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Serial Dependence in Human Visual Perception and Decision-Making

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"The eye sees only what the mind is prepared to comprehend."

Henri Bergson

Contents

LIST OF PUBLICATIONS

Publications and manuscripts included in the thesis main body

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ABSTRACT

Decisions about a current visual stimulus are systematically biased by recently encountered stimuli, a phenomenon known as serial dependence. In human vision, for instance, we tend to report the features of current images as more similar — i.e., an attractive bias — or more different — i.e., a repulsive bias — to those seen a few seconds earlier. While the phenomenology is clear-cut, the nature and underlying mechanisms have continued to be hotly debated for decades.

In this thesis, I first provide an extensive review of the main research paradigms, the key factors determining the two opposite biases, and the theories about the underlying mechanisms of serial dependence. The review also focuses on the challenge of establishing a relationship between serial dependence and the concept of object continuity, specifically whether serial dependence assists in maintaining the perceptual continuity of visual features and objects.

Second, I investigate whether serial dependence selectively applies to low-level visual features and objects, and whether it integrates past and present information to form a more accurate perception by reducing current uncertainty, as suggested by Bayesian accounts. My findings reveal that serial dependence does neither selectively apply to low-level features nor to objects. Moreover, I demonstrate that the integration of past and present information does not facilitate perception by reducing current uncertainty.

Third, I further examine the role of the number of intervening stimuli and task relevance, in addition to the time interval between current and past stimuli, which has often been considered a criterion for serial dependence. The findings here indicate that serial dependence is modulated by an interplay of time, the number of stimuli, and task relevance, suggesting that no single criterion or general temporal tuning can independently define serial dependence.

Last, I explore the format of history in serial dependence — what propagates from the past to the present — to determine whether it is the mere history of visual stimuli or the history of internal representations that is integrated. My findings support the latter, demonstrating that serial dependence arises from internal representations, wherein diverse visual features are condensed into the essential formats required by a given task.

Taken together, serial dependence is an intriguing yet complex phenomenon. The research I present in this thesis highlights its influence on visual information processing at various stages and its simultaneous modulation by multiple factors during a task, resisting simplification into a single criterion.

Keywords : serial dependence, opposite history biases, task relevance, object continuity, orientation perception

RÉSUMÉ

Les décisions en réponse à un stimulus visuel actuel sont systématiquement biaisées par les stimuli récemment rencontrés, un phénomène connu sous le nom de dépendance sérielle. Dans la vision humaine, par exemple, nous avons tendance à rapporter les caractéristiques des images actuelles comme étant plus similaires — c'est-à-dire un biais attractif — ou plus différentes — c'est-à-dire un biais répulsif — à celles vues quelques secondes auparavant. Bien que la phénoménologie de la dépendance sérielle soit claire, sa nature et ses mécanismes sous-jacents continuent de faire l'objet de débats animés depuis des décennies.

Dans cette thèse, je présente d'abord une revue approfondie des principaux paradigmes de recherche, des facteurs clés déterminant les deux biais opposés, et des théories associées aux mécanismes sous-jacents de la dépendance sérielle. La revue se concentre également sur le défi d'établir une relation entre la dépendance sérielle et le concept de continuité de l'objet, en particulier si la dépendance sérielle aide à maintenir la continuité perceptive des caractéristiques et des objets visuels.

Deuxièmement, j'examine si la dépendance sérielle s'applique sélectivement aux caractéristiques visuelles et aux objets de bas niveau, et si elle intègre les informations passées et présentes pour former une perception plus précise en réduisant l'incertitude actuelle, comme le suggèrent les comptes bayésiens. Mes résultats révèlent que la dépendance sérielle ne s'applique ni sélectivement aux caractéristiques de bas niveau ni aux objets. De plus, je démontre que l'intégration des informations passées et présentes ne facilite pas la perception en réduisant l'incertitude actuelle.

Troisièmement, j'examine en outre le rôle du nombre de stimuli intervenant et de la pertinence de la tâche, en plus de l'intervalle de temps entre les stimuli actuels et passés, souvent considéré comme un critère de dépendance sérielle. Les résultats ici indiquent que la dépendance sérielle est modulée par une interaction du temps, du nombre de stimuli et de la pertinence de la tâche, suggérant qu'aucun critère unique ou accord temporel général ne peut définir la dépendance sérielle indépendamment.

Enfin, j'explore le format de l'historique — l’information qui se propage du passé au présent — dans la dépendance sérielle, pour déterminer s'il s'agit simplement de l'historique des stimuli visuels ou de celui de leurs représentations internes qui est intégré. Mes résultats soutiennent cette dernière hypothèse, démontrant que la dépendance sérielle découle de représentations internes, où diverses caractéristiques visuelles sont condensées dans les formats essentiels requis par une tâche donnée.

Dans l'ensemble, la dépendance sérielle est un phénomène intrigant mais complexe. La recherche que je présente dans cette thèse met en évidence son influence sur le traitement de l'information visuelle à divers stades et sa modulation simultanée par plusieurs facteurs au cours d'une tâche, résistant à la simplification en un seul critère.

Mots-clés : dépendance sérielle, biais historiques opposés, pertinence de la tâche, continuité de l'objet, perception de l'orientation

INTRODUCTION

What we see is not a photographic snapshot of the external world but a complex blend of past experiences, previous decisions, and echoes of prior stimuli. Our interpretation of the continuous stream of sensory information is deeply embedded in our prior knowledge. Past, therefore, does not vanish, but instead shapes the present.

On one hand, prior experiences guide our perception and allow us to create plausible interpretations of an otherwise fluctuating, uncertain world. Consider driving on a rainy day: the visual scene is noisy, and the view of cars and traffic signs is intermittently obscured. Yet, we maintain a coherent representation of our surroundings, making decisions and taking actions based on sensory information that is often fragmented and unreliable. On the other hand, past experiences can also lead to illusions and systematic biases in vision. A notable example is the waterfall illusion: after staring at a waterfall continuously for several seconds, our subsequent gaze on a stationary scene can create the illusory perception that static scenes seem to ascend (Mather et al., 1998). This begs the question: how does the past simultaneously aid and hinder our vision?

To unravel the influence of the past, serial dependence is the critical phenomenon, reflecting the dependency of the current perception and perceptual decisions on the recent past. It has been traditionally considered a simple product of mechanisms that provide visual stability (J. Fischer & Whitney, 2014; Cicchini et al., 2014). Yet, as I intend to present to you here, serial dependence is actually far more than that.

Serial Dependence

Pioneering research by J. Fischer and Whitney has re-introduced serial dependence in 2014 (J. Fischer & Whitney, 2014). Through a series of behavioral experiments with human participants, the researchers have demonstrated that the orientation of a visual object —a Gabor patch— was consistently reported more similar to the orientations of objects encountered within the previous 10-15 seconds. In other words, changes in object orientation from one trial to the next were underestimated. Later, numerous studies have reported serial dependence for various attributes, from basic ones, such as orientation (John-Saaltink, Kok, Lau, & De Lange, 2016; Liberman, Zhang & Whitney, 2016; Samaha, Switzky, & Postle, 2018; Cicchini, Mikellidou, & Burr, 2018), position (Manassi et al., 2018), color (Barbosa & Compte, 2019), to more complex ones, like facial expressions (Liberman, Manassi & Whitney, 2018), numerosity (Fornaciai & Park, 2018), confidence (Samaha et al., 2019), timing (Roseboom, 2019), esthetics (Kim et al., 2019). Serial dependence has been also studied in different modalities such as auditory (Alais et al. 2015; Motala, Zhang & Alais, 2020), tactile (Hachen et al. 2020), odor (Van der Burg et al., 2022) and even in the behaviours of non-human primates (Papadimitriou, Ferdoash & Snyder, 2015; Barbosa et al., 2020; Stein et al., 2020).

While serial dependence has garnered significant attention recently, the investigation into its effects resonates with a topic of long-standing interest, with roots extending back to the mid-20th century. For instance, Pratt (1933) has investigated the relation of the time and errors made in psychophysical tasks. Likewise, Needham (1935) has examined the effect of time intervals in sequential comparison tasks. They have demonstrated that the difference in successive stimuli can be either overestimated or underestimated, with these estimation errors being modulated by the interval between the successive stimuli.

Remarkably parallel to contemporary research, in 1968, Holland and Lockhead have investigated the impact of preceding stimuli on the judgments of current stimuli, particularly in the context of absolute loudness judgments. Their work, titled 'Sequential Effects in Absolute Judgments of Loudness' (1968), demonstrated that the loudness of a current stimulus was judged as either more similar or more different to the preceding loudness, depending on the recency of successive stimuli. They coined the terms ‘assimilation’ and ‘contrast’ to denote these opposing sequential effects, which are now referred to respectively as ‘attractive’ and ‘repulsive’ in the serial dependence literature.

The following sections will focus on serial dependence in human vision, elucidating its two contrasting forms and underlying factors. These sections will summarize recent findings from the literature and introduce the central debates concerning the nature and role of serial dependence. At the end of Introduction, an overview of the upcoming chapters will be presented for the reader's convenience.

Two Opposite Forms

Traditionally, serial dependence has been considered an attractive (or positive) bias that pulls current judgments towards the recent stimulus history. For instance, when individuals are asked to determine the orientation of a grating stimulus, their responses are systematically biased toward the orientations observed in prior trials (J. Fischer & Whitney, 2014), as illustrated in Figure I.1A.

Recent studies expand on this understanding by reporting a repulsive (or negative) form of serial dependence, in which current perceptual decisions are biased away from previous stimuli (as in Figure I.1B). This repulsive bias has been observed for the stimuli encountered far in the past (Fritsche, Mostert, & de Lange, 2017), in the absence of memory maintenance (Czoschke et al., 2018) and explicit decisions (Pascucci et al., 2019), and for the task irrelevant or to-be ignored stimuli (Rafiei et al., 2021).

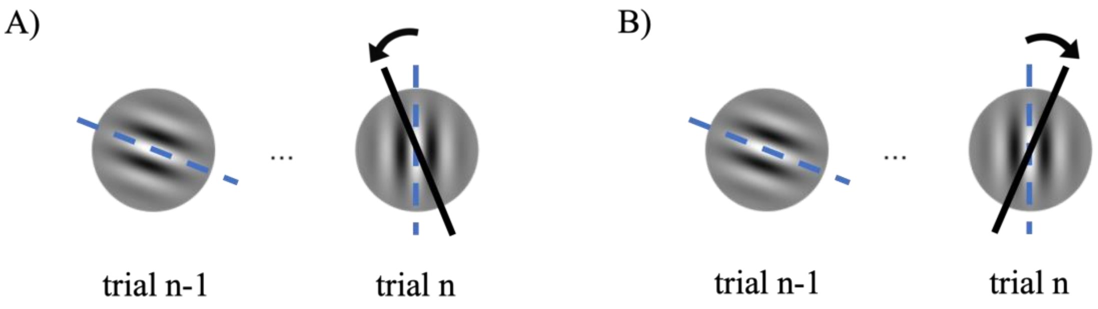

Figure I.1. Illustration of the Two Opposite Forms of Serial Dependence.
(A) Attractive form, where the current judgment of the grating stimulus orientation (trial n) is shifted towards the orientation of the previous grating stimulus (trial n-1). **(B)** Repulsive form, where the current reported orientation deviates away from the orientation of the prior stimulus. The blue dashed lines represent the actual orientations, while the black solid lines represent the reported orientations of the stimuli.

Key Factors

To date, research has uncovered a number of factors that can determine or modulate serial dependence, each exerting distinct effects on its attractive and repulsive forms. The following sections will briefly exemplify the principal factors examined in this thesis. It is important to acknowledge, however, that there are additional factors beyond the list here, and future research may continue to expand on this list (also see Chapter 1 for a review).

Attention

Attention is widely accepted as a fundamental factor in serial dependence. A range of studies employing diverse paradigms have demonstrated that attractive bias is gated by attention (J. Fischer & Whitney, 2014; Fritsche & de Lange, 2019; Pascucci et al., 2019); current decisions are attracted toward the past only when the previous stimulus was attended. When a prior stimulus is either unattended (J. Fischer & Whitney, 2014) or deliberately ignored (Rafiei, et al., 2021), a repulsive effect is observed in subsequent decisions.

Given the role of attention in shaping serial dependence, one might wonder how this influence varies across different types of attentional focus. Research has indicated that attractive bias can manifest through spatial attention directed at a prior stimulus location (J. Fischer & Whitney, 2014; Kiyonaga et al., 2017). Similarly, the literature often posits that serial dependence emerges at the object level (-i.e., object-based attention, Liberman et al., 2014; Liberman et al., 2018), further supporting the notion that attentive focus on distinct stimulus features might not be essential, provided there is spatial attention to the object.

But what happens when attention shifts to specific features of an object rather than the object as a whole? Many perceptual tasks do not necessitate attending to an entire object; instead, attention is required on specific features of visual objects, such as size, color, or motion (Maunsell & Treue, 2006; White & Carrasco, 2011; Saenz, Buracas & Boynton, 2003). This brings into focus another variant of attention: feature-based attention. In this cognitive process, attention is selectively allocated to specific features within the visual field, enabling individuals to efficiently process relevant visual information in the environment while ignoring or filtering out irrelevant ones (Treue & Trujillo, 1999; Baldassi & Verghese, 2005).

Indeed, research directly investigating the role of feature-based attention in serial dependence highlights significant modulation (Fritsche & de Lange, 2019; Collins, 2022). For instance, in an orientation adjustment task, when the previously attended feature of an object pertains to size, current orientation judgments present weaker attraction to the orientation of previous objects, though the attraction does not completely disappear. Moreover, the specificity of feature-based attention seems to have distinct effects on different types of biases. Notably, Fritsche and de Lange (2019) also revealed that repulsive bias remains unaffected by this type of attention. This finding raises the question: Could the nature of serial dependence be contingent on the type of attentional mechanism engaged? Such questions highlight the nuanced relationship between attention and serial dependence, suggesting a complex interplay that future research may further elucidate.

Task relevance

Task relevance, closely associated with attention, emerges as another key components, shaping the form of serial dependence. Attraction typically occurs for stimuli deemed relevant to a task, while a repulsive bias predominantly arises from those considered irrelevant (Rafiei et al., 2021; Ceylan & Pascucci, 2023). But what precisely constitutes task relevance, and how is it defined across different experimental conditions?

Different from attention, task relevance, by definition, necessitates performing a task and making decisions about stimuli. For instance, investigating the role of task relevance, Rafiei et al. (2021) employed a visual search task with multiple distractors and a target, where each item remained attended until the target —distinctly tilted one compared to the rest— was detected. The orientations of distractors were found to induce repulsion, whereas those of the target induced attraction in subsequent judgments. Although initially attended to, such repulsive bias might be attributed to the active removal of distractor representations from working memory once they are deemed irrelevant (Shan & Postle, 2022). In paradigms requiring feature-based attention, different features of the same object may be classified as relevant or irrelevant, depending on the task demands (Fritsche et al., 2017; C. Fischer et al., 2020). These paradigms might permit encoding the features into working memory according to their relevance immediately following stimulus onset (Shan & Postle, 2022).

Despite variations in how relevance is construed, there is a general agreement that attractive and repulsive biases in orientation judgments stem from task relevant and irrelevant information, respectively. Importantly, studies employing different tasks and stimuli have observed attraction towards stimuli typically considered irrelevant, an effect evident in numerosity judgments (Fornaciai & Park, 2018).

Uncertainty

Various studies have reported critical modulations by uncertainty in serial dependence (Cicchini et al., 2018; Van Bergen & Jehee, 2019; Gallagher & Benton, 2022; Manassi et al., 2018; Ceylan, Herzog & Pascucci, 2021; Fulvio, Rokers, & Samaha, 2023). Manassi et al. (2018) even proposed that attractive biases may manifest only when a stimulus is sufficiently uncertain. The concept of uncertainty, however, is not uniformly defined across studies. It can refer to an objective measure of sensory precision or can be a subjective measure about individual performance (Meyniel et al., 2015; Samaha et al., 2019; Fritsche et al., 2019).

As an objective measure of sensory precision, the level of uncertainty can be defined by spatial frequency (Cicchini et al., 2018), noise (Kim & Alais, 2021), luminance contrast (Manassi et al., 2018; Fulvio, Rokers, & Samaha, 2023), or even to sensory statistics (Van Bergen & Jehee, 2019). Indeed, it is widely suggested that when the previous stimulus offers more reliable sensory information (i.e., less uncertain) than the current one, perceptual decisions tend to attract more to the past (Cicchini et al., 2018; Van Bergen & Jehee, 2019; Manassi et al., 2018). This tendency aligns with Bayesian frameworks in visual perception that advocate for a weighted integration of visual cues to produce optimal predictions (Trommershauser, Kording & Landy, 2011; Van Bergen & Jehee, 2019). Yet, this integration is not always optimal, and the modulation by the uncertainty has been found limited to the level of current uncertainty (Ceylan et al., 2021; Gallagher & Benton, 2022).

Moving beyond sensory precision, subjective confidence can be considered a measure of uncertainty (Meyniel et al., 2015), which has been shown to modulate attractive serial dependence (Samaha et al., 2019; Suárez-Pinilla, Seth & Roseboom, 2018). For instance, Samaha et al. (2019) have demonstrated that stimuli reported with higher confidence in the past generate more attraction in current judgments.

Working memory

Working (or short-term) memory is a prominent focus in serial dependence. Research has suggested that attractive serial dependence arises through the active engagement of working memory (Fritsche et al., 2017; Bliss et al., 2017; Stein et al., 2020; Barbosa et al., 2020; C. Fischer et al. 2020), with attraction to past stimuli intensifying when stimulus information is retained in working memory, especially for extended periods, up to approximately 10 seconds. Beyond this timeframe, the attraction tends to diminish, giving way to repulsion (Bliss et al., 2017).

In pathological conditions like anti-NMDAR encephalitis and schizophrenia, where working memory is compromised (Morgan & Curran, 2006; Gilmour et al., 2012), the expected attractive bias becomes disrupted, as shown by Stein et al. (2019). Notably, research has demonstrated that, in tasks demanding the active employment of working memory, decisions of individuals with schizophrenia systematically deviate away from past stimuli, in contrast to the emergence of attractive bias seen in their healthy counterparts (Stein et al., 2019). It becomes evident that without the typical functioning of working memory, the attraction of past stimuli on current decisions is not only weakened but can even be reversed, suggesting a fundamental role for working memory in shaping serial dependence.

Passage of time

Unlike other systematic biases and illusions, such as aftereffects (Gibson & Radner, 1937), attractive serial dependence can emerge rapidly for stimuli shortly presented (<1 seconds) approximately 3 to 15 seconds in the past, corresponding to 1 to 4 trials in typical paradigms (J. Fischer & Whitney, 2014). Yet, this does not imply that the strength of the bias remains uniform within this timeframe. Instead, attraction gradually diminishes with time or with trials, eventually disappearing (J. Fischer & Whitney, 2014). Following this, repulsion tends to emerge for stimuli presented longer ago, up to approximately a few minutes (Fritsche et al., 2020). These durations, however, are estimations drawn from standard orientation adjustment tasks and may differ in other experimental paradigms (Fornaciai and Park, 2018). Notably, tasks requiring immediate responses do not always generate attractive bias (Fritsche et al., 2017; Bliss et al., 2017).

Furthermore, Bliss et al. (2017) provided a detailed analysis of the time course of serial dependence by varying both the inter-trial interval (ITI) and inter-stimulus interval (ISI) across trials. Their research revealed that attractive bias gradually increases with a longer delay following the stimulus and, conversely, decreases with a shorter delay following the response, suggesting a more complex temporal tuning than the mere passage of time.

Feature space proximity

It has been proposed that attraction to past stimuli increases when the past and present stimuli are visually similar (J. Fischer & Whitney, 2014; Fritsche et al., 2019; Rafiei et al., 2021). This similarity can be observed within the features of the same stimulus (e.g., orientations: Fritsche & de Lange, 2019; Rafiei et al., 2021) or across different objects (e.g., faces: Liberman et al., 2018). For instance, Fritsche and de Lange (2019) report an attractive bias for small orientation differences and a reference-like repulsive bias for differences greater than approximately 50°. In line with this, Rafiei et al. (2021) demonstrate that the opposite bias, which emerge due to task relevance manipulations in their research, can be further modulated by the similarity between the inducer and the test item. Additionally, Liberman et al. (2018) demonstrate that attractive bias occurs only for identical stimuli (e.g., face stimuli of the same identity) or for sufficiently similar stimuli (e.g., face stimuli of the same race), and disappears for distinct stimuli (e.g., face stimuli of different genders).

Like uncertainty, however, feature space proximity can also be a subjective measure of similarity, influenced by factors such as expertise (Turbett et al., 2019), and is therefore prone to individual differences (Zhang & Whitney, 2017).

Major Debates

On the nature

One of the most controversial issues at the center of serial dependence research concerns its origins: whether it is a perceptual or post-perceptual phenomenon. A substantial body of evidence indicates that serial dependence can arise in relation to a previously viewed stimulus, regardless of whether it was reported, and can influence the appearance of subsequent stimuli (Fischer & Whitney, 2014; Liberman et al., 2014; Manassi et al., 2018). Therefore, these studies suggested serial dependence as a perceptual phenomenon, possibly resulting from changes in sensory encoding. However, post-perceptual accounts challenge early findings, showing that the attractive serial dependence is only possible with the presence of decisions (Pascucci et al., 2019), induce with the memory maintenance (Bliss et al., 2017; Czoschke et al., 2018) and requires conscious awareness (Kim et al., 2020).

A useful approach in understanding the nature of serial dependence was first suggested by Cicchini et al. (2021), differentiating the 'source' and the 'site of action' concepts in the investigation of the phenomenon. Employing this differentiation enables researchers to address whether serial dependence originates from a perceptual or post-perceptual stage and whether we observe its effects at various stages. Taken this approach, in their study Cicchini et al. (2021) suggested that positive serial dependence can arise at a later decisional stage which propagates down to an early perceptual stage where the effects become more prominent.

Another approach aims to address the nature of serial dependence by disentangling the opposite forms of serial dependence (Fritsche et al., 2017). Recent studies employing this approach suggest that these opposite forms can co-exist: the attractive bias emerges at post-perceptual stages, while the repulsive form arises at earlier perceptual stages (Fritsche et al., 2017; Pascucci et al., 2019). Consequently, these forms possess distinct underlying mechanisms and temporal tuning profiles, leading to unique modulations by various factors. This divergence may as well imply that they play different roles in visual perception and perceptual decisions.

On the role

The traditional approach to serial dependence characterizes it as an attractive bias, proposing that the visual system integrates similar visual information over time to create a smoother, more stable and continuous perception of external world, with the (attractive) serial dependence emerging as a consequence (Fischer & Whitney, 2014; Kiyonaga et al., 2017; Cicchini et al., 2018; Van Bergen & Jehee, 2019). Building on this, J. Fischer and Whitney (2014) introduced the theoretical concept of 'continuity field,' which delineates the spatio-temporal tuning profile of attractive serial dependence. The continuity field was introduced to highlight and rationalize the existence and role of the phenomenon. Continuity field is now considered as mechanisms that "smooth out" perception over time, counteracting noisy fluctuations and disruptive changes such as those caused by saccades, head movements, occlusions, and various forms of visual noise (Cicchini et al., 2018).

Existing models of serial dependence rely on Bayesian and adaptive filtering frameworks in which serial dependence is an optimal tool for reducing visual uncertainty (Cicchini et al., 2018; Fritsche et al., 2020; Van Bergen & Jehee, 2019). Bayesian theories suggest that the brain is essentially a 'Bayesian predictor,' constantly updating its predictions about the current state of the world based on prior experiences (Kersten, Mamassian, & Yuille, 2004). Analogous to a Kalman filter in systems control (Cicchini et al., 2014; Burr & Cicchini, 2016), this process facilitates predictive coding in perception (Taubert, Alais, & Burr, 2016). In the context of vision, this implies that our current perception is an optimal composite of both immediate sensory information and our recent visual history.

Nonetheless, the literature involves conflicting evidence on the functional role of serial dependence (J. Fischer & Whitney, 2014; Cicchini et al., 2017; Fritsche et al., 2018; Pascucci et al., 2019; Ceylan et al., 2021; Gallagher & Benton, 2022), and Bayesian accounts cannot entirely explain these discrepancies.

Overview of Thesis

Over the past decade, serial dependence has become one of the central phenomena in visual perception and cognition research. However, the true nature and role of this phenomenon remain elusive. The existing literature presents conflicting results, leaving many questions unanswered. Key questions include: What constitutes ‘the past’ in serial dependence? Is perceptual stability the sole role of serial dependence? How do time and stimuli interact within a sequence of events? In the following chapters, I will explore these questions and introduce additional ones, aiming to offer alternative perspectives.

In **Chapter 1**, I will review serial dependence research over the past decade, highlighting the main paradigms and models used. Additionally, I will focus on the concept of object identity and the challenge of discerning its relation to serial dependence.

It is often suggested that attractive serial dependence serves to stabilize perception by reducing external noise. According to this theory, current visual stimuli are perceived as more similar to preceding ones, especially when the past stimuli are already similar and less uncertain. However, what determines similarity? Is past uncertainty the only factor, independent of current uncertainty? To address these questions, in **Chapter 2**, I will investigate whether serial dependence is selective to specific features and objects, and whether it becomes more attractive only when the past is less uncertain.

The continuity field has been proposed as the spatiotemporal tuning profile of attractive serial dependence, indicating that more recent stimuli exert a greater influence than those in the distant past. However, it is unclear whether serial dependence is merely a passage of time, or whether the number of stimuli or events tunes serial dependence. Therefore, in **Chapter 4**, I will disentangle the roles of time, stimuli, and task within a sequence of events and investigate whether serial dependence simply reflects the passage of time.

Despite extensive research, it is still unclear what exactly is ‘the past’ that leads to serial dependence and forms the opposite biases. Answering these pivotal questions could offer deeper insights into the origins and underlying mechanisms of serial dependence. In this regard, in **Chapter 5**, I will explore whether the past in serial dependence is merely a sensory history.

Finally, in the last chapter, I will summarize and discuss the findings of this thesis.

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CHAPTER 1: A Survey into Serial Dependence

Serial dependence in visual perception: A review

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Abstract

How does the visual system represent continuity in the constantly changing visual input? A recent proposal is that vision is serially dependent: stimuli seen a moment ago influence what we perceive in the present. In line with this, recent frameworks suggest that the visual system anticipates whether an object seen at one moment is the same as the one seen a moment ago, binding visual representations across consecutive perceptual episodes. A growing body of work supports this view, revealing signatures of serial dependence in many diverse visual tasks. Yet, the variety of disparate findings and interpretations calls for a more general picture. Here, we survey the main paradigms and results over the last decade. We also focus on the challenge of finding a relationship between serial dependence and the concept of 'object identity', taking centuries-long history of research into account. Among the seemingly contrasting findings on serial dependence, we highlight common patterns that may elucidate the nature of this phenomenon and attempt to identify questions that are unanswered.

Introduction

While walking down a street, the information that light brings to our eyes is constantly changing. Every time we move and shift our gaze around, every time that cars and people go by, the details of the scene change. Yet, we maintain a sense of continuity in what we perceive: the tree beside the street is perceived as the same tree seen a moment ago, despite constant interruptions and changes in our view. This is a remarkable ability, and the best technology and engineering are yet to design a machine that can do this as well as the human brain can.

How does the brain maintain continuity in a world of change? Numerous recent results suggest that the visual system uses the recent past to inform perception in the present, exploiting the autocorrelation of events in the visual world (Burr & Cicchini, 2014; Fischer & Whitney, 2014; Kiyonaga et al., 2017; Kristjánsson, 2022; Pascucci & Plomp, 2021). Central to this idea is *serial dependence* (see Figure 1 and Box 1), a behavioral bias where current visual decisions are biased by the history of stimuli seen before (Fischer & Whitney, 2014).

Over the past decade, the study of serial dependence has increased considerably, lining up with well-established research on the role of the recent past in perception and cognition. Recent findings show that perceptual decisions are systematically attracted or repelled by the history of prior stimuli, revealing effects that are pervasive and evident in seemingly any sort of visual task. This has fostered frameworks where such serial dependence is assumed to mediate our experience of object continuity.

What is the nature of serial dependence? How are attractive and repulsive biases involved in the temporal integration and segregation of visual input? At what level of processing and representation do these effects occur? And how does the visual system determine what matches what from one moment to the next? In addressing these questions, first, we survey the literature on serial dependence, focusing on the main paradigms and findings (Section 2), and the factors that seem to play a role (Section 3). Next, we discuss challenges to establishing a direct link between serial dependence and object continuity (Section 4). Finally, we present a historical overview of the main frameworks and computational approaches dedicated to serial dependence over the last century (Section 5). The goal is to provide a comprehensive background for future research, reviving centuries-old questions and raising new ones.

Box 1.

Serial dependence

Serial dependence has a long history in psychology and psychophysics, starting from the adoption of scaling methods and the finding of systematic effects in psychophysical reports that extend over trials. Two such effects were termed *assimilation* —when perceptual reports were positively correlated with previous stimuli and responses— and *contrastive effects* —when the sign of this serial correlation was negative (see Section 5).

More recently, the term *serial dependence* has been used to describe, typically, a positive bias to judge present stimuli as more similar to recent stimuli than they are —i.e., a form of assimilation. In particular, serial dependence involves a systematic bias in perceptual decisions during psychophysical tasks, which are attracted towards aspects of the stimulus presented one or a few trials before. For instance, the decision about the orientation of a visual stimulus is biased towards the orientation of the stimulus seen before (Figure 2-3).

Originally, however, the term comes from time-series analysis and refers to statistical dependencies between events that are close in time (Huitema, 1986). Compared to serial- and auto-correlation, serial dependence implies any linear or non-linear relationship that can be used to predict future events from the past. It describes a unidirectional effect (the past affects the present and not the other way around), but no causality —a third unknown variable may be the true source mediating the effect. From this perspective, serial dependence is neither a mechanism nor a phenomenon exclusive to vision and cognition, but a property of a time series (e.g., of behavioral and neural data).

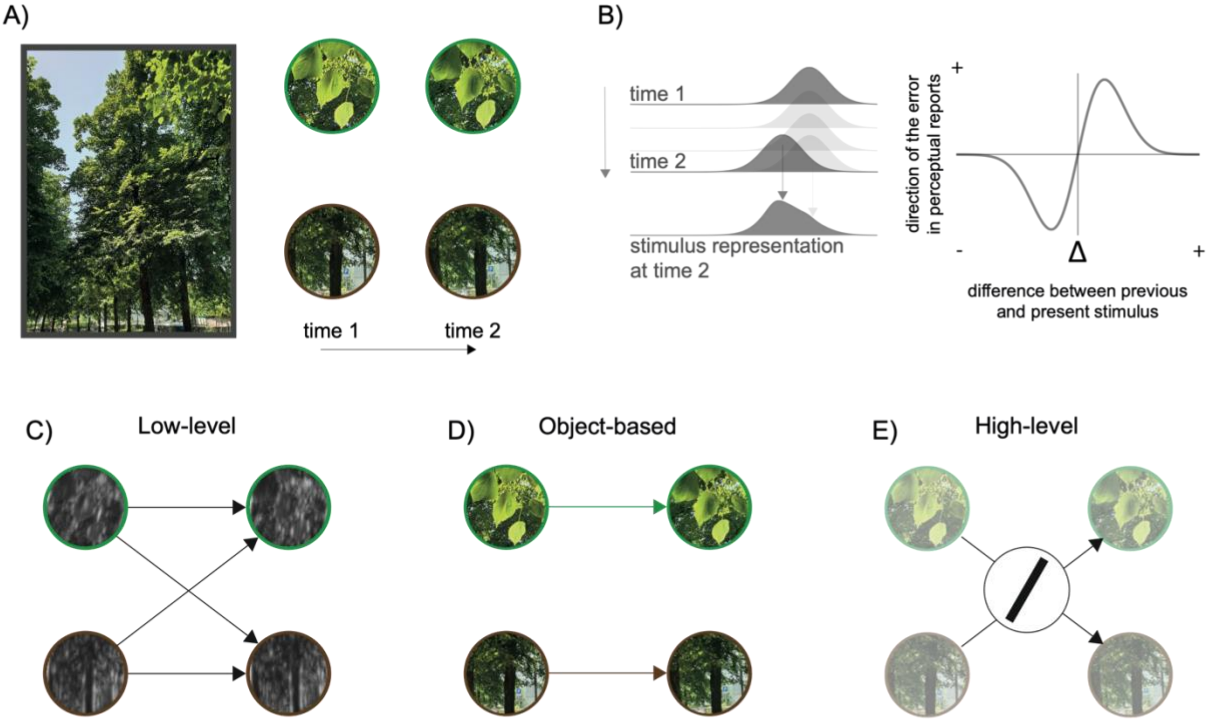

Figure 1. Serial dependence in visual perception and decision making. A) Our everyday environment is made of relatively stable and temporally correlated visual features: as we take a walk in the park, the objects around us (e.g., the leaves and trees) tend to remain the same, despite changes in luminance patterns and viewpoints. B) To exploit such temporal continuity, the representation of a visual object (here illustrated as a probability distribution over stimulus space) can propagate from one moment to the next, biasing visual representations towards the recent past. This leads to systematic errors in perceptual decisions, which tend to be pushed towards the direction of the previous stimulus. C-E) Three possible scenarios illustrating different accounts of the nature of representations involved in serial dependence; two different objects —the leaves and the tree— are shown inside green and brown circles, respectively: C) serial dependence can occur at the level of low-level visual features (e.g., orientation, motion, color) and independently of object-level representations; D) serial dependence can occur only for visual features of the same object; E) serial dependence can occur at more abstract levels of representation, where features of objects are extrapolated and reduced to elementary representations required by the task (e.g., both the tilt of the tree and of the leave can be represented as a tilted line). Note that, as in the ‘low-level’ scenario, high-level serial dependence can be object independent. (The picture in A is from Parc de Milan, Lausanne, Switzerland).

Serial dependence paradigms

Serial dependence has been investigated with a variety of paradigms, involving different types of stimuli, responses, and analysis. This has led to disparate, often seemingly contradictory, findings. Here we focus on work with behavioral methods (see Box 2 for imaging research) 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.

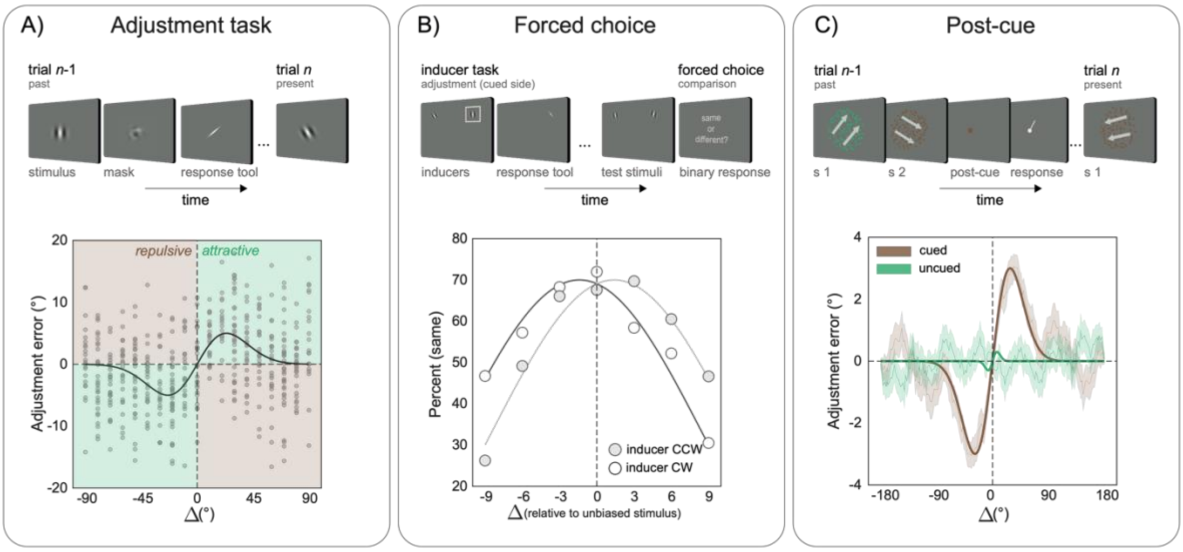

Figure 2. Typical paradigms and findings in serial dependence research. A) In a standard orientation adjustment task, an oriented stimulus (e.g., Gabor) is briefly presented and followed by a noise mask. After the mask, observers reproduce the perceived orientation of the Gabor by rotating a response tool (here a simple line). Serial dependence is seen in the adjustment errors (grey dots in the bottom plot) as a function of the difference in orientation between consecutive trials (Δ: previous minus present orientation). Typically, errors deviate towards the direction of the previous stimulus orientation (attractive bias, highlighted in the green regions of the plot), when Δ is small, following the shape of the first derivative of a Gaussian function (black curve). The dots in the bottom plots are from a simulated observer. B) An example of a sequential dual task in which an adjustment task is followed by a forced-choice task. One of two stimuli (the inducer) is cued in the adjustment task and observers reproduce its orientation. In the 'test' display, two other stimuli are presented, one at the same location as the inducer. In the forced-choice task, observers make a perceptual judgment (e.g., comparison or equality judgment) about the two test stimuli. Serial dependence is evident in the forced-choice task, as a shift in the perceived orientation of the stimulus at the inducer location, compared to the stimulus at the other '*unbiased*' location. The plot shows a simulated pattern of data resembling the findings of Fritsche and colleagues (Fritsche et al., 2017), where the inducer caused repulsive biases: to be perceived as identical to the unbiased stimulus, the test stimulus at the inducer location had to be slightly tilted in the opposite direction of the inducer (positive Δs indicate when the unbiased stimulus was more clockwise). C) The typical structure of a post-cueing paradigm investigating serial dependence in motion direction between trials containing two clouds of moving dots. A post-cue indicates the color of the cloud to report. The plot shows a simulated pattern of results based on the findings from Fischer and

colleagues (Fischer et al., 2020): serial dependence is influenced by the congruency between the feature cued on present and previous trials.

Adjustment tasks

In the method of adjustment, a brief stimulus is followed by a response tool that resembles one of the stimulus' features (e.g., the orientation, size, and so on). Participants adjust the tool to match their perception of the feature. This method is also known as a 'delayed reproduction task' or simply 'reproduction task'.

Typically, adjustment errors are biased by features on the preceding trials. In Fischer and Whitney (2014), the stimulus was an oriented Gabor presented for 500 ms followed by a noise mask for 1000 ms. After 250 ms from the offset of the mask, participants rotated a line to reproduce the orientation of the Gabor (see Figure 2A). On average, adjustment errors (reported minus true orientation) were positively related to the difference in orientation (Δ) between the previous and the present stimulus, showing a bias towards the previous orientation of about 10° for Δ near 20° —at the peak of the bias, perceptual reports were halfway between the present and prior orientation.

The pattern in Fischer and Whitney (2014) has been widely replicated, even though the magnitude of the effect can vary (e.g., from 1° to 10°, Fritsche et al., 2017). This pattern reveals key aspects of serial dependence. First, the effect of stimulus similarity: the bias is larger when the previous and present stimuli are similar (e.g., when Δ is small) and fades out as their difference increases, forming the typical S-shape that can be approximated by the fit of the first derivative of a Gaussian function (see Figure 2A, 3 and Box 3). Secondly, the bias is still evident from stimuli up to three trials back (10-15 seconds).

Some systematic properties, like the effect of stimulus similarity and the temporal decay of serial dependence, seem to hold for a variety of adjustment tasks involving features such as shape (Collins, 2022; Manassi et al., 2019), numerosity (Cicchini et al., 2014; Corbett et al., 2011; Fornaciai & Park, 2018b), facial identity (Liberman et al., 2014), color estimation (Barbosa & Compte, 2020), gaze direction (Alais et al., 2018), emotional expressions (Liberman et al., 2018), aesthetic judgments (Kim et al., 2019), spatial position (Manassi et al., 2018), and even for stimulus ensembles (Manassi et al., 2017; Pascucci et al., 2019)

What role does the adjustment tool play in serial dependence? Because the response tool usually resembles the relevant feature of the stimulus, the bias could partly be due to the response itself and the tendency to adjust the tool similarly to the previous trial (hysteresis in motor responses). Fischer & Whitney (2014, experiment 2) removed the response tool on 25% of trials, finding that serial dependence is largely unaffected by the presence and use of a response tool. Similarly, serial dependence occurred without responses in Manassi et al. (2018), although the bias was significantly larger when a response was required. Cicchini, Mikellidou & Burr (Cicchini et al., 2017) decorrelated the effect of the stimulus and the response by asking participants, on half of trials, to reproduce the orthogonal instead of the actual orientation (90° away from the true one). They demonstrated that the attractive bias is maximal when the stimulus and the response match, but absent when the response is orthogonal to the stimulus, corroborating the idea that the response tool itself plays no role.

While the response tool might not be necessary, how the stimulus is reproduced reflects the last instance of how the stimulus was perceived and remembered (Cicchini et al., 2014). Indeed, most of the variance in adjustment errors is explained by the feature reproduced on the previous trial, rather than the physically presented one (Pascucci et al., 2019). This latter observation is in line with studies demonstrating that, in adjustment tasks, the strength of serial dependence is also a function of post-perceptual or post-encoding factors, such as the confidence in the last decision (Samaha et al., 2019; Suárez-Pinilla et al., 2018) and the presence of an active task (Bae & Luck, 2020; Pascucci et al., 2019; Pascucci & Plomp, 2021).

Adjustment tasks also involve visual working memory, as the stimulus is reproduced ‘offline’ —when no longer on screen— and needs to be briefly held in memory so the bias may partly be due to interference between the previous and current memory trace of the stimulus. While Fischer and Whitney (2014) have shown that serial dependence is independent of any explicit memory of prior stimuli —i.e., it occurs even though participants are unable to recall the previous stimulus from working memory, other studies have reported an increase in the bias towards prior stimuli with increased retention time of the present stimulus before the adjustment response, suggesting that visual working memory may still contribute to and modulate the strength of serial dependence (Bliss et al., 2017; Fritsche et al., 2017; Mei et al., 2019).

Beyond standard adjustment tasks, other studies have used variants of this method to target more specific aspects of serial dependence. In the *sequential no-report* paradigm, stimuli are presented in a rapid stream with only occasional adjustment responses, leading to independent history of stimuli and reports —i.e., the previous stimulus does not necessarily correspond to the last report (Pascucci et al., 2019; Pascucci & Plomp, 2021). In this paradigm, prior stimuli and prior reports have opposite effects: the bias towards prior stimuli is repulsive, or attractive but weaker than the one towards prior reports, indicating the coexistence of two independent forms of serial dependence. In Kim, Burr, Cicchini, and Alais (Kim et al., 2020), an adjustment task was combined with binocular rivalry and serial dependence occurred only when the previous stimulus was consciously perceived but not suppressed by binocular rivalry. Similarly, Cicchini, Benedetto & Burr (Cicchini et al., 2021) combined the surround tilt illusion with an orientation adjustment task. In the tilt illusion, a surrounding configuration of oriented Gabors biases the perceived orientation of a central target. When this illusion was induced on the preceding trial, adjustment errors were biased towards the illusory orientation, rather than the actual one; however, the effects of the previous (illusory) orientation occurred before the illusion arose on the current trial. This led the authors to conclude that serial dependence originates at a late processing stage —i.e., after spatial context effects, but affects early processing stages.

In sum, these findings have exploited the high resolution of adjustment tasks, in which the stimulus and responses are sampled in quasi-continuous space, to reveal fundamental and consistent aspects of serial dependence. These include the effect of the similarity between current and prior stimuli, the co-existence of multiple and even opposing biases, the temporal decay of serial dependence, and, importantly, the dependence of the bias on how the previous stimulus is perceived, remembered and eventually reported.

Forced-choice tasks

Disentangling whether serial dependence occurs in perception or at some later, decisional or memory stage is challenging. Adjustment tasks, for instance, involve both perceptual and post-perceptual aspects —i.e., the stimulus must be held in memory for the time required to adjust the response and the reproduction response requires a post-perceptual decision about the stimulus feature. A more direct test of perception would be to use forced-choice tasks where influences of post-perceptual factors, such as the post-stimulus retention time, are minimized. As an example: an *inducer* stimulus might be presented at one location and subsequently, two stimuli appear, one at the location of the inducer, the other at a neutral location. Asking observers to compare a feature of the two stimuli can reveal whether the inducer has changed the perceived features of the stimulus (see Figure 2B).

In Fischer and Whitney (2014), the inducer was one of two simultaneously presented Gabors. Observers were cued to reproduce the orientation of this Gabor in a typical adjustment task. On each trial, the adjustment response was followed by the presentation of two additional

Gabors, and observers were forced to choose the Gabor that was oriented more counterclockwise. 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). Using a very similar paradigm, however, Fritsche and colleagues (Fritsche et al., 2017) found that the stimulus at the previous location caused a *repulsive* bias upon the perceived orientation of the subsequent Gabor, in tasks where forced choices involved both comparative (e.g., which one is more clockwise?) and equality judgments (e.g., is their orientation the same?). Cicchini and colleagues (Cicchini et al., 2017) failed to replicate this repulsive effect but found an attractive bias when the inducer was oriented 5° away from the current stimulus (instead of 20° as in Fritsche et al., 2017).

As with adjustment tasks, forced-choice tasks have been used to study the influence of prior stimuli and responses. Pascucci and colleagues (2019) have shown that even a choice made in the absence of any sensory stimulus (e.g., pure noise), can alter the sensitivity in a future perceptual task. In Feigin and colleagues (Feigin et al., 2021), prior choices about the location of a stimulus biased current location judgments, independently of changes in the stimulus color or the response keys. Conversely, prior choices about the stimulus color did not affect current location judgments, even if the two responses involved the same response keys. Feigin and colleagues (2021) concluded that serial dependence is strongly influenced by the task relevance of a visual feature and driven by prior choices, rather than the stimulus itself. Similarly, Zhang and Alais (Zhang & Alais, 2020), showed that the stimulus *percept*, rather than the physical stimulus per se, attracts subsequent perceptual choices, whereas the motor response might even produce a repulsive effect. The authors also focused on the source of inter-individual variability in serial dependence, an aspect evident in adjustment tasks as well (Bliss et al., 2017; see also Figure 2C), and found that some subjects rely more on prior stimuli but others on prior responses (Zhang & Alais, 2020). While, collectively, these studies indicate a clear involvement of prior choices and post-perceptual decisions in serial dependence, there is also evidence of a pure stimulus effect, independent of choice and response, as shown by Fornaciai and Park (Fornaciai & Park, 2018a) in a forced-choice numerosity task where the inducer stimulus required no task.

Forced-choice paradigms have also revealed how different aspects of stimulus history can lead to opposite biases. Alais, Leung, and Van der Burg, (Alais et al., 2017) tested forced choice of motion direction, finding positive serial dependence for motion and a simultaneous repulsive effect due to orientation signals arising from motion streaks. Taubert and colleagues

(Taubert, Alais, et al., 2016) reported strong positive serial dependence for gender but repulsive effects for facial expression, arguing that perception integrates temporally stable attributes (gender), but segregates changeable ones (expression).

In contrast to adjustment tasks, forced-choice tasks involve binary responses with a reduced number of stimulus categories and there seems to be little one-to-one correspondence between the effects reported with one and the other method, particularly in the domain of visual orientation. For instance, in forced-choice tasks, serial dependence is maximal for Δ's of 5-10°, while it is absent or repulsive for Δ's of 20°; in adjustment tasks, the peak bias towards the previous stimulus is usually at around 20°, and much smaller for 5° (Cicchini et al., 2017; Fischer & Whitney, 2014; Murai & Whitney, 2021). In other studies, however, serial dependence in forced-choice tasks occurs even for Δs larger than 30° and beyond the range found in adjustment tasks (Zhang & Alais, 2020). These discrepancies may simply reflect different tasks and paradigms, but they also raise the important question of whether the effects reported with one method versus another truly and unequivocally reflect the same cause. A potential method to resolve these discrepancies could be to design adjustment and forced choice tasks that are fully comparable within the framework of signal detection theory (see for example Tomassini et al., 2010). It seems likely that serial dependence is shaped by the task type, whether the task involves perceptual or post-perceptual processes and whether the critical dimensions are categorical or continuous. One potential explanation is that the influence of prior events depends on the 'narrative' imposed by the task: when there are only two categories, the bias is due to the stimulus category (or choice) on the preceding trial; when stimuli vary along a continuum, the bias becomes more fine-tuned to gradual differences between stimuli.

Classification

Another family of paradigms can be broadly pooled under the term "classification" tasks. Classification tasks are extensions of forced-choice methods, where more than two stimulus categories are available for choice or considered in the analysis. Manassi, Kristjánsson & Whitney (2019) used a 3-alternative image classification task involving a simulated visual search task reminiscent of medical image search. They created 48 morphs between three random shapes and found that shape classification was strongly influenced by recent visual stimuli, with a 7% increase in errors towards the previous image. Murai and Whitney (2021) used a reverse correlation technique with classification images. A high-contrast clockwise or counterclockwise inducer Gabor was presented before the appearance of a low-contrast Gabor embedded in noise, or a noise image alone. By recovering the internal template used for deciding whether a Gabor was present or absent, Murai and Whitney found a bias in the template toward the orientation of the preceding, irrelevant high-contrast Gabor. These findings indicate that serial dependence adapts to the paradigm at hand, revealing potentially maladaptive biases (e.g., a bias in search tasks akin to medical image search; but see Beckstead et al., 2017) and biased internal decision templates.

Post-cueing paradigms

A defining feature of serial dependence is the direction and temporal order of events: a stimulus presented in the past exerts an effect on the present, not the other way around (see Box 1). However, attractive and repulsive biases can also be found when the order of events is inverted: a later stimulus influences decisions on a preceding one. In Fornaciai and Park (Fornaciai & Park, 2020b), multiple stimuli were memorized on one trial and a post-cue indicated the relevant one. They showed that a future stimulus can cause systematic biases in the judgment of a preceding stimulus, very similar to serial dependence effects. This may suggest that serial dependence is simply a form of memory interference, and that event order is not crucial. However, a key difference is that standard serial dependence paradigms do not require active working memory maintenance and the ‘inducer’ stimulus, always presented in the past, becomes irrelevant in the present.

In a study by Czoschke and colleagues (Czoschke et al., 2019), participants memorized two consecutively presented clouds of drifting dots and were subsequently cued to report the drift direction of the first or second cloud. The biases were repulsive from the drift direction memorized within trials, but attractive from those memorized on preceding trials. This argued for positive serial dependence across-trials, and repulsive serial dependence within-trials, compatible with repulsive interference between simultaneous working memory representations. Fischer and colleagues (Fischer et al., 2020) then demonstrated that across-trial serial dependence can be affected by task-relevant contextual features, such as the color or serial position indicated by a post-cue (see also Section 4.2).

In general, while post-cueing paradigms deviate from the typical approach of measuring serial dependence with a single stimulus on each trial, they are powerful tools to understand how stimulus information is bound together within and across memory episodes.

Box 2.

Neural correlates of serial dependence

Functional Magnetic Resonance Imaging (fMRI)

Compared to the vast amount of behavioral work, only a few studies have been performed on the neural underpinnings of serial dependence. In one of the first, Schwiedrzik and colleagues (Schwiedrzik et al., 2014) used fMRI in a task with multistable stimuli to disentangle the effects of perceptual hysteresis (e.g., positive serial dependence) from those of adaptation. They found that these two opposite biases, revealed in many other following works, as we discuss in this review, reflect distinct neural circuits: hysteresis 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 adaptation is restricted to activity changes in early sensory areas.

In a later study, John-Saaltink and colleagues (John-Saaltink et al., 2016) demonstrated that prior stimuli modulate activity in early sensory cortex, with an effect highly specific to V1. Notably, the effects were not due to the prior stimulus itself but to the reported stimulus even on error trials, where the reported stimulus did not match the physical one.

Within the Bayesian framework, van Bergen and Jehee (van Bergen & Jehee, 2019) used fMRI decoding techniques to decode representations of sensory uncertainty in probabilistic distributions derived from population-level activity. They found that the uncertainty decoded from the activity in the early visual cortex can be related to the strength of serial dependence, showing that, at least when comparing the relative uncertainty between two trials (e.g., high to low and low to high), the behavioral bias reflected optimal cue combination (larger serial dependence when the sensory uncertainty decoded on the previous trial was lower).

Electroencephalography (EEG) and transcranial magnetic stimulation (TMS)

Leveraging the high temporal resolution of EEG, other works have investigated the electrophysiological correlates and temporal dynamics of serial dependence. Several 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 & Park, 2020a). An important finding comes from the work of Barbosa and colleagues, which demonstrated that latent traces of prior stimuli can be reactivated by the onset of a new event (e.g., the start of a new trial), likely causing interference with the representation of a new stimulus and serial dependence effects (Barbosa et al., 2020; Stein et al., 2020). Using TMS, these authors also provided evidence for a causal link between the reactivation of memory traces in the prefrontal cortex and serial dependence in behavior (Barbosa et al., 2020; see also Neto & Bartels, 2021).

Key factors determining serial dependence

Stimulus parameters

Section 2 demonstrates that serial dependence can seemingly occur in virtually any visual task, with different stimuli and processing demands. But a few key parameters can be considered necessary and sufficient: 1) the stimulus on the present trial should be weak, uncertain, and briefly presented; 2) stimulus duration and strength on the preceding trial must be controlled to minimize visual adaptation and negative aftereffects; 3) visible trails or after-images of the previous stimulus must be avoided (e.g., with backward masking); 4) serial dependence is typically stronger when the previous stimulus is attended to and task-relevant (but see Fornaciai & Park, 2018a); 5) the distance between previous and present stimuli on the dimension of interest (e.g., orientation) must be relatively small.

Uncertainty

Serial dependence is strongly influenced by uncertainty in the task. Uncertainty is inversely related to the stimulus duration, contrast, spatial frequency, and visibility (Ceylan et al., 2021; Cicchini et al., 2018; Manassi et al., 2018; Pascucci et al., 2019), but can also be modulated by the internal states of the observer, independently of the stimulus, such as performance confidence (Samaha et al., 2019; Suárez-Pinilla et al., 2018) and the focusing of attention (Fischer & Whitney, 2014; Fritsche & de Lange, 2019; Rafiei, Hansmann-Roth, et al., 2021).

It is generally agreed that serial dependence, particularly the positive form, increases when uncertainty is high. However, exactly how uncertainty modulates the effects of prior stimuli is still debated. For instance, a few models of serial dependence based on Bayesian and ideal observer principles, predict that the effect of uncertainty depends on the previous trial — when the preceding stimulus is reliable and the present one is not, the bias towards the past is stronger, following classic models of optimal cue integration and Bayesian principles (van Bergen & Jehee, 2019; Cicchini et al., 2018; Knill, 2007; Körding & Wolpert, 2006). But studies testing the effect of relative uncertainty have reported increased serial dependence for both spatial frequency and noise (Ceylan et al., 2021; Cicchini et al., 2018; Gallagher & Benton, 2022) when the *present* stimulus is uncertain, independently of the uncertainty of the previous one.

Several potential explanations for this still await to be fully explored (Ceylan et al., 2021; Gallagher & Benton, 2022). For example, the uncertainty in the previous stimulus might deteriorate with time, leading to broadly tuned priors or 'decisional templates' that are uninformative about previous uncertainty. When these broad priors are combined with the current stimulus, the effects depend mostly on the uncertainty in the current stimulus.

Attention

Another important aspect to consider is top-down processing. While some studies have revealed serial dependence with virtually no task, by simple exposure to a series of stimuli (Fornaciai & Park, 2018a; Murai & Whitney, 2021), it is nevertheless clear that attention plays an important role.

Initial evidence for this comes from Experiment 4 in Fischer and Whitney (2014), where 8 Gabors were presented on a circle and one was pre-cued for attention. When the attended location was constant between trials, there was positive serial dependence but not when the cued location changed, and the effects decreased as the distance between attended locations increased. Crucially, the direction of serial dependence was reversed for non-attended locations—i.e., a repulsive bias (Fischer & Whitney, 2014).

For feature-based attention, Fritsche and De Lange (2019) demonstrated that serial dependence in orientation is drastically reduced when attention is directed to the size and not the orientation of the stimulus. Attentional modulations may also partly explain results from 'sequential no-report' paradigms, where sequences of non-reported stimuli may be given less attention, leading to repulsive rather than attractive serial dependence (Pascucci et al., 2019; Pascucci & Plomp, 2021).

A complementary question is how serial dependence affects attention. This has been addressed with visual search tasks. In Collins (Collins, 2020), the detection of an orientation singleton was affected by whether serial dependence pushed the representation of the singleton toward or away from the distractors presented in the same display. Rafiei and colleagues (Rafiei, Hansmann-Roth, et al., 2021) assessed serial dependence due to recently ignored distractor stimuli, showing that prior non-attended items lead to a repulsive bias upon current visual targets. Conversely, attended items led to attractive biases. Notably, this was not only seen for visual search targets but also in the representation of a single stimulus presented after the search had been performed (Rafiei, Chetverikov, et al., 2021).

Taken together, studies on the role of attention suggest that positive serial dependence requires top-down attentional processing, and that attention may ‘gate’ whether serial dependence is positive (for previously attended items) or negative (for previously unattended items).

Processing stages

A contentious issue has been whether serial dependence reflects effects upon perception or whether they are higher-level, related to decisional processes or working memory. While Fischer and Whitney (2014) initially suggested that positive serial dependence occurs as early as primary visual cortex, several findings indicate that the bias might originate at later processing stages, which involve visual awareness (Kim et al., 2020), attention (Fischer & Whitney, 2014; Fritsche & de Lange, 2019), decisions (Feigin et al., 2021; Pascucci et al., 2019) or working memory (Bliss et al., 2017; Fritsche et al., 2017). While these latter studies point to the involvement of top-down aspects related to the task at hand, there is also evidence of serial dependence with no explicit task (Fornaciai & Park, 2018a; Murai & Whitney, 2021), which suggests that, under some circumstances, the effect can be ascribed to purely ‘bottom-up’ perceptual history.

Notably, even if serial dependence originates at late processing stages, it could still affect early processing stages — e.g., by altering the phenomenological appearance of stimuli. Several results are consistent with this. Cicchini and colleagues (2020) showed that serial dependence may act before spatial context effects (e.g., the spatial tilt illusion), which are typically assumed to arise relatively early in visual processing. In line with this, many top-down effects have been claimed to penetrate perceptual processing (Firestone & Scholl, 2014) making such late-to-early history effects feasible. However, as the majority of studies have used adjustment tasks that are prone to many sources of biases (see Section 2.1), any consensus on the phenomenological consequences of serial dependence, particularly in the context of adjustment tasks, has yet to be reached.

A related question is to what extent prior and present representations at multiple levels interact (Trapp et al., 2021). For example, Ceylan, Herzog, and Pascucci (2021) have shown that serial dependence can occur for elementary visual features with completely distinct stimuli (e.g., the scenario in Figure 1E), suggesting that the bias may also involve relatively abstract representations, independently of the continuity of stimulus identity —i.e., orientation might be commonly represented as a tilted line, even if it belongs to different visual objects (Ceylan et al., 2021; Kwak & Curtis, 2022). Crucially, when serial dependence is observed for low-level features belonging to different visual objects, there are two candidate explanations: this might reflect perceptual history effects at low-level processing stages, independently of the object (Goettker & Stewart, 2022), or effects of high-level representations that reflect how information is maintained in working memory (Kwak & Curtis, 2022). In other words, the orientation of a current stimulus may be biased toward the orientation of a perceptually distinct previous stimulus, because the bias occurs at early orientation processing levels (e.g., V1) or because 'orientation' is the relevant feature and can be represented as a single line. Disentangling these two possibilities or understanding their reciprocal contribution to serial dependence is a key future step.

More generally, the variety of existing paradigms and findings indicate that serial dependence is a multifactorial phenomenon, where prior perception, memory, decision-making, as well as the specific requirements of the task, conjointly influence decisions about current stimulus features.

Retinotopy

Different stages of visual processing have been related to different levels of retinotopy. For example, many adaptation and negative aftereffects are retinotopic so that the adapter and test stimulus must be at very similar locations (Boi et al., 2011). Similarly, feature integration has been long assumed to occur in retinotopically organized feature maps (Treisman & Gelade, 1980; but see Boi et al., 2011).

Several studies have reported a broad tuning of serial dependence in retinal coordinates, spanning more than 15° of the visual field. That is, the previous stimulus continues to influence current decisions even when the current stimulus is 15° away, but the effects decrease with distance. Collins (Collins, 2019) presented a Gabor stimulus at various locations and manipulated the spatiotopic and retinotopic reference frames. In the key manipulation, observers had to saccade toward the new location of a fixation spot presented before the stimulus. In one condition, the Gabor was presented at the same location as on the previous trial, but the retinal location changed because of the saccade (spatiotopic). In another condition, both the saccade and the stimulus landed in a new position that matched the previous Gabor location in retinotopic, but not spatiotopic coordinates (retinotopic). Collins (2019) found that serial dependence was stronger in the retinotopic condition, consistent with the broad tuning of the ‘continuity field’ proposed by Fischer and Whitney (2014), and mirroring receptive fields in higher-level visual areas, such as the inferior temporal cortex. Mikellidou and colleagues (Mikellidou et al., 2021) asked observers to perform an orientation reproduction task under two conditions, either with their head fixed (egocentric condition) or tilting their head by 40° before stimulus appearance (allocentric, e.g., world-centered condition). When the egocentric and allocentric coordinates were in conflict, serial dependence was mostly allocentric. So, while these two studies are seemingly in conflict, they support the initial findings of Fischer and Whitney, involving both retinotopic and allocentric tuning. A potential explanation is that whether serial dependence is retinotopic or spatiotopic might depend on the fast time scale of spatial remapping during saccades compared to the slow remapping during yaw rotations (Mikellidou et al., 2021). Another possibility is that feature integration shifts towards non-retinotopic processing for integration over relatively long timescales (Wutz et al., 2016). Collins (2019) also argued that the spatial tuning window of serial dependence might be broader than initially claimed (e.g., 22°), which may explain the lack of any spatial tuning in studies presenting the stimuli 10° apart (Fritsche et al., 2017).

Opposite directions

The studies reviewed above have revealed both repulsive and attractive serial dependence. These opposite biases occur both from single stimuli in the past, and from stimuli at multiple time scales.

For effects of a single stimulus in the immediate past, there are reports of repulsive biases only (Bae & Luck, 2019, 2020; 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, 2019; Rafiei, Chetverikov, et al., 2021; Rafiei, Hansmann-Roth, et al., 2021; Stein et al., 2020).

Some studies suggest that negative biases dominate when previous stimuli are not attended (Fischer & Whitney, 2014) or task-irrelevant (Pascucci et al., 2019; Pascucci & Plomp, 2021), and when increased duration and strength promotes negative adaptation-like aftereffects (Bliss et al., 2017; Fischer & Whitney, 2014; Manassi et al., 2018). Other work indicates that direction may depend on proximity in feature space, with positive serial dependence when the stimuli are similar and negative biases when they differ (Fritsche & de Lange, 2019; Rafiei, Chetverikov, et al., 2021; Rafiei, Hansmann-Roth, et al., 2021).

Recent models of serial dependence argue that the two biases reflect effects at different processing stages (Fritsche et al., 2020; Pascucci et al., 2019), broadly described as lower-level (repulsion) and higher-level (attraction). These stages involve different temporal dynamics: perceptual decisions are attracted towards the most recent history (e.g., a few seconds in the past), whereas perception is systematically repelled away from more remote history (e.g., minutes in the past) (Fritsche et al., 2020; Gekas et al., 2019; Pascucci et al., 2019). Ultimately, these opposing biases interact, leading to classic patterns, where attraction for small stimulus differences is accompanied by repulsion for larger differences (Figure 3). Repulsive biases may reflect long-lasting visual adaptation, while attractive biases may reflect higher-level processes, such as decision inertia or working memory interference (Fischer et al., 2020; Fritsche et al., 2017, 2020; Pascucci et al., 2019). While this is supported by the higher spatial tuning and task independence of negative biases, in line with typical adaptation effects (Fritsche et al., 2020; Pascucci & Plomp, 2021) the exact nature of these biases and their involvement in different tasks are still debated. Alternative explanations involve repulsive biases that may arise from the active removal from working memory of information that is no longer relevant (Shan & Postle, 2022) and the use of prior stimuli as a reference for current decisions (DeCarlo & Cross, 1990; Stewart et al., 2005).

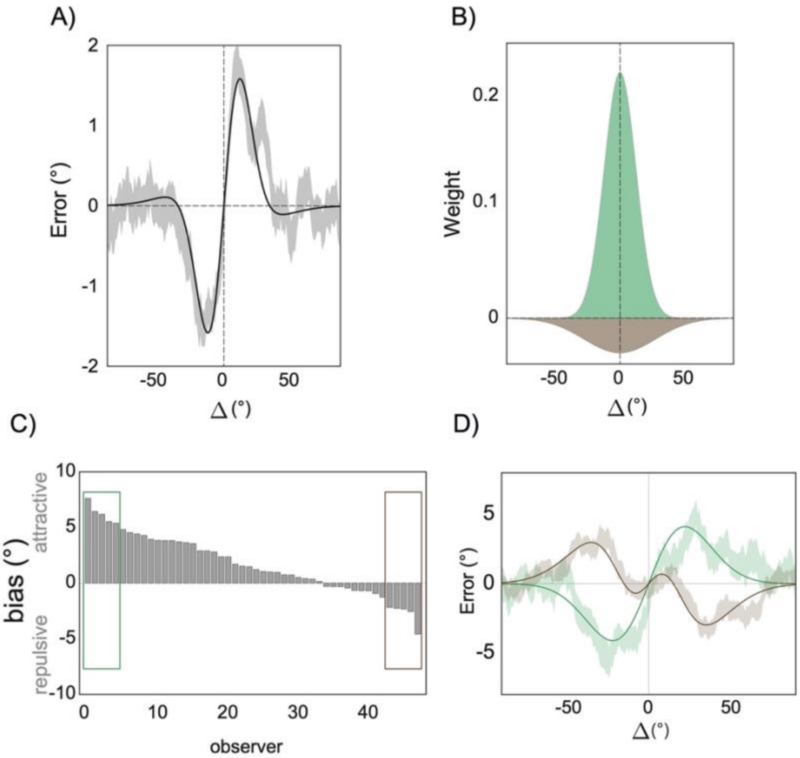

Figure 3. Contrasting forces in serial dependence. A) Serial dependence is typically positive when the difference between the previous and present stimulus is small, and slightly negative when the difference is large (Δ, here indicating the difference in orientation between the previous and present stimulus, data are from 48 subjects performing an orientation adjustment task with low spatial frequency Gabors (Ceylan et al., 2021). B) The coexistence of these two opposite biases can be modeled as the additive effect of a weighting function narrowly tuned toward the recent past (the green distribution) and one more broadly tuned away (the brown negative distribution). If observers weigh the previous stimulus according to the two distributions, the resulting pattern resembles A). C) Inter-individual variability in the dominance of the positive and negative components of serial dependence. Typically, the positive bias dominates; some subjects, however, show no bias or only negative serial dependence. D) Two curves with a difference of Gaussian fit depicting the pattern for the top 5 observers showing positive serial dependence (green, corresponding to the green square in C)) and the top 5 observers showing only negative biases (brown, corresponding to the brown square in C). The proportion of subjects showing positive serial dependence in this dataset is 70% with an effect size of *d'* = 0.63 (Cohen's d).

The problem of object continuity

Object continuity

If serial dependence is involved in maintaining perceptual continuity, there must be a way of solving the problem of "what matches what" from one view to the next: Do feature A at time *t* and feature B at time *t+1* belong to the same object?

Spatiotemporal correlations among multiple features are crucial for object continuity (Treisman & Gelade, 1980): without binding features that covary in time and space, we would clumsily fail in any object discrimination and recognition tasks (Kahneman et al., 1992). Many studies have shown that serial dependence is larger when two visual features are similar and close in space and time. This has fostered the notion that serial dependence is strictly related to object processing and the spatiotemporal feature correlations that define object continuity. However, a key question is whether serial dependence is *causal* to or *contingent* upon the experience of object continuity.

Collins (2021) proposed two possible scenarios. Firstly, object features may be bound in visual working memory, and serial dependence operates on "object-level" representations and is therefore object-selective (see Figure 1D). A second option is that serial dependence operates directly on elementary features. In this scenario, the visual system assumes that similar features in close spatial and temporal proximity belong to the same object. Both scenarios overlap with the definition of the continuity field (Fischer & Whitney, 2014) as a mechanism that promotes the continuity of object representations by smoothing over spurious changes in object features —changes that *generally* do not reflect an object change. Yet, the first possibility implies no direct causal role of this mechanism in object continuity: to operate on "object-level" representations, object identity must first be established, at each time point —i.e., serial dependence is contingent on object continuity. The second possibility instead advocates a causal role, as the experience of object continuity depends on how the visual system combines elementary features and infers their common sources over time. The paradox, however, is that in this latter scenario serial dependence does not need to be contingent on object continuity and may occur for similar visual features that belong to different objects (see Figure 1C and 1E).

How features are integrated into object representations is a fundamental question in perception. The link between serial dependence and object continuity may provide new insights into this relationship. But this involves a chicken-egg problem since it is difficult to separate the definition of a "visual object" from the definition of serial dependence: if objects are temporally continuous in terms of locations and features, how can we distinguish whether serial dependence operates on object-level representations or on spatially and temporally similar visual features, which tend to be an object in the first place?

In the following sections, we describe several approaches to this question, by testing the role of feature similarity (Section 4.2), feature conjunctions (Section 4.3), and object identity (4.4).

Feature similarity

Work on serial dependence has tended to focus on how prior visual features influence the judgment of current ones. What we mean by ‘feature’ is any property of a stimulus that can be quantified along a single dimension. This includes elementary features typically used in vision research, such as orientation, motion, or size, but also more complex and abstract properties such as facial emotions and attractiveness. In all these cases, features —and related judgments— can vary in quasi-continuous space (e.g., the full circle for circular features, a linear continuum for size). This quasi-continuous space provides a high-resolution sampling of perceptual biases, which can reveal mixtures of attractive and repulsive biases and their relation to proximity in feature space.

Serial dependence in judgments about visual features is well established (Section 2). The effects show systematic tuning in feature space: errors tend to be more biased toward prior features when the difference between the previous and current feature is small —the effect of feature similarity or proximity. Several studies, particularly using orientation, have also shown that, as the distance between features increases, the bias reverses, becoming repulsive. For example, Fritsche and de Lange (2019) reported that typical positive serial dependence for small orientation differences between inducer and test is accompanied by a smaller repulsive bias for orientation differences larger than 45-50° (see also Bliss et al., 2017 and Figure 2). Similar patterns have been reported in studies manipulating task relevance and attentional roles of inducers (Rafiei, Chetverikov, et al., 2021; Rafiei, Hansmann-Roth, et al., 2021).

The presence of both attractive and repulsive biases can have at least two explanations. One involves mechanisms that simultaneously push decisions toward prior similar features and away from different ones —a behavior reminiscent of excitatory/inhibitory activity in working memory circuits (Stein et al., 2020), another, the coexistence of positive serial dependence and adaptation-like negative aftereffects (Fritsche et al., 2017, 2020; Pascucci et al., 2019; Pascucci & Plomp, 2021). Note that, to generate typical serial dependence patterns (Figure 2A-B), the repulsive component should be more broadly tuned than the attractive one, and we believe that this aspect is an interesting topic for future research. Another explanation is that these feature space effects depend on the ‘objecthood’ assigned to a given feature change (Liberman et al., 2016; Pascucci & Plomp, 2021): when two features presented at consecutive moments are similar enough, the perceptual system integrates them into an object. Conversely, when the change is sufficiently large, they might be differentiated as separate objects.

Feature similarity effects may reveal the resolution with which the perceptual system can distinguish changes in a visual feature. However, a clear understanding of the mechanisms that lead to this mixture of positive and negative biases, and their relation to object processing is still lacking. Manipulating a single feature cannot provide a conclusive answer, as effects of feature similarity can also be found when objects change (Ceylan et al., 2021). Future research should look at whether feature tuning is affected, for instance, by the interval between trials, since the expected feature variability of an object might depend on time.

Feature conjunctions

Another approach to addressing the relation between serial dependence and object processing is to manipulate conjunctions of features: objects are, by definition, made up of multiple features that covary in time and space.

A straightforward way to test the role of feature conjunctions is to include changes in a ‘context’ feature— in tasks that involve the judgment of another feature (the ‘content’ feature). So, in tasks requiring the judgment of visual orientation or direction of motion (content feature), the stimuli may change color (context feature). Several studies have shown that when context changes are task-irrelevant, serial dependence is unaffected by the context feature: decisions on the current orientation are biased towards prior stimuli, independently of color changes in the stimulus. Assuming that irrelevant features still define object identity in the natural world, these results indicate that serial dependence occurs at a more abstract level of representation than the one where features are integrated (Figures 1C and E).

Studies using post-cueing have, however, revealed that context features can modulate serial dependence, depending on task relevance (see Section 2.4). In Fischer and colleagues (2020), two clouds of moving dots with different colors were presented on each trial, one after the other. A post-cue indicated the color (or the serial position) of the cloud for which participants should reproduce the motion direction. Between trials, serial dependence was largest for stimuli with a matching context feature (e.g., same color, same serial position), but, crucially, only if the context feature was task-relevant (if color was the cued feature to indicate the relevant dot cloud). In other experiments, changes in spatial and, to a lesser extent, serial position affected serial dependence even if these changes were task-irrelevant, suggesting that spatial and serial position might be more automatically integrated into object representations in working memory. Recent work by Houborg and colleagues demonstrates, however, that unless required by attention set and task context, serial dependence is independent of the integration of elementary visual features into objects, or content-context integration (Houborg et al., submitted). In this study, serial dependence in orientation occurred irrespective of changes in the color of stimuli and even when participants were explicitly asked to discriminate the stimuli based on their color.

Collins (2021) found that serial dependence in shape judgments occurred despite changes in the orientation of the object, but was larger if the orientation of the object was constant. The same pattern was found when facial emotional expressions were the content feature and identity was the context feature: serial dependence occurred regardless of identity but was larger when identity on the current and previous trials matched. Consistently, Taubert, Van der Burg and Alais (Taubert, van der Burg, et al., 2016) tested a paradigm reminiscent of online-dating applications finding that serial dependence in attractiveness judgments of faces was larger when the orientation (upright or inverted) of the face was the same on consecutive trials. Also, Liberman and colleagues (2018) suggested that serial dependence in emotional expression judgments was selective for gender but not ethnicity, suggesting that gender differences create larger dissimilarity between faces than ethnicity (at least for their face stimuli).

Manipulations of feature conjunctions have yielded a wide spectrum of results suggesting that, while not being a prerequisite, effective continuity in feature conjunctions can modulate serial dependence. Serial dependence may therefore occur both at the level of individual features and for objects with integrated features and the particular task demands might determine which pattern occurs (Collins, 2021). Furthermore, serial dependence for feature conjunctions may also depend on whether the context feature is completely task-irrelevant or can interact with the processing, and the relevance of the content feature.

These results suggest that serial dependence is not necessarily contingent on object continuity since it occurs even when the secondary features of an object change. But they also suggest a potential causal role: serial dependence reflects the binding of sequential instances of the same feature in close spatiotemporal proximity. While this might be directly related to the spatiotemporal correlations that characterize the features of the same object in the natural world, it might lead to idiosyncratic biases in empirical settings where serial dependence occurs despite changes in context features.

Object identity

In the studies above, object identity is generally defined by stimulus similarity (whether the consecutive stimuli share features). Other studies have investigated the effects of object identity without necessarily tying it to stimulus similarity.

For instance, the coherent behavior of objects passing behind occluders creates a strong sense of continuity (Carey & Xu, 2001; Spelke et al., 1995), a technique widely used in the film industry (called the "cowboy switch"). A stunt double performs a difficult action and then disappears behind an occluder, before being substituted by the original actor. This trick leads to the impression that the same actor did the whole scene. Leveraging this phenomenon, Liberman, Zhang & Whitney (Liberman et al., 2016) presented a sequence of Gabor stimuli on two sides of a rectangle. In one condition, the Gabor moved across the screen, passing behind the rectangular occluder with either a coherent or an incoherent trajectory. In another condition, the same Gabors were presented statically, one after the other, on either side of the rectangle. Perceptual decisions on the orientation of the final Gabor were influenced by the orientation of the preceding Gabor only when the motion of the Gabor was coherent so that it seemed to pass behind an occluder. This shows how object identity and continuity can be manipulated by exploiting the dynamics of real-world objects. This also shows that when object representations are established with real-world dynamics, serial dependence is contingent on object representations, rather than simple visual features.

As in the example above, testing the role of object identity goes beyond manipulating single features and feature conjunctions, but requires the representation of an object and its spatiotemporal properties. The studies described in Section 4.3, where complex stimuli like faces were manipulated, can also assess the effects of object identity. Indeed, what we call 'context change' is often a change in the face shown from one trial to another. Since faces are not easily reduced to low-level features and require holistic processing (McKone et al., 2001; Sigurdardottir et al., 2015), face changes can be considered changes in visual objects. As mentioned, these studies show that serial dependence occurs when objects are constant and the features change (e.g., for changes in the viewing angle of a face; Liberman et al., 2014), and even when there are major changes in the object itself (Ceylan et al., 2021).

Another potential 'litmus' test for the role of object identity is to keep the content feature constant while changing all other object features. For instance, Ceylan and colleagues (2021) found positive serial dependence for orientation judgments even when the stimulus changed in spatial frequency or changed *completely* (e.g., a Gabor stimulus turning into a symmetric dot pattern). Similarly, using naturalistic stimuli in virtual reality, Tanrikulu, Pascucci and Kristjánsson (Tanrikulu et al., 2021) showed that serial dependence in orientation judgments was the same whether an object (e.g., a regular toothbrush) was constant, or switched to another object within the same category (an electric toothbrush), or even to a different object from a different category (i.e., a sword). Goettker and Stewart (Goettker & Stewart, 2022) also demonstrated that serial dependence in oculomotor responses to dynamic stimuli occurs between completely different objects (moving car vs. blob). Finally, serial dependence can be found between sequential (i.e., number of events over time) and simultaneous (i.e., number of items in space) numerosity representations and between semantic (presenting a numeral) and simultaneous representations of numerosity magnitudes (Fornaciai & Park, 2022).

The results reviewed in sections 4.1-4.4 indicate that serial dependence occurs at many levels, from features independently of object identity, to objects, which can then affect features. However, the findings do not point to an unequivocal functional role for serial dependence in object processing and show that serial dependence might be modulated by, but is not necessarily contingent upon, object identity and continuity. As proposed by Houborg and colleagues (submitted), at least when observers have to perform a task, the perceptual system may operate by parsimony, summoning feature conjunctions and holistic processing only when strictly required by the task, while otherwise reducing the complexity of its representations to the lowest-dimensional format possible (e.g., representing features like orientation and motion direction as ‘tilted lines’ and discarding other features; Kwak & Curtis, 2022). This entails the prediction that the complexity of processing on the current trial determines the complexity of the information that propagates to the next trial.

Our review of the paradigms, findings and theoretical challenges of serial dependence has so far revealed a complex and multifaceted phenomenon. This can also be seen in the multitude of models that have been proposed in nearly a century of research. In the following, concluding part of this review, we will provide a general overview of the main modeling frameworks of serial dependence.

A brief history of research on history biases

The study of serial dependence has been accompanied by numerous conceptual and modeling accounts to explain the behavioral patterns and establish the inherent computational principles. Notably, old and new challenges echo one another. Some of the recurring questions involve the nature of repulsive and attractive effects, the relation of these biases to perception and working memory, the role of uncertainty, and the putative functional role in everyday vision. In this final section, we provide a brief overview of a century of models and frameworks of serial dependence, intending to look back to move forward.

Historical models

The classic laws of psychophysics have historically relied on a static relationship between stimulus and sensation (e.g., Weber's law). Some recognized the importance of sequential effects —the judgment of a sensation depends not only on the present stimulus but also on preceding events. Hence, alternative forms of psychophysical functions incorporated a dynamic component that could account for sequential effects in traditional magnitude scaling tasks. The approach involved finding a term that could complete a given psychophysical law (e.g., Stevens' power law; Stevens, 1957) with a temporal component (DeCarlo & Cross, 1990). Two effects were mostly considered: *assimilation* — a form of positive serial dependence, and *contrast* — a form of negative serial dependence. Their nature represented a point of divergence for different theoretical frameworks.

In the *perceptual/memory* model of sequential effects (Cross, 1973; DeCarlo & Cross, 1990) information about immediately preceding stimuli was incorporated in Stevens' power law, with a parameter determining the direction, attractive or repulsive, of the effect. The resulting equation could reflect either systematic influences of previous stimulus intensity on current perception (a purely proactive effect) or interference between current and prior perception in memory (Lockhead & King, 1983).

The models above sought to make psychophysical functions dynamic, echoing the intuition behind Helson's adaptation-level theory (Helson, 1948, 1964): Helson (1948) claimed that 'any momentary state of the system [represents] a quasi-stationary process in dynamic equilibrium' (p.298) and '[f]or every excitation-response configuration there is assumed a stimulus which represents the pooled effect of all the stimuli and to which the organism may be said to be tuned or adapted' (Helson, 1947, p.2).

Beyond systematic effects from previous stimuli, other models have focused on *response heuristics* in perceptual judgments. These models assumed that observers in psychophysical experiments tend to repeat previous responses under uncertainty (Garner, 1953; Ward & Lockhead, 1971). Forms of heuristics also include psychological phenomena where prior events are implicitly or explicitly used to predict the next outcome (Budescu, 1985; Kahneman & Tversky, 1972). Heuristics of this kind can induce biases where present stimuli are judged as similar to previous ones but different from more remote ones, under well-known fallacies (gambler's or hot-hand fallacies), where a structure is expected in random sequences —i.e., that after a few repetitions, a change is more likely. Response heuristics and perceptual/memory effects have been considered complementary components of sequential dependencies (DeCarlo & Cross, 1990).

Conceptually distinct accounts are based on the relativity of perceptual judgments (Stewart, 2007; Stewart et al., 2005). Judgments are always made about both immediate and long-term context: perceptual decisions are relative and rely on comparing successive stimuli. Trial history, therefore, affects the perceived distance between the present and the prior stimulus, leading to assimilative (attractive) or contrastive (repulsive) effects depending on stimulus similarity (Hsu, 2021).

Other frameworks, inspired by Thurstonian models, involve *criterion-setting* accounts. The assumption is that responses cause a momentary shift in the location of the response criterion along the stimulus continuum (Treisman & Williams, 1984). According to an influential model of this sort, criterion shifts are mediated by two opposite mechanisms that operate under adaptive principles based on the non-randomness of real-world events. The *tracking* mechanism relies on the fact that prior perceptual judgments reflect the best guess about the current state of the world. Consequently, prior responses shift the criteria to facilitate the repetition of prior observations, leading to positive serial dependence. The *stabilization* mechanism relies on the fact that the non-randomness of external events is typically short-lasting, and as the interval increases, the present stimulus becomes less likely to be similar to the past one, causing negative serial dependence (Hsu, 2021; Treisman & Williams, 1984).

Despite clear differences between these models, they face the same challenge of dealing with: 1) two, potentially simultaneous but opposing mechanisms causing attraction/assimilation and repulsion/contrast; 2) multiple stages, from early perceptual effects to higher-level effects due to memory and decisions, an aspect usually reflected, but not fully captured, in the classic dichotomy between *stimulus* and *response*; and 3) the functional role of these opposite biases.

Recent models

The recent interest in serial dependence has seen the rise of new models grounded on more contemporary theoretical and computational frameworks, focusing mostly on modeling results from adjustment tasks with circular features, like orientation or motion. The modeling, therefore, differs from studies with magnitude scaling, absolute judgments, identification, and categorization. Additionally, the mechanisms behind sequential biases may differ between linear or circular stimulus spaces and prothetic or metathetic continua. Nevertheless, important commonalities have emerged. These recent models can be broadly distinguished by whether they rely on *mechanistic* principles and *hardwired* components, *cognitive/perceptual architectures*, or *rational* principles.

Mechanistic models

The labeled-line population coding model of serial dependence originally proposed by Fischer & Whitney (2014) belongs to the first category. In this model, positive serial dependence is implemented as a change in the response gain or shift in the tuning function of a population of low-level visual neurons encoding orientation information —i.e., a mechanism *hardwired* in early visual processing. A labeled-line orientation model is composed of a set of neurons "voting" for their preferred orientation and generating a population response profile whose mean or maximum represents the 'perceived' orientation. The Gain model involves a phasic gain increase in the response of previously stimulated neurons which bias their individual and population response to the present stimulus. This model expresses the core idea behind the 'continuity field': a mechanism that binds information based on feature similarity, spatial proximity, and (relatively long) time intervals, by temporarily increasing the receptivity of visual neurons responding to specific features and objects (Fischer & Whitney, 2014).

Other examples of mechanistic models come from the perspective of serial dependence as a visual memory effect, suggesting that hysteresis in perceptual decisions arises from the interplay between activity-based and activity-silent neural states in working memory. According to the bump-reactivation hypothesis (Barbosa et al., 2020; Stein et al., 2020), neuronal activity from preceding trials remains imprinted in synaptic connections as activity silent states in the prefrontal cortex. In close analogy with the principle behind sonar and echolocation (Wolff et al., 2017), a new sensory impulse reignites these hidden states, causing an ‘echo’ of past activity patterns in the processing of new sensory information (Bae & Luck, 2019).

Cognitive/Perceptual architectures

Models based on *cognitive/perceptual architectures* have been proposed to account for the coexistence of attractive and repulsive serial dependence. These models typically employ a simple two-stage architecture of encoding and decoding. The *Two-process* model represents the first example where a simple two-layer neural network generated data consistent with simultaneous negative and positive serial dependence (Pascucci et al., 2019). A low-level input layer resembling a neural population selective to basic visual features is followed by a readout layer decoding the input. Serial dependence emerges from short-term plasticity and slowly decaying weights in synaptic connections amongst the layers, introducing bias and inertia in the decoding of sequential sensory signals (Ceylan et al., 2021; Pascucci et al., 2019). This model is agnostic regarding the computational goals of this bias but assumes a form of neuronal adaptation causing repulsive biases at lower stages.

Rational models

Rational models of serial dependence embed explanatory and generative models with the computational goal of optimality and Bayesian principles. Cicchini and colleagues (Cicchini et al., 2018) proposed an Ideal Observer model where serial dependence follows the rules of optimal cue integration: previous and present stimuli are combined according to their relative uncertainty, with reliable stimuli weighted more highly than unreliable ones. A related approach is the probabilistic model of van Bergen and Jehee (van Bergen & Jehee, 2019) which incorporates an internal model of the transition distribution of natural orientation changes in a Bayesian model where prior and present stimuli are optimally combined. Similarly, Kalm and Norris (Kalm & Norris, 2018) proposed a Bayesian filter where current decisions combine information from present stimuli and a mixture of prior states, taking into account more than one trial in the past. This line of modeling makes the computational goal of serial dependence explicit: to use prior sensory input to optimize perception, reduce uncertainty, and minimize noise. A simplified version of these models, where only the uncertainty associated with the present (but not the previous) stimuli is taken into account, has recently been proposed to explain the lack of evident ‘optimal’ combination between consecutive stimuli (Ceylan et al., 2021).

Building on the models above, Fritsche and colleagues (Fritsche et al., 2020) combined a cognitive/perceptual architecture with rational and normative principles, formalizing a Bayesian and efficient observer model of serial dependence. As in previous attempts, this model embeds an encoding and a decoding stage. Efficient coding schemes at the encoding stage promote long-term repulsive effects where the encoding of a new stimulus feature is shifted away from the prevailing stimulus statistics over minutes in the past. An ideal Bayesian observer decodes the input from the encoding stage using the most recent stimuli as priors. Hence, both short-term attraction and long-term repulsion, originating at different stages of processing, contribute to the final decision. More recent work within Bayesian frameworks, suggests that interindividual variability in positive serial dependence might be due to different beliefs about the temporal statistics of the environment (Glasauer & Shi, 2022).

Discussion

Our aim was to provide a “state of the art” overview of serial dependence in vision, trying to highlight the main themes and identify critical future questions. A major challenge is that the findings do not paint a single clear picture and small tweaks to paradigms can cause serial dependence patterns to differ largely. For example, the peak biases and whether they are attractive or repulsive seem to differ by whether the tasks involve adjustment, forced choice, or classification. A key challenge is to try and determine what conditions cause what sort of serial dependence. Our hope is that our summary will help with identifying issues for further investigation.

We also highlight some theoretical problems inherent in the literature –serial dependence is assumed by many accounts to promote object continuity, but the level of representation involved, whether it is about features, objects, or abstract information, is still unclear. Eventually, perceptual decisions often deal with complex and manifold events, incorporating many levels, from physical aspects of the stimulus to abstract descriptors and categories. One possibility is that serial dependence operates opportunistically, depending on the circumstances and the requirements of the task. Hence, serial dependence may involve different levels of processing and may lead to biases with diverse characteristics in different tasks. Whether the bias occurs at the level of features, integrated objects, or more abstract representations, could depend on the most parsimonious representation that the brain can use to perform a given task.

Box 3.

Analysis methods for serial dependence

The analysis of serial dependence involves quantifying systematic relationships between the decision on the current trial and the history of events on preceding trials. The exact pipeline depends on the type of task and data (e.g., adjustment responses or forced choices). We here provide a brief description of standard approaches used in different contexts.

Adjustment tasks

For simplicity, we will use orientation adjustment tasks as an example, but the analyses described here equally apply to color, direction, or any other continuous stimulus.

Data preparation: adjustment errors are computed as the angular (or linear) difference between the reported and the actual orientation in each trial. Typically, adjustment errors are widely scattered. To correct for outlier errors and unlikely reports, a correction is often performed by removing trials according to an arbitrary cutoff (e.g., 30°; Cicchini et al., 2018), standard deviation-based thresholds (e.g., 3 sd; Fritsche et al., 2017), or other parametric approaches (e.g., Grubb's test; Pascucci et al., 2019). Adjustment times are also used to clean the data, for instance, by removing trials with responses faster than 500 ms or slower than 10 s (Ceylan et al., 2021). In some cases, the trial following an outlier (e.g., a guess), is also removed, since no meaningful serial effects can be expected following a trial in which the observer had a lapse of attention or guessed the response. An additional procedure is to demean the cleaned errors to remove systematic tendencies to reproduce the stimulus in one direction or another (e.g., CW or CCW). Because adjustment errors are prone to other sources of biases, including, for instance, anisotropies and category boundary effects in orientation estimation, some authors have usually corrected for non-linearities in the stimulus space (van Bergen & Jehee, 2019; Manassi et al., 2018; Pascucci et al., 2019). This has been done with different methods, from fitting sinusoidal to polynomial functions on the errors over stimulus space, to clean the data of biases, such as the cardinal or orientation bias and category biases in color space. Standard and validated approaches for this step have yet to be reached.

A largely unaddressed issue concerns the influence of swap errors on serial dependence. Swap errors refer to an observer reporting the wrong item in a working memory task. In serial dependence, an observer might report the previous instead of the current target, simply because of a 'swap' rather than a combination of the prior and current percept. Almeida, Barbosa & Compte (Almeida et al., 2015) reported that in a typical working memory task, swaps and attractive bias co-occur. As swap errors appear as a 100% bias, even a few swaps could create the appearance of spurious serial dependence.

Model fitting: the magnitude of the serial dependence in adjustment errors is computed by fitting the first derivative of a Gaussian function (abbreviated as DoG) to the errors as a function of Δ (the difference between the previous stimulus feature and the current one). The typical form of this function is:

$$y = \mathit{\Delta} awce^{-(w\Delta)^2}$$

where y is the adjustment error (single trial or averaged over trials and smoothed over Δ), α is the amplitude of the DoG curve multiplied by the constant $c = \sqrt{2}/e^{-0.5}$, which scales the amplitude to the curve peak in y units (e.g., degrees), and w is the inverse of the curve width. Note that, besides approximating the main pattern, the form of this function also reflects two important aspects of serial dependence, which can be decomposed into a linear component $\mathit{\Delta} a$, which implies a systematic relationship between errors and previous stimuli, and a Gaussian weighting component, centered on 0, which accounts for the fading of the relationship as $\mathit{\Delta}$ increases.

The most used parameter to determine the magnitude of serial dependence is the amplitude or half-amplitude of the DoG function (α). While this is usually estimated on the aggregate data of many subjects, to avoid the pitfalls of aggregated data, the DoG fitting procedure can be expanded to allow for variability between individual participants by fitting a mixed effects model (Pascucci et al., 2019). Another modeling approach is to fit a hierarchical Bayesian model to the data (Sadil et al., 2021). In this model, the authors accounted for individual differences and rotational biases as well.

As mentioned throughout the manuscript, serial dependence patterns also contain a combination of attractive and repulsive components, an aspect that simple DoG curves fail to capture. Alternative functions have been proposed to overcome this limitation (Bliss et al., 2017). Because of the putative nature of these opposite biases, a plausible approach would be to use the difference between two Gaussian functions, one accounting for the positive and one for the negative component (see Figure 3A-B) —i.e., the classic ‘Mexican-hat’ profile. This, however, would come at the expense of model complexity.

Model-free approaches: an alternative approach to model fitting is to compute the average error in a range of Δ values, typically close to zero. For example, subtracting the average error for Δ in the 1–25◦ range from the average error in the corresponding negative range (Samaha et al., 2019) quantifies the amount of systematic deviation of errors from zero —this deviation or ‘bias’ is positive for attractive serial dependence and negative for repulsion. This approach is a straightforward way of quantifying serial dependence with few assumptions, particularly useful when limited data points are available, which is often the case in analyses for a single observer. Restricting the analysis to values of Δ close to zero is reasonable when serial dependence effects are expected in this range. A disadvantage of this approach, which also applies to the DoG fitting procedure described above, is that it does not allow capturing more complex patterns across the entire Δ range. While attractive biases are typically present for small Δ, repulsive biases appear for larger Δ. One way to address this problem would be to use more than a single bin, discretizing Δ as a function of several distances between the previous and present stimulus (e.g., 3-4 bins from ‘close’ to ‘far’), then analyzing the data with standard repeated-measures approaches.

Statistical analysis
Statistical testing is commonly performed using a permutation approach on the parameter of interest, typically the half-amplitude α of the DoG function (Fischer & Whitney, 2014; Fritsche et al., 2017). A null distribution of α is obtained by fitting the DoG function to a large number of randomized datasets generated by randomly flipping the sign of errors in each trial (or shuffling the correspondence between single-trial Δ and errors). The proportion of such datasets that is more extreme than the parameters from the DoG function fitted to actual data denotes *p*, which can be interpreted in the same way as the p-value in standard frequentist statistics. Comparisons between conditions can be performed using a similar permutation approach by shuffling the labels of the conditions for each randomized dataset. This approach has been often used for aggregated data from multiple subjects. In the framework of non-linear mixed-model analysis, the final estimate of the parameters and their uncertainty can be used to quantify statistical significance (Pascucci et al., 2019).

Forced-choice
When the task involves a choice between two alternatives, results are typically analyzed using a psychometric function, in which stimulus value predicts response. Serial dependence can be quantified as a shift in the threshold or point of subjective equality (PSE) of the psychometric function. For example, in comparing which one of two stimuli is tilted more clockwise, the PSE corresponds to the point of ‘no difference’. A shift in the PSE can be informative of whether the perception of the current stimulus has been affected by a preceding inducer, with attractive and repulsive biases that depend on the direction of the shift (Fritsche et al., 2017). Beyond PSE, more sophisticated statistical models have been also proposed to quantify or account for serial biases in psychophysical forced-choice tasks (Gekas et al., 2019).

Future directions

In our review, we have laid emphasis on several open or unresolved questions. As a final step, we list some key issues that can be fundamental fuel for future research:

1. What is the role of the ‘task’ in serial dependence? Several studies have shown serial dependence without any explicit task while others support a clear role of attention and top-down, task-related factors (Section 3.4). One direction for future research could be to understand what the absence of a task implies, and under which conditions a stimulus is completely unattended to and not processed further. Whether serial dependence occurs for information that is irrelevant in our daily vision or only for attended features is a crucial question. Hence, the role of the ‘task’ must be clarified.
2. When do ‘objects’ become objects in serial dependence? As one of the core sections highlighted (Section 4), it is still unclear under which conditions serial dependence

keeps track of objects, as they appear to us in real life. Future research might focus on more realistic stimuli and environments (e.g., virtual reality) to use familiar objects that we usually interact with every day.

3. What is the potential connection between serial dependence and other temporal biases such as attentional priming (Kristjánsson & Ásgeirsson, 2019; Pascucci et al., 2012), distractor learning and habituation (Geng et al., 2019; Turatto et al., 2018, 2019; Turatto & Pascucci, 2016), feature distribution learning (Chetverikov et al., 2020) and the persistence of event- and object-files (Pascucci & Plomp, 2021; Scholl, 2007)?
4. A fundamental future step will be to develop and test models of serial dependence that can conjointly account for neural and behavioral results, adhering to the rule of parsimony. Many existing models have an increasingly complex structure and number of parameters, undermining their ability to generalize and account for peculiar aspects of serial dependence. What is the minimum structure of a flexible model that can account for repulsive and attractive biases? What are the missing ingredients?
5. Outside the laboratory, what is the purpose of serial dependence? Are the effects in real life larger or smaller, depending on the actual properties of real stimuli (e.g., their weight, size, physical distance, intrinsic dynamics and so on)?
6. To what extent are the effects of temporal context (e.g., serial dependence) analogous to those of spatial context? Any overarching and sufficiently flexible theoretical framework of serial dependence should take into account the relationship between spatial and temporal context and whether a single model can account for both.

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CHAPTER 2: Serial Dependence Across Features and Objects

Serial dependence does not originate from low-level visual processing

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Abstract

Perception depends not only on the current sensory input but also on the preceding history of stimuli. In serial dependence (SD), for example, the orientation of a Gabor patch is mistakenly reported as more similar to previous trials than it actually is. This bias is typically observed for moderate orientation differences (<45°) and extends over a few trials in the past. It is hotly debated whether SD originates at perceptual or post-perceptual, e.g., decisional, stages. Here, we provide evidence for the latter hypothesis. We presented Gabor patches with different spatial frequencies or Gabors intermingled with dot patterns. Even though stimuli were perceptually clearly dissimilar, we found robust SD effects arguing against any perceptual account. These findings suggest a re-evaluation of current models and theoretical accounts of SD.

Introduction

We live under the impression of perceiving the world simply as it is. Yet, perception is systematically distorted by all sorts of spatial and temporal contexts, strikingly evident in many illusions. In the temporal domain, studies on *serial dependence* (SD; Fischer & Whitney, 2014) have shown that human perception of a current stimulus is systematically biased towards stimuli presented just before. In a typical SD task, for example, observers adjust the orientation of a Gabor patch in a series of trials (Fig. 1). Even though the interval between consecutive Gabors can be substantially long (e.g., up to 5 seconds), responses to the present Gabor are systematically biased toward orientations seen a few trials before.

It is widely believed that SD is perceptual (Cicchini et al., 2017; Fischer & Whitney, 2014; Manassi et al., 2018) but several works support the involvement of *post-perceptual* processes (i.e., working memory, decision-making; Fritsche et al., 2017; Bliss et al., 2017; Pascucci et al., 2019). Although simplistic, the perceptual/post-perceptual dichotomy has been widely used in the attempt to elucidate the mechanisms behind SD (Fritsche et al., 2017; Pascucci et al., 2019), particularly in relation to negative forms of serial dependence, like adaptation and aftereffects, which have a clear perceptual nature (Gibson, 1937). A more useful distinction is between the *source* and the *site of action* of SD (Cicchini et al., 2020), i.e., whether SD originates at a perceptual or post-perceptual stage and whether it affects future processing at early or later stages. By this distinction, it is possible to hypothesize, for instance, that SD emerges post-perceptually (late source) and affects early visual processing and stimulus appearance in the next trial (early site).

In the purely perceptual view (source and site of action are related to low level processing), SD is often explained by a so-called *continuity field*, which combines features of similar stimuli within an extended region of space (~15° of visual angle) and time (~10-15 seconds) into a single percept (Fischer & Whitney, 2014). The underlying idea is that the visual world is relatively stable within short temporal windows and, hence, previous events can be used as priors for the present percept, reducing the effect of external noise and providing stability across eye movements (Cicchini et al., 2018; van Bergen & Jehee, 2019). Models of SD are thus in the Bayesian and adaptive filtering spirit where prior and current stimuli are combined depending on their relative reliability (Cicchini et al., 2018; Fritsche et al., 2020; van Bergen & Jehee, 2019).

Evidence in support of the post-perceptual view comes from studies showing that SD is driven by post-perceptual aspects, such as working memory and decision-making processes

(Fritsche et al., 2017; Pascucci et al., 2019; but see Cicchini et al., 2017), requires conscious and attentional processing (Fritsche & de Lange, 2019; Kim et al., 2020) and does not occur for behaviorally irrelevant stimuli (Fischer & Whitney, 2014). Accordingly, alternative models have been suggested related to decisional rather than continuity fields (Pascucci et al., 2019).

Here, we tested whether SD originates from low- or high-level processing. We presented Gabor patches with a high and a low spatial frequency (SF) within the same block of trials (Experiment 1) or Gabors intermixed with symmetric dot patterns (Experiment 2). The rationale is that these stimuli do not only differ in their appearance but also share very limited processing. At the earliest stages of vision, for instance, Gabors with different spatial frequencies are processed by distinct neuronal populations (Georgeson, 1973; Ware & Mitchell, 1974). The orientation of the dot patterns, instead, requires the computation of symmetry, which occurs only for neurons in higher visual areas such as, for instance, the lateral occipital cortex, V4 and V7 (Bertamini et al., 2018; Sasaki et al., 2005; Wang et al., 2016). Hence, if SD occurs only between Gabors of the same SF, our results speak for a perceptual effect. However, if SD occurs between different Gabors or even between Gabors and dot patterns, a purely perceptual account can be ruled out.

General Methods

Ethics statement

The study was approved by the local ethics committee in accordance with the Declaration of Helsinki (except for preregistration) (World Medical Organization, 2013).

Apparatus

Stimuli were presented on a gamma-corrected VG248QE monitor (resolution: 1920 x 1080 pixels, refresh rate: 120 Hz) and were generated with custom-made scripts written in Matlab (R2013a) and the Psychophysics Toolbox (Brainard & Vision, 1997), running on a Windows-based machine. Experiments were performed in a darkened room, and participants sat at 57 cm from the computer screen, with their head positioned on a chin rest. All stimuli were presented on a grey background (62.66 cd/m^2).

Participants

A total of 48 healthy participants (two independent groups of 24, age range of 18-40 years, 10 females in Experiment 1 and 11 females in Experiment 2), mostly from the EPFL and the University of Lausanne, participated in the study for a monetary reward (20 CHF/hour). All participants had normal or corrected-to-normal vision and were naïve as to the purpose of the experiments. Visual acuity was tested with the Freiburg Acuity test, and a value of 1 had to be reached with both eyes open (Bach, 1996). Written informed consent was collected from all participants in advance. Participants were instructed to maintain their gaze at the centre of the screen for the entire duration of the experiment.

Stimuli and procedures

An example of a trial sequence in Experiment 1 is illustrated in Figure 1A-B. Each trial started with a green fixation dot (0.5˚, 500 ms) followed by a central Gabor lasting 500 ms. Gabor stimuli were Gaussian-windowed sinusoidal gratings with a peak contrast of 25% Michelson and a Gaussian envelope of 1.5°. The spatial frequencies of Gabor stimuli were either 0.33 (Low SF) or 1 (High SF) cycle(s) per degree. After the Gabor, a noise mask was presented, centred at the same location for 500 ms. Masks were white-noise patches of the same size of the Gabor stimuli with a peak contrast of 95% Michelson, smoothed with a symmetric Gaussian low-pass filter (filter size = 1˚, SD = 2˚). After a blank fixation interval of 500 ms, a response tool was presented at the same location as the Gabor. The response tool was a dark grey circular frame surrounding the location of the previous Gabor with two symmetric dots (0.5° of diameter) that marked the extremities of an imaginary oriented line. This response tool was designed to reduce the effect of additional physical orientation signals in stimulus-related serial dependence. On each trial, the orientation of the response tool was set randomly, and participants were asked to adjust it until it matched the perceived orientation of the Gabor. The response tool was rotated by moving the computer mouse in the upward (clockwise rotation) or downward (counterclockwise rotation) directions, and the final response was confirmed by pressing the keyboard space bar. After a random intertrial interval (500–1000 ms), a new trial started. Gabor stimuli were assigned random orientations in each trial, covering the entire orientation range (0-179°, in steps of 1°).

There were three main conditions in Experiment 1, performed in separate blocks. In the Low SF and High SF conditions, low or high spatial frequency Gabors were presented for the entire block of trials. In the Mixed SF condition, the two types of stimuli were randomly intermixed. The order of the three blocks was balanced across participants.

In Experiment 2 (Figure 1C), we presented symmetric patterns of dots (Sym Dots) instead of the high spatial frequency Gabor. Sym Dots stimuli consisted of a symmetric pattern of 18 light grey dots (0.2° of diameter) created starting from a grid of 1.64 x 3.75°. The grid was divided into 8 x 8 equally sized squares, and the centre of each square was used as the dot location. Dot locations were determined with the following rule: two randomly selected columns of the 8 x 8 grid of squares contained 3 dots, while the remaining contained only 2 dots. A small jitter (0-0.015° in the x-axis; 0-0.05° in the y-axis) was added to the location of each dot. Symmetry was obtained by adding a mirrored version of the generated grid on the other side, interleaving the two specular patterns with an empty column. This empty midline represented the imaginary target orientation to be reported. Different orientations were presented by applying a rotation matrix to the entire pattern. Note that, on each trial the dot pattern was regenerated resulting in a sequential presentation of stimuli defined by the same features, but with highly variable configurations (see also Wang et al., 2016). Besides the use of symmetric dot patterns instead of high-frequency Gabors, all other aspects of Experiment 2 were identical to Experiment 1.

At the beginning of each experiment, participants were provided written and verbal instructions and performed a sequence of practice trials under the supervision of the experimenter. Practice trials were not analysed but served to ensure that participants understood the task. Experiments consisted of 3 blocks of 200 trials each, for a total of 600 trials and lasted approximately 1 hour.

Analysis

Before statistical analysis, trials containing and following absolute adjustment errors larger than 3 standard deviations from the mean and reaction times smaller than 500 ms or larger than 10 seconds were removed from subsequent analyses. The first trial of each block was also removed (overall, less than 5% of trials were discarded). Adjustment errors were computed as the difference between the reported and the actual orientation in each trial, bounded to ± 90°. In Experiment 1, participants performed the task with an average absolute error of 8.01 ± 1.81°

and average reaction times of 1.63 ± 0.42 seconds. In Experiment 2, the average absolute error was 7.35 ± 1.66° and the average reaction times were 1.46 ± 0.39 seconds.

To quantify serial dependence, we pooled the adjustment errors of all participants (Fritsche et al., 2020) and fitted a derivative of Gaussian function (DoG) of the form:

$$error = \Delta \alpha w c e^{-(w\Delta)^2} \tag{1}$$

where Δ is the difference between the previous and current stimulus orientation, α is the amplitude of the DoG curve scaled by the constant $c = \sqrt{2}/e^{-0.5}$ to match the curve peak and w is the inverse of the curve width. The best-fitting DoG was estimated by solving a constrained non-linear minimization problem with the sum of squared residuals as the cost function (Fritsche et al., 2020; Manassi et al., 2017). Constraints were imposed on both parameters to ensure algorithm convergence ($\alpha = [-20,20], w = [0.02,0.07]$, parameters initialized at $\alpha = 2, w = 0.05$). DoG functions were fitted to group data, separately for each condition of interest, and the amplitude parameter α was used to quantify the bias. Statistical testing was performed using a permutation approach. A null distribution of SD amplitudes was obtained by fitting eq. [1] to surrogate datasets generated by randomly flipping the sign of errors in each trial 10000 times (Fritsche et al., 2020). The null distributions were used to derive p-values as the proportion of surrogate α parameters larger than the observed ones. The comparison between conditions was performed using a similar permutation approach but shuffling the labels of the conditions for each surrogate dataset.

In the analysis of the Mixed block in Experiment 1, we evaluated the qualitative predictions of two models of SD. In both models, adjustment responses were approximated by a simple adaptive filter of the form:

$$y_n = (1 - w)x_n + wx_{n-1} \tag{2}$$

where y is the adjustment response in trial n, x the stimulus orientation and w the weight assigned to the orientation in the previous trial $(n - 1)$. In the ideal observer model, weights were computed as a combination of the uncertainty associated to present and past stimuli, according to the following equation:

$$w_n = \frac{\sigma_n^2}{\sigma_n^2 + \sigma_{n-1}^2 + \Delta^2} \tag{3}$$

in which σ is the uncertainty in the present (n) and past $(n-1)$ stimuli and the squared term Δ accounts for the fading of SD effects as the distance between consecutive orientations increases (Cicchini et al., 2018). The alternative model was a simplified version of eq. [3] in which weights depended only on the uncertainty in present sensory input:

$$w_n = \frac{1}{2 + (\Delta/\sigma_n)^2}. \tag{4}$$

Two σ parameters were estimated independently for Low ($\sigma = 8.21°$) and High SF Gabors ($\sigma = 4.41°$) by minimizing the difference between the peak SD predicted by eq. [4] and the observed DoG amplitude in blocks of only Low or High SF. The two σ were then used in eq. [3-4] to predict the data in the Mixed SF block.

All model-based analyses were paralleled by a model-free approach to control that results were not affected by fitting the data to the group average (e.g., neglecting the variability at the individual level) or by model fitting artifacts. In the model-free approach, we subtracted the average error for Δ in the 1-25° range from the average error in the corresponding negative range of Δ (Samaha et al., 2019). The resulting index, quantifying the amount of systematic deviation of the errors with respect to zero (either in the positive or negative direction) was used for subsequent analysis. Effect sizes (Cohen's *d'*) were obtained from the model-free results. The means and standard errors of the means (SEM) shown in Figure 2-3 were computed using a moving average on the adjustment errors of individual subjects (Fritsche et al., 2017). Moving average windows were centred on the actual Δ with a length of ±7° for the data of an entire block of trials (e.g., Figure 2A, 3A) and ±12° for subsets of trials within the Mixed condition of both experiments (e.g., Figure 2C, 3C), to compensate for the smaller amount of trials in Mixed blocks.

Results

In Experiment 1, we presented Gabors with an SF of either 0.33 or 1 cycle(s) per degree. Participants reproduced the orientation of the Gabors by adjusting the angle of an imaginary line between two response dots (Figure 1A). Serial dependence was tested in separate blocks with Gabors having only low (Low SF), only high (High SF), or mixed spatial frequencies (Mixed SF; see Figure 1A-B). In accordance with previous findings, in blocks with only low or high SFs, adjustment errors were positively related to the difference between the previous and present Gabor orientation (Δ): more clockwise errors occurred when previous orientations were more clockwise, and the opposite was true for counter-clockwise differences (Figure 2A). We quantified the size of this effect as the amplitude (α) of derivative of Gaussian functions (DoG) and validated this model-based analysis by an additional model-free analysis (Samaha et al., 2019; see Methods).

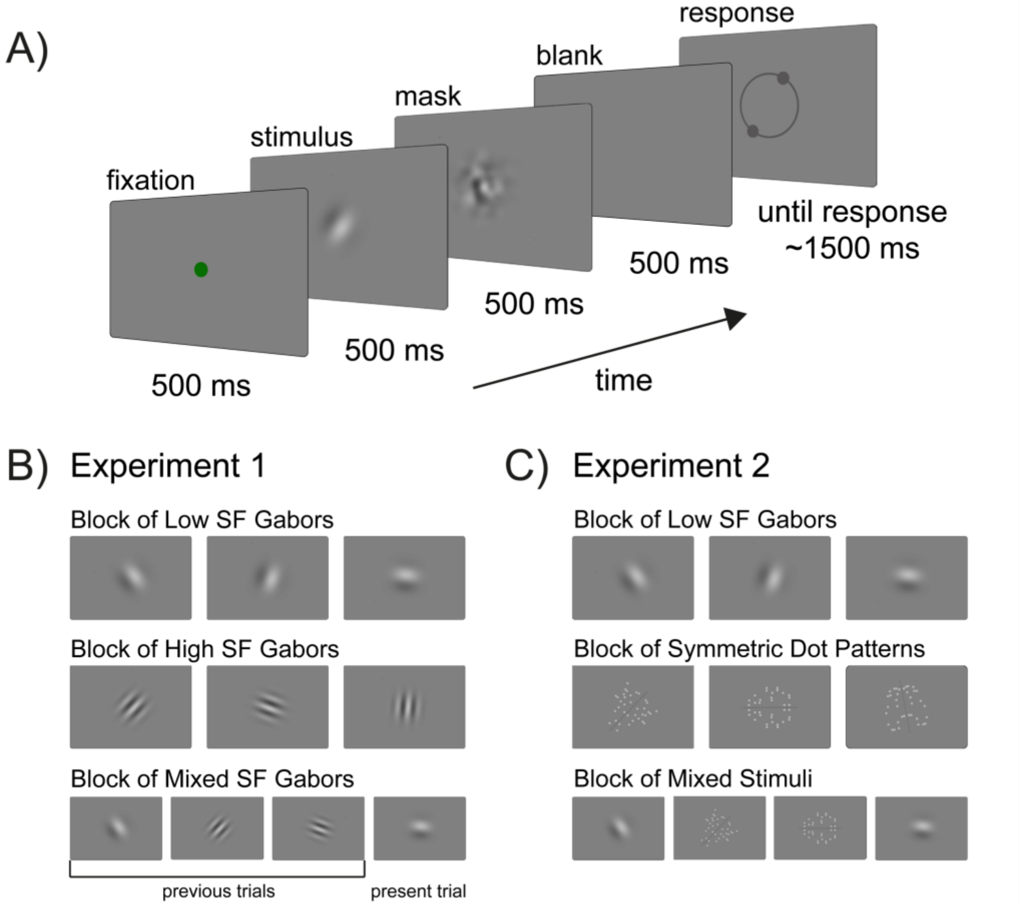

Figure. 1. A) Example of a trial sequence in the orientation adjustment task. Participants saw an oriented Gabor stimulus at the centre of the screen, followed by a noise mask. After a blank interval, participants reported the orientation of the stimulus by adjusting the angle of an imaginary line connecting two dots connected by a thin circle. B) In Experiment 1, separate blocks contained Gabors with low (Low SF; .33 cpd), high (High SF; 1 cpd), or mixed (Mixed SF) spatial frequencies. In the mixed block, Gabors of low and high spatial frequencies were randomly interleaved. C) In Experiment 2, High SF Gabors were replaced by patterns of symmetric dots, and participants reproduced the tilt based on the angle of the symmetry axis. The symmetry axis is indicated by the dashed black lines (not presented in the experiment). The order of blocks was counterbalanced across participants. Stimuli are not drawn to scale.

As shown in Figure 2A, SD occurred in the blocks with only Low or High SF Gabors (Low SF: peak SD = 2.9°, $p < 0.001$; model-free: $t(23) = 6.83$, $p < 0.001$, $d' = 1.39$; High SF: peak SD = 1.56°, $p < 0.001$; model-free: $t(23) = 2.94$, $p = 0.007$, $d' = 0.60$). SD was larger for

Low SF Gabors compared to High SF Gabors (Low vs. High: *p* = 0.005; model-free: *t*(23) = 2.50, *p* = 0.02; *d'* = 0.51, paired t-test). Importantly, SD occurred also in the mixed blocks where Low and High SF were randomly intermixed (Mixed: peak SD = 1.77°, *p* < 0.001; model-free: *t*(23) = 5.26, *p* < 0.001; *d'* = 1.07).

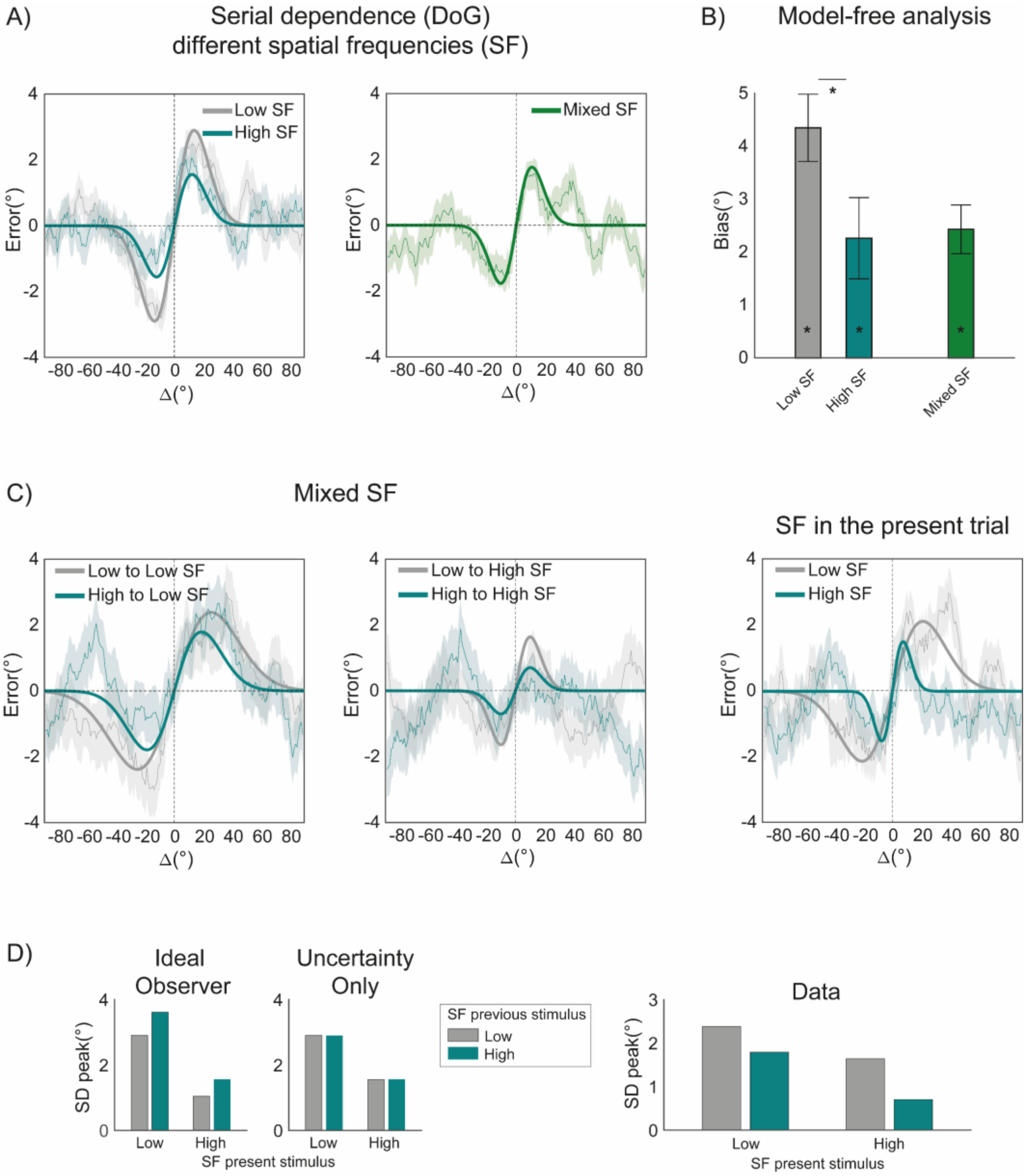

Figure. 2. A) Adjustment errors as a function of the difference between the orientation of the previous and the present Gabor (Δ), fitted by a derivative of Gaussian function (DoG). The left panel shows the adjustment errors and fits for all trials in the separate blocks with either Low or High SF Gabors. The right panel shows the results for all the trials in the Mixed SF block. Thinner lines and shaded regions represent the bootstrap estimate and standard deviation of the participants' average errors. B) Model-free analysis quantifying the SD bias as the difference between the average of errors in a positive (from 1° to 25°) and negative (from -1° to -25°) range of the Δ variable (see Methods). Error bars show the standard error of the mean (SEM). Asterisks indicate significant differences. C) SD in the Mixed SF block as a function of whether the actual trial contained a Low SF (left panel) or a High SF Gabor (central panel). The two curves in each panel indicate whether a Low or a High SF Gabor was presented in the trial before. The right panel visualizes the overall SD for Low and High SF in the actual trial of

the Mixed SF block. D) Qualitative predictions of the Ideal Observer and the Uncertainty Only model, along with the observed peaks of SD amplitude in the four combinations of present and past stimuli within the Mixed SF block. The Ideal Observer model predicts larger SD when the SF of the previous stimulus is high rather than low, and the largest effect occurs in the High-to-Low SF case. The Uncertainty Only model predicts no difference due to the previous SF but an overall larger SD for Low SF Gabors. Our results (bottom bar plot) showed an opposite trend to the one predicted by the Ideal Observer model.

In line with previous reports (Cicchini et al., 2018), SD is larger for the low spatial frequency Gabors, supposedly because they contain weaker orientation signals due to the fewer stripes. But why did SD occur in Mixed SF blocks? One possibility is that SD reflects a mechanism to reduce uncertainty in a task-relevant feature (e.g., orientation), independently of changes in other aspects of the stimulus (e.g., spatial frequency) (Cicchini et al., 2018; Kim et al., 2020). For instance, uncertainty in a sequence of orientation signals can be reduced by combining weaker stimuli (e.g., Low SF Gabors) with more reliable ones (e.g., High SF Gabors). Alternatively, SD depends on post-perceptual processes that are independent of the uncertainty of previous stimuli and affected only by the quality of current sensory input.

We illustrate these two alternatives using the predictions of two simple models of SD (Figure 2D; see Methods). In the Ideal Observer model (Cicchini et al., 2018), sequential stimuli are combined optimally, i.e., more reliable stimuli (High SF) induce larger SD on more uncertain ones (Low SF). In a simpler alternative model (Uncertainty Only model), SD is overall larger for more uncertain stimuli (Low SF), but there is no effect of the uncertainty in the previous trial. We used these simple models to qualitatively compare their predictions against the observed patterns of SD in the Mixed SF blocks (see Supplementary Materials and Figure S1 for a model comparison based on alternative and more sophisticated models of SD). To this aim, we estimated the peak of SD curves (DoG amplitude) separately for trials in the four combinations of the present and past SF (Low to Low, High to Low, Low to High and High to High). Qualitatively, the results provided no support for the Ideal Observer model. The SF in the previous trial had no effect on SD for both Low SF (Low-to-Low vs. High-to-Low: $p = 0.23$; model-free: $t(23) = 0.79$, $p = 0.43$) and High SF Gabors (Low-to-High vs. High-to-High: $p = 0.80$; model-free: $t(23) = 0.23$, $p = 0.81$). This pattern is consistent with the predictions of the Uncertainty Only model (Figure 2D and S1), namely, that SD is overall larger for Low SF and unaffected by previous SF. A direct comparison of SD for Low and High SF in the Mixed block confirmed a significant increase in the width of the Low SF curve (Low SF vs. High SF, permutation $p < 0.05$), but no difference in the amplitude (permutation $p > 0.05$), in line with an overall larger bias toward previous orientations in the presence of Low SF

Gabors (model-free analysis comparing errors in the ±45° range: $t(23) = 3.67$, $p = 0.001$, $d' = 0.75$, paired t-test; Figure 2C, rightmost panel). We also found that, in Mixed SF blocks, SD for High SF stimuli was less pronounced compared to SD in only High SF blocks (Low-to-High SF: peak SD = 1.6°, $p = 0.01$; model-free: $t(23) = 1.82$, $p = 0.08$; High-to-High SF: peak SD = 0.70°, $p = 0.21$; model-free: $t(23) = 0.79$, $p = 0.43$). This suggests that participants were even less uncertain in reporting the orientation of High SF stimuli when they were intermixed with Low SF stimuli. Overall, however, the results of this experiment indicated that the two types of stimuli were not combined in an optimal way.

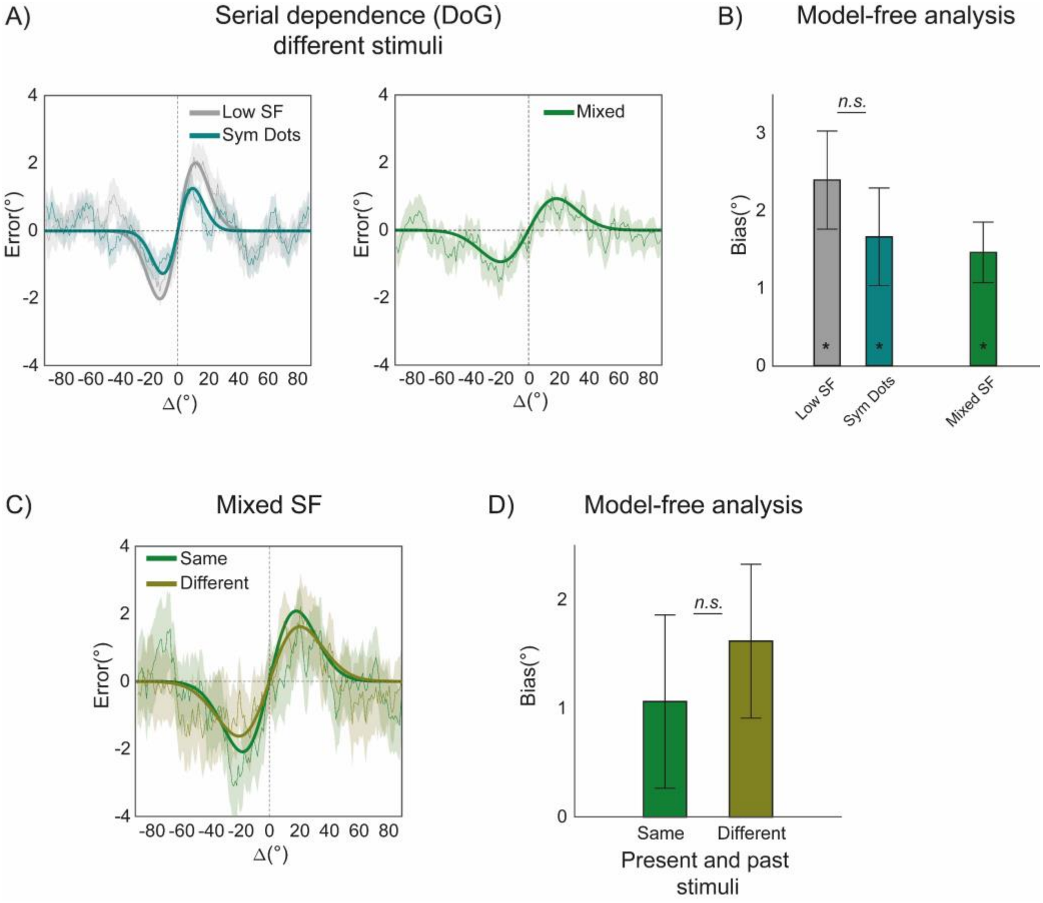

Figure. 3. A) Serial dependence and DoG fits for each block of Experiment 2. B) Model-free analysis confirming SD in all blocks, including blocks where different stimuli were intermixed (Mixed). C-D) SD in Mixed blocks was equally affected by whether the previous trial contained the same or a different stimulus.

In Experiment 2, we tested whether SD occurs even between completely different stimuli. We used the same paradigm as in Experiment 1 but substituted the high-frequency Gabor with a pattern of symmetric dots (Sym Dots; Figure 1C). The two stimuli appear as clearly different and are also processed at distinct stages of the perceptual stream (Wang et al., 2016), thus, SD between them would be incompatible with a purely perceptual bias. When tested in separate blocks, SD occurred for both Gabors and dot patterns (Figure 3A-B; Low SF: peak SD = 2.02°, $p < 0.001$; model-free: $t(23) = 3.78$, $p = 0.001$, $d' = 0.77$; Sym Dots: peak SD = 1.26°, $p < 0.001$; model-free: $t(23) = 2.64$, $p = 0.015$, $d' = 0.54$), without significant difference between blocks (Low SF vs. Sym Dots: $p = 0.07$; model-free: $t(23) = 1.45$, $p = 0.16$; $d' = 0.30$, paired t-test). Crucially, SD was also present in trials of the Mixed block (Mixed: peak SD = 0.94, $p = 0.004$; model-free: $t(23) = 3.74$, $p = 0.001$, $d' = 0.76$) and was equally affected by whether the previous trial contained an identical or a different stimulus (Figure 3C-D; same vs. different stimulus: $p = 0.33$; model-free: $t(23) = -0.44$, $p = 0.66$; $d' < 0.10$). Taken together, these results show that SD occurs for different visual features and stimuli.

Discussion

With two straightforward experiments, we provided evidence that the source of SD is post-perceptual. SD occurred for stimuli differing in basic features (Gabors with either Low and High SF; Experiment 1) and for entirely different stimuli (Gabor patches and dot patterns; Experiment 2). Hence, SD originates at a stage where the selectivity to specific stimulus features is lost.

Our findings have clear implications for our understanding of SD. First, previous work has often claimed that SD originates and acts at the earliest stages of visual processing (e.g., in primary visual cortex; Fischer & Whitney, 2014; John-Saaltink et al., 2016). Here we have shown that SD is incompatible with such a proposal since SD lacks the selectivity to basic visual features, which is a hallmark of early visual processing.

Second, we found that SD depends on both the decision in the previous trial and mostly on the visual quality of the present, but not on the past, stimulus (Experiment 1; Mixed SF condition). This pattern suggests that a simple Ideal Observer model is not a complete account of SD (Cicchini et al., 2018). The Ideal Observer predicts that more reliable stimuli (e.g., High SF Gabors) induce stronger SD on more uncertain ones (e.g., Low SF Gabors). This prediction was supported in a recent neuroimaging study showing that the uncertainty represented in brain activity is related to behavioural SD: more reliable sensory representations induce stronger SD on more uncertain ones (van Bergen & Jehee, 2019). However, the authors contrasted only conditions with low-to-high and high-to-low uncertainty trials. It is possible that the difference reported in their study was exclusively due to the current and not to the previous uncertainty. In the work of van Bergen and Jehee (2019), the authors also proposed a more complex ideal observer model that incorporated an internal model of the transition distribution of natural orientation changes (van Bergen & Jehee, 2019). In principle, this model can account for the lack of an effect of the previous uncertainty in our Experiment 1. For instance, if the transition distribution is broad and independent of past SF, small uncertainty differences in previous stimuli can be wiped out. It should be noted, however, that a broad transition distribution would produce comparable results to a broad decisional template that is independent of the uncertainty in past stimuli, in line with the explanation proposed here (see supplementary Figure S1).

The lack of an effect of the previous stimulus uncertainty can be alternatively explained by the fact that, in naturalistic environments, low spatial frequency stimuli tend to be more stable across time than high spatial frequency ones (van Bergen & Jehee, 2019). This may strengthen priors that increase SD after low, rather than high spatial frequency stimuli, reversing the pattern predicted by the ideal observer model. Further research may help to clarify the role of uncertainty and internal priors by using manipulations other than spatial frequency. Similarly, in evaluating the role of sensory uncertainty, we compared the predictions of the Ideal Observer model with the Uncertainty Only model. This comparison was performed using a subset of trials from one condition (Mixed SF block), leading to a reduced number of datapoints. Further research focusing exclusively on this model comparison could help to confirm and better characterize the observed patterns. Nevertheless, even if the results were qualitatively not identical to the uncertainty only model, they showed a trend opposite to the predictions of the ideal observer.

Our results, particularly those of Experiment 2, are also inconsistent with a purely Bayesian account of visual SD. Bayesian models of SD rely on the idea that our visual system uses previous stimuli as priors for present perception, exploiting the fact that stimuli in the natural world rarely change over short times (Cicchini et al., 2018; Fritsche et al., 2020; van Bergen & Jehee, 2019). In this view, the computational goal and functional role of SD is to maintain perceptual continuity and visual stability (Cicchini et al., 2018; Fischer & Whitney, 2014). This goal can be fulfilled only by a mechanism that is selective to stimulus type, i.e., combining oranges and apples has no benefit. Hence, SD for entirely different stimuli is difficult to reconcile within the framework of Bayesian perception.

We provided evidence that SD occurs beyond early perceptual processing. This may still leave open the possibility that SD involves distributed sensory areas, rather than decisional biases (Collins, 2019). SD, however, typically requires awareness (Kim et al., 2020), attention

(Fritsche & de Lange, 2019) and decisions (Pascucci et al., 2019). This makes it unlikely that SD is exclusively bounded to sensory circuits and occurs without post-perceptual factors coming into play.

Whereas we conclude that the source of SD is not perceptual, we cannot rule out that SD ultimately leads to changes in the appearance of the next stimulus, i.e., that the *source* is post-perceptual but the *site of action* is perceptual (Cicchini et al., 2020). Post-perceptual decisions (Pascucci et al., 2019), as well as other recurrent processes involving higher-level areas (Kim et al., 2020), may still interfere with the decoding of orientation signals at different levels of the sensory stream, producing distortions in the appearance of both Gabors and dot stimuli. However, this late interference, which is independent of features and stimuli, suggests a common and central mechanism for SD, arguing against a continuity field in early sensory processing. A central mechanism might well explain SD in many distinct domains of processing (Liberman et al., 2018; Liberman & Whitney, 2015) and finds support in recent evidence of SD across different stimulus features and formats (Fischer et al., 2020; Fornaciai & Park, 2019). Fischer and colleagues (2020), for instance, found that SD occurs after changes in task-irrelevant features but is reduced after changes in task-relevant ones (Fischer et al., 2020). Consistently with our view, this suggests that the information carried over from one trial to the next is strictly related to the task and not to the low-level properties of stimuli. Our findings also accommodate the fact that higher subjective confidence on previous reports amplifies SD independently of signal quality (Samaha et al., 2019).

In line with previous work, we propose that SD originates from post-perceptual *decisions* (Fritsche et al., 2017; Pascucci et al., 2019). This conclusion is restricted to the type of positive SD observed here and in similar studies. Other forms of SD, for example visual adaptation and negative aftereffects, are clearly of perceptual nature. Similarly, other reports showing that SD is selective for sensory modality (Fornaciai & Park, 2019) and for the ear of origin in auditory perception (Ho et al., 2019) are more difficult to frame in this view. We cannot exclude the coexistence of two sources of positive SD, one purely perceptual and the other post-perceptual (Cicchini et al., 2017), with the former fading out swiftly during inter-trial intervals and the latter dominating.

Taken together, our findings provide evidence that SD emerges at post-perceptual stages where previous events affect present reports depending on the quality of the available sensory input. The next question is, therefore, what exact mechanisms are responsible for SD. Post-perceptual accounts of SD have proposed a role for decision inertia, by which previous perceptual decisions become attractor points for reading out and interpreting present sensory input (Pascucci et al., 2019). The fact that SD lasts only a few trials suggests the involvement of typical expectation mechanisms that emerge during sequential decisions in a random series of events. Consistently with well-known cognitive and reasoning biases, indeed, humans tend to underestimate changes in a short sequence of random events while overestimating variations over the longer term (Croson & Sundali, 2005; Pascucci et al., 2012). This perfectly fits with initial reports showing positive SD for short runs (e.g., 3-4 trials) and negative dependence for trials further in the past (Fritsche et al., 2020; Gekas et al., 2019).

Two recent studies have proposed a candidate mechanism for the neuronal implementation of SD that can provide a parsimonious explanation of our results. In the bump-reactivation hypothesis (Barbosa et al., 2020; Stein et al., 2020), neuronal activity from the previous trial remains imprinted in synaptic connections in the prefrontal cortex, as a latent and activity-silent pattern. Silent activity patterns are then reactivated by external cues signaling the beginning of a new trial (e.g., a fixation cue), ultimately causing serial biases in working memory. As the last representation that is held in memory most likely corresponds to the task-relevant decision, which is abstracted from low-level features, this model can perfectly explain the SD between stimuli differing in low-level aspects.

Our findings open a new avenue into the post-perceptual processes involved in SD. Post-perceptual processes can include inertia in decision-making (Pascucci et al., 2019), as well as the tendency to reiterate the same stimulus-response mapping rule (Hommel, 2004), choice repetition (Akaishi et al., 2014) and working-memory biases (Fritsche et al., 2017). Interestingly, it has been shown that when a different response tool is used for stimuli of different categories (e.g., response images are faces of the same or different gender as the target stimulus in a facial expression adjustment task), SD effects can be selective to the category of the preceding stimulus (Liberman et al., 2018). This suggests a role for how decisions are mapped into specific response tools that may be an important aspect for future research.

In conclusion, our results provide clear evidence that SD is not a perceptual effect but involves later processing stages where the selectivity to features and stimuli is lost.

Supplementary Material

Ideal Observer and Two-Process: model comparison

In explaining the results of the Mixed SF block in Experiment 1, we compared the predictions of two simple models of serial dependence (SD), the Ideal Observer, and the Uncertainty only model. Both models were considered in their basic form, including only the effect of the stimuli in the previous trial and a single parameter to account for the uncertainty associated with present and past stimuli (Cicchini et al., 2018; see Methods and main text). Here we show that the comparison between more sophisticated models, with variables in circular space and a weighted mixture of past states (10-back trials), would essentially return the same qualitative predictions. To this aim, we used a modified version of the Two-Process model of SD (Figure S1, see caption for details). In this model, stimulus encoding and decoding occur at two sequential stages (Pascucci et al., 2019) and SD may involve the combination of the uncertainty encoded from past and present stimuli (e.g., as in the Ideal Observer) or the combination of previous decisions (decoded stimuli) with only present stimulus uncertainty (e.g., as in the Uncertainty only model). In the figure below, it is straightforward to see that when SD is modeled as a combination of present and past sensory uncertainty (Figure S1A-C), the effect is larger for high-to-low SF stimuli (i.e., the Ideal Observer behavior). Instead, when SD is modeled as a combination of present stimuli with past decisions (e.g., with their own history and shape; Figure S1B-D), the model can effectively reproduce the data both quantitatively and qualitatively (details in the caption).

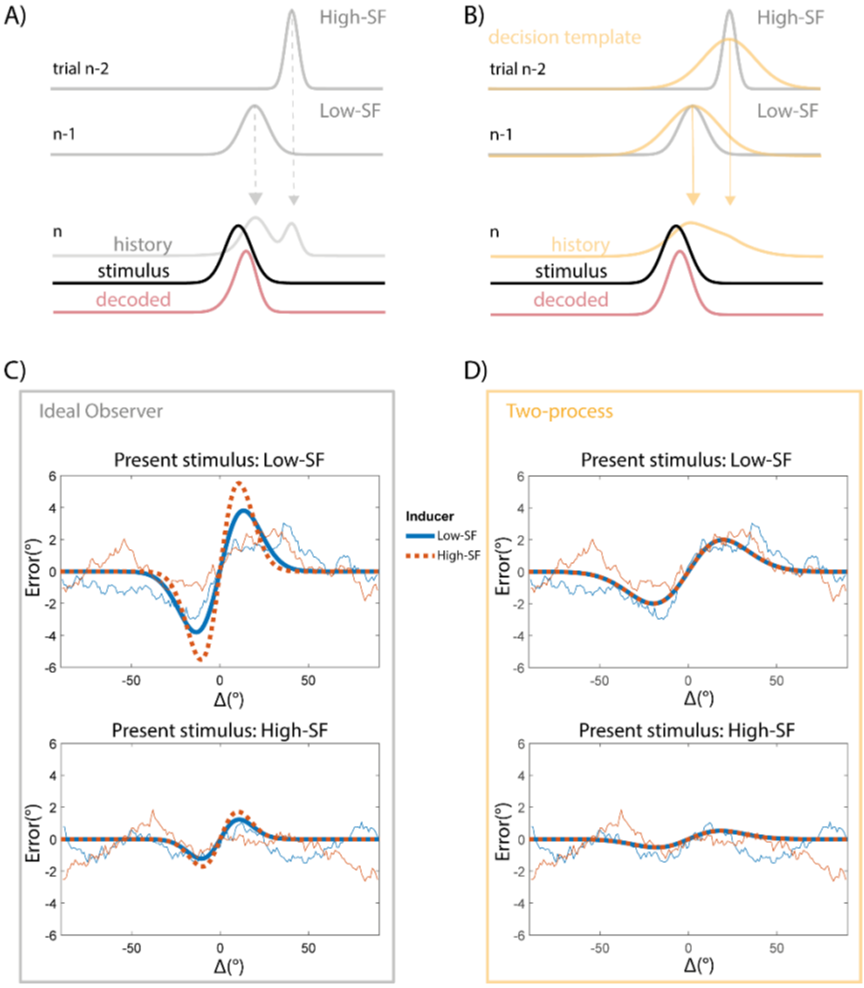

Figure S1. A modified version of the Two-Process model. The model has a hierarchical structure with an encoding and a decoding stage (Pascucci et al., 2019). At the encoding stage, sensory uncertainty is approximated by the width (concentration parameter) of a Von Mises distribution (gray curves; Kalm & Norris, 2018). At the decoding stage, orientation signals are decoded from the circular mean of the Von Mises distribution. The effect of the previous trials is modeled by including a memory component with an exponential decay over 10 trials. SD results from combining present sensory input with a weighted mixture of past trials (Kalm & Norris, 2018). A) In the Ideal Observer type of model, SD results from a combination of present and past sensory uncertainty. B) In the Two-Process model (equivalent to the Uncertainty Only model), SD is a combination of past decisions with present sensory signals. Past decisions are modeled as Von Mises distributions with their own width and history (orange curves). C-D) Predictions of the models for the conditions in Mixed blocks, showing an improved quantitative fit but identical qualitative pattern compared to the simpler models used in our work. Curves are DoG fits of the model predictions. Thick lines are the running averages of all subjects.

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CHAPTER 3: Serial Dependence, Time, and Number of Stimuli

Attractive and repulsive serial dependence: the role of task relevance, the passage of time, and the number of stimuli

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Abstract

Visual decisions are attracted towards features of previous stimuli. This phenomenon, termed *serial dependence*, has been related to a mechanism that integrates present visual input with stimuli seen up to 10-15 s in the past. It is believed that this mechanism is ‘temporally tuned’ and the effect of prior stimuli fades with time. Here, we investigated whether the temporal window of serial dependence is influenced by the number of stimuli shown. Observers performed an orientation adjustment task where the interval between the past and present stimulus and the number of intervening stimuli varied. First, we found that the direction — repulsive or attractive— and duration of the effect of a past stimulus depends on whether the past stimulus was relevant to behavior. Second, we show that the number of stimuli, and not only the passage of time, plays a role: the effect of a stimulus at a fixed interval depends on the number of other stimuli shown after. Our results demonstrate that neither a single mechanism nor a general tuning window can fully capture the complexity of serial dependence.

Introduction

Perceptual decisions depend not only on the characteristics of the stimulus available at the moment but also on the history of events before. For example, decisions about the orientation of a visual stimulus can be systematically biased by the orientation of stimuli seen a few seconds before, a phenomenon known as *serial dependence* (Fischer & Whitney, 2014).

Studies over the past decade have reported serial dependence in a variety of visual tasks (Kiyonaga et al., 2017; Pascucci et al., 2023), showing effects that last approximately 10-15 s and decline as a function of time: a stimulus presented 5 s before has a stronger influence on current decisions than a stimulus presented 10 s before (Fischer & Whitney, 2014; Manassi et al., 2018, 2019). In most of these studies, serial dependence is *attractive*, which means that present stimuli are judged as more similar to previous stimuli than they truly are. The time course of this attractive bias has been often related to the temporal tuning of a mechanism, termed *continuity field* (Collins, 2019; Fischer & Whitney, 2014), which integrates prior and current visual input, exploiting the seconds-long autocorrelation of events in the natural world (van Bergen & Jehee, 2019; Kalm & Norris, 2018). The consistency of the temporal tuning window of serial dependence has been considered a hallmark or a defining criterion of continuity fields (Manassi et al., 2019).

Most of the findings on serial dependence, however, come from paradigms in which 10-15 s correspond to 2-3 stimuli, shown on consecutive trials. This leaves it unclear whether the temporal window of serial dependence would change depending on the number of presented stimuli (Fischer & Whitney, 2014; Manassi et al., 2019, 2021). That is, the influence of a stimulus presented 10 s before might change depending on how many other stimuli are presented in between.

Previous work on the temporal dynamics of serial dependence has mostly focused on the effect of the passage of time. For instance, it has been shown that the bias towards prior stimuli increases with the inter-trial interval and with the interval before the current stimulus is reported (Bliss et al., 2017; Fritsche et al., 2017; see also Bilacchi et al., 2022). Such findings indicate that the strength of serial dependence varies during working memory intervals but cannot tell whether the number of stimuli plays a role. Other studies have found attractive biases towards decisions made in the past, even when increasing the number of stimuli between the current and the previous decision (Pascucci et al., 2019; Pascucci & Plomp, 2021). Crucially, these works have shown that stimuli presented —but not reported— in the interval between perceptual decisions can cause systematic repulsive, and not attractive biases, suggesting that, at least under some conditions, the direction and temporal dynamics of serial dependence are largely dictated by the structure of the task at hand.

Studies investigating the role of task relevance have also shown that not all the stimuli falling within the temporal window of serial dependence are necessarily integrated. For instance, Fischer et al. (2020) presented participants with two clouds of moving dots in different colors on each trial, displayed in succession. A post-cue indicated which of the two clouds, based on either color or serial position (e.g., the 'context' feature), they were to reproduce the motion direction of. Serial dependence in reporting motion directions was highest between trials for stimuli with a matching context feature, but only when that feature was important for the task at hand (e.g., for stimuli with the same color when color was the relevant feature cued on consecutive trials). Similarly, Ceylan et al. (2021b) presented observers with two overlayed features, a cloud of moving dots and an oriented Gabor, and found that only the feature cued and reported on the previous trial induced serial dependence on the following trial. Moreover, there is extensive evidence that attention to the previous stimulus, due to its relevance for the task, is a prerequisite of many forms of serial dependence reported in the literature (Fischer & Whitney, 2014; see Pascucci et al., 2023 for a review). In agreement with several other findings (Feigin et al., 2021; Pascucci et al., 2019; Pascucci & Plomp, 2021; but see Fornaciai & Park, 2018; Murai & Whitney, 2021), these works suggest that, within the time window in which serial dependence is typically found, there can be strong modulations of the effect due to the behavioral relevance of prior stimuli.

None of the above studies, however, has presented a systematic investigation of the relationship between the number of stimuli and the interval of time, a critical aspect in understanding the temporal dynamics of serial dependence.

To this end, we performed two experiments, using a modified version of the standard orientation adjustment task. In both experiments, we varied the number of intervening stimuli and the time interval between a stimulus shown in the past and the stimulus that participants had to reproduce in the present (see Figure 1). If serial dependence is exclusively a function of time, the stimulus shown at a given interval in the past should always produce the same bias, independently of how many other stimuli are presented in between.

Overall, we found that, in addition to the passage of time, two main factors play a role: the relevance of the previous stimulus to the task and the number of intervening stimuli. We discuss how all these factors together contribute to serial dependence —i.e., the bias eventually measured in behavioral reports, beyond a single mechanism and a general tuning window.

General Methods

Ethics statement

The study was approved by the local ethics committee in accordance with the Declaration of Helsinki (except for preregistration) (World Medical Organization, 2013).

Apparatus

All experiments were run on a gamma-corrected VG248QE monitor (resolution: 1920 x 1080 pixels, refresh rate: 120 Hz) in a darkened room. Stimuli were generated with custom-made scripts written in MATLAB (R2013a) and the Psychophysics Toolbox and presented on a grey background (62.66 cd/m^2). Participants sat at 57 cm from the computer screen, with their head on a chin rest.

Participants

We recruited 20 healthy participants (12 females, age range of 18-35 years) for Experiment 1 and 20 participants (11 females, age range of 18-35 years) for Experiment 2. All participants had normal or corrected-to-normal vision according to the Freiburg Visual Acuity test (Bach, 1996) and were paid (20 CHF/hour) after completing the experiments. Written informed consent were collected from all participants in advance.

Stimuli and procedures

Experiment 1

Figure 1 illustrates the sequence of events in one trial of Experiment 1. Each trial started with a placeholder (a white circular frame with a diameter of 7°), indicating the upcoming stimulus location, which lasted until the end of a response. After 1000 ms, a Gabor stimulus (noise: 50%, peak contrast: 25% Michelson, spatial frequency: 0.75 cycle/°, Gaussian envelope: 1.5°) was presented inside the placeholder for 500 ms. Depending on the number of stimuli within the trial (two, three, or four), the next Gabors appeared with an inter-stimulus interval (ISI) of

12, 6, or 4 s. Following the last Gabor and an interval of 500 ms, a response tool was presented. The response tool was made of two small triangles placed at the opposite ends of the placeholder, drawing an imaginary line. Participants rotated the response tool to reproduce the orientation of the last Gabor by moving a computer mouse upward (clockwise rotation) or downward (counter-clockwise rotation) and clicking the left mouse button to confirm the final decisions. The subsequent trials started after a random intertrial interval (1000–2000 ms).

In regular trials (80%), the time interval between the first and the last Gabor was always between 12-13 s. To reduce the expectations on the trial sequence and to preserve attention on each Gabor, we included catch trials (20%) in which the sequence could stop earlier (e.g., after one, two, or three stimuli) and the responses were collected right after the sequence ended. Stimulus orientations were assigned randomly (0-179°, in steps of 15°, jittered +/-7°).

Before the experiment, all participants were provided written and verbal instructions. To ensure that participants understood the task, they performed two blocks of four practice trials under the supervision of the experimenter. The experiment consisted of 8 blocks of 26 trials each, for a total of 208 trials, and lasted approximately 1 hour.

Experiment 2

As illustrated in Figure 4, trials consisted of a single Gabor, or two Gabor stimuli sequentially presented. In trials with two stimuli, the ISI between the two and the delay following the last Gabor and before the response was 2000 ms. As in the first experiment, participants reproduced the orientation of the last Gabor by rotating the response tool. In Experiment 2, we removed the placeholders and used a response bar for a simplified design. To facilitate the attractive bias to the past, we used noise-free Gabor stimuli with lower contrast (peak contrast: 15% Michelson) and lower spatial frequency (0.56 cycle/°), in line with parameters used in prior studies (Cicchini et al., 2018; Manassi et al., 2018). Similarly, to achieve a complete picture of the direction and strength of these biases across the entire orientation distance range, as typically done in prior work, we used orientation distances in the ±90° range. In this experiment, we set the number of catch and regular trials to the same proportion (50% each), to ensure that participants were not paying more attention to the second Gabor, because it was more likely to be the target. In the catch trials, the response tool was presented following the first Gabor and a delay of 2000 ms.

After written and verbal instructions, participants performed eight practice trials under the experimenter's supervision before starting the experiment. The experiment consisted of 10 blocks of 30 trials each, for a total of 300 trials, and lasted approximately 45 minutes.

Analysis

Before data analyses, we excluded trials with high adjustment errors (larger than 45°) or slow adjustment times (longer than 10 s). Following the first outlier removal, trials with adjustment errors of more than 1.5 interquartile ranges above the upper quartile or below the lower quartile were further removed. Additionally, two participants were excluded in the first experiment, one showing strong repulsive effects in all conditions, with values larger than 3 standard deviations from the average bias of the group, the other showing poor performance (a standard deviation of errors before cleaning larger than 45° and more than 20% of outlier trials). Participants performed the task with an average absolute error of 6.07 ± 1.06° and average reaction times of 1.92 ± 0.55 s in Experiment 1, and an average absolute error of 7.36 ± 1.06° and average reaction times of 1.73 ± 0.42 in Experiment 2.

To quantify serial dependence, we used a 'model-free' approach (Ceylan et al., 2021a; Samaha et al., 2019) in the analyses of both experiments. In Experiment 1, for each participant, we first binned the adjustment errors based on the acute angle distance between the previous and the present orientations (Δ) as 'close' (1-25°) and 'far' (26-50°). In Experiment 2, Δ distances ranged between -90 and 90°; therefore, we binned the adjustment errors for the distances as 'close' (1-30°), 'mid' (31-60°), and 'far' (61-90°). Then, we subtracted the averaged errors for positive orientation distances from those for negative orientation distances within each bin. In this way, for each participant and bin, we estimated the magnitude of the serial dependence bias, representing the deviation of the errors towards (attractive bias) or away (negative bias) from the previous orientation. The estimated biases were submitted to repeated-measures ANOVA and paired student t-tests for the statistical analyses (see Results). This non-parametric approach was preferred over widely used model-fitting approaches because it considers both attractive effects, typically larger for small orientation differences, and repulsive effects, which become more evident for larger orientation differences (Fritsche & de Lange, 2019). For statistical reports, *p*-values are reported up to the 3rd decimal.

In the analysis of inter-individual differences in Experiment 1, we considered the bias for the close orientation distance bin as a function of the inducer presented at 4 s ISI. The bias was used to predict the effect of the previous target at close orientation bins, by means of linear regression. The averages shown at 6 s and 12 s ISI in Figure 3D are biases at close orientation distances for the two inducers shown before the 4 s ISI inducer in trials where the sequence contained 4 stimuli (e.g., 3 inducers and 1 target).

Results

Experiment 1

Observers were presented with a sequence of oriented Gabor stimuli and reproduced the orientation of the last one (see Figure 1). On each trial, two, three, or four Gabors were presented one after the other. In the condition with two stimuli, the inter-stimulus interval (ISI) was 12 s. In the condition with three and four stimuli, the ISI between each stimulus was 6 and 4 s, respectively. Hence, the last Gabor (e.g., the one they had to respond to) was always presented at least 12 s from the first one, but with a different number of stimuli and ISI in between. We will refer to the last Gabor as *target* and to the non-reported stimuli in the sequence as *inducers*. By *last inducer*, we refer to the inducer directly preceding the target, without other stimuli in between. By *first inducer*, we refer to the inducer at the beginning of the sequence, which could or could not be followed by other inducers. These definitions held for 80% of the trials. In the remaining 20% of 'catch' trials, the sequence was interrupted randomly, and observers reported the orientation of one of the inducers (either the first, second, or third, randomly selected). Catch trials were included to avoid observers focusing exclusively on the last part of the trial. In catch trials, adjustment responses were slightly less precise compared to regular trials (group-average standard deviation [σ] of the errors in regular trials: 7.48°, σ in catch trials: 8.16°, $t(17) = -3.03$, $p = 0.007$, $d' = 0.71$).

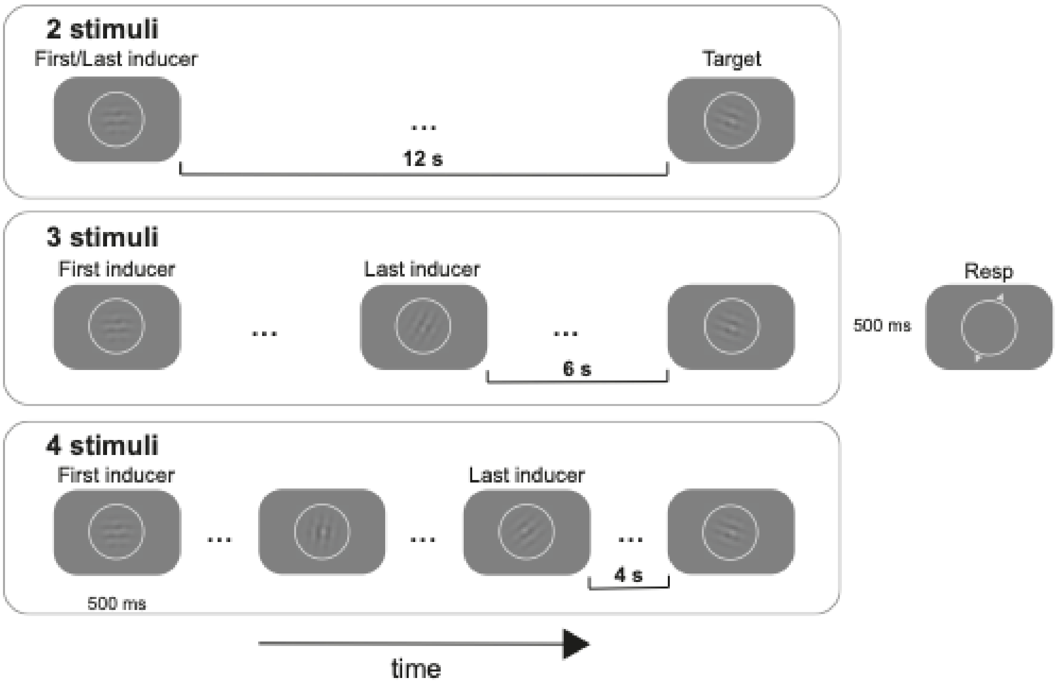

Figure 1. Stimuli and paradigm in Experiment 1. On each trial, observers were presented with a sequence of Gabor stimuli (inducers) and reproduced the orientation of the last one (target). A single trial could contain 2, 3, or 4 stimuli. Stimuli were presented inside a placeholder (white circular frame) and the response was made by adjusting the orientation of an imaginary line connecting two triangles at the extremities of the circular frame. Stimuli are not drawn to scale.

In the analysis of serial dependence, we focused on 1) the effects of previous targets and inducers; 2) the effect of the number of intervening stimuli; 3) the effect of the passage of time (ISI) in the absence of intervening stimuli.

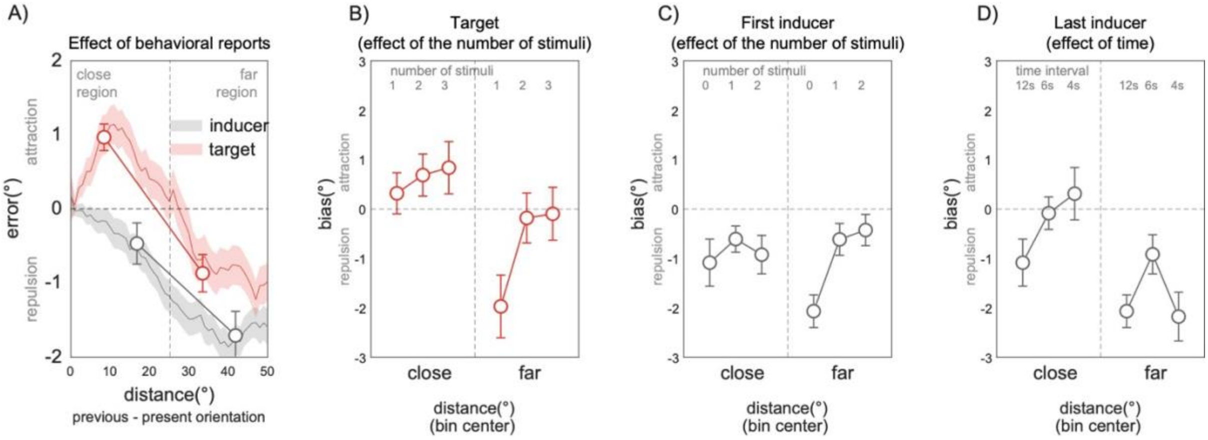

Figure 2. Results of Experiment 1. A) Serial dependence is attractive when measured on the previous target orientation (red curve) and repulsive for the inducers' orientation (gray curve). Continuous lines with shadow bars

are the running average with one standard deviation computed at the group level (Ceylan et al., 2021a). Dots represent the approximation of the curve by binning the bias at the two orientation distances (close and far regions). The inducer condition in this first plot includes the effect of all the inducers presented immediately before the target; the target condition includes the effect of all the targets reported on the previous trial, including catch trials. B) The bias from the previous target's orientation as a function of the orientation distance (bins) to the current target and the number of intervening stimuli (1, 2, 3). C) The bias from the first inducer presented at the beginning of the sequence, as a function of the orientation distance to the target and the number of additional inducers presented before the target. D) The bias from the last inducer in the sequence, as a function of the time (ISI) between the last inducer and the target. Error bars are standard errors of the mean (SEM). Note that, except for A), catch trials were excluded from the rest of the analyses and plots.

Effect of targets and inducers

Overall, errors were systematically biased towards the orientation of the previous target, showing the typical pattern of attractive serial dependence: errors were more clockwise when the previous target orientation was clockwise to the present one and the other way around when counterclockwise. Conversely, the effect of inducers was reversed: inducers caused a strong repulsive effect particularly when the orientation difference between the inducer and the current target was large (see Figure 2A).

To statistically compare the influence of the previous target and the last inducer, we computed a measure of bias at two orientation distance bins (see Figure 2A and Methods). We submitted the bias to a repeated-measures ANOVA with factors Distance (close vs. far) and Stimulus type (target [including also the target in catch trials] vs. inducer [including all inducers shown immediately before the target]), revealing a significant main effect of Distance ($F(1,17) = 40.66$, $p < 0.001$, $\eta_p^2 = 0.71$) and a main effect of Stimulus type ($F(1,17) = 14.73$, $p = 0.001$, $\eta_p^2 = 0.46$) without an interaction between the two ($F(1,17) = 2.07$, $p = 0.17$, $\eta_p^2 = 0.11$). The bias due to the previous target orientations was positive (e.g., attractive) for close orientation distances ($t(17) = 5.36$, $p_{holm} < 0.001$, $d' = 1.26$, paired t-test vs. 0) and negative when orientations were far ($t(17) = -3.46$, $p_{holm} = 0.006$, $d' = 0.82$), in line with previous findings (Fritsche & de Lange, 2019). Conversely, the bias due to the last inducer orientation was strongly repulsive for far orientation distances ($t(17) = -5.26$, $p_{holm} < 0.001$, $d' = 1.24$) but absent for close orientation distances ($t(17) = -1.70$, $p_{holm} > 0.05$).

Effect of the number of intervening stimuli

We then focused on the effect of the targets and inducers as a function of the number of intervening stimuli. In the analysis of serial dependence from the previous target (including only the targets in regular trials), a repeated-measures ANOVA with factors Distance (close vs. far) and Number of stimuli (1, 2, 3) revealed a significant main effect of Distance ($F(1,17) = 12.85$, $p = 0.002$, $\eta_p^2 = 0.43$) and of Number of stimuli ($F(2,34) = 3.95$, $p = 0.028$, $\eta_p^2 = 0.19$), but no interaction ($F(2,34) = 0.90$, $p = 0.42$, $\eta_p^2 = 0.05$; Figure 2B).

In the analysis of serial dependence from inducer stimuli in regular trials, we considered the bias due to the very first stimulus in the sequence (*first inducer*, see Figure 2C), as a function of the number of stimuli that occurred after (0, 1, 2). A repeated-measures ANOVA revealed only a main effect of the Number of stimuli ($F(2,34) = 4.00$, $p = 0.027$, $\eta_p^2 = 0.19$), but no main effect of Distance nor interaction (both $p > 0.05$).

Effect of the passage of time (ISI)

We further evaluated the effect of the ISI between the last inducer and the current target in regular trials, in the absence of other intervening stimuli (Figure 2D). A repeated-measures ANOVA with factors Distance (close vs. far) and ISI (12, 6, 4 s) revealed a significant effect of both Distance ($F(1,17) = 20.57$, $p < 0.001$, $\eta_p^2 = 0.55$) and ISI ($F(2,34) = 3.94$, $p = 0.029$, $\eta_p^2 = 0.19$), with no interaction between the two ($F(2,34) = 3.02$, $p = 0.062$, $\eta_p^2 = 0.15$).

The main results of the analyses reported above can be summarized as follows: 1) Inducers caused repulsive biases; targets caused attractive biases (Figure 2A). 2) Both attractive and repulsive biases were influenced by the number of stimuli: with more intervening inducers, the attractive bias towards previous targets increased, while the repulsive bias of the very first inducer decreased (Figure 2B-C). 3) Inducers closer in time to the current target caused less repulsion and a tendency towards attraction (Figure 2D).

Inter-individual differences

Focusing on this last result, we investigated whether the decrease of repulsive biases for inducers presented 4 s before the current target could actually reflect an increase in the attractive component tied to these stimuli. A clear difference between targets and inducers is that target stimuli were behaviorally relevant and required an adjustment response. If the relevance of the stimulus is the determinant of the direction of the bias, some participants might have expected the inducers at the end of the trial —i.e., close to the moment of the target, to be target stimuli, strengthening their positive effect on future decisions.

To evaluate this, we explored inter-individual differences in the direction of the effect of the most recent inducer. We found large inter-individual variability in the effect of the inducer presented 4 s before, with individual patterns going from strong attraction to repulsion (Figure 3A). At the individual level, the direction and strength of this bias were inversely related to the effect of the previous target (Figure 3B). Observers showing larger attractive biases towards the most recent inducer were less influenced by the previous target. Observers showing strong repulsion from the inducer were more attracted by the previous target's orientation (slope of a linear model predicting the previous target effect at close distances with the strength of the inducer effect at close distances: -0.263± 0.08, $p = 0.009$, $R^2 = 0.35$, Figure 3C). Also, for the subset of observers showing strong attractive biases towards the inducer at 4 s ISI, the bias quickly turned into repulsion for the other inducers presented at 6 and 12 s ISI (Figure 3D).

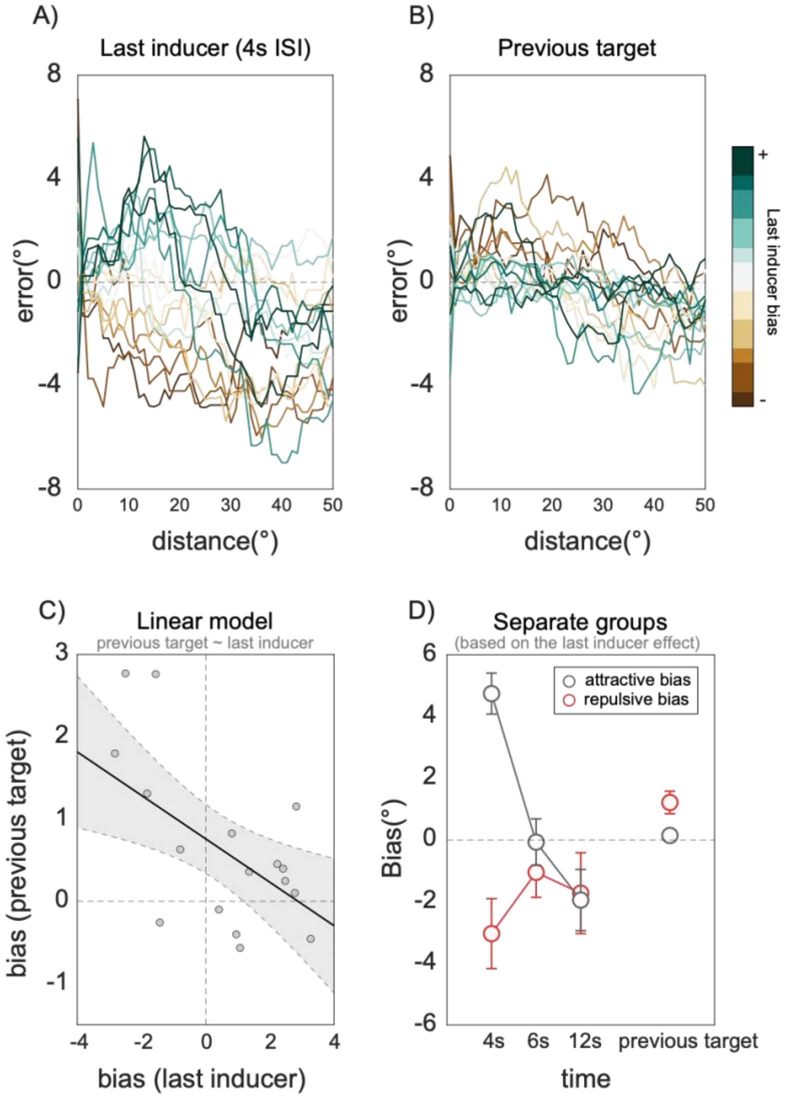

Figure 3. Results of the inter-individual analysis in Experiment 1. A) When considering the effect of the inducer presented 4 s before, individual patterns show clear variability, from strong attraction to repulsion. B) At the individual level, the direction and strength of the effect of the inducer 4 s before were inversely related to the effect of the previous target. The curves in A-B are individual moving averages (window size = 21°). The color scale is based on the direction of the effect of the inducer: strong attraction corresponds to the dark-green extremity of the scale; strong repulsion to the brown extremity. The ordering of colors in B is based on A, to highlight the inverse relationship. C) Predictions and confidence intervals of a linear model explaining the bias due to the previous target with the bias due to the inducer 4 s before the current target. The data points are individual biases for close distances only. D) Plot of two separate groups of observers depending on the effect, attractive or repulsive, of the last inducer.

Experiment 2

A clear result in Experiment 1 is the repulsive effect of inducers. One explanation is that observers paid less attention to inducers, expecting the target to occur later, as evident from the poorer performance in catch trials. Repulsive biases have been often reported as a consequence of reduced attention to the previous stimulus (Fischer & Whitney, 2014; Fornaciai & Park, 2019; Pascucci et al., 2019; Rafiei et al., 2021). To ensure that participants were equally attending to inducers and targets, in Experiment 2 we presented only one (a single target) or two stimuli on each trial (an inducer followed by a target). Hence, each stimulus had a 50% probability to be the target (see Figure 4). To further minimize repulsive effects, we also decreased the contrast, spatial frequency, and duration of the stimulus, while increasing the stimulus-response interval (Bliss et al., 2017; Ceylan et al., 2021a; Cicchini et al., 2018; Manassi et al., 2018).

The standard deviation of errors in trials with only one target stimulus (group-average of errors σ: 9.67°) was still slightly but significantly larger compared to trials where the target was preceded by an inducer (group-average σ of errors: 8.68°, $t(19) = -4.85$, $p < 0.001$, $d' = 1.08$).

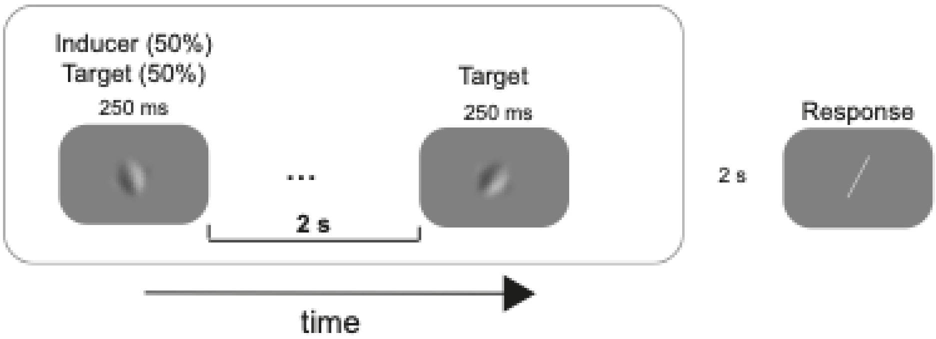

Figure 4. Stimuli and paradigm in Experiment 2. On each trial, observers were presented with only one or two Gabor stimuli. When there were two stimuli, observers had to reproduce the orientation of the second. Stimuli were shorter in duration and lower in contrast and spatial frequency compared to Experiment 1. Stimuli are not drawn to scale.

In the analysis of serial dependence, we computed the bias at three orientation distance bins (see Methods). First, we evaluated the effect of targets and inducers. A repeated-measures ANOVA revealed a significant main effect of Distance ($F(2,38) = 6.75$, $p = 0.003$, $\eta_p^2 = 0.26$) and a main effect of Stimulus type (target vs. inducer, $F(1,19) = 21.64$, $p < 0.001$, $\eta_p^2 = 0.53$) as well as an interaction between the two ($F(2,38) = 6.48$, $p = 0.003$ $\eta_p^2 = 0.25$). In line with the results of Experiment 1, errors were attracted towards previous targets and repelled away from the inducer (Figure 5A).

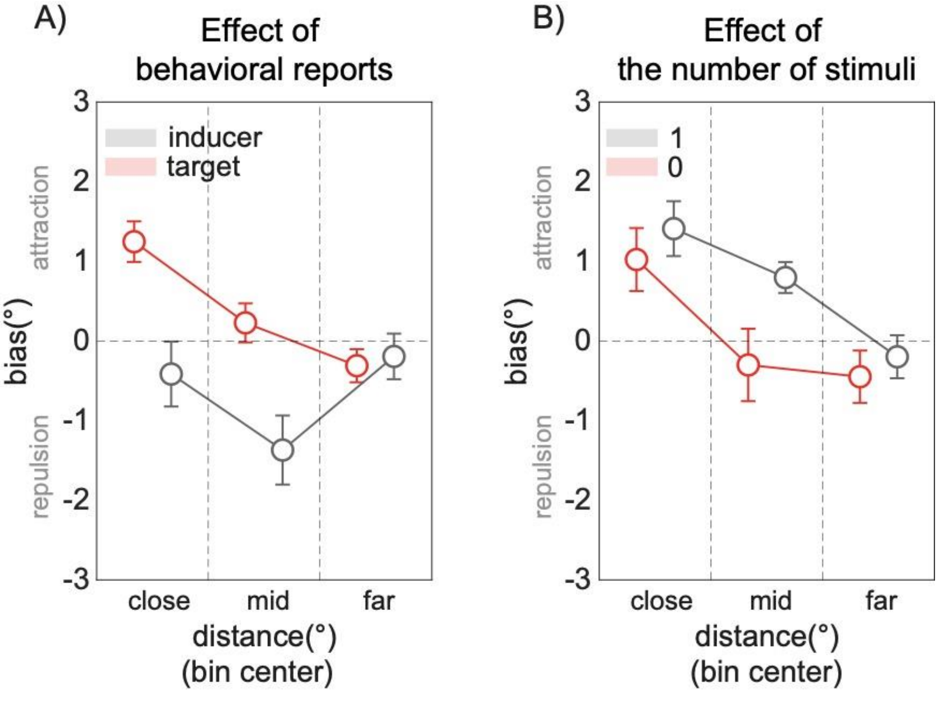

Figure 5. Results of Experiment 2. A) As in Experiment 1, the inducer (non-reported) stimulus caused a repulsive bias (gray dots and line); the previous target caused an attractive bias (red dots and line). B) The attractive bias towards the previous target increased when the current trial contained an inducer (gray dots and line), compared to when it contained only one target (red dots and line). Error bars are SEM.

Second, we evaluated whether the attractive bias was modulated by the presence of an inducer, shown after the previous target. According to the results of Experiment 1, intervening inducers should increase the attractive bias towards previous targets. A repeated-measures ANOVA with factors Distance and Number of stimuli revealed a significant main effect of Distance ($F(2,38) = 13.42$, $p < 0.001$, $\eta_p^2 = 0.41$), but no main effect of Number of stimuli nor interaction (both $p > 0.05$; Figure 5B). Further exploratory t-test analysis motivated by the results of Experiment 1, however, revealed a significant difference in the 'mid' orientation distance bin, where the attraction towards the previous target was larger if the previous target was followed by an inducer ($t(19) = -2.32$, $p_{holm} = 0.047$, $d' = 0.52$; other differences at 'close' and 'far', $p_{holm} > 0.05$, one-tailed t-test, testing the hypothesis of a difference larger than 0). Hence, although the effect of intervening inducers was not evident across all distance bins, the direction of the effect for the 'mid' distance bin was coherent with the results of Experiment 1.

Discussion and Conclusions

We investigated serial dependence as a function of the time interval and number of stimuli between the current and previous stimulus. In two experiments, observers reproduced the orientation of a stimulus (target) shown after a sequence of other stimuli with a variable number and ISI (inducers).

One of the main results of this study, confirmed in both experiments, is the opposite effect of targets and inducers. Targets caused attraction, whereas inducers caused repulsion, despite being the same stimulus (e.g., a Gabor). Continuity fields predict only attractive biases because similar stimuli are integrated over time, independently of the task (Collins, 2019; Fischer & Whitney, 2014). Clearly, such a prediction fails to explain the present results.

What is the nature of the repulsive bias? Several studies suggest that the direction of serial dependence —i.e., repulsive or attractive— depends on attention (for a review: Pascucci et al., 2023). When the previous stimulus is not attended to, the bias is repulsive (Fischer & Whitney, 2014; Fornaciai & Park, 2019; Pascucci et al., 2019; Rafiei et al., 2021). In our paradigm, particularly in Experiment 1, observers might have paid less attention to inducers at the beginning of the trial, leading to poorer performance in catch trials and a negative bias from these stimuli. Note that, compared to other studies where repulsive biases were induced by completely and explicitly unattended stimuli (Fischer & Whitney, 2014), participants in our paradigm were instructed to pay attention to the inducers because of catch trials. Indeed, the difference in performance between catch and regular trials was only in the order of 1°, indicating that inducers were still attended to and remembered, even though with less precision than the target in regular trials.

Another possibility is that, while initially attended to, stimuli that require no response —i.e., like the inducers used here, are actively removed from working memory (Shan & Postle, 2022). Although the underlying mechanisms are still debated (Fulvio & Postle, 2020), the consequence of active removal might be a systematic bias away from the previous stimulus, consistent with the one observed in our experiments (Fritsche et al., 2020; Shan & Postle, 2022). Alternatively, it is also possible that stimuli requiring no response are implicitly used as a reference for future decisions, leading to reference-repulsion effects (DeCarlo et al., 1990; Stewart et al., 2005).

Under the present paradigm, we cannot disambiguate the exact origins of the repulsive bias. Nevertheless, in this and similar experiments, the direction of serial dependence effects depends strongly on whether the previous stimulus required a response (Pascucci et al., 2019; Pascucci & Plomp, 2021). We propose that the switch of the bias, from repulsive to attractive, has to do with the maintenance and active recall of prior stimulus information when an impending task is expected (Fischer et al., 2020; Pascucci et al., 2019). This, and only this, can explain why the target orientation, reported far back in time and followed by other stimuli, was the only orientation causing an attractive bias.

While inducers shown at the beginning of the trial caused systematic repulsion, we found clear inter-individual variability in the effect of the inducer presented 4 s before the target. This finding adds to a body of evidence showing considerable inter-individual variability in the direction of serial dependence effects (Bliss et al., 2017) as well as in the effect of prior stimuli and responses (Glasauer & Shi, 2022; Zhang & Alais, 2020). In the specific context of our task, it is plausible that the source of this inter-individual variability was the degree to which different participants expected the target to occur later. Those employing such a strategy might have considered inducers occurring later —i.e., 4 s before the target, as potential targets, leading to an increase of the attractive bias.

At the group level, the attractive bias towards the inducer at 4 s ISI was inversely related to the effect of the target on the preceding trial. Participants showing strong attractive biases towards the inducer showed no effect of the previous target. Participants showing only repulsive effects showed stronger attraction towards the previous target (Figure 3D). This indicates that attractive serial dependence is a function of the number of stimuli exerting an attractive bias within a given time window: the attractive bias of a stimulus shown more than 12 s before decreases if a new and more recent stimulus also exerts an attractive bias.

The primary interest of this work was on the temporal dynamics of serial dependence, considering the role of the passage of time and the number of intervening stimuli. It is generally believed that both time and intervening stimuli reduce the effect of prior information (Kanai et al., 2007). Here, however, we report a case of the opposite: in serial dependence, intervening stimuli can actually boost the influence of stimuli shown far back in time. In both our experiments, intervening inducers increased the attractive bias towards the previous target (Figure 1B and 5B), a finding that has not been reported before. We argue that this is due to the additive co-existence of repulsive and attractive biases: additional stimuli carrying only repulsive effects (e.g., the inducers) nullify and flatten the repulsive component tied to the previous target, eventually increasing the attractive bias towards the previous target.

In sum, we showed that the temporal dynamics and direction of serial dependence effects are non-trivial aspects that depend largely on the details of the task. Existing studies have reported purely attractive (Ceylan et al., 2021; Fischer & Whitney, 2014; Fornaciai & Park, 2018; Manassi et al., 2018; Murai & Whitney, 2021), purely repulsive (Bae & Luck, 2019, 2020; Fornaciai & Park, 2019), or a mixture of attractive and repulsive serial dependence (Bliss et al., 2017; Fritsche & de Lange, 2019; Pascucci et al., 2019; Pascucci & Plomp, 2021). In most of these studies, the stimulus was always presented and reproduced at relatively fixed temporal intervals (e.g., every 4-5 s). By varying the frequency of stimuli and reports, we found an interplay between repulsive and attractive biases. Our findings demonstrate that, even in simple tasks where the same stimulus is shown at consecutive moments in time, the direction of serial dependence is dictated by the balance between these opposing biases. The effects that are ultimately measured in behavior —i.e., serial dependence— are modulated by the relevance of the stimulus to the ongoing task, the passage of time, and the number of intervening stimuli, and cannot be reduced to a single mechanism, nor a general temporal tuning window of integration in vision.

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CHAPTER 4: The Format of The Past in Serial Dependence

The format of the internal representations in serial dependence

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Abstract

Perceptual decisions are biased toward prior stimuli and prior decisions. It is believed that this bias, termed *serial dependence* (J. Fischer & Whitney, 2014), underlies a mechanism that stabilizes perception, combining similar stimuli over time. Here we show that serial dependence does not necessarily combine similar stimuli. We presented a cloud of moving dots and an oriented Gabor, fused into a single stimulus. Observers were intermittently cued to attend to either the motion or the Gabor. When the task was to reproduce the ‘tilt’ of the attended feature (e.g., either the direction of motion or the Gabor orientation), observers systematically combined the two: perceptual decisions on the Gabor orientation were biased toward the motion direction reported in the previous trial and vice versa. This occurred when trial-by-trial decisions were based on a common attribute of the two visual features (e.g., the ‘tilt’), whereas reporting the motion speed did not affect reproducing the orientation of a subsequent Gabor. This evidence suggests that serial dependence does not rely on the history of external stimuli. Rather, it operates on a reduced dimension of sensory input where the temporal information that is combined depends on the format of perceptual decisions.

Introduction

A major goal of the perceptual system is to maintain stable representations across sequential decisions and actions. It is likely to this goal that perceptual and cognitive processes show signatures of serial dependence (J. Fischer & Whitney, 2014; Fritsche et al., 2020; C. Fischer et al., 2020). Serial dependence occurs when the content of present perception, decisions, and memory is dependent on previous events (C. Fischer et al., 2020; Fritsche, Mostert & de Lange, 2017; Pascucci et al., 2023). A wealth of new evidence indicates that this temporal dependency is intrinsic to basic perceptual tasks, involving simple features like orientation and motion (Fritsche & de Lange, 2017; Ceylan, Herzog & Pascucci, 2021; C. Fischer et al., 2020). This leads to the idea that the brain relies on the recent history of visual features to smooth perceptual representations in time. Yet, serial dependence may occur at several stages of processing (Pascucci et al., 2023), and the format of the representations involved —i.e., what is the information that propagates across perceptual episodes, remains debated (Liberman et al., 2016; C. Fischer et al., 2020; Pascucci & Plomp, 2021; Ceylan et al., 2021; Collins, 2022; Houborg et al., 2023). For instance, does the perceptual system rely on the history of multiple features, even when tracking their individual changes would be wasteful and unnecessary?

Serial dependence has been linked to changes in the appearance of visual stimuli (J. Fischer & Whitney, 2014; Collins, 2020; Fornaciai & Park, 2020; Cicchini, Benedetto & Burr, 2021; Manassi & Whitney, 2022; Liberman et al., 2022). Within this perspective, recent visual inputs within a close spatial region tend to merge, fostering smooth and continuous perceptual experiences. Such integration is thought to be reflected in continuity fields, which capture the spatiotemporal tuning profile of sensory-level integration in serial dependence (J. Fischer & Whitney, 2014). The similarity of visual inputs promotes this integration, whereas distinct percepts, such as those resulting from occlusion or noise, are typically segregated.

Previous research has highlighted the influence of visual similarity on serial dependence (Fritsche & de Lange, 2019; Rafiei et al., 2021). For instance, when a Gabor stimulus is presented with similar tilt angles successively (e.g., 30˚ followed by 35˚), current orientation judgments are drawn more towards the prior stimulus orientation than when angles are more distinct (e.g., 30˚ followed by 75˚) (Fritsche et al., 2019). Yet, such findings do not definitively address the depth of integration in visual experiences or pinpoint exactly what is being integrated in serial dependence.

If this integration primarily occurs at the sensory level, serial dependence would strictly involve the physical attributes of stimuli. As an analogy, one would not expect the orientation of a tree to be judged as more similar to that of a recently observed traffic light pole. However, evidence suggests that individuals can exhibit such integrative behaviors across diverse stimuli (Ceylan et al., 2021; Tanrikulu et al., 2021).

Another layer of complexity emerges when considering the stage of feature or object identity formation. If serial dependence occurs before establishing feature or object identity, then current orientation judgments should be influenced by the previously observed stimuli, even if a different aspect of the stimulus (e.g., size or shape) was attended to (Collins 2022). Consequently, when stimuli are attended to in the same spatial location (spatial attention), they should be integrated independently of any other feature where the attention is allocated (feature-based attention). Yet, findings suggest that feature-based attention, such as focusing on a stimulus's size or shape (Fritsche & de Lange, 2019; Collins 2022), has a profound effect on serial dependence, indicating that the integration stage might surpass mere sensory processing.

Studies on emotional facial expressions provide valuable insights into the level of integration. Faces are complex objects composed of multiple features, such as attractiveness, emotions and ages (Kanwisher, McDermott & Chun, 1997). Research indicates that serial dependence in judgments of emotional facial expressions arises from integration at the sensory feature level, but only after the object identity is established (Liberman, Zhang, & Whitney, 2016; Liberman et al., 2018). For instance, current emotional facial expressions are judged more similar to past expressions primarily when faces of the same gender are presented. Interestingly, this effect persists even when faces belong to different ethnicities, suggesting that while gender may act as an 'object filter', ethnicity does not. This distinction underscores that facial emotional expressions might not be sufficiently distinct across ethnicities to categorize faces as separate objects.

However, there are conflicting perspectives on this. For example, previous research posits that even when tasks require individuals to report a single feature of a stimulus, such as orientation, secondary features like color do not disrupt serial dependence (Houborg et al., 2023). Thus, a judgment on the orientation of a green Gabor might still be influenced by the orientation of a previously seen red Gabor. But the question arises: is color, like ethnicity in facial expressions, not serving as an object filter in this context?

The constructs of feature and object identity are multifaceted, and their links to perceptual continuity and serial dependence are vast and varied. A comprehensive review by Pascucci et al. (2023) provides an in-depth exploration of these connections. Drawing from the literature and previous findings, it is speculative at best to pin down the exact mechanisms of serial dependence. Whether the integration occurs before or after object identity is established remains a question. Perhaps the visual system adopts an alternative format, abstracting internal representations. This might suggest that, for instance, tilts are what get integrated in orientation judgment taks in serial dependence.

Here we investigated the format of the representations involved in serial dependence, aiming to identify the information that propagates across perceptual episodes. We used an experimental paradigm in which two visual features, a cloud of moving dots and an oriented Gabor, were fused into a single stimulus (see Figure 1A). In each trial, observers were cued to reproduce either the Gabor orientation or the direction of motion, by adjusting a circular response tool (see Methods). When these features are presented separately, adjustment errors are typically biased toward the orientation/motion direction presented in the previous trial (C. Fischer et al., 2020; J. Fischer & Whitney, 2014). Clockwise errors occur when the previous stimulus is more clockwise and the other way around for counter-clockwise errors. The bias increases when the difference between two stimuli (Δ) is small and approximates the shape of the first derivative of a Gaussian function (*DoG*, see Figure 2A-B and Methods).

We presented the two features simultaneously to address specific hypotheses (see Figure 2 in Results). First, perceptual decisions may rely on the actual history of individual features, independently of the task (Fornaciai & Park, 2018). In this case, decisions on the Gabor orientation would be biased toward the previous Gabor, and decisions on the motion direction would be biased toward the previous motion direction. Second, the bias may be modulated by feature-based attention (Fritsche & de Lange, 2019). In this case, serial dependence could be weaker or absent when the different feature is attended/cued in consecutive trials. A third scenario is that decisions rely on the history of the common attribute that is relevant for the task: the ‘tilt’. In this case, decisions would be biased towards the orientation/motion direction reported in the previous trial, independently of whether the same feature was attended or not.

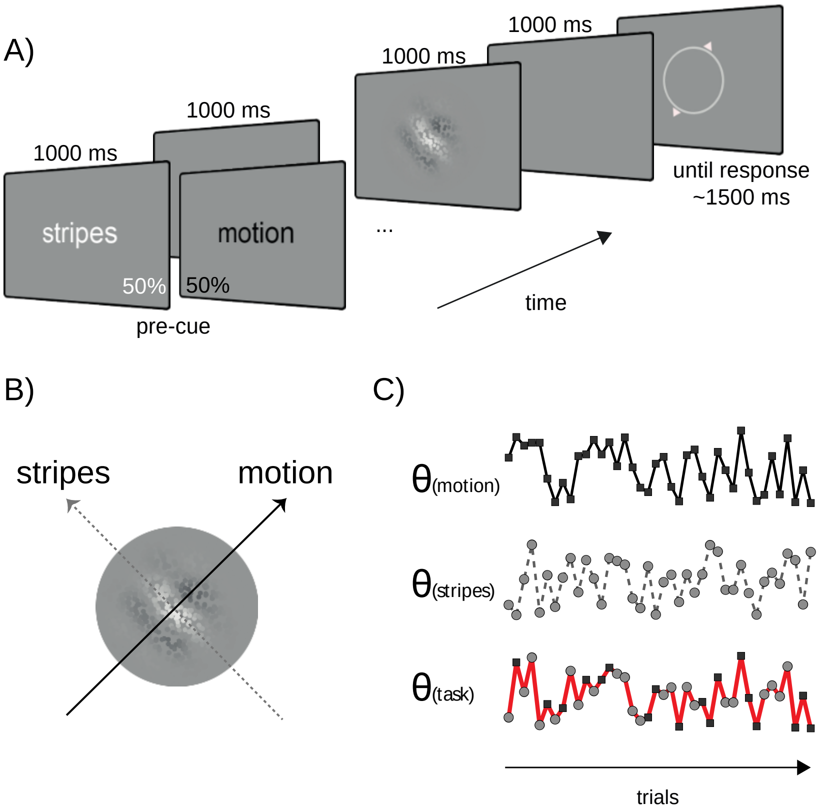

Figure 1. Experimental Paradigm. (A) This schematic illustrates the sequence of a single trial in the orientation adjustment task. At the beginning of each trial, observers received a pre-cue indicating which feature to report: either the orientation of the Gabor (stripes) or the axis of dot motion (motion), with equal probability for either option. Subsequent to the pre-cue, the stimulus (a random dot kinematogram - RDK) is centrally displayed. Following a brief blank interval, observers were presented with a response tool that consisted of a thin circular frame with two markers that delineate an imagined line. Observers rotated the markers on the circular frame to match the current feature orientation. **(B)** The illustration of the fused stimulus. The stimulus contained two visual features; the dots moving on one axis and the tilted stripes. **(C)** Trial-by-trial feature orientation manipulations. The graph depicts the independent variation of orientation signals across consecutive trials, represented by theta (Θ) values. For each trial, two orientation signals are shown: $\Theta_{(motion)}$ derived from the dot motion and $\Theta_{(stripes)}$ from the Gabor tilt. These orientations were assigned randomly from 0 to 179 degrees (in steps of 1°). The red line and $\Theta_{(task)}$ indicates the orientation that was pre-cued and subsequently reported by observers.

General methods

Ethics statement

The study received local ethics committee approval in accordance with the Declaration of Helsinki, except for preregistration (World Medical Organization, 2013).

Apparatus

Experiments were run on a gamma-corrected VG248QE monitor with a resolution of 1920 x 1080 pixels and a refresh rate of 120 Hz. Custom-made scripts, written in MATLAB (R2013a) and using the Psychophysics Toolbox (Brainard & Vision, 1997), were used to design the experiments and were run on a Windows-based computer. Stimuli were presented on a grey background with a luminance of 62.66 cd/m². The experiments took place in a darkened room, with participants seated 57 cm away from the computer screen, and their heads were positioned on a chin rest.

Participants

41 healthy participants (21 in Experiment 1 and 20 in Experiment 2, age range of 18-40 years) took part in the study for a monetary reward (20 CHF/hour). All participants had normal or corrected-to-normal vision and were naïve as to the purpose of the experiments. Freiburg Acuity test was applied to each participant to test the visual acuity, and only participants who obtained the minimum binocular acuity score of 1 (Bach, 1996) proceed to the experiments. Written informed consents were given by all participants in advance.

Stimuli and procedures

We conducted two behavioral experiments in which participants were always presented with two visually overlapping features simultaneously and pre-cued to report the properties of one or the other. The two features obtained by modulation the luminance of a random dot kinematograms (RDK: diameter of ~5°, 1000 dots, dot diameter of ~0.15°, 10% noise) with the contrast pattern of a Gaussian-windowed sinusoidal grating (peak contrast: 50% Michelson, Gaussian envelope: ~2.5°, spatial frequency: 0.33 cycle/°, noise: 40%). In this way, a single stimulus contained the dots moving on one axis and the tilted stripes. An example of a trial sequence in Experiment 1 and Experiment 2 is illustrated in Figure 1A. Each trial started with a pre-cue written either as “stripes” or as “motion” indicating whether the orientation of Gabor or the orientation of motion axis should be reported. The pre-cue was followed by a central stimulus. After a delay of 1000 ms, a response tool was presented at the same location as the stimulus. The response tool was a light grey circular frame with two symmetric triangles of which connected by an imaginary oriented line, reducing the effect of additional physical orientation signals (Ceylan et al., 2021). The initial orientation of the response tool was random at each trial. Participants rotated it by moving the computer mouse upward (clockwise rotation) or downward (counter-clockwise rotation) until it matched the perceived orientation of stripe or motion-axis and clicked left on the mouse to confirm the final decision. Each trial started after a random intertrial interval (500–1000 ms) and stimuli were assigned random orientations (0-179°, in steps of 1°). In Experiment 2, the motion task was a speed discrimination task, and the motion axis was task irrelevant. Therefore, participants reported the speed of dot-motion using a computer keyboard (e.g., S key: slow, F key: fast) instead of reproducing the motion axis. The task was the same for the stripes as in the first experiment.

Before the start of each experiment, participants were instructed written and verbal as well as they performed 20 practice trials under the supervision of the experimenter to ensure that participants understood the task. Experiments consisted of 5 blocks of 80 trials each, for a total of 400 trials and lasted approximately 1 hour.

Analysis

Before statistical analysis, we applied a two-step process to eliminate outliers from individual trial adjustments. First, any error exceeding 45 degrees was deemed a lapse and thus discarded. We also excluded any trial with adjustments slower than 10 seconds. After this exclusion, the errors underwent an additional round of processing to adjust for mean values and to eliminate any systematic reporting bias. This was achieved by taking the residuals of a fourth-degree polynomial fitted to the response errors as a function of the current orientation (Manassi et al., 2018; Van Bergen & Jehee, 2019; Pascucci et al., 2019). After the initial exclusion, we further removed any trials with extreme errors, defined as being greater than 1.5 interquartile ranges either above the upper quartile or below the lower quartile. Subsequently, the data, now free from any systematic bias and extremes, were normalized by subtracting the mean. Less than 10% of trials were excluded in both experiments. Following this, participants were excluded if they showed poor performance (where the percentage of outlier trials exceeded 20%) or displayed strong repulsive effects (values larger than 2 standard deviations from the group’s average bias). This led to exclusion of two participants in the first experiment and one participant in the second experiment.

Adjustment errors were computed as the difference between the reported and the actual orientation in each trial, bounded to ± 90°. In Experiment 1, participants performed the Gabor orientation task with an average absolute error of 5.88 ± 4.67° and average reaction times of 1.50 ± 0.70 seconds, and Motion axis task with an average absolute error of 7.79 ± 5.88° and average reaction times of 1.50 ± 0.76 seconds. In Experiment 2, the average absolute error in the orientation task was 4.69 ± 3.72° and the average reaction times were 1.66 ± 0.78 seconds while the average accuracy was 97.41% ± 4.46 and the average reaction times were 0.64 ± 0.15 seconds in speed discrimination task.

We used a model-free approach (Ceylan et al., 2021; Samaha, Switzky & Postle, 2019) to quantify serial dependence. For each participants, we subtracted the average error for the acute angle distance between the previous and the present orientations (Δ) in the 1-45° range from the average error in the corresponding negative range of Δ. In this way, we estimated the magnitude of the serial dependence bias, representing the deviation of the errors toward (attractive bias) or away (negative bias) from the previous orientation. The estimated biases were tested with Student t-tests for the statistical analyses (see Results). Effect sizes (Cohen's *d'*) were obtained from the model-free results. For statistical reports, p-values are reported up to the third decimal. In Figures 3A-B and 4A-B, we presented adjustment errors as a function of Δ, fitted by a derivative of Gaussian function (DoG) following the same procedure as in Ceylan et al. (2021). However, these results are only used for the qualitative inspection and not included in the subsequent analyses.

Results

In our study, we presented two features simultaneously fused into a single stimulus to test three hypotheses: 1) Decisions are based on the history of individual features independently of the task, 2) Bias is modulated by feature-based attention, and 3) Decisions depend on the history of the task-relevant reduced format: the 'tilt' (See Introduction and Figure 2 caption for details). We tested these predictions on the behavioral data obtained from 39 healthy observers.

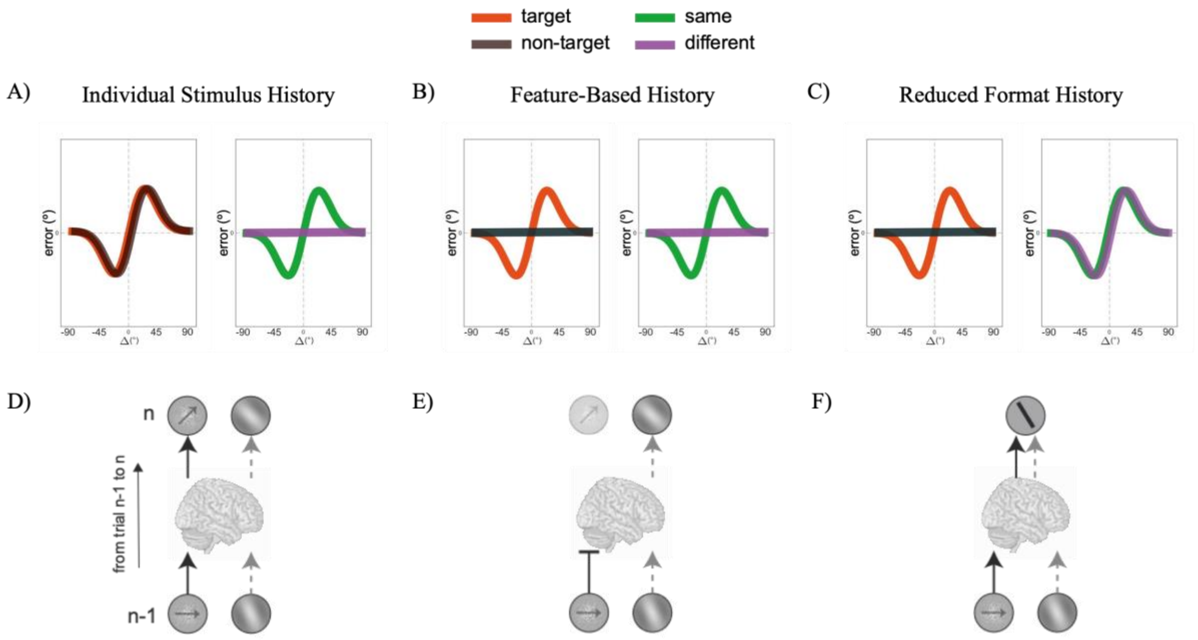

Figure 2. History Hypotheses. The upper panel displays the qualitative predictions of serial dependence across three hypotheses, visualized using hypothetical fits of the derivative of Gaussian function (DoG). DoG fits represent the predicted patterns of adjustment errors as a function of the angular difference between the orientation of the previous and the present featue (Δ). Different colors represent types of previous stimulus features. The lower panel presents schematic diagrams that demonstrate the hypothesized transfer of information from one trial to the next, corresponding to each scenario depicted in the upper panel. Arrows signify the presence of serial dependence, whereas their absence suggests a lack of shared history influencing current judgments. Solid and dashed lines symbolize the feature types within the stimulus, representing motion and Gabor patterns, respectively. **(A)** Individual Stimulus History: Serial dependence is solely linked to the history of stimulus independently of the task at hand. It arises only for the feature from the preceding trial that matches the feature reported in the current trial, regardless of whether the previous stimulus was reported. **(B)** Feature-Based History: Serial dependence is modulated by feature-based attention. It occurs only for the feature attended in the previous trial and increase when the previous feature type is same as the one in the current trial. **(C)** Reduced Format History: Serial dependence pertains to the shared task-relevant format. A non-reported feature does not yield serial dependence and the type of reported feature does not modulate serial dependence. **(D)** Individual Stimulus History: This schematic illustrates that each feature type maintains its trajectory of influence, irrespective of its target status in the previous trial. A previous non-target motion feature can induce serial dependence on a current target motion feature, but a previous target Gabor feature will not affect the current motion judgments. **(E)** Feature-Based History: Depicted here is a scenario where attention to a particular feature type modulates serial dependence. The absence of an arrow from the previous motion feature to the current Gabor target indicates that differing feature types (motion vs. Gabor) from one trial to the next do not exhibit shared history, thereby reducing or eliminating serial dependence in this case. **(F)** Reduced Format History: In this hypothesis, the feature type is immaterial; what matters is the task-relevant information—orientation. Thus, orientation information from a target feature in one trial leads to serial dependence in the subsequent trial, regardless of feature type. The tilt symbol in the current trial signifies that only orientation information is relevant for task performance, predicting that orientation from any feature type will share a common history and influence orientation judgments in the following trial.

In Experiment 1, we evaluated the group average bias due to the feature that was cued (and reported – *target*), and to the one that was only exposed (but not reported – *non-target*) in the previous trial. When considering the relationship between adjustment errors and the *target* feature, we found strong serial dependence. Responses were systematically biased toward the tilt of the previously reported feature, (target feature amplitude: 1.46 ± 1.33°; $t(1,18) = 4.77$, $p < 0.001$, $d' = 1.09$) as shown in Figure 3C. Conversely, the feature *exposed* but irrelevant in the previous trial did not affect adjustment responses, leading to a flat bias (non-target feature amplitude: -0.30 ± 1.17°; $t(1,18) = -1.11$, $p = 0.280$, $d' = -0.26$; Difference of amplitudes: 1.76 ± 1.84°; $t(1,18) = 4.15$, $p < 0.001$; $d' = 0.95$). This confirmed that serial dependence occurs mostly for behaviorally relevant features that are under the current and previous focus of attention (Fritsche & de Lange, 2019; Pascucci et al., 2019; Pascucci & Plomp, 2021).

While the results of this analysis align with the second scenario and appear in agreement with previous work (Fritsche & de Lange, 2019; Pascucci et al., 2019; Pascucci & Plomp, 2021), they cannot reveal whether serial dependence occurred only when the *same* feature was cued in the previous and present trial or even for *different* features (Ceylan et al., 2021). This latter possibility would provide evidence in favor of the third scenario. To disentangle this, we ran a further analysis separating trials in which the cued feature in the previous trial was the same as in the present (e.g., the Gabor orientation followed by the Gabor orientation) or was a different one (e.g., the motion direction followed by the Gabor orientation). Surprisingly, as shown in Figure 3D, serial dependence was comparable between the two conditions (Same target feature amplitude: 1.19 ± 2.05°; $t(1,18) = 2.54$, $p = 0.021$, $d' = 0.58$; Different target feature amplitude: 1.78 ± 1.89°; $t(1,18) = 4.11$, $p < 0.001$, $d' = 0.94$; Difference of amplitudes: -0.59 ± 2.99°; $t(1,18) = -0.86$, $p = 0.403$; $d' = -0.20$). Hence, in trials where the cued feature changed, observers systematically combined the previous motion axis with the present Gabor orientation and vice versa.

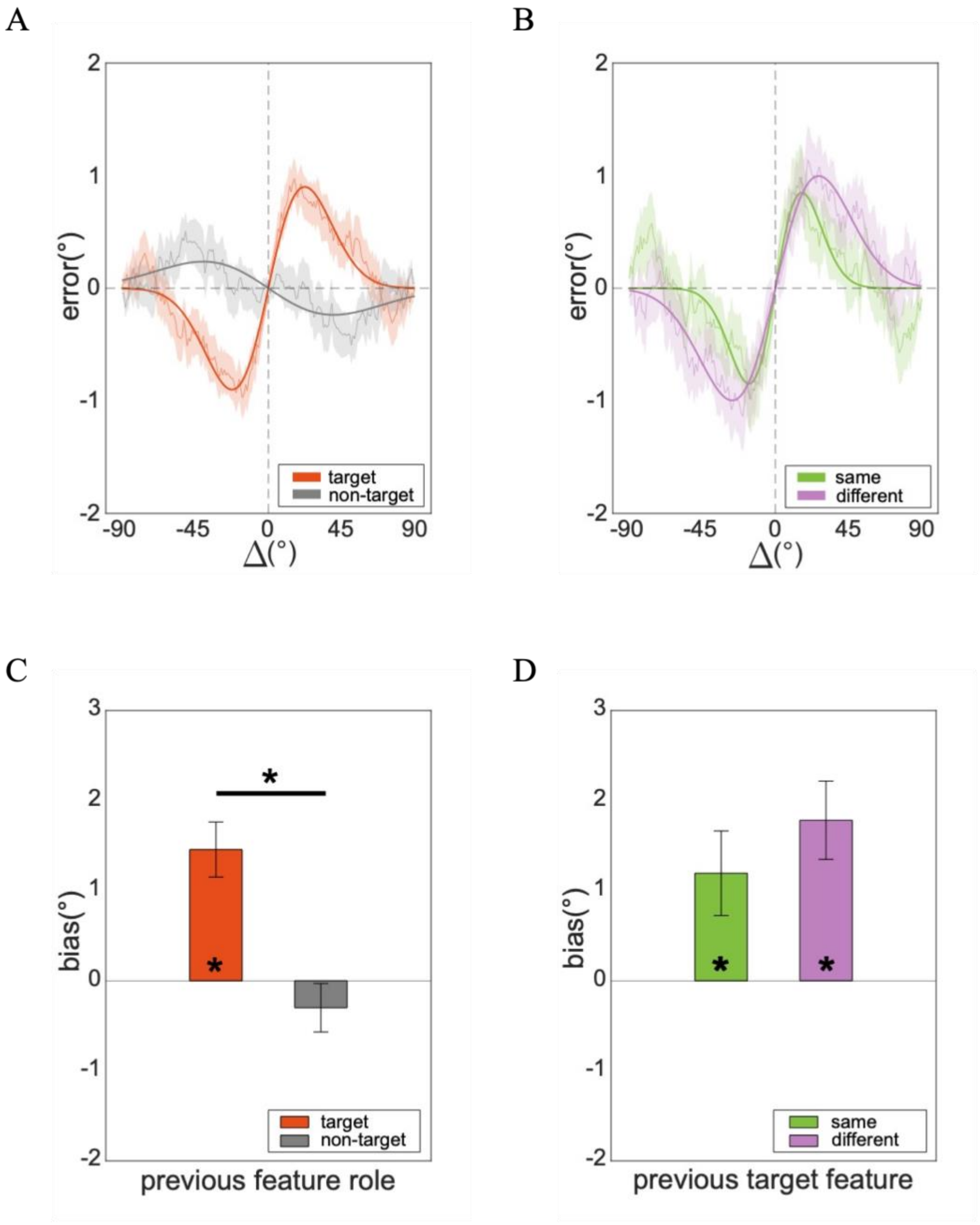

Figure 3. Serial Dependence in Experiment 1: (A-B) Adjustment errors as a function of the angular difference between the orientation of the previous and the present feature (Δ), fitted by a derivative of Gaussian function (DoG). Thinner lines and shaded regions represent the bootstrap estimate and standard deviation of the participants' average errors. **(A)** Serial dependence for the previous Target (in red) and Non-Target (in dark-grey) feature. **(B)** Serial dependence when the previous target is of Same (in green) and Different (in purple) type as the target feature in the current trial. **(C-D)** Model-free analyses quantifying serial dependence bias as the difference between the average of errors in a positive (from 1° to 45°) and negative (from -1° to -45°) range of the Δ variable. Error bars represent the standard errors of the mean (SEM). Asterisks indicate statistically significant differences ($p < 0.05$).

These findings have an unequivocal interpretation: perceptual decisions do not necessarily track the history of visual features but rely on a reduced dimension determined by the task, lending clear support to our third scenario. Moreover, they clarify the type of attentional processing involved in serial dependence (Fritsche & de Lange, 2019): attending to a specific feature (e.g., motion) does not prevent serial dependence to a different feature (e.g., Gabor orientation) if there is a common relevant dimension that the two features share (e.g., the 'tilt'). To further prove this point and to confirm that simply attending to motion (and not specifically to the direction of motion) is not sufficient, we ran a second experiment.

In Experiment 2, we used the same stimulus and varied the speed of motion in the could of dots. A separate group of participants was intermittently cued to report either the motion speed, with a binary choice response (slow vs. fast), or the Gabor orientation as in the first experiment. By asking participants to focus on a different attribute of the cloud of dots, the direction of motion was no longer a source of bias for the perceptual decision about the Gabor orientation in the next trial. As result, in line with Experiment 1, serial dependence occurred in current Gabor orientation judgments exclusively for the previously cued feature (Target feature amplitude: 0.64 ± 1.18°; $t(1,18) = 2.39$, $p = 0.028$, $d' = 0.55$), and interestingly, this time we observed a repulsive bias for the exposed but not reported stimuli (Non-target feature amplitude: -0.59 ± 1.14°; $t(1,18) = -2.23$, $p = 0.038$, $d' = -0.51$; Difference of amplitudes: 1.23 ± 1.84°; $t(1,18) = 2.92$, $p = 0.009$; $d' = 0.67$, Figure 4C). Additionally, consistent with the Reduced Format predictions, current orientation judgments were attracted towards previous orientations only when the cued feature pertained to the tilt (i.e., the Gabor orientation) and not the speed (Same target feature amplitude: 1.43 ± 1.92°; $t(1,18) = 3.23$, $p = 0.005$, $d' = 0.74$; Different target feature amplitude: -0.17 ± 1.42°; $t(1,18) = -0.52$, $p = 0.610$, $d' = -0.12$; Difference of amplitudes: 1.60 ± 2.53°; $t(1,18) = 2.75$, $p = 0.013$; $d' = 0.63$, Figure 4D).

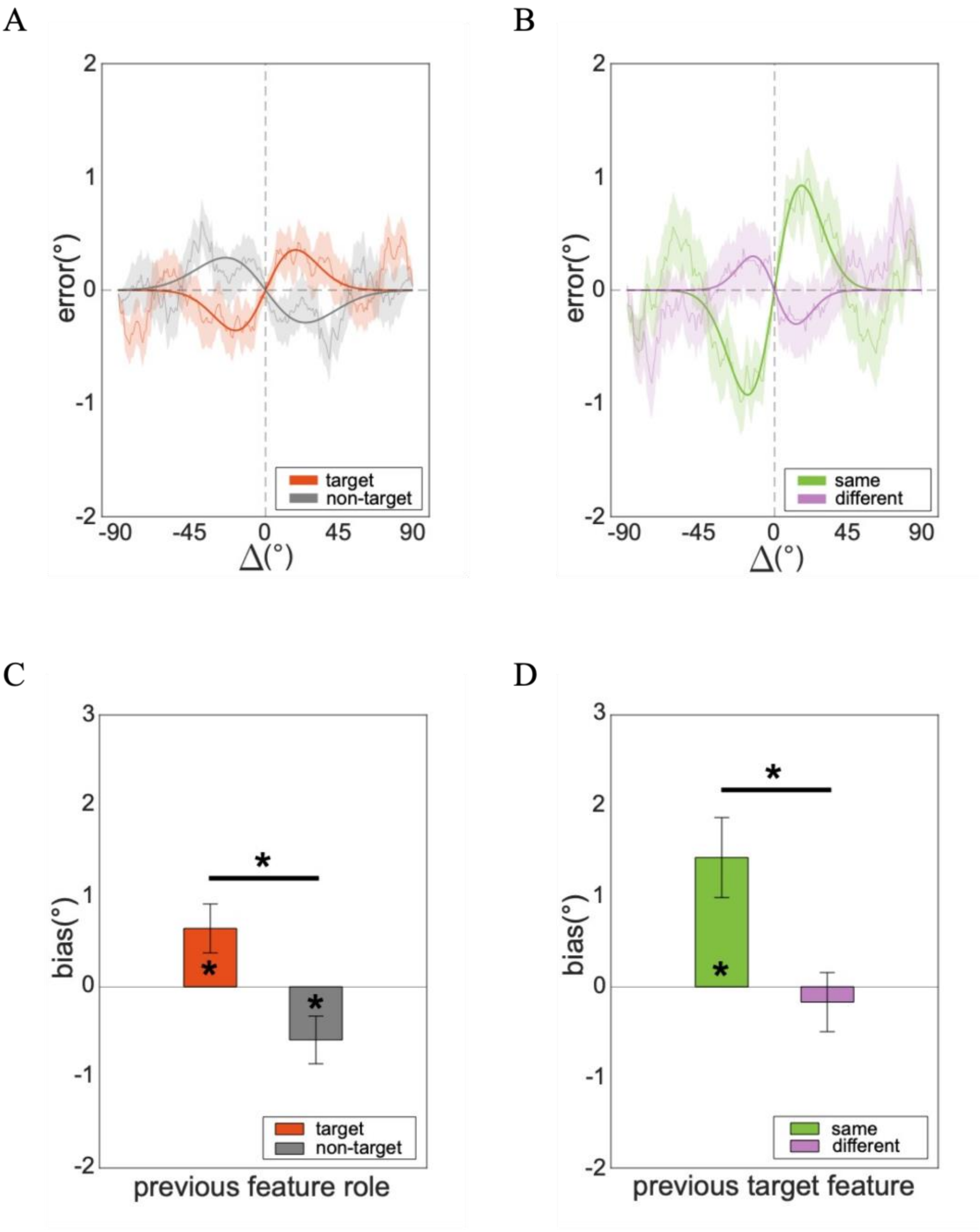

Figure 4. Serial Dependence in Experiment 2: (A-B) Adjustment errors as a function of the angular difference between the orientation of the previous and the present feature (Δ), fitted by a derivative of Gaussian function (DoG). Thinner lines and shaded regions represent the bootstrap estimate and standard deviation of the participants' average errors. **(A)** Serial dependence in adjustments of Gabor orientation in the current trial for the previous Target (in red) and Non-Target (in dark-grey) feature. **(B)** Serial dependence in adjustments of Gabor orientation when the previous target is Same (i.e., Gabor, in green) and Different (i.e., Motion, in purple) type as the target feature in the current trial (i.e., Gabor). **(C-D)** Model-free analyses quantifying serial dependence bias as the difference between the average of errors in a positive (from 1° to 45°) and negative (from -1° to -45°) range of the Δ variable. Error bars represent the standard errors of the mean (SEM). Asterisks indicate statistically significant differences ($p < 0.05$).

Discussion

In this study, we investigated serial dependence in perceptual decisions for stimuli containing two visual features. We found a systematic bias toward the previous trial when decisions were made upon a common attribute of the two features —i.e., the tilt: the previous direction of a cloud of moving dots biased the present decision on the orientation of a contrast pattern and vice versa. This bias occurred independently of the individual history of the two features and only when the common attribute was attended and task-relevant. We, therefore, report a clear case in which serial dependence is 1) stimulus-independent and 2) strongly modulated by attention and task relevance.

The independence of the bias from the individual history of the two features does not imply that serial dependence is completely unrelated to perception, neither it marks the involvement of a specific stage of processing. We interpret this result as moving beyond the ongoing debate about the perceptual or post-perceptual dichotomy (J. Fischer & Whitney, 2014; Cicchini et al., 2014; Liberman et al., 2014; Liberman et al., 2018; Manassi et al., 2018, Fritsche et al., 2017; Fritsche et al., 2020; Pascucci et al., 2019; Kim et al., 2020; Ceylan et al., 2021; Manassi, Murai & Whitney, 2023; Cicchini et al., 2024). Serial dependence may occur at different stages (Pascucci et al., 2023) or at a single stage that flexibly adapts to the task. In all cases, drawing a sharp line might be reductive. Given the continuum between decisional, attentional, memory, and perceptual processes, for instance, the bias may originate late (e.g., during decisions or in working memory) and affects early stages of processing in the next trial according to feedback and recurrent schemes (Fornaciai & Park. 2022; Fulvio, Rokers & Samaha, 2023). We do, however, provide an important piece of evidence about the representational format of serial dependence. Our findings demonstrate that serial dependence does not necessarily reflect the history of what we see, in terms of individual changes in external features and objects. We show that serial dependence relies on internal representations, also called *priors* in previous work (Hohwy, 2017; Van Bergen & Jehee, 2019), that depend strictly on the format of perceptual decisions and may not be tied to the actual history of sensory input. While at first this can be viewed as a bug, more than a feature, it could indeed underly a cost-effective strategy to maintain stable and low-dimensional representations across perceptual decisions, by reducing the dimensionality of sensory input to the attribute required for behavior (Kwak & Curtis, 2022; Pascucci et al., 2023).

Our results also confirm that attention plays a key role in serial dependence (J. Fischer & Whitney, 2014) since the bias was evident only when the common attribute of the two features was cued and actively attended. But the type of attention involved requires a more sophisticated definition of *feature-based* attention (Fritsche & de Lange, 2019), given that attending to distinct features (e.g., the dots motion or the Gabor orientation) did not prevent the temporal combination of their common attribute.

Hence, we demonstrated that serial dependence acts on a reduced dimension of sensory input that is relevant for behavior, after condensing all irrelevant aspects of sensory input. This may not be the only possible form of serial dependence and could represent a case that dominates under the present experimental context. Yet, the bias is in all respects identical to the one reported in many studies using a single visual feature and adjustment response tasks, which makes a generalization legitimate. This is precisely where the significance of our study emerges, as it provides a crucial contribution to understanding the representational nature of serial dependence, suggesting a sophisticated perceptual mechanism that prioritizes behavioral relevance over the fidelity of sensory history.

The primary focus of this study was on the format of representations that propagate from one trial to the next in serial dependence. Prior research has primarily examined serial dependence with the same type of stimuli presented and reported in sequence. However, natural environments expose us to multiple sensory inputs simultaneously, many of which are irrelevant to our immediate tasks. Drawing inspiration from such natural scenes, our study investigated serial dependence in a novel context, using fused stimuli where two distinct features were spatiotemporally overlaid. In concurrence with earlier research (Ceylan et al., 2021; Tanrikulu et al., 2023), our results indicate that serial dependence can manifest across distinct features, suggesting that it is not exclusively tied to the history of the stimulus. Accordingly, we propose that serial dependence might operate at more abstract internal representations, where various stimulus features are condensed into the basic formats required by a given task. For example, the orientation of stripes and the motion axis of dots may both be reduced to representations of a tilted line (Kwak & Curtis, 2022).

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GENERAL DISCUSSION

Summary

Serial dependence is a long-standing topic that has received renewed interest in the past decade. Despite considerable research to date, the true nature and role of this phenomenon are yet to be fully understood. The goal of this thesis was to elucidate the origin and role of serial dependence in human vision. Multiple lines of evidence, gathered through psychophysical methods, are presented to distinguish between the perceptual and post-perceptual nature of serial dependence and to identify the key cognitive factors at play.

In **Chapter 1**, I provided a detailed review of the major paradigms, methodologies, and findings in serial dependence research over the past decade. Importantly, this represents the first comprehensive review in the serial dependence literature, aimed at guiding future research by identifying common factors amidst a range of contrasting findings. The chapter also highlighted that serial dependence emerges from a complex interplay among the stimulus, task environment, and cognitive processes.

Moreover, the chapter addressed ongoing theoretical debates regarding the role of serial dependence in maintaining object continuity. Although it is widely believed that serial dependence facilitates object continuity, there is disagreement over the precise level at which this process occurs—whether it is at the feature, object, or abstract level. The review posited that serial dependence is not fixed; instead, it adjusts to the demands of different tasks, suggesting that various tasks might induce distinct biases. These biases are contingent on the brain's selection of the simplest and most efficient representation to execute the given task.

In **Chapter 2**, I addressed a critical yet previously neglected question: Does serial dependence occur for entirely dissimilar features and stimuli? Through two behavioral experiments, I demonstrated that serial dependence is not exclusive to basic physical properties of stimuli or to the visual objects themselves. Moreover, the influence of serial dependence is determined by the uncertainty of the current stimulus, not the previous one. These results suggest that serial dependence may not be merely a low-level perceptual bias since it is not selective to specific features or objects. The extent of its contribution to enhancing visual perception is also questionable as it adjusts based on the present level of uncertainty only. While Bayesian theories suggest that serial dependence fosters perceptual stability by reducing current uncertainty through bias towards previous less uncertain stimuli, my findings challenge this view, casting doubt on the Bayesian perspective of serial dependence.

In **Chapter 3**, I investigated the roles of time, number of stimuli and the task relevance in serial dependence through two behavioral experiments. The results revealed that serial dependence is jointly modulated by time, number of stimuli, and task relevance, with these factors interacting with each other. This interaction implies that no single criterion can independently define serial dependence. Specifically, the influence exerted by a past stimulus can vary depending on the number of intervening stimuli, challenging previous research that identified time as the sole criterion for serial dependence.

Furthermore, my findings contradicted the broadly accepted notion of serial dependence as predominantly attractive. In certain contexts, stimuli not directly reported (referred to as inducers) could induce a repulsive bias, leading to the current stimulus being perceived as dissimilar to its predecessors. This observation adds a layer of complexity to our understanding of serial dependence, suggesting that the phenomenon cannot be simplified to a singular mechanism or a general temporal window of integration in vision.

In **Chapter 4**, I further disentangled the perceptual and post-perceptual nature of serial biases. Specifically, I examined the origins of attractive biases—whether they stem from a history of stimuli and feature-selective representations or from task-relevant internal representations. By employing a novel task across two behavioral experiments, I uncovered that attractive biases in current orientation judgments are confined to task-relevant internal representations and manifest only when the preceding task involved orientation. These findings support a post-perceptual origin for attractive serial dependence.

Distinct Origins of Two Opposite Biases

Previous research (J. Fischer & Whitney, 2014; Cicchini et al., 2017; Manassi et al, 2019; Fornaciai et al., 2018) posits that attractive serial dependence is a perceptual phenomenon, reflecting a shift in the *appearance* of the current stimulus towards previously seen stimuli. According to this theory, attractive bias might emerge during sensory encoding, where the previous stimulus alters the current orientation-tuning, leading the current orientations to be perceived more similar to the preceding one. On the other hand, this thesis presented multiple evidence indicating that attractive serial dependence emerges at a visual processing stage beyond encoding. For instance, Chapters 2 and 4 demonstrated that attractive serial dependence does not selectively apply to the physical properties of stimuli.

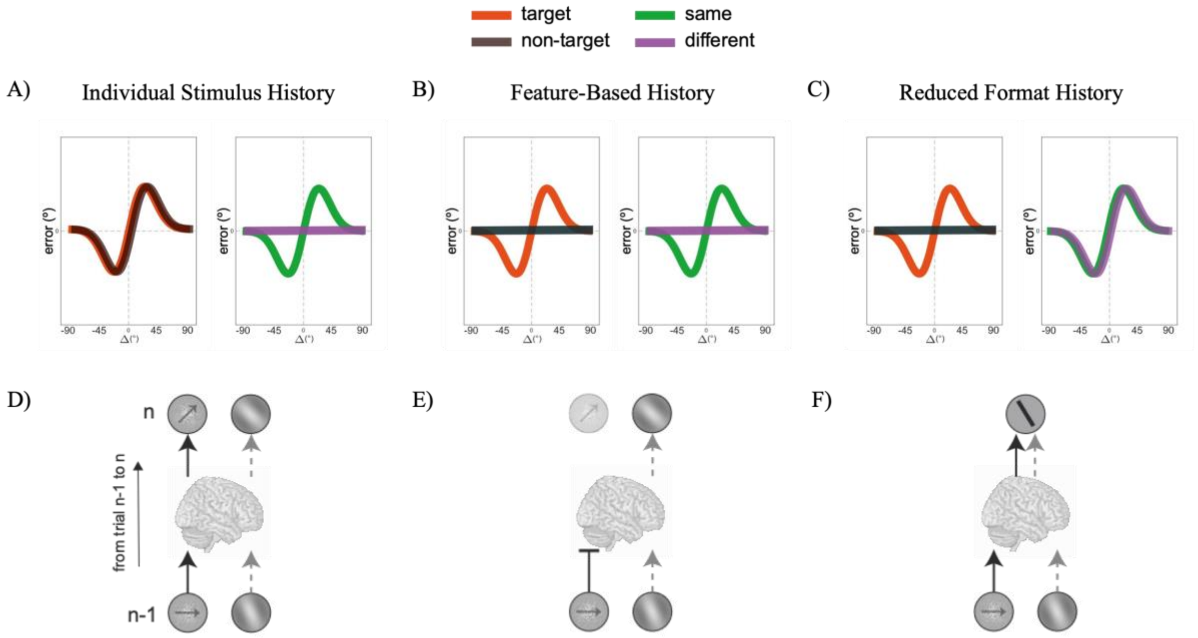

Figure D.1. Serial Dependence Hypotheses. The upper panel displays the qualitative predictions of serial dependence across three hypotheses. The lower panel presents schematic diagrams that demonstrate the hypothesized transfer of information from one trial to the next, corresponding to each scenario depicted in the upper panel. **(A)** and **(D)** Individual Stimulus History: Serial dependence is solely linked to the history of stimulus independently of the task at hand. **(B)** and **(E)** Feature-Based History: Serial dependence is modulated by feature-based attention. **(C)** and **(F)** Reduced Format History: Serial dependence pertains to the shared internal representations reduced to task relevant format (Details are provided in Chapter 4 Figure 2 caption).

Had serial dependence originated at earlier stages of visual processing, it should have applied only to visually similar stimuli—as strongly proposed by perceptual accounts —, negating the presence of an attractive bias in experiments where I used profoundly different stimuli

(Chapters 2 and 4). This is because, in the initial stages of visual information processing, the visual system operates with high specificity to basic features like orientation and spatial frequency (Blakemore, Muncey, & Ridley, 1973). Such specificity results in varied neural activity in the primary visual cortex (V1/V2) even for slightly different stimuli. However, as processing progresses to advanced stages, this specificity diminishes, particularly as neurons develop larger receptive fields for complex stimuli, losing the specificity to low-level properties such as orientation (Zhang, & Tadin, 2019). Given this hierarchical framework, a bias applicable only to specific stimuli and basic features would suggest early-stage origin in the visual system. Adaptation, a well-documented *perceptual* phenomenon, exemplifies this principle. It necessitates prolonged exposure to the same feature or stimulus, causing sensory receptors to become less responsive (Kohn, 2007). The tilt-aftereffect, a well-studied effect of orientation adaptation, results in a shift in perceived orientations away from preceding ones, showing high selectivity to sensory properties (He & MacLeod, 2001).

The attractive bias that is not confined by sensory properties may suggest the engagement of post-perceptual mechanisms, such as working memory and decision-making. Notably, in my experiments the attended objects or features changed randomly across trials (Chapters 2 and 4). Perceptual accounts would predict the attractive bias only when the same feature is attended across successive trials (e.g., from Gabor to Gabor only). However, I observed comparable attractive biases both when the same feature was reported consecutively and when it changed (e.g., the biases were similar whether from motion to stripe or from motion to motion in Chapter 4). These findings may provide additional evidence for an attractive serial dependence in the task relevant representations rather than the appearances of the stimulus (see Figure D.1).

Moreover, Chapter 4 presents evidence that feature-based attention can significantly modulate attractive bias, supporting post-perceptual accounts (Fritsche & de Lange, 2019). Importantly, this modulation is contingent on variations of task formats (e.g., speed vs. orientation), rather than differences in stimulus formats (e.g., motion orientation vs. Gabor orientation). For instance, in Experiment 1, when the orientation of motion was reported in the previous trial, current decisions on stripe orientations were attracted to previous stimuli (and vice versa), showing no modulation due to feature-based attention. Conversely, in Experiment 2, when the previously reported feature was the speed rather than the orientation of motion, current decisions on stripe orientations were not attracted to previous stimuli. Similar findings were previously presented by Fritsche & de Lange (2019), showing that attractive bias was significantly reduced in orientation judgments if the previously attended feature pertained to size rather than orientation, while the adaptation-like repulsive bias remained unchanged. These findings provide evidence for the involvement of post-perceptual mechanisms in attractive bias, while the repulsive biases appear to be of a perceptual nature since they were not modulated by attentional manipulations. When the task requires a decision about a different property (e.g., speed or size), orientation information becomes task-irrelevant; therefore, it is unlikely to be maintained in, and retrieved from, working memory. Therefore, at least in my experiments, attractive serial dependence is not stimulus-driven but task-driven (as hypothesized in Reduced Format History in Figure D.1, also see Chapter 4).

Consequently, making a perceptual decision might be a prerequisite for attractive serial dependence. Consistent with this notion, the results from Chapter 3 revealed that when the same object was attended but not reported, no attractive bias was observed. Instead, an adaptation-like repulsive bias occurred, in line with previous research (Fritsche et al., 2017; Pascucci et al., 2019; Pascucci & Plomp, 2021). Importantly, these opposite biases did not conform to the traditional temporal tuning of perceptual bias (i.e., continuity field, J. Fischer & Whitney, 2014). An attractive bias was found for stimuli reported in the more distant past, while a repulsive bias emerged for stimuli that were attended to (but not reported) more recently. Interestingly, this repulsion diminished as the number of intervening stimuli increased — a finding not explained by the continuity field theory. This alternative tuning suggests distinct origins for repulsive and attractive biases. It is plausible that reported stimuli were engaged within the same history and facilitated attraction, attended (but not reported) stimuli were disengaged in working memory, leading to repulsive biases (Pascucci et al., 2019; Pascucci & Plomp, 2021; Biryukov et al., 2021; Blonde et al., 2023).

While making a perceptual decision may be crucial, research (see Supplementary Projects) indicate that it does not always lead to attraction in subsequent trials. Attractive biases in these experiments appeared only in decisions preceded by trials with a response delay, which allowed for the maintenance of information in working memory. In contrast, trials preceded by immediate responses exhibited no such biases. This pattern aligns with findings from previous research (Bliss et al., 2017; Stein et al., 2020; Barbosa et al., 2020), where retention periods were manipulated. These previous studies collectively reveal that attractive biases only emerge when there is a response delay, allowing for engagement with working memory.

The findings outlined in this thesis propose distinct mechanisms for the two opposite forms of serial dependence: stimulus-driven repulsive bias and task-driven attractive bias. Attractive bias is posited to arise at a post-sensory encoding stage, engaging higher-level conscious processing mechanisms. In contrast, repulsive bias may originate during the sensory encoding, potentially induced by the absence of a task. The effects of both forms can be observed at multiple stages of decision-making, including perception, with one form dominating the other depending on various factors (see Chapter 1).

The Role of Serial Dependence

Another controversial topic in serial dependence research is its role in the visual system. Previous research has followed two major rationales to address the potential roles of attractive serial dependence: 1) it provides a coherent perception and promotes perceptual continuity by integrating similar percepts over time, and 2) it functions as a tool to reduce current visual uncertainty, combining uncertain information with more reliable one for optimal perception.

Throughout this thesis, I have consistently demonstrated that attractive serial dependence can be observed between entirely distinct visual features and stimuli (Chapters 1, 2, 4), and can have a different temporal tunning profile (Chapters 3, 4) than the one suggested to promote perceptual continuity (i.e., continuity field, J. Fischer & Whitney, 2014). These findings challenge the notion that this type of bias contributes to coherent perception, as there is no apparent benefit in integrating completely different visual properties for the sake of perceptual continuity.

Yet, continuity can be explored beyond perception, extending into areas such as memory (Bliss et al., 2017; C. Fischer et al., 2020; Collins 2022). For instance, Bliss et al. (2017) highlight the emergence of attractive bias as a result of temporal autocorrelation in visual working memory rather than in perception. C. Fischer et al. (2020) suggest that the congruency between content (task-related or top-down properties) and context features (stimulus-related or bottom-up properties) helps link objects encoded in working memory (referred to as object-files; see Kahneman et al., 1992), facilitating attractive serial dependence. While this could be interpreted as serial dependence being a product of such mechanisms, they also raise the possibility that the mechanisms ensuring object continuity might be further promoted by attractive serial dependence. This is reminiscent of the 'chicken-egg' problem discussed in Chapter 1 and aligns with scenarios proposed by Collins (2022).

Moreover, previous studies have collectively suggested that the visual system employs serial dependence as a strategy to mitigate stimulus uncertainty, particularly when the preceding stimulus is less uncertain than the subsequent one. These studies have utilized principles of Bayesian and adaptive filtering to model serial dependence (Cicchini et al., 2018; Van Bergen & Jehee, 2019). To further investigate, I examined the performance of two models in predicting the strength of bias across stimuli with varying levels of uncertainty (Chapter 2).

Specifically, I utilized an ideal observer model (Cicchini et al., 2018), predicting a stronger attraction when prior stimulus is less uncertain (i.e., high spatial frequency Gabor), and alternatively provided an uncertainty-only model that predicts a stronger attraction when the current stimulus is more uncertain (low spatial frequency Gabor) independently of the preceding uncertainty. Behavioral results showed the opposite trend to the ideal observer model; bias was highest when successive stimuli more uncertain, which was successfully captured by the uncertainty-only model, and it reduced when the previous stimulus was less uncertain. This indicates that attractive serial dependence is a bias induced by the uncertainty, not necessarily aiming to reduce this uncertainty for optimal perception.

In summary, as elaborated in Chapter 1, perceptual continuity is a hard topic with overlapping definitions involving features and objects (the criteria defining ‘features’ and ‘objects’) and the concept of continuity itself (see ‘The Problem of Object Continuity’ in Chapter 1). While the literature is abundant with both direct and indirect evidence highlighting the link between perceptual continuity and serial dependence, establishing causality between the two remains a challenging endeavor and requires more direct investigations. The results presented in this thesis question the conventional notion that functional serial dependence facilitates perceptual continuity or reduces uncertainty. Instead, the findings suggest that serial dependence may introduce a systematic error, or 'bug', induced by the current uncertainty.

The Past in Serial Dependence

What exactly is “the past” that influences “the present” in serial dependence? Is it the appearance of the stimulus, the memory representation accessed in working memory for decision-making, or the response representation itself? Does this representation mirror the stimulus, or does it adopt simplified formats within working memory? Addressing these questions is vital for understanding the nature and role of serial dependence; however, finding definitive answers is challenging due to conflicting results in the existing literature.

The prevailing consensus in the literature highlights the critical role of attention, with attractive bias being gated by attention (J. Fischer & Whitney, 2014; Fritsche & de Lange, 2019). Based on this understanding, it appears that sensory information filtered by attention in the past serves as the source of attractive serial dependence. However, as previously discussed, research indicates that attention per se is not sufficient to observe the attractive bias; the stimulus information must be maintained in working memory (Bliss et al., 2017; Fritsche et al., 2017; Stein et al., 2020; Barbosa et al., 2020), and a decision must be made (Fritsche et al, 2017; Akrami et al., 2018; Pascucci et al., 2019). The latter suggestions raise the possibility that working memory representations or even response representations could be the potential sources of attractive serial dependence.

Although unattended stimuli can also be stored in working memory (LaRocque, Lewis-Peacock & Postle, 2014; Christophel et al., 2018), they tend to exert rather repulsive effects on subsequent decisions (Shan & Postle, 2022). This might suggest that working memory might function more as a modulator and the source of attractive bias remain as attended stimulus in the past. Alternatively, this could mean that simply maintaining information in memory is not enough, the information needs to be actively accessed in working memory (Barbosa et al., 2021). This insight supports the critical role of decision in serial dependence. Observers are likely encouraged to access the information when a task requires a response. Otherwise, information that is maintained shortly—but not retrieved—might generate a repulsive bias in subsequent decisions (Shan & Postle, 2022).

Several studies have argued that making a decision is not essential for a subsequent trial to manifest an attractive bias (Fischer & Whitney, 2014; Suárez-Pinilla et al., 2018; Fornaciai, &

Park, 2018). This could potentially be due to the unpredictability of no-response trials in these studies (Fritsche, 2020), leading observers to make implicit decisions (without behavioral responses), which initiates the use of working memory. Consistent with this idea, Pascucci et al. (2019) demonstrated that the attractive bias disappears when observers are explicitly instructed not to make a decision. Replicating the latter finding, explicit 'stop' instruction given in the past (referred to as a stop signal in cognitive control research, Zhang & Li, 2012) has been found to induce repulsion in upcoming decisions (Ceylan & Pascucci, 2023). Additionally, the extent of repulsion increases when the likelihood of making a decision is higher in the subsequent trials. Stop signals may prompt the removal of stimulus representations from working memory, a process found to induce repulsion (Shan & Postle, 2022), especially when upcoming trials are expected to require a response (Ceylan & Pascucci, 2023). These findings suggest that past working memory representations are the source of serial dependence, leading to attractive bias when accessed and repulsive bias when removed.

Moreover, previous research (Sadil, Cowell & Huber, 2023) has showed an attractive bias to the previous responses and not to previous stimuli. This observation might indicate that the representation generated during past responses might serve as the source of attractive bias, thereby drawing current decisions towards it, independent of the stimulus. While this theory could explain the lack of attractive bias in the absence of responses, other findings (Cicchini et al., 2017; Ceylan & Pascucci, 2022) challenge this idea. Dissecting the roles of stimulus and response in serial dependence, recent research has presented evidence that, while response representations can modulate attraction, they are not the main source of it (see Supplementary Projects). Attractive bias was observed across trials requiring different types of responses and increased when observers needed to map circular stimulus information to linear responses. This trend may indicate modulation by either response representation or stimulus-response mapping. Mapping circular information to a linear space might introduce additional uncertainty, which, as demonstrated in Chapter 2, tends to amplify attractive bias. Additionally, research found attractive bias absent only in trials preceded by immediate responses. This outcome supports the notion that working memory representations, even those maintained for brief periods, serve as the source of serial dependence (Bliss et al., 2017; Fritsche et al., 2017; Barbosa et al., 2020).

Up to this point, the evidence suggests that working memory representations (i.e., the information that is maintained and accessed) constitute 'the past' serving as the source of attractive bias. However, the extent to which these representations accurately reflect the stimulus remains unclear. My findings (in Chapters 2 and 4) imply that attractive biases do not emerge due to replicas of sensory input or stimulus-copy representations. Instead, it appears that attractive bias is generated by task-relevant internal representations (see Figure D.1).

This proposition is supported by the robustness of the attractive biases (in Chapters 2 and 4) to changes in the physical properties of stimuli. For instance, in Chapter 2, I observed that reports on the orientations of dotted patterns were attracted to the orientations of Gabor stimuli, and vice versa. Similarly, in Chapter 4, I found attractive biases between the orientations of motion axes and the orientations of stripes. In these experiments, while the stimuli were distinct, the reported properties—the orientation—were common. Therefore, it is unlikely that the source of the attractive bias is a stimulus-copy representation in working memory. A recent neuroimaging study demonstrated that the motion of a cloud of dots could be decoded into a single line, representing the motion axis information (Kwak & Curtis, 2022). Visual system might filter redundant sensory information, reducing it to an elementary format that is relevant for decision-making. These reduced formats accessed in working memory might be the source of attractive bias instead of the stimulus-copy representations, as suggested by Houborg et al. (2023) and Tanrikulu et al.(2023) (also see Chapters 1 and 4). This would explain the lack of attractive bias when the previously reported property was different than the current one (in Chapter 4; Fritsche & de Lange, 2019; Collins, 2022).

The contribution of my work to the existing literature resides in the complexity of the stimuli employed. In Chapter 4, I utilized a Random Dot Kinematogram (RDK) wherein changes in dot luminance produced a Gabor-like feature on the moving dots. In Experiment 1, the motion speed was same across trials and was irrelevant to the task; therefore, only two types of orientation information—derived from the stripes and motion axes—were provided. Observers were pre-cued to report the orientation of one feature while ignoring the other.

This scenario likely required the deployment of multiple distinct selective attention mechanisms, each underpinned by top-down (voluntary and goal-driven) attentional control. These mechanisms might include feature-based attention, which allows for the detection of motion over static images (Cavanagh & Alvarez; 2005); object-based attention with an allocentric perspective, employed to group stripes and dots separately and segregate one object from another (Egly et al., 1994); and space-based attention with an egocentric perspective

(Posner et al., 1980), which facilitates attention to a single dot (or a stripe) and its direction, as opposed to the entire cloud of dots (or multiple stripes). Different strategies for detecting target versus non-target properties might have been used by different observers, or even variably applied across trials by individual observers. Regardless, Experiment 1 demonstrated that attractive bias robustly occurred, irrespective of the specific attentional source or mechanism in use. In other words, while the sensory representations might have differed significantly due to the engagement of potentially various attentional sources, the compact representation, 'orientation', was consistent across trials.

On the other hand, in Experiment 2, the speed of the dots changed randomly across trials and was task relevant. The same strategies used in Experiment 1 would have been beneficial in Experiment 2 as well; hence, the absence of attractive bias in Experiment 2 could be attributed to the disagreement of compact representations of the reported feature, namely speed and orientation. This observation provides compelling evidence that the source is the reported compact representations, not the attended stimulus-copy representations. This is because the attended motion, which still conveys orientation information, did not induce attraction. It is also plausible that the faster speed became salient, possibly leading to the utilization of bottom-up (involuntary and stimulus-driven) processes (Melloni et al., 2012), which could induce repulsion, interrupting the attraction. Also, temporal attention might have played a more significant role in Experiment 2 than in Experiment 1 due to the manipulation and relevance of speed. However, this factor is unlikely to explain the absence of attractive bias since the task was binary, and the speed of the motion was easily detectable.

Overall, my findings suggest that neither stimulus nor response representations alone can account for the past that serves as the source of serial dependence. Attractive biases arise from compact representations that are maintained in and accessed from working memory during decision-making. Conversely, repulsive biases may originate from the removal of sensory representations from working memory or/and from adaptation-like aftereffects. Importantly, these repulsive biases continue to be associated with the stimulus and, consequently, with sensory properties.

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APPENDIX A: Supplementary Study

Dissecting serial dependence: the effect of the response type, stimulus-response mapping, and retention interval

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Abstract

Human perceptual decisions exhibit attractive serial dependence and are biased towards prior events. The increasing interest in this phenomenon has raised debates about whether serial dependence originates from the history of prior stimuli or responses. Moving beyond this simple distinction, we present a series of experiments addressing a key issue: whether serial dependence originates from the sensory stimulus or the post-perceptual processes involved in mapping the stimulus to a response. Participants performed an orientation judgment task with alternating types of responses. We found attractive serial dependence regardless of the specific stimulus-response mapping. In particular, perceptual decisions were attracted towards the previous trial orientation, despite changes in the response tool and modality, from linear to circular continuous responses, and even binary choices, albeit with varying degrees of strength. However, we observed this effect only when the response from the previous trial was delayed and not provided immediately after the stimulus. We propose that the primary source of attractive serial dependence lies neither in the stimulus nor the type of response, but rather in the maintenance of information within working memory.

Significance Statement

Our perceptual decisions are always influenced by prior events, a phenomenon known as attractive serial dependence. It is debated at which stage serial dependence originates, whether at the level of perception, memory, or decisional and response-related processes. Using a novel experimental design, we disentangled stimulus perception from stimulus-response mapping stages and found intact serial dependence due to past stimuli, regardless of changes in the response mapping and response tool used. The response type only exerted a modulatory effect. Crucially, attractive serial dependence manifested when there was a delay between the stimulus and the response in the preceding trial. Our findings suggest that the source of serial dependence neither lies in the stimulus nor the response, but rather in the maintenance of information within working memory.

Introduction

Perceptual decisions are biased by the history of prior events, a phenomenon known as serial dependence [1,2]. Serial dependence is evident in a variety of perceptual tasks [3] and is typically characterized by a bias in judging current stimuli as more similar to the past than they truly are. Despite the growing research on this phenomenon and its central role in recent models of perception [4–7], the nature of serial dependence remains highly controversial.

One of the central challenges in the study of serial dependence is determining the role of the 'stimulus' and the 'response'. This seemingly oversimplified distinction raises deeper questions about the origins of serial dependence effects and whether they are primarily driven by recent perceptual history (the 'stimulus' effect), or result from post-perceptual processes, such as memory and decision-making (the 'response' effect) [8–14]. Despite its reductive nature, this dichotomy has significant implications for understanding the neural mechanisms and computational principles underlying serial dependence [13,15].

In classic paradigms, distinguishing between the effects of the stimulus or the response is not only challenging but nearly impossible because the two are highly correlated. For example, in adjustment tasks, participants report a stimulus feature, like its orientation, by reproducing it with a response bar [2]. Thus, the stimulus and response are quite similar, making it challenging to access how the 'stimulus' is perceived, as experimenters rely mainly on the information provided by the response. Additionally, since participants often use the same visual tool for responses in every trial, the response itself can act as a 'stimulus,' potentially contributing to serial dependence [2].

However, the majority of studies have employed paradigms in which stimuli and responses are highly correlated, making them both potential sources of the measured serial dependence effects. Attempts to eliminate response-related influences by removing the response tool in some trials have yielded mixed results, with instances of intact or only reduced serial dependence without responses [1,11], no serial dependence [16,17], or even repulsive biases [13,18]. Ultimately, none of the existing paradigms seems capable of unequivocally disentangling the contributions of different stages, ranging from how the stimulus is perceived to how it is stored in memory, mapped to a response, and, most importantly, determining at which of these levels the events of the previous trial influence the current one. A seemingly consistent finding is that serial dependence increases with the memory retention interval in the current trial, that is, of the interval between the stimulus and the related response. This suggests that at least the way stimulus information is internally manipulated in preparation for a response plays a role [8,10].

One of the key aspects not taken into account is the role of stimulus-response mapping stages. If serial dependence is significantly influenced, if not determined, by processes related to the response, then the effects should be specific to the type and image of the response used. For instance, when the task requires reproducing the orientation of a stimulus, using a circular response image in one trial and a linear tool with a different stimulus-response mapping in another should make a difference. Conversely, if serial dependence solely arises from the influence of the recently presented stimulus, the format of the response tool should have little or no impact. Crucially, to the best of our knowledge, no studies have tested the effect of interleaving different response images and mappings in serial dependence.

To this aim, we conducted four experiments in which participants judged the orientation of a stimulus in a series of trials. We manipulated the type of response required, ranging from the conventional orientation adjustment task involving a rotating response bar (circular response) to tasks that involved mapping the circular feature (i.e., orientation) to a linear or binary scale. We then assessed serial dependence in blocks where the two types of responses were used separately or sequentially intermixed, focusing on the effects of different stimulus-response mapping on the typical bias in adjustment reports.

Our results demonstrate that serial dependence occurs regardless of the specific response tool and type of stimulus-response mapping. Previous stimuli systematically biased current perceptual decisions, whether the previous and current trials involved linear, circular continuous responses, or binary choices, albeit with varying degrees of strength. Notably, in a final experiment involving interleaved trials with circular adjustment responses and trials with immediate binary choices after the stimulus, thus minimizing retention intervals, we observed a significant reduction in serial dependence after binary choices. This finding suggests that not only the retention interval in the current trial [8,10] but also the one in the previous trial, plays a key role.

Taken together, our collection of experiments shed novel insights into the nature of attractive serial dependence: the systematic bias towards the past is neither solely due to the physical stimulus perceived nor the format and mapping of the response required. Instead, our findings support the idea that, while these factors may all have a modulatory role, attractive serial dependence is primarily driven by the temporary retention of stimulus information in working memory.

Results

Experiment 1

In Experiment 1, 28 participants reproduced the orientation of a low-contrast and briefly presented Gabor patch in two conditions (see Figure 1). In one condition, they made adjustments by rotating a response bar, similar to traditional serial dependence experiments [1]. Consequently, in this scenario, the mapping between the stimulus and the response space was a direct correspondence, since both the stimulus feature and the response were circular (*circular* condition). In the other condition, participants indicated the perceived orientation by placing a point on a line, which included cardinal and oblique orientations as reference markers. Therefore, the circular space of the stimulus feature did not align with the linear space of the response, and a transformation from circular to linear space was required for the stimulus-response mapping (*linear* condition). Both conditions were conducted in separate blocks as well as in an intermixed block where linear and circular responses were alternated (*mixed* condition).

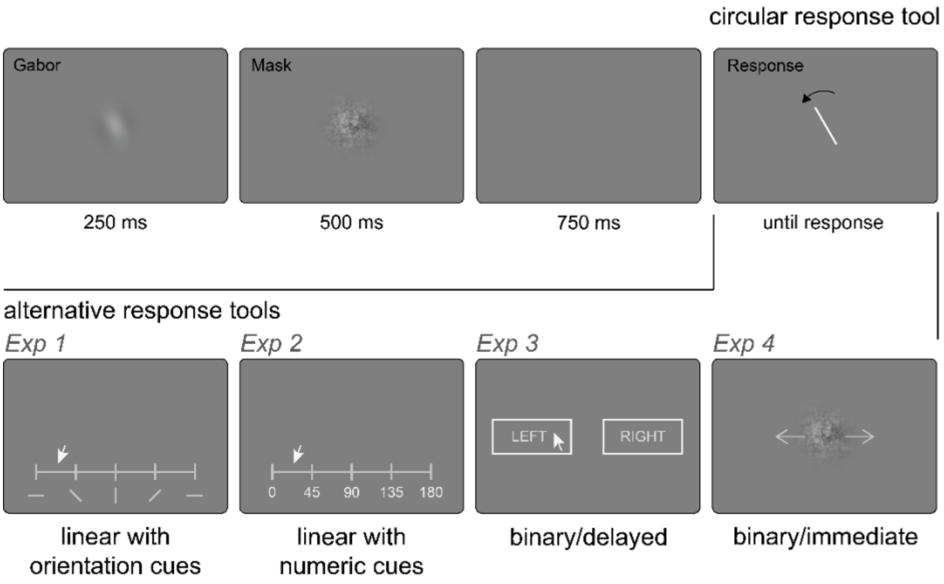

Figure 1. Main paradigm and variations across the set of experiments. In a typical orientation adjustment trial, participants reproduced the orientation of a Gabor by rotating a circular response tool (top row, see Methods). In four experiments, we introduced a second response type requiring mapping of the circular feature (e.g., orientation) to a linear response tool (Exp 1-2, bottom row) or a binary response tool (Exp 3-4, bottom row). The binary response (forced choice) was delivered after a delay (Exp 3) or immediately after the Gabor stimulus (Exp 4). Trials with circular and alternative response tools were performed both in separate blocks and intermixed, alternating within the same block (mixed condition). Stimuli are not drawn to scale.

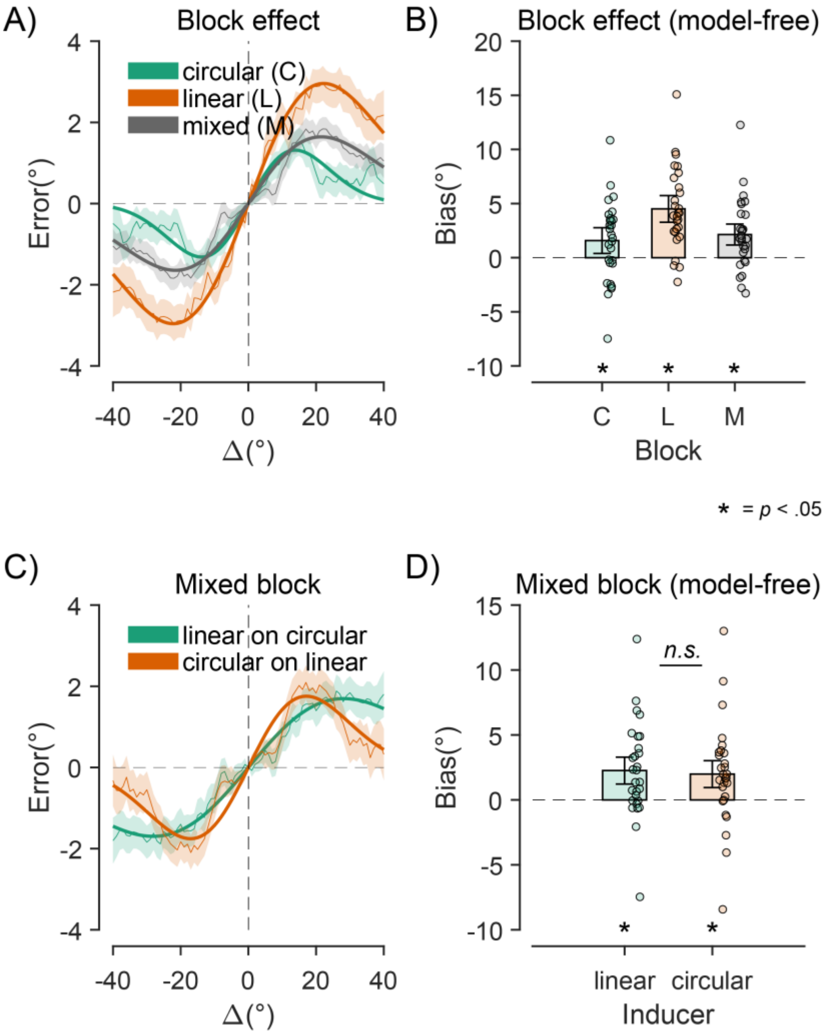

Figure 2. Results of Experiment 1. A) Errors as a function of the difference in orientation between stimuli presented on consecutive trials (Δ: previous minus present orientation). The best-fitting δoG is superimposed on each serial dependence curve. Separate curves represent data from circular, linear, and mixed response tools. Symmetric patterns for negative and positive Δ are obtained after folding the errors as in [19]. Shaded bars are 1 standard deviation (std) of the running average of errors (moving window of 15°) computed on the aggregated data of all observers. B) Complementary results from the model-free analysis with a non-parametric estimate of the bias in each block. Positive values mean attractive bias towards the previous orientation. Error bars are 95% CI. C) Serial dependence in the mixed block as a function of whether the previous stimulus required a linear response and the current one a circular response (linear on circular) or the other way around (circular on linear). D) Model-free bias for the two conditions within the mixed block (e.g., the same conditions as in C, with the same color coding).

First, we examined whether serial dependence occurred in both conditions when performed in separate blocks, as a prerequisite for testing whether serial dependence persisted across response types in the mixed block (Figure 2A-B). Both the circular and linear conditions demonstrated significant attractive serial dependence, although the half-amplitude values (α, see Methods) were larger in the linear condition (*circular*: $\alpha = 1.31°$, $p_{\text{perm}} = .003$; *linear*: $\alpha = 2.95°$, $p_{\text{perm}} < .001$). When evaluating serial dependence overall in the mixed condition, the bias fell between the levels observed in the linear and circular conditions performed individually (*mixed*: $\alpha = 1.64°$, $p_{\text{perm}} < .001$). This difference between conditions was confirmed through a one-way repeated-measures ANOVA on the non-parametric, model-free estimate of the bias (see Methods; $F(2;54) = 7.83$, $p = .001$). Importantly, in the mixed condition where the response type alternated and changed from one trial to the next (Figure 2C-D), we found equivalent levels of serial dependence between linear-on-circular and circular-on-linear trials (*linear-on-circular*: $\alpha = 1.69°$, $p_{\text{perm}} < .001$; *circular-on-linear*: $\alpha = 1.75°$, $p_{\text{perm}} < .001$; difference: $\alpha = -0.05°$, $p_{\text{perm}} = .445$), a result also confirmed via model-free analysis ($t(27) = 0.37$, $p = .70$, paired t-test, Cohen's $d = 0.07$).

Therefore, attractive serial dependence persisted regardless of the required stimulus-response mapping and the type of response tool presented. It is worth noting that, the magnitude of the bias differed between the individual blocks and the mixed condition. Notably, when the circular response tool was used within the mixed block (in the *linear to circular* condition), the bias was more pronounced, in contrast to the block with only circular responses, even though the difference was not significant (model-free: $t(27) = 0.90$, $p = .37$, paired t-test, Cohen's $d = 0.17$). Conversely, the pattern was reversed and significant for the linear response tool: the mixed block showed diminished bias compared to the block with only linear responses (model-free: $t(27) = -2.93$, $p = .006$, paired t-test, Cohen's $d = -0.55$; marginally significant after Bonferroni correction for a family of 9 tests, with significance level $\alpha_{\text{crit}} = .0056$).

Experiment 2

The findings from Experiment 1 indicate that serial dependence is not influenced by the type of response or the processes involved in mapping the perceived stimulus to the required response. Moreover, Experiment 1 clearly demonstrates that the image of the response tool itself plays a minimal role, as we found serial dependence in intermixed trials, even though linear and circular response tools were perceptually clearly distinct. Therefore, this suggests a primary effect of the stimulus.

However, there is an alternative explanation to consider. It is possible that the presence of visual cues, such as orientation reference markers, could have prompted participants to retain the circular representation of the stimulus orientation until the moment of response. Thus, the observed serial dependence might still result from how stimulus information was internally stored, rather than the perception itself.

To prevent any use of circular features at the stimulus-response mapping stage, in Experiment 2 (N = 27), we removed the oriented visual cues from the response tool and replaced them with numeric orientation cues representing five equally spaced points on the line (see Figure 1, bottom row). Participants were trained in a practice session to associate each number to the corresponding orientation.

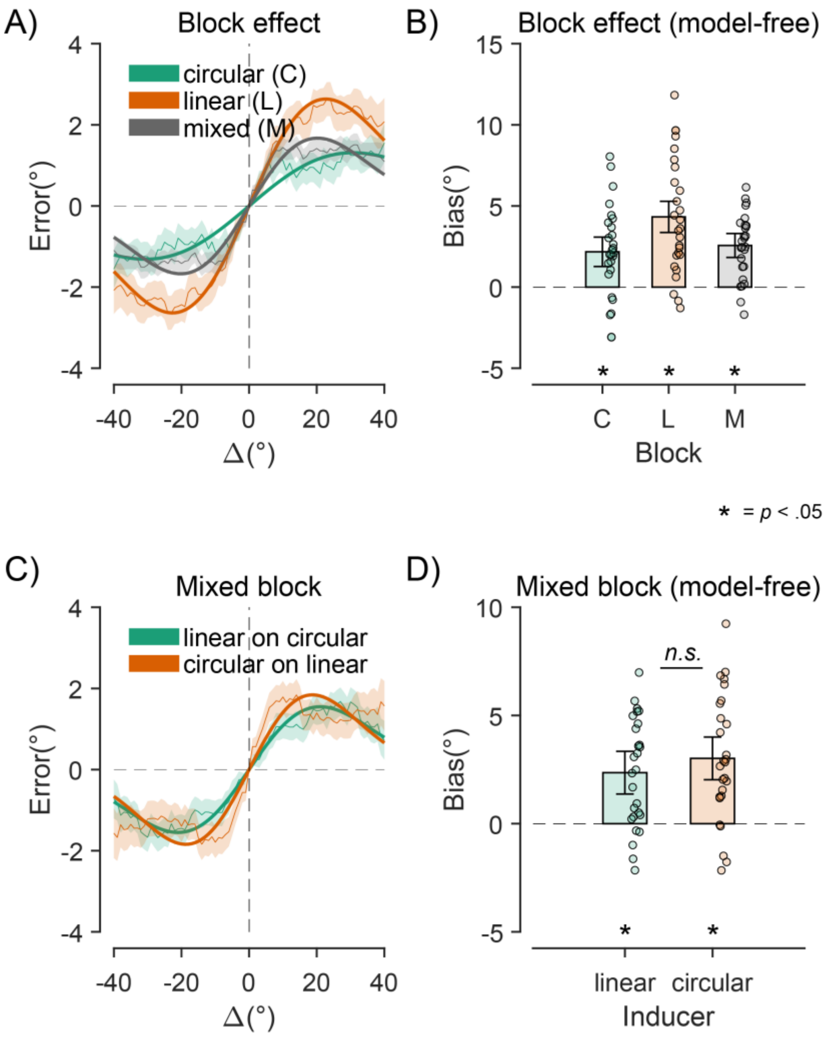

Figure 3. Results of Experiment 2 with the same color coding and format as in Figure 2. A-B) Serial dependence, δoG fit (A), and model-free bias (B) for the three blocks of Experiment 2. C-D) Serial dependence δoG fit (C), and model-free bias (D) for the alternating response type conditions in the mixed block.

As in Experiment 1, we initially examined serial dependence in separate blocks involving linear or circular response tools (Figure 3A-B). The results demonstrated significant serial dependence in both conditions, with a larger effect in the linear condition (*circular*: $\alpha = 1.31°$, $p_{\text{perm}} < .001$; *linear*: $\alpha = 2.63°$, $p_{\text{perm}} < .001$). The overall level of serial dependence in the mixed condition fell in between, consistent with the pattern in Experiment 1 (*mixed*: $\alpha = 1.67°$, $p_{\text{perm}} < .001$; ANOVA on model-free: $F(2;52) = 7.24$, $p = .001$). Furthermore, in the mixed condition of Experiment 2, serial dependence remained comparable between linear-on-circular and circular-on-linear trials (Figure 3C-D; *linear-on-circular*: $\alpha = 1.54°$, $p_{\text{perm}} < .001$; *circular-on-linear*: $\alpha = 1.84°$, $p_{\text{perm}} < .001$; difference: $\alpha = -0.29°$, $p_{\text{perm}} = .246$; model-free paired t-test: $t(26) = -0.97$, $p = .338$, $d = -0.18$). This suggests that the effect observed in Experiment 1 and replicated in Experiment 2 is not specific to the type of visual cues used for mapping orientations in the linear response tool.

As in Experiment 1, we also observed a trend for different patterns of serial dependence between the mixed condition and the other blocks. In particular, linear responses exhibited a trend for a smaller bias in the mixed blocks compared to blocks with fixed response types (model-free: $t(26) = -1.86$, $p = .073$, paired t-test, Cohen's $d = -0.35$), but no difference or trend was evident for the circular response case (model-free: $t(26) = 0.33$, $p = .740$, paired t-test, Cohen's $d = 0.06$).

Experiment 3

Our first two experiments confirm that the type of response and the stimulus-response mapping do not have an impact on serial dependence. This could suggest that the effects observed are primarily driven by the perception of the Gabor image, the 'stimulus', rather than any post-perceptual aspects related to the response. However, despite asking participants to map orientations to a linear space, it is still plausible that the requirement to report a continuous circular feature led participants to retain a circular feature orientation in memory [20–22] and map it onto a linear response only at the end. If this were the case, the retention of a circular feature in memory could have contributed to the observed serial dependence.

In Experiment 3 (N = 27), we replaced the linear response tool with a binary task, specifically a forced-choice task. Participants were asked to indicate whether the stimulus was tilted to the left or right relative to the vertical by moving the mouse cursor to one of two response options and pressing the 'space' button (Figure 1). By using a binary task, we eliminated the need for participants to recall and map any circular feature to the response. Instead, they could detect the left or right tilt during perception and store this binary variable in memory. As the primary aim was to measure the effects of the binary task on the classic serial dependence in adjustment responses, the experiment consisted of one block with a circular condition and one block with a mixed condition, where binary and circular responses were alternated.

As expected, attractive serial dependence was evident in the circular condition (Figure 4A-B; *circular*: α = 2.65°, $p_{\text{perm}} < .001$). However, importantly, it was equally evident in the mixed condition, where participants were required to provide binary responses for previous stimuli (*mixed*: α = 2.24°, $p_{\text{perm}} < .001$; difference: α = 0. 41°, $p_{\text{perm}} = .218$; model-free paired t-test: t(26) = 0.79, *p* = .432, *d* = 0.15). Thus, attractive serial dependence persisted even when participants were not asked to recall and map a circular feature to the response but reported the perceived tilt, relative to vertical, with a binary choice.

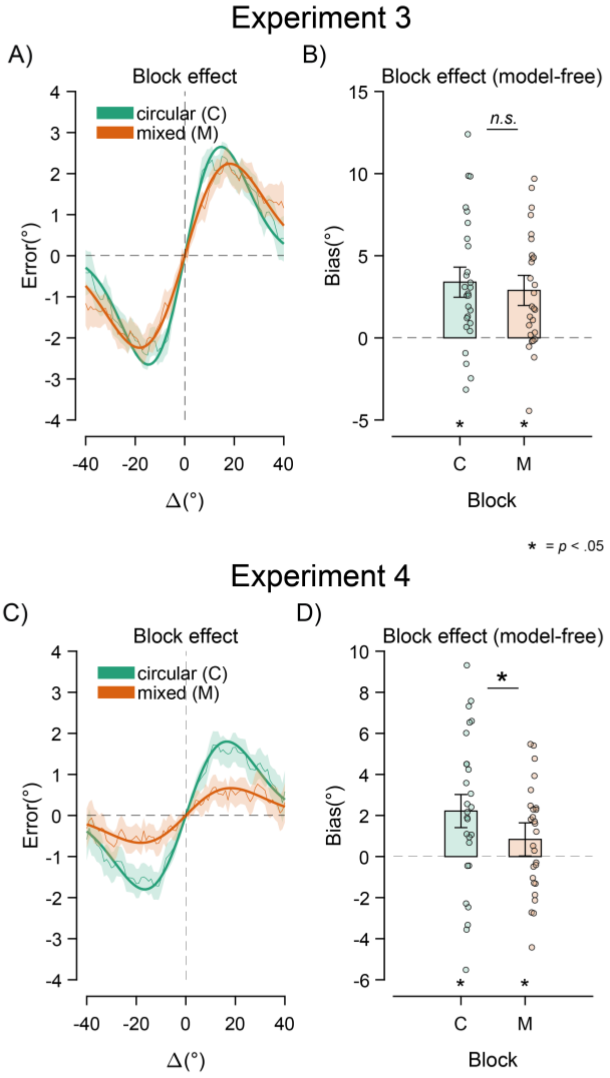

Figure 4. Results of Experiments 3-4. A-B) Serial dependence, δoG fit (A), and model-free bias (B) in Experiment 3, for the block with only circular response tool (green, circular) and for the block in which a circular response was preceded by the binary choice (orange, mixed). C-D) Serial dependence, δoG fit (C), and model-free bias (D) in Experiment 4, for the block with only circular response tool (green, circular) and for the block in which a circular response was preceded by the binary choice (orange, mixed). The binary choice was delayed in Experiment 3, whereas it was delivered immediately after the stimulus in Experiment 4 (see Methods and Figure 1). Note that Experiment 4 was the only experiment showing a significant difference in serial dependence, in which the bias was absent after immediate binary responses, compared to the significant serial dependence observed in all other conditions of all experiments (see Results).

Experiment 4

The results reported so far provide evidence against the involvement of the response tool and the format of response in serial dependence. Furthermore, these findings suggest that how the stimulus is maintained in memory, which may depend on the response format required, may also not play a role.

In this final experiment, we tested whether information maintenance in working memory is relevant at all. Twenty-seven participants performed the orientation adjustment task, similar to the previous experiments, in one block of trials. In a second block, adjustment responses were interleaved with a binary forced-choice task. However, unlike Experiment 3, the forced-choice responses were given immediately after the stimulus, starting from the onset of the mask. This meant that no memory maintenance was required, as the retention interval was minimal, and any information about the stimulus could be discarded during the presentation of the noise mask (see Figure 1). To maintain consistency with the other experiments, the interval between trials was kept comparable for both adjustment and binary choice trials (see Methods).

Importantly, while serial dependence was evident in the circular condition when only adjustment responses were considered (*circular*: $\alpha = 1.80°$, $p_{\text{perm}} < .001$), the effect was much decreased and non-significant when adjustment responses were preceded by the binary choice task (*mixed*: $\alpha = 0.66°$, $p_{\text{perm}} = .088$; difference: $\alpha = 1.13°$, $p_{\text{perm}} = .007$; model-free paired t-test: $t(26) = 2.48$, $p = .019$, $d = 0.47$). This particular condition, the only one showing a clear reduction and no significant serial dependence across our set of experiments (Figure 4C-D), supports the role of memory maintenance and retention intervals in serial dependence.

This pattern aligns with the role of post-perceptual factors in attractive serial dependence proposed in previous studies [10,13,23]. Importantly, studies involving similar alternations of forced-choice and adjustment trials, have also documented repulsive effects of prior stimuli on forced-choice responses [10]. An exploratory analysis of serial dependence in our binary task seems to confirm this finding (see Supplementary Material).

Discussion

Serial dependence is a ubiquitous aspect of human decisions, evident in any perceptual task [2,3]. The recent interest in this phenomenon, from both an empirical and computational point of view [2], has raised debate on the underlying mechanisms and stages of processing involved. In this study, we present a series of experiments addressing a key issue: whether serial dependence originates from the physical stimulus or the post-perceptual processes involved in mapping the stimulus to a response.

Our results demonstrate that: 1) serial dependence occurs irrespective of the type of response and the response space required, 2) it occurs with little or no contribution of the image used to respond, but the response type can modulate the intensity of the bias and 3) attractive serial dependence manifests when there is a delay between the stimulus presentation and the delivery of the response on the preceding trial.

Previous studies have used statistical and computational models [5,12,13], as well as paradigms tailored to dissociate serial dependence from the stimulus and the response [1,9,10,13,17,18,24]. These studies have shown that, under some conditions, prior stimuli and responses can even have opposite effects [10,12,13,17,18,25], but the broader debate on the stages of processing involved in serial dependence has remained controversial [2]. None of the existing studies, however, has exhaustively evaluated the role of stimulus-response mapping stages, which is crucial to disentangle stimulus perception from internal processes related to retaining and mapping stimulus information for decision-making and responses. Our findings demonstrate that the presence of attractive serial dependence is unaffected by trial-to-trial changes in the type of response, even when switching between binary forced-choice, continuous linear, and circular adjustment responses. Thus, the specific response space and the image of the response tool itself are not major determinants.

However, our experiments indicate that, although not a determinant, response mapping does influence serial dependence. We observed that the bias towards prior stimuli was more pronounced when participants reported the stimulus orientation in the linear space as opposed to the circular space, especially when comparing blocks where these response tools were used separately (Experiment 1-2). This might be because serial dependence tends to increase in conditions of uncertainty [20]. Mapping orientation to the linear space may have introduced an additional source of uncertainty, leading to a stronger bias towards prior stimuli. Additionally, we found trends and patterns in Experiments 1 and 2 suggesting that serial dependence varied in strength between blocked and mixed conditions. Specifically, the linear response tool exhibited stronger serial dependence in the blocked condition compared to the mixed condition. This suggests that uncertainty and the tendency to exhibit systematic biases with a particular response tool may also depend on the presence and intermittent use of another response tool that allows for more precise responses (e.g., the circular response tool, see Table 1).

The finding that the response tool modulates, rather than determines, serial dependence is also important because previous research has primarily focused on manipulating stimulus parameters [4,20,26], with little attention to the role of stimulus-response mapping processes. Future studies must account for aspects of the response tool, even when using circular responses, as the often-overlooked parameters of the response tool can significantly influence the strength of serial dependence, without necessarily implying a direct effect of perceptual history.

Our final experiment, the only one showing no serial dependence after binary forced-choice tasks, appears in line with the involvement of post-perceptual processes. That is, not only the perception of the stimulus but also the delay after the stimulus and before the response matters. Compared to Experiment 3, where binary choices were made with the same delay as adjustment responses, the immediate response required in Experiment 4 disrupted attractive serial dependence. The most plausible explanation is that attractive serial dependence necessitates the temporary storage and maintenance of prior stimulus information in working memory, even for brief durations [8,10,18,27]. According to several frameworks, visual working memory maintenance appears to be the stage at which prior stimuli imprint neural circuits, leading to their persistence for several seconds [28,29].

Recently, some studies have reframed the problem of the processing stages involved in serial dependence by distinguishing between the 'source,' where serial dependence originates, and the 'site,' where it manifests [2,13,23]. Within this distinction, there is evidence from adjustment tasks supporting a post-perceptual source but a perceptual site. For example, Cicchini and colleagues demonstrated that attractive serial dependence originates after but influences perception before spatial context effects, which are thought to emerge relatively early in visual processing [23]. In line with this, our results are consistent with serial dependence originating late, not simply from the perception of prior stimuli, and cannot deny the possibility of a direct effect on the perception of current stimuli (but see Supplementary Material).

Overall, our findings support memory and decision-making accounts of serial dependence, emphasizing the crucial role of retaining stimulus information for the task at hand [8,13,20,21,27,30–32]. It is worth noting that even in experimental conditions where explicit memory is prevented by eliminating any task requirements [33,34], there is no guarantee that memory maintenance, even for a brief and sufficient period, is not involved [35].

The present series of experiments strongly suggests that information is retained in working memory and carries over from one trial to the next in a specific format. Even when participants were asked to map the stimulus onto different response spaces, they exhibited a bias toward the actual feature of the stimulus in its original physical space (e.g., circular). It is plausible that in the tasks used, participants retained an ‘orientation code’ in memory and mapped it onto the linear or binary space only when responding. Importantly, this ‘stimulus code’ does not necessarily need to closely reflect the initial perception of the stimulus but can be a more compact and basic representation that serves the purpose of the task, such as an oriented line [22]. This may explain why serial dependence occurs even for entirely distinct objects, as long as they share a common task-relevant feature [20,21,32].

In summary, our findings suggest that neither the stimulus nor the response alone can explain attractive serial dependence. While the type of response and stimulus-response mapping can influence the strength of the bias, they do not determine its presence. The bias toward prior stimuli becomes particularly evident when memory maintenance is required.

Methods

Ethics statement

The study was approved by the local ethics committee under the Declaration of Helsinki (except for preregistration) [36]. This study was not preregistered.

Apparatus

The stimuli were generated and presented online via PsychoPy v.2022.2.4 [37,38].

Participants

Experiments were performed online and included 119 participants, (30 in Experiment 1 [28 after exclusion], 13 females; mean age: 27.3; 29 in Experiment 2 [27 after exclusion], 8 females; mean age: 26.6; 30 in Experiment 3 [27 after exclusion], 9 females; mean age: 28.4; 30 in Experiment 4 [27 after exclusion], 10 females; mean age: 26.34), recruited through the Prolific platform (www.prolific.ac) [39,40] and Pavlovia (https://pavlovia.org), with a monetary reward of £10/hour (average experiment duration was 45 minutes). We aimed at more than 15 subjects per experiment based on prior work reporting medium-to-large effect sizes (e.g., Cohen's $d' > 0.5$) in the strength of serial dependence and the effect of experimental manipulations with approximately 15 subjects [13,17]. All participants were naïve as to the purpose of the experiments.

Stimuli and procedures

Figure 1 illustrates the main aspects of the paradigm. After a blank interval of 2000 ms, a Gabor stimulus (peak contrast of 15% Michelson, the spatial frequency of 0.33 cycles-per-degree [cpd], and a Gaussian envelope of an approximate size of 1.5°, 200 pix) was presented at the center of the screen for 250 ms and followed by a noise mask (90% contrast, 500 ms duration, 200 pix). Each trial involved the presentation of a Gabor stimulus for 250 ms. The Gabor could have any orientation within the circular space ranging from 1° to 180°. However, the absolute difference in orientation between two successive Gabor stimuli could not exceed 40°. We imposed this restriction as attractive serial dependence in orientation tends to reach its maximum effect within the 10-40° range of orientation differences. Beyond this range, the effect diminishes or even transforms into repulsion. Secondly, the chosen analysis method (detailed below) is based on the narrower range of orientation differences where serial dependence is typically stronger [2]. The Gabor was followed by a noise mask for 500 ms and after 750 ms from the mask, participants had to report the orientation of the presented Gabor (except in Experiment 4, see below).

The main manipulation in each experiment was the type of response required and the response tool used. In all four experiments, one of the blocks consisted of a classical adjustment task, and another block consisted of trials with a classical adjustment task and an alternative type of response, always presented in alternating order. Experiments 1 and 2 also included additional blocks with the only alternative type of response trials.

In the classical adjustment task trials, observers rotated a response bar to match the perceived orientation of the Gabor (adjustment task). The adjustment response was made by moving the mouse upward and downward and confirming by pressing the space button (left mouse button in Experiment 4).

In Experiment 1, we used a linear response tool as an alternative to the circular adjustment tool, thus requiring a different stimulus-response mapping. Observers selected with the mouse cursor on the linear scale the orientation they previously saw. The scale had five ticks from 0 to 180 degrees with 45-degree steps. Each tick was labeled with a bar representing the corresponding orientation.

Experiment 2 also involved a linear response tool. To avoid visual cues to orientation, each tick on the scale was labeled with a corresponding degree number from 0 to 180 degrees with 45-degree steps.

In Experiment 3, the alternative response involved a forced-choice binary task. Observers selected whether the Gabor orientation was rotated to the left or the right with respect to vertical. They were instructed to move their mouse to the placeholder on the screen with the text "LEFT" if it was left tilted and with the text "RIGHT" if it was right tilted, and after it, press the space button.

Experiment 4 also involved a forced-choice binary response. The main difference from Experiment 3 is that observers were now instructed to give a report as soon as they saw the mask. The mask image included images of transparent arrows to the left and the right, indicating that the report should be made immediately. After the forced-choice report, the blank interval before the next trial was 4.25 seconds long instead of the 2 seconds used in classical adjustment trials in order to maintain approximately comparable inter-trial intervals between the stimuli as in the other experiments. The forced-choice report was made with the left and right keys on the computer keyboard.

Blocks with only one type of report consisted of 82 trials. Blocks with mixed types of reports consisted of 163 trials. The order of blocks was counterbalanced across participants.

Before each experiment, participants were provided written instructions and performed a sequence of practice trials for each type of report. Practice trials included feedback and were not analyzed further. Participants were instructed to maintain their gaze at the center of the screen for the entire duration (breaks excluded). All stimuli were presented on a grey background.

Analysis

At the level of individual trials, we removed outliers in adjustment responses (adjustment task and linear report task) in a two-step procedure. First, adjustment errors were computed as the acute angle of the difference between the reported and true orientation. Errors larger than 45° were considered lapses and removed. The remaining ones were demeaned and cleaned from outliers identified as values more than 1.5 interquartile ranges above the upper quartile or below the lower quartile. Additionally, adjustment trials slower than 10 s were excluded from further analysis. Less than 20% of trials were excluded across all experiments. After outlier exclusion, errors were further pre-processed by mean-centering and removing any systematic bias in reporting orientation for each response space by taking the residuals of a 4-th degree polynomial fitted to the response errors as a function of the current orientation [7,11,13]. Subjects were excluded if the percentage of outlier trials exceeded 20%. Table 1 shows the number of tested and excluded subjects, the average standard deviation of adjustment errors, and the proportion of correct responses in all experiments. The average adjustment times ranged from 2.53 sec. to 2.64 sec. for circular response tools; from 2.12 to 2.14 sec. for linear; 1.57 sec. for binary in Experiment 3; 0.75 sec. for binary in Experiment 4.

Experiment	N	Excluded	Condition	Eσ (°)/pc
1	30	2	*circular*	9.7(°)
			linear	11.11(°)
			mixed(circular)	10.22(°)
			mixed(linear)	11.11(°)
2	29	2	*circular*	9.21(°)
			linear	10.7(°)
			mixed(circular)	9.23(°)
			mixed(linear)	10.49(°)
3	30	3	*circular*	9.95(°)
			mixed(circular)	10.12(°)
			mixed(binary)	0.92 (pc)
4	30	3	*circular*	9.57(°)
			mixed(circular)	9.07(°)
			mixed(binary)	0.88 (pc)

Table 1. Summary of performance metrics across experiments and conditions involving different response tools. Eσ: standard deviation of adjustment errors. Pc: proportion of correct responses in binary forced-choice tasks.

In the analysis of serial dependence, errors were analyzed both using a model-based and a model-free approach [20]. The model-based analysis consisted of fitting a 1st derivative of a Gaussian function [1] to the adjustment errors as a function of the variable Δ, obtained as previous minus current orientation. The δoG has the following form:

$$error = \Delta \alpha w c e^{-(w\Delta)^2}$$

where c is a constant $c = \frac{\sqrt{2}}{e^{-0.5}}$ and w is the inverse of the curve width. The half-amplitude parameter α quantifies the deviation of the errors, in degrees, from the actual orientation, as a function of Δ variable: positive values of α indicate a systematic deviation of errors towards the orientation of the preceding stimulus, and negative values indicate a deviation away —i.e., repulsion. The parameters of the δoG function were estimated on the aggregate data of all participants, by solving a constrained non-linear minimization problem with the sum of squared residuals as the cost function. Model fitting was performed separately on each condition of interest. Statistical significance of the half-amplitude parameter was assessed via bootstrap resampling and surrogate null statistics, by randomly shuffling the sign of adjustment errors and comparing the observed α with the distribution of surrogate α (N = 5000). Serial dependence between conditions was compared by randomly shuffling the condition labels 5000 times and comparing the distribution of the resulting differences against the observed one.

In the model-free approach, we subtracted the average error for Δ within the positive Δ range from the average error in the corresponding negative Δ range [20,41]. The resulting index, quantifying the amount of systematic deviation of the errors from zero (either in the positive or negative direction) was used for subsequent analysis.

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APPENDIX B: Other Study

Feature distribution learning by passive exposure

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Abstract

Humans can rapidly estimate the statistical properties of groups of stimuli, including their average and variability. But recent studies of so-called *Feature Distribution Learning* (FDL) have shown that observers can quickly learn even more complex aspects of feature distributions. In FDL, observers learn the full shape of a distribution of features in a set of distractor stimuli and use this information to improve visual search: response times (RT) are slowed if the target feature lies inside the previous distractor distribution, and the RT patterns closely reflect the distribution shape. FDL requires only a few trials and is markedly sensitive to different distribution types. It is unknown, however, whether our perceptual system encodes feature distributions automatically and by passive exposure, or whether this learning requires active engagement with the stimuli. In two experiments, we sought to answer this question. During an initial exposure stage, participants passively viewed a display of 36 lines that included one orientation singleton or no singletons. In the following search display, they had to find an oddly oriented target. The orientations of the lines were determined either by a Gaussian or a uniform distribution. We found evidence for FDL only when the passive trials contained an orientation singleton. Under these conditions, RT's decreased as a function of the orientation distance between the target and the mean of the exposed distractor distribution. These results suggest that passive exposure to a distribution of visual features can affect subsequent search performance, but only if a singleton appears during exposure to the distribution.

Introduction

Humans can extract meaningful information from complex visual scenes in a fraction of a second. Most of the information that is available in the immediate ‘gist’, takes advantage of statistical regularities and redundancies typically found in the visual world. Similar objects are often arranged into groups defined by distributions of low-level features, like color, orientation, size, and location. This provides the visual system with the opportunity to form coarse, global representations, without recognizing individual details: “there is a big basket of small red apples on the left side of the grocery shop”. But how coarse are these global representations that are automatically and effortlessly available?

A large body of evidence indicates that humans can rapidly extract basic statistical summaries, like the average and variability of an ensemble of similar stimuli (Ariely, 2001; Whitney & Leib, 2018). Recent studies, however, demonstrate that the perceptual system can quickly learn even more complex and detailed aspects of stimulus distributions, such as the whole shape of a distribution of visual features. In studies of *feature-distribution learning* (FDL; Chetverikov et al., 2016, 2017b, 2017a), for instance, observers are presented with a sequence of visual search trials containing a singleton target embedded in a set of distractors (see Figure 1). After only a few exemplars of distractors drawn from a particular distribution of features, the visual system learns the shape of the distribution and uses this information to guide future search: searching for a new target becomes easier if the target lies outside the distribution of previous distractors and harder if the target lies *inside* the previous distractor distribution (a role-reversal effect; Kristjánsson & Driver, 2008). In this way, the response time functions reflect the shape and characteristics of the distractor distribution. This suggests that even when ensembles are not directly relevant for behavior (e.g., a set of distractors in a search task), the brain encodes detailed representations of their properties, beyond summary statistics, which can ultimately aid the detection of task-relevant outliers. This form of learning has been observed for both colors (Chetverikov et al., 2017b) and orientation (Chetverikov et al., 2016), for various distributions types (even bimodal ones, Chetverikov et al., 2017a) and occurs implicitly, since observers cannot explicitly judge distribution shapes, even though the learning strongly affects their search performance (Hansmann-Roth et al., 2021).

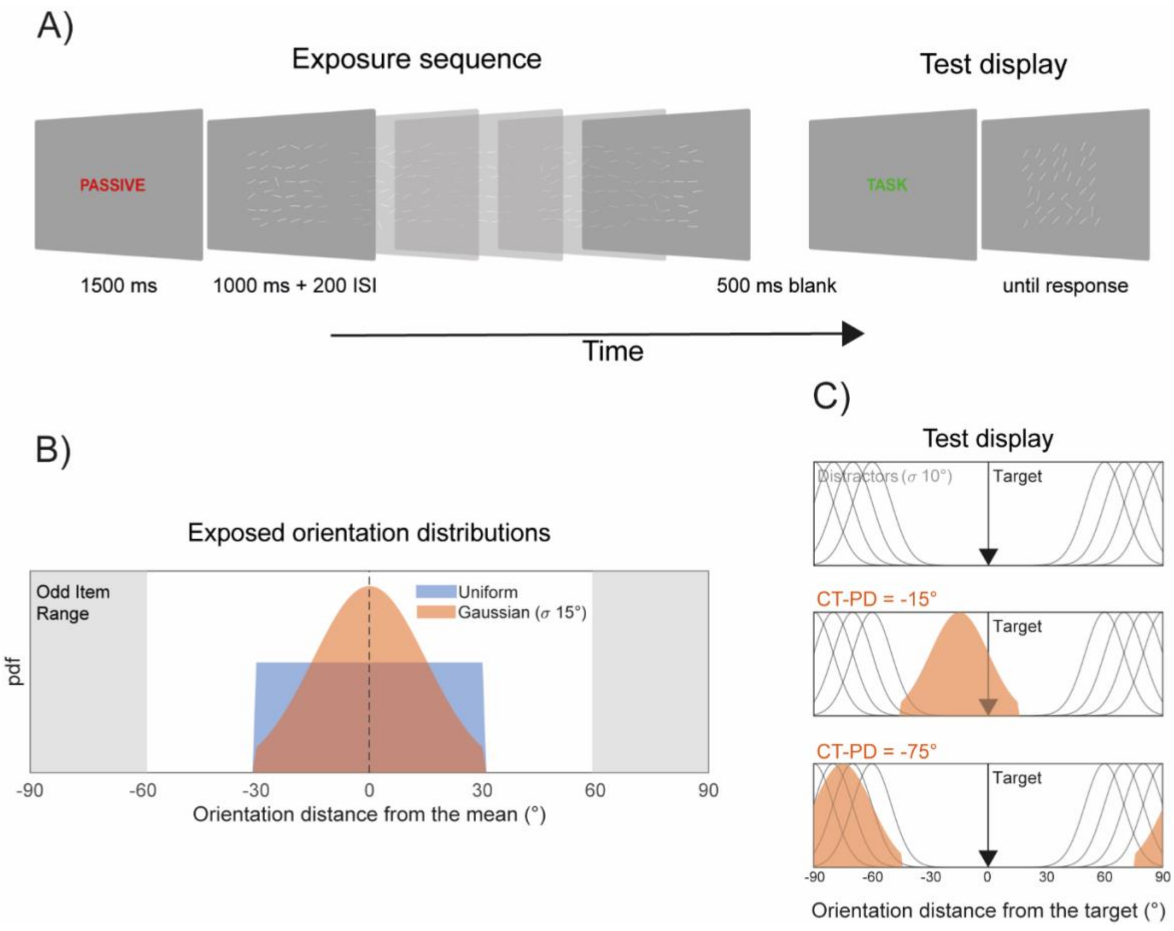

Figure 1. Trial structure and main variables. A) Example of a sequence of displays in one trial. Participants were instructed by a written cue to passively view the display (exposure sequence) or to perform a visual search (test display). In the visual search task, they had to report the location of the oddly oriented target (upper vs. lower quadrant). B) In the exposure sequence, the orientations in the ensemble of lines were drawn according to two different distributions, a truncated Gaussian, and a uniform distribution. One oddly oriented line with orientation distance of ± 60-90° from the ensemble mean, was included in the exposed displays of Experiment 1, but not in Experiment 2. C) In the test display, distractors followed a Gaussian distribution with 10° of standard deviation and a mean located between ±60° and ±90° away from the target orientation (gray curves). The target orientation was presented at different distances from the mean of the exposed distractors distribution (current-target previous-distractor distances, CT-PD; orange Gaussian distribution in the example).

An important question concerning this learning is whether such detailed statistical representations are encoded automatically and independently of a task —i.e., by simple exposure. In FDL, observers are engaged in a search task that requires them to segment out a potential target from a set of task-irrelevant features. In most of our everyday routines, however, we are not constantly engaged in visual search. Yet, learning the distribution of visual features can help to maintain an accurate representation of our visual environment while maximizing our ability to identify outliers and relevant changes in the environment. In line with this, research has shown that our attentional and perceptual systems constantly learn the characteristics of the visual input, even while idling, giving rise to phenomena of latent learning and plasticity (Turatto et al., 2018; Won & Geng, 2020). In studies of the habituation of the attentional capture response, for example, simple exposure to a repetitive onset stimulus can prepare the attentional system for resisting capture by the same onset in the context of a task (Turatto et al., 2017, 2018; Turatto & Pascucci, 2016).

While feature distribution learning from active search has been found to aid visual performance, this mechanism would be more useful if it can also operate more generally, outside this task-specific context. In the present work, we, therefore, asked whether passive exposure to sets of oriented lines coming from distributions of orientations can induce feature distribution learning effects that modulate visual search during a subsequent active search task. We used a modified FDL paradigm, presenting a sequence of five displays containing 36 oriented lines. All the lines were oriented according to either a Gaussian or a uniform distribution (see Methods and Figure 1), except for one oddly oriented line resembling the target of a typical FDL display. In a departure from typical FDL methods, within short blocks with sequences of trials with oriented lines, observers were asked to passively view each display without performing any explicit task. After the sequence, a single *test* display was presented, requiring observers to perform a search task, reporting the location of the singleton target (upper vs. lower half of the screen). For the test display, that probed the signatures of FDL, search times were analyzed as a function of the angular distance between the mean of the prior distractor distribution and the orientation of the test target (the Current-Target/Previous-Distractor distance, CT-PD) (Chetverikov et al., 2019).

Methods

Participants

A total of 40 healthy participants (24 in Experiment 1 and 16 in Experiment 2, age range of 19-35 years, 18 females), from the EPFL and the University of Lausanne, participated in the study for a monetary reward (20 CHF/hour). All participants had normal or corrected-to-normal vision and were naïve as to the purpose of the experiments. Before the experiments, visual acuity was tested with the Freiburg Acuity test (Bach, 1996). A value of 1 or above reached with both eyes open was used as the selection criterion. The sample sizes were selected based on previous FDL studies. All participants gave written informed consent, and the study was approved by the local ethics committee under the Declaration of Helsinki (apart from preregistration) (World Medical Organization, 2013).

Apparatus

Stimuli were presented on a gamma-corrected VG248QE monitor (resolution: 1920 x 1080 pixels, refresh rate: 120 Hz) and were generated with custom-made scripts written in Matlab (R2013a) and the Psychophysics Toolbox (Brainard, 1997), running on a Windows-based machine. Experiments were performed in a darkened room and participants sat at 57 cm from the computer screen, with their head positioned on a chin rest.

Stimuli and procedure

In both experiments, trials were arranged into short mini-blocks comprising an exposure sequence of five displays (1000 ms each, separated by a 200 ms blank screen), followed by a single test display (see Figure 1). All stimuli were presented on a grey background. A colored written cue (1500 ms) indicated the upcoming sequence of exposed displays (the word ‘PASSIVE’, written in red) or the test display (‘TASK’ written in green). Each display contained 36 white lines of 1° length, arranged in a 6-by-6 array within a 14° square centred at the fovea. A small jitter was added to the location of each line within each cell of the 6-by-6 array (jitter range: ±0.5°) to prevent uniform appearance.

During the exposure stage, the orientation of each line was drawn from a truncated Gaussian distribution (standard deviation (σ): 15°, cut-off at ± 30° [2σ] from the mean) or a uniform distribution (range: ± 30° from the mean), in separate and intermixed mini-blocks consisting of 5 learning trials and a test trial. A ‘seed’ mean orientation of both distributions was randomly selected for each mini-block and remained the same for the 5 learning trials of each mini-block. In Experiment 1, the exposure displays always contained a singleton line, oriented between ±60° and ±90° away from the mean of the distribution. In Experiment 2, no singleton line was present in the passively viewed displays during the exposure sequence.

On test trials, the orientation of the target line was drawn from among a set of 12 angular distances (from -75° to +75° in steps of 15°) from the seed mean of the previous sequence of exposed distributions. The distance between the target line orientation and the previous distribution mean defined the Current-Target/Previous-Distractor distance (CT-PD). The distractor distribution of orientations in the test display was always Gaussian with σ of 10° and the mean located between ±60° and ±90° away from the target orientation. Note that the true circular mean of the orientations shown in each display of the learning trials could slightly differ from their seed mean. This is because orientations were randomly redrawn in each display, sampled from truncated Gaussian or uniform distributions with the chosen seed mean. However, these variations were negligible (standard deviation of the difference between the true circular mean and the seed mean across trials, subjects, and experiments: <1.60°) and well below the 15° steps of the CT-PD variable used to model changes in search times (see Analysis).

The target line in the test display could be presented in one of the 36 possible locations. Participants were asked to report the location (upper vs. lower half of the screen) of the target line by pressing the ‘i’ (upper) or ‘j’ (lower) keys of a computer keyboard as quickly as possible. The test display remained on the screen until a response was made. Two types of feedback were used to ensure that participants engaged in the task and maintained a high accuracy rate. First, error feedback (the word ‘error’, written in black) was presented following incorrect responses. Second, a score was calculated on each mini-block (as in previous work, Chetverikov et al., 2019), and the average score was shown after every 33 mini-blocks.

At the beginning of each experiment, participants were provided with written and verbal instructions and performed a sequence of practice trials under the supervision of the experimenter. Practice trials were not analyzed further but served to ensure that participants understood the task. The experiments consisted of 264 mini-blocks with 8 breaks, lasting approximately 1 hour.

Analysis

Trials with errors and response times slower than 1 second or faster than 200 ms were excluded from the analysis, following guidelines from previous work (Chetverikov et al., 2019) (34.6% in total for Experiment 1, 23.8% for Experiment 2). Participants performed with an average accuracy of 94±4% in Experiment 1 and 93±4% in Experiment 2. In Experiment 2, one participant was excluded due to average response times larger than 2 seconds, well beyond the threshold recommended in previous FDL studies (Chetverikov et al., 2019).

To evaluate the effect of the exposed distributions on search times, the relationship between single-trial log-transformed response times and the CT-PD variable was modeled with a set of five different models. These included a model assuming no effect of CT-PD on the log-transformed search times, defined as a model with only a 'constant' parameter (e.g., an intercept) and no parameter associated with the CT-PD variable (see Table 1). The other models assumed effects of various forms. In particular, the Linear model predicted a linear relationship between CT-PD and search times, the Uniform model predicted a step-like shift of search times in the CT-PD range, whereas the remaining models predicted effects that followed Gaussian and truncated-Gaussian distributions. Note that the truncated-Gaussian and uniform distributions corresponded to the one used to generate the exposure distributions. The explicit mathematical form of each model is reported in Table 1. All models were fitted by minimizing the negative log-likelihood of the data given the parameter values, using a quasi-Newton optimization algorithm (MATLAB's *fminunc* function). For each model, the Bayesian information criterion (BIC; Schwarz, 1978) was computed as $BIC = -2 * logL + k * log(n)$, where $logL$ is the maximum log likelihood value under each model, k is the number of parameters in each model (see Table 1) and n is the total number of data points. Model comparison was performed for the two types of exposed distributions separately, by subtracting all BIC values from the largest one. Differences in BIC (ΔBIC) larger than 2 are considered positive evidence against the model with the higher BIC (Raftery, 1995).

Experiment		1		2	
		Distribution		**Distribution**	
Model	**Function**	Gaussian BIC	Uniform BIC	Gaussian BIC	Uniform BIC
Constant	$y = a$	-619.24 *Δ = 0*	-528.72 *Δ = 0*	-67.73 *Δ = 6.65*	-2.31 *Δ = 6.26*
Linear	$y = a + b\lvert x\rvert$	-620.57 *Δ = 1.32*	-531.81 *Δ = 3.09*	-62.25 *Δ = 1.17*	3.32 *Δ = 0.61*
Uniform	$y = \begin{cases} a, & \lvert x\rvert \leq 2\sigma \\ b, & \lvert x\rvert > 2\sigma \end{cases}$	-623.9 *Δ = 4.65*	-533.44 *Δ = 4.71*	-62.03 *Δ = 0.95*	3.94 *Δ = 0*
Gaussian	$y = a + 2be^{\left(-\frac{\lvert x\rvert^2}{2\sigma^2}\right)}$	-620.87 *Δ = 1.62*	-530.59 *Δ = 1.87*	-61.10 *Δ = 0.02*	3.82 *Δ = 0.12*
Truncated-Gaussian	$y = \begin{cases} a, & \lvert x\rvert \leq 2\sigma \\ a + 2be^{\left(-\frac{\lvert x\rvert^2}{2\sigma^2}\right)}, & \lvert x\rvert > 2\sigma \end{cases}$	-620.93 *Δ = 1.68*	-530.65 *Δ = 1.92*	-61.08 *Δ = 0*	3.82 *Δ = 0.12*

Table 1. The set of models used in both experiments and the BIC of each model for trials with uniform and Gaussian distributions presented during exposure. The ΔBIC against the model with the higher BIC in each model comparison is reported below the BIC value. The model with the higher BIC is indicated by $\Delta = 0$. In all equations, y stands for the log-transformed, single-trial search times, x is the CT-PD variable in degrees (see Methods), a models the intercept, b is either the slope of the Linear model, the offset of the Uniform model or the amplitude of the Gaussian models (Gaussian and Truncated-Gaussian) and σ is the standard deviation of the Gaussian function.

Model comparison was paralleled with a two-way repeated-measures ANOVA with factors: Distribution Type (2 levels) and CT-PD (6 levels, from 0° to 75° in steps of 15°, considering the absolute value of the original CT-PD levels). For the ANOVA analysis, the response times of each participant were averaged across CT-PD levels. In the location priming analysis of Experiment 1, we compared response times as a function of whether the location of the singleton in the last exposure display was the same or different from the location of the test singleton, using paired t-test analysis.

Results

Experiment 1

In Experiment 1, where observers passively viewed arrays of orientated lines where one item was an orientation singleton, there was strong learning of the orientation distributions beyond the average or range. But there was little evidence that observers learned differences between the Gaussian and uniform distributions.

To evaluate whether the orientation distribution in the exposure displays affected performance on the test trial, we compared how well a set of models fit the shape of response times (RT) as a function of CT-PD (see Table 1). The set of models included a model with only a constant (i.e., no effect of the prior distractor distribution), a linear and a Gaussian model, and a uniform and a truncated-Gaussian model that resembled those used in generating the original distributions of the exposed orientations (see Figure 2A and Table 1).

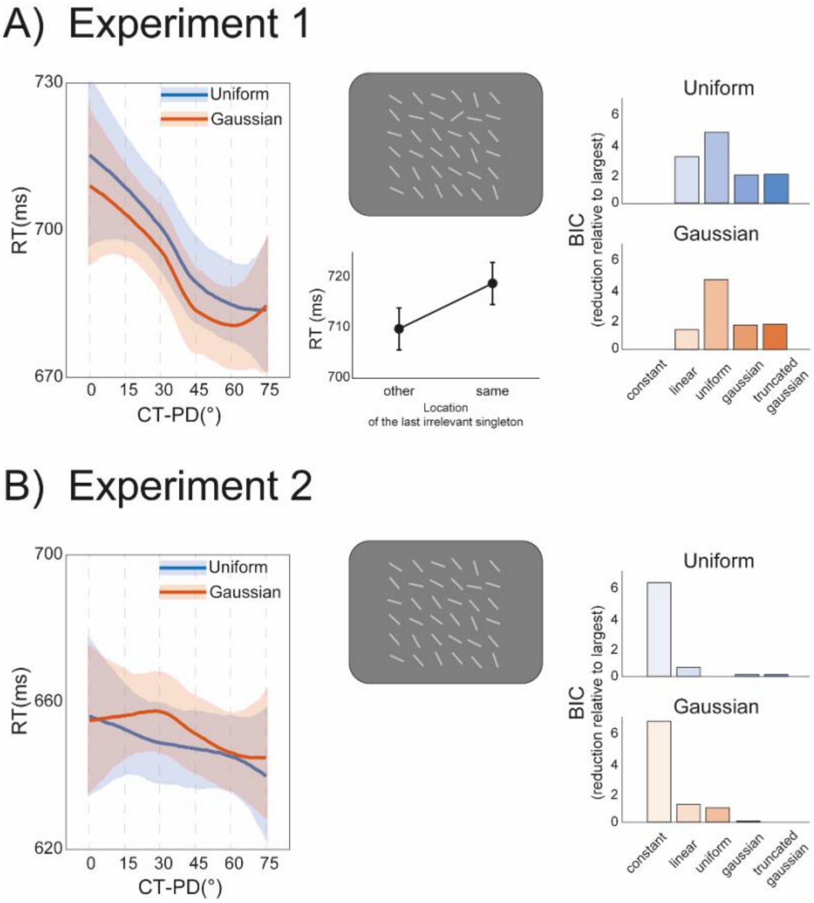

Figure 2. Results of Experiment 1 and 2. A) In Experiment 1, the exposed set of distractors contained a singleton orientation (as in the example display). Despite the absence of an explicit task, participants learned the distractors distribution during exposure, as evident from the decrease of response times (RT) as the angular distance between the previous distractors mean and the current target orientation increased (current target – previous distractor, CT-PD), a typical hallmark of FDL. According to Bayesian Information Criterion analysis (BIC), all models assuming an effect of the exposed distractors distribution performed better than a model assuming no effect (right panel, see also Table 1). This pattern was comparable across exposure sequences in which a uniform (blue bars) and a Gaussian distribution (red bars) were presented. The singleton line in Experiment 1 captured attention, causing significant negative location priming effects (response times were slower when the test target appeared at the same location of the last exposed singleton, line plot in the bottom-central panel). This involuntarily attentional capture likely caused the implicit learning of the distractors' distribution. B) In Experiment 2, in which the singleton line was removed during exposure (as in the example display), FDL did not occur and a model assuming no effect of the previous distractor distribution performed better than all the other models (BIC plot, right panel).

All models assuming an effect of the prior distractor distribution performed better than the model assuming no effect (see Table 1; minimum ΔBIC across model comparisons against the constant = 1.32). In particular, model comparison through the Bayesian Information Criterion (BIC; Schwarz, 1978), revealed positive evidence favoring the uniform over the constant and over the other models (all ΔBIC > 2, except for the comparison ‘uniform vs. linear’ in the condition with uniform distractor distributions: ΔBIC = 1.62).

This pattern was similar for the two types of distributions observers were exposed to during the learning trials. This means that observers' search times were clearly affected by the distribution of orientations during the exposure stage, and while this result was further supported by a significant main effect of CT-PD, in a two-way repeated-measures ANOVA with the factors Distribution Type X CT-PD (main effect of CT-PD: F(5,115) = 6.86, $p < 0.001$, $\eta_p^2 = 0.23$), the main effect of Distribution Type and interaction were not significant. While we would normally expect a main effect of Distribution Type, the results from the model comparison show that observers can passively learn the characteristics of a distribution of features, beyond the simple average. However, the learned characteristics did not allow sufficient resolution to distinguish between the shape of the uniform and the Gaussian distributions.

One potential explanation for this form of learning is that the presence of a singleton, although not task-relevant, per se, might have triggered automatic attentional capture mechanisms that lead to the implicit learning of the distractor features. That is, the singleton may have captured attention because it was an outlier in the orientation distribution and was implicitly represented and learned. To evaluate this possibility, we inspected potential priming effects due to the location of the irrelevant singleton in the last exposure display before the test trial. A small but significant negative priming effect revealed that search times were slower when the singleton during the last learning trials was in the same quadrant as the target singleton (t(23) = -2.24, $p = 0.035$). This confirmed that observers were not completely immune to the presence of a singleton at the exposure stage, and therefore, FDL might have been due to the automatic segmentation of a singleton from the distribution of features. In other words, the feature contrast causes singleton detection which is, in turn also connected with the learning of distributions. To address this point more directly, we performed Experiment 2 in which no singleton appeared during the exposure stage.

Experiment 2

As in the first experiment, observers passively viewed the display during the exposure trials and were tested on a single test trial. No evidence of an effect of the exposed distributions from the learning trials was found in this experiment (see Figure 2B and Table 1), with all the models performing worse than the constant only model (constant model against each of the other models with higher BIC, all ΔBIC > 4), and no significant main effect or interaction in the two-way repeated-measures ANOVA with factors Distribution Type X CT-PD (all *p's* > 0.05). This means that the presence of a singleton during the learning trials in Experiment 1, was crucial for triggering FDL by passive viewing.

Discussion

Recent work has shown that human observers can rapidly learn rich and detailed representations of distributions of visual features (Chetverikov et al., 2016, 2017a), above what is proposed in summary statistics accounts (Cohen et al., 2016). Here we asked whether this form of learning, in which the attentional system represents the full shape of a distribution of visual features, occurs during passive viewing or whether it requires active visual search.

We found that passive exposure to distributions of visual features in the absence of an explicit search task can affect future search performance, provided that the passively viewed displays contain a singleton element. In previous work, observers also performed a singleton search on the learning trials, and the RT patterns following learning tracked the precise shape of the learned distributions. It was possible to distinguish, for instance, learned representations that resembled the shape of Gaussian, uniform, and even more complex distributions (Chetverikov et al., 2016, 2017b, 2019). In Experiment 1, observers' performance was affected by the distribution of features during the exposure stage, beyond the simple average, but the resulting RT patterns did not allow us to distinguish between the Gaussian and the uniform distributions. One explanation for the inability to distinguish different distribution types is that this form of learning is eventually shaped and refined by the repeated attentional selection of a target singleton during active search. The detection of a deviant 'outlier' during singleton search may indeed be mediated by an implicit representation of the statistical properties of the whole display (Haberman & Whitney, 2012). Once the active process of segmenting out a deviant from the same distribution of features is reiterated a few times, the shape of the distribution is learned and temporarily stored in detail. Several findings reinforce this idea, suggesting that statistical representations are the building blocks of segmentation and categorization processes

(Im et al., 2021; Khayat & Hochstein, 2018; Utochkin, 2015). In line with this, the most likely explanation for our results is that the irrelevant singleton on passive trials triggered an unsolicited and involuntary attentional capture, which in turn, led to the automatic segmentation of a deviant from the distribution, and a coarse representation of the distribution's shape. This is supported by the absence of learning after removing the singleton from the passive trials of Experiment 2, and even more, by the negative location priming effect found in Experiment 1. The negative location priming suggests that participants did encode the irrelevant singleton (and its location) during passive viewing. This, in turn, impaired performance when the target appeared in the same location as the previous singleton, a form of negative priming typically observed at the location of previously irrelevant and distracting stimuli (Fox, 1995). We therefore speculate that the involuntary detection of a deviant singleton left a coarse trace of the statistical distribution of visual features from which the singleton was an outlier. In more active conditions, where the singleton is the target of a visual search, the characteristics of the distribution may be learned and retained more in detail (Chetverikov et al., 2016).

An alternative explanation is that search times were affected by the difference between the singleton orientation and the search target: search times could have been faster when the search target was similar to the singleton and slower as their difference increased. Since the odd item range was always far from the exposed distribution mean, this could have led to the gradual decrease in search times as the CT-PD distance increased (and the similarity between the singleton and the target increased). Because the CT-PD and the singleton-target difference in orientation were highly negatively correlated, due to the experimental design, it is not possible to fully disentangle between the role of one or the other, which could be an interesting question for future research. Nevertheless, both explanations are consistent with the idea that the presence of a singleton triggers an automatic capture and segmentation of the display, which could be mediated by activity in saliency maps that operate as early as in primary visual cortex (Li, 1999, 2002).

Our results add to the emerging field of research showing latent forms of short-term plasticity in the attentional system. These studies have provided evidence of basic and non-associative forms of learning, like habituation of the attentional capture response, after passive and task-free exposure to single stimuli (Turatto et al., 2018; Turatto & Pascucci, 2016; Won & Geng, 2020). Here we show that involuntary attentional capture and singleton segmentation can foster more complex forms of learning in which the properties of a distribution of visual features are latently and automatically learned. The dependence of passive FDL on the presence of an outlier might be functionally meaningful: constantly learning the entire statistics of irrelevant features in the visual world might be redundant and resource-consuming; learning the distribution of features that signal a ‘surprise’, can aid the attentional system in directing resources more efficiently when such surprise becomes relevant for behavior.

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