampal activation remain elevated in NR trials but not in RR ones? One possibility is that after a trial involving no action, both visual attention and motor readiness are more keenly tuned for the next trial. Indeed, our results revealed higher activity in brain networks associated with executive control and performance monitoring during NR trials compared to RR ones. Recent studies suggest that history biases depend largely on the expectation of making a perceptual decision and the subsequent attention state; when individuals pay more attention to the current stimulus, the influence of the preceding one diminishes (Ceylan & Pascucci, 2023b; Pascucci et al., 2023). It is worth noting that this sharpened focus on the current stimulus is likely facilitated by the absence of motor activity in the preceding trial. However, we cannot entirely dismiss other factors, such as the frequency distribution of the "Response" and "No-response" trials, as potential contributors. For instance, stimuli from the less frequent "No-response" trials might be more easily disregarded or even cause an opposite effect (Ceylan & Pascucci, 2023b). Nevertheless, our findings point to more efficient encoding and accurate retention of the current duration during NR trials. This prevents inter-trial memory interference and reduces historical bias. This neural efficiency may reflect a strategic allocation of cognition resources for processing sequential stimuli and optimizing performance (Chanales et al., 2017; Hsieh et al., 2014).

Our findings are broadly consistent with prior studies on non-temporal sequential dependence, corroborating the idea that sequential biases are influenced by the reactivation of the memory trace (de Azevedo Neto & Bartels, 2021; Fornaciai & Park, 2020b; Ranieri et al., 2022; Sheehan & Serences, 2022;

Zhang & Luo, 2023). For instance, an EEG study employing an auditory pitch categorization task revealed that past information - be it pitch, category choice, or motor response - stores their respective features in memory. These stored features are only reactivated by the corresponding features in the current trial, thereby shifting current neural encoding and giving rise to sequential biases (Zhang & Luo, 2023). In the present study, we observed similar dynamics: a negative modulation in the hippocampus by prior reproduction on current encoding, as well as a negative correlation between hippocampal BOLD signals and sequential dependence index. These findings further collectively underscore the crucial role of memory in shaping inter-trial sequential biases.

5.2 The contributions of the current studies

5.2.1 For the understanding of time perception

The investigations presented in this study significantly enrich our understanding of time perception. The time perception is of particular interest to researchers due to its realization in the brain. Unlike vision or other sensory modalities, there are no dedicated sensory organisms for "time." Thus, perceived duration is the result of the processing of event itself, and is highly sensitive to manipulation by, for example, the size, value or emotional effect of the stimulus whose duration is to be judged (Droit-Volet, 2016; Wehrman, Kaplan, et al., 2020).

The serial dependence effect in time perception observed in the current study showed that the perception of a temporal interval is biased toward the previous interval, and further enriched the traditional internal clock model (pacemaker counter or oscillator device). The internal clock model (pacemaker counter or oscillator device) proposes that humans and other animals measure the duration of events using a dedicated internal clock. It consists of a pacemaker that generates pulses, a switch that controls the flow of pulses, an accumulator that counts the pulses, and a comparator that compares the accumulated value with a reference memory. The internal clock model assumes that the perception of time is proportional to the number of pulses accumulated during an event. However, the model had no assumptions on inter-trial dynamics. The serial dependence effect in time perception suggests that internal-clock may not operate independently, rather those components, such as the pacemaker, accumulator, are context-dependent, influenced by mental states, emotions, memory, attention, and expectation (Shi, Church, et al., 2013; Wittmann, 2009). This process uses information from different sources, such as the sensory input, the previous experience, and the current goals, to construct a temporal representation of events. In other words, our internal clock does not operate like the physical clock, the latter independent of surrounding events.

5.2.2　For the understanding of serial dependence

　　Fisher and Withney's study (2014) on serial dependence affects reactive research interests in inter-trial sequential dependence, although the topic has been historically investigated a century ago (Fernberger, 1920; Hollingworth, 1910; Turner, 1931). However, there is still ongoing debate regarding the underlying mechanisms of the bias, whether it originates from the perceptual or the post-perceptual processes (Bae & Luck, 2020; Ceylan et al., 2021; Fischer & Whitney, 2014; Fritsche et al., 2017; Liberman et al., 2016; Pascucci et al., 2019). Our behavioral and neural findings revealed that for sequential dependence in time perception to occur, action component is essential, and the lingering memory trace from a preceding stimulus in working memory also contributes to sequential biases. Furthermore, our studies demonstrated the assimilation to the prior stimulus in both duration discrimination and reproduction tasks, indicating its general applicability across diverse tasks. However, the influence of task relevance in sequential effects showed distinct patterns in these two task types. Overall, our studies suggests that the origin of this temporal sequential dependence is likely rooted in high-level, post-perceptual decisional and integrational processes (Bae & Luck, 2020; Ceylan et al., 2021; Fritsche et al., 2017; Kiyonaga, Scimeca, et al., 2017; Pascucci et al., 2019; Roach et al., 2017).

　　It should be noted, however, that our findings do not dismiss the potential influences originating from the perceptual stage, as commonly identified in studies involving non-temporal stimuli (Czoschke et al., 2019; Fornaciai & Park, 2018a, 2020b; Togoli et al., 2021). Convergent evidence shows that serial dependence could emerge at different stages. For example, evidence has emerged where irrelevant stimuli, whether they are response-irrelevant inducers (Fornaciai & Park, 2018a) or simultaneously presented irrelevant (Czoschke et al., 2019), can either attract or repulse estimates in subsequent tasks. Intriguingly, these studies tend to position these task-irrelevant inducers close in time to the target (e.g., within a second in Togoli et al., 2021), which could promote potential perceptual integration. Well-documented phenomena, like ensemble perception (Whitney & Yamanashi Leib, 2018), show a tendency to attract individual items toward the ensemble mean (Baykan, Zhu, Allenmark, et al., 2023; Baykan, Zhu, Zinchenko, et al., 2023; Nakajima et al., 1992; Zhu et al., 2021). Notably, our findings reveal that the nature of the task plays a crucial role in shaping serial dependence in time perception, suggesting a task-specific impact on working memory usage. The study opens avenues for future research by highlighting the role of task-specific factors in shaping sequential dependence, proposing a universal phenomenon impacting various perceptual domains. Because of this, a more thorough understanding of the effects of assimilation in temporal judgments extends beyond the interval timing community, reaching into broader discussions about decision-making.

5.3 Outlook and future research

The renewed perspective on sequential effects presented in this work raises several questions calling for future empirical and theoretical work. Firstly, to clarify the relationship between the central tendency effect and serial dependence effect in time perception can provide a thoughtful understanding of how the brain integrates the prior information. In the current studies, we used the post-cue paradigm to confirm that the sequential effect in the time domain relies heavily on late decision stages that engage action. It is essential to highlight that in our study, since both prior task-relevant trials and task-irrelevant trials covered the same duration range, we cannot conclusively determine if central tendency would differ when task-relevant and task-irrelevant trials span different ranges. Nonetheless, the response-driven common cause hypothesis does suggest a possible variation in central tendency biases (Roach et al., 2017; Wang et al., 2023). It would be interesting for further studies to validate this prediction. Therefore, the distinct sequential effects by task relevance we noted in time perception might also be relevant to other perceptual domains, presenting an intriguing avenue for future research.

Further empirical research is also necessary in order to investigate the sequential effects by separating the serial dependence effect and the decisional carry over effect. Most research on serial dependence to date has adopted the method that choices are highly correlated with stimulus, for example, in the temporal judgment task, longer (shorter) intervals will be judged more often as "longer" ("shorter"). Therefore, sorting trials by previous stimulus duration leads to groups with unbalanced previous choices (and vice versa). Hence, the sorted trials have confounding influences of prior stimuli and prior response. This can lead to biased estimations of the effects and missed detections (when the two cancel one another out). In the current work, we mainly observed the temporal assimilation towards prior intervals in all studies, and strong response repetition bias in the decisional carryover effect. However, some studies found repulsive serial dependence effects and attractive decisional carryover effects from previous trials on current duration estimates (Li et al., 2023; Wiener et al., 2014). Additionally, recent studies have further exposed a strong influence of prior response on duration judgment and the influence of prior stimulus was negligible (Wehrman et al., 2023; Wehrman, Wearden, et al., 2020). A further design and analysis that separates the influence of the prior stimuli and the prior response may be of use in explaining the more complex aspects of sequential effects.

Additionally, recent research has explored the impact of feedback on the serial dependence effect, yielding inconsistent findings across different perception domains. Some studies suggest that providing feedback decreases the serial dependence, but other research posits that the feedback increases the serial dependence. For instance, in a numerosity discrimination task (Fornaciai & Park, 2022), serial dependence in numerosity estimates was induced by both dot arrays and symbolic numbers, implicating high-level processing stages that involve abstract information processing and judgment. Interestingly,

providing feedback in this task heightened serial dependence, indicating that external information at the judgment level modulates the weight of past information. The role of feedback here is to confirm or correct perceptual estimates, potentially enhancing confidence and reliability, thereby increasing the influence of the previous stimulus on the current one. Conversely, research on three-dimensional (3D) motion perception (Fulvio et al., 2023) revealed that feedback eliminates serial dependence. In this study, participants judged the direction of a rotating sphere with different contrast levels, and feedback on accuracy was provided selectively on some trials. Serial dependence varied with the contrast of the current stimulus, with lower contrast leading to more bias from the previous stimulus direction. Furthermore, feedback eliminates serial dependence, regardless of the contrast level. The researcher proposed that stimulus contrast and performance feedback may affect sensory uncertainty in the current trial. Higher contrast or feedback weakened serial dependence, indicating enhanced accuracy and reduced sensory uncertainty, thereby overriding the influence of past stimuli. Feedback, in this context, acts as a corrective signal that updates the perceptual system by providing information about the true state of the stimulus, reducing reliance on prior expectations, and preventing serial dependence. Notably, the limited studies on the role of feedback in the serial dependence effect underscores the necessity for further investigation into this complex phenomenon, especially regarding how feedback influences serial dependence.

Finally, it is important to consider individual differences in the future experiment given the fact that not every single observer shows serial dependence. The reliability of attractive serial dependence is well-established in many studies and perceptual domains: there is significant positive serial dependence, and there are stable individual differences (Kondo et al., 2022). However, the repulsive aftereffects observed in relatively few observers—whether these repulsive effects are actually stable—is far less clear and has yet to be demonstrated. For example, Glasauer and Shi (2022) showed that individual beliefs of temporal continuity can impact the magnitudes of the sequential bias. Those with a high belief in temporal continuity yielded strong attraction effects. Many studies have suggested that serial dependence operates at multiple levels of processing (Kiyonaga, Manassi, et al., 2017; Liberman et al., 2014, 2018), and, accordingly, we would expect individual differences in serial dependence may depend on how they form the prior and integrate the information into the current estimates. An analysis of individual differences in serial dependence would again be useful in this respect.

5.4 Conclusion

This dissertation provided strong empirical evidence to understand the behavioral and neuropsychological mechanisms underlying serial dependence of time perception. Our studies revealed assimilation effects in time perception and highlighted several factors that modulate the temporal

sequential dependence. Firstly, our research emphasized the distinctive role of task relevance in sequential effects during time discrimination and reproduction tasks. While the assimilation effect in the time discrimination task was unaffected by task relevance, it was notably stronger in the time reproduction task following the same duration task. Our findings thus imply that a reassessment of the existing evidence for sequential dependence, considering its potential association with the specific nature of the task, may be beneficial. Furthermore, our studies dissected sequential biases in space and time using a unified setting, revealing distinct sequential biases. Time blends through assimilation, while direction skews via dominant repulsion, with time particularly influenced by the preceding task. The research highlights that sensory processing and adaptation are key in shaping sequential biases in coherent motion direction, while working memory and post-perceptual processes have a greater effect on the bias in time reproduction. Moreover, increasing the working memory load intensified both the attraction in timing and repulsion in direction tasks. The distinct pattern of sequential biases between time and space potentially links to the dual roles of working memory in retrieving and discarding information, which presents an exciting avenue for further research. The fMRI study investigated neural mechanisms that underlie serial dependence in time perception and revealed that action or not in a preceding trial significantly influences sequential dependence in time perception. When a reproduction task follows passive viewing, both memory and striato-thalamo-cortical networks actively engage, effectively nullifying any sequential biases. In contrast, back-to-back reproduction tasks result in subdued hippocampal activity, which in turn gives rise to prominent sequential biases. Intriguingly, these biases show a negative correlation with individual levels of hippocampal activation. Our findings highlight that sequential biases in time perception do not solely arise at the perceptual stage but also crucially involve the post-perceptual processes. Here, the hippocampus plays a key role in linking sensory representation to responses. Overall, our studies revealed the assimilation effect toward the prior stimuli in time perception and supported the post-perceptual processes involved in the underlying mechanism of serial dependence in time perception.

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