Continuity in perception

Contrasting serial dependence, aftereffects and learning of ignored information.

Christian Houborg

Thesis for the degree of Philosophiae Doctor

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Abstract

English abstract.

When we are viewing the environment around us, we are exposed to an overwhelming continuous stream of information: not everything can be processed at once, and the perceptual system must pick and choose. We must direct our attention and select stimuli of interest while ignoring or discarding irrelevant information in order to solve daily tasks and problems. An effective tool to simplify such a daunting task is for the perceptual system to chunk information together. Various pieces of spatial and temporal information can be used to bind several features which correlate in space and time into singular objects. However, because the visual world is ambiguous and prone to noise, correctly combining and selecting similar yet distinct features and objects is still an ambitious undertaking. Prior assumptions and expectations of our visual environment provide additional aid. They do this, for example, by assuming that objects and their defining features are stable entities which are maintained over time and taking advantage of such stability and regularities over time. Additionally, maintaining representational maps containing predictions of relevant or irrelevant locations or features associated with objects further eases the task of sorting the vast amounts of continuous visual information. A vast number of history-driven biases in attention and behavior have been demonstrated experimentally to improve performance when locating and discriminating between visual stimuli. Encoding of sequentially presented stimuli is attentionally facilitated when stimuli share a feature or location. Similarly, if such characteristics occur within the same object, attentional effects are spread within the entire object. The continuous flow of information can be subject to transient changes, such as blinking and changes in lighting, requiring a mechanism which employs this general predictability in order to maintain perceptual stability despite such transient changes. Serial dependence, a general attraction to previously viewed stimuli information, has been proposed as such a perceptual smoothing mechanism (J. Fischer & Whitney, 2014). It is proposed that perception is smoothed, and perceptual decisions of present stimuli are influenced by past stimuli within a spatial and temporal continuity field. Further, attention has been deemed a crucial factor: perceptual decisions about attended stimuli are attracted towards previously attended stimuli. In the papers of this thesis, we further explore the role of attentional selection in serial dependence by employing and adapting spatial, feature-based, and object-based attentional and serial dependence paradigms. In the first paper, we investigated representation traces left over after attentional filtering of irrelevant stimuli when spatially suppressed. Observers performed two tasks sequentially: first, they performed a discrimination task while ignoring a distractor Gabor, reproducing the orientation of a

Gabor afterwards. Notably, we did not observe a difference between suppressed or non-suppressed distractors, which equally interfered with perceptual decisions of the reported Gabor. This showed that perceptual decisions are biased away from the features of recent distractors. Such effects could be caused by either attentional filtering or active removal of irrelevant traces of information. We speculate that distractors were processed to the extent that they left a trace or interfered with other ongoing traces of prior stimuli. In the second paper, we studied the role of feature-based attention and task demands related to secondary contextual features. Participants performed either a detection task, responding to a cued color, or a discrimination task, actively responding differently to two colors, while a sequence of red or green Gabors were presented; the orientation of the last Gabor was reproduced. We observed that during the detection task, attraction only occurred towards the target color, whereas during the discrimination task perceptual decisions were attracted to previous stimuli regardless of color. The results provide further evidence that serial dependence is modulated by task demands and task contextual information. They further suggest that serial dependence can operate on features and does not need object representations, i.e., attraction can occur between features of different objects. We propose an account of parsimony, wherein the representation required by the task determines what information is propagated from one instance to another. Finally, in the third paper, we investigated the tuning of serial dependence to object representations, employing object-based attention by presenting a Gabor at one of the ends of two triangles. When the previous Gabor was presented within the same object, we observed a widening of the range of relative orientation differences in which attraction took place. We suggest an increase in stimulus sensitivity caused by attentional employment based on objects. Overall, our results show that task demands, attentional facilitation and filtering processes have an important and nuanced role in serial dependence.

Keywords:

Serial dependence; visual attention; spatial attention; feature-based attention; object-based attention.

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Contents

List of Figures

List of Original Papers

This thesis is based on the following original publications, which are referred to in the text by their Roman numerals (I, II, III, ... [as needed]):

I. Houborg, C., Pascucci, D., Tanrikulu, Ö. D. & Kristjánsson, Á. (2023). The effect of visual distractors on serial dependence. Journal of Vision, 23(12):1. https://doi.org/10.1167/jov.23.12.1.

II. Houborg, C., Tanrikulu, Ö. D., Kristjánsson, Á. & Pascucci, D. (2023) The role of secondary features in serial dependence. Journal of Vision, 23(5):21. https://doi.org/10.1167/jov.23.5.21.

III. Houborg, C., Kristjánsson, Á. & Pascucci, D. Object-based processing reduces feature tuning in serial dependence. Submitted for review in Psychonomic Bulletin & Review

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Declaration of Contribution

Christian Houborg made contributions for designing and programming of experiments, Planning and performing data collection, data analysis, and writing the paper manuscripts. The thesis was written by Christian Houborg.

Árni Kristjánsson and David Pascucci provided supervision and contributed to experiment design, data analysis, writing the paper manuscripts and thesis.

Ömer Dağlar Tanrıkulu made contributions to experiment design (paper I and II) and programming (paper I) and provided additional supervision and support.

1 Introduction

When taking a walk in the forest, at the beach, or down through your local university campus, it is hard not to notice how vast and rich in information the visual scene captured by our eyes is. When taking a single glance in a random direction, there are more single pieces of information than we could seemingly ever process, counting every single leaf in the forest, the grains of sand at the beach, the activity, people, books, and information at the university. Nevertheless, with the aid of our perceptual organs, and our brain, we are able to avoid getting lost, and are able to navigate these visual scenarios filled to the brim with information, some pieces of it relevant for successful navigation to the end destination of our walk, other pieces of information irrelevant, red herrings, that will take us down other pathways we might not wish to tread on the current planned trajectory.

Luckily, the majority of the world, and we ourselves, remain stable over time, which allows us to build experience and expectancies which we, and the perceptual system, can take advantage of. We can use this collection of experience to build templates that guide our navigation, templates of relevant stimuli to search for, which guide us to our current goal: Certain wooden signs, a particular pattern of foliage, trees, or bushes, that mark the correct path for our journey. Similarly, we build expectancies and templates of irrelevant stimuli, which waste our energy, which we can then avoid, ignore, or in other ways disengage from more efficiently to spare our limited energy for the walk ahead of us. One fundamental challenge facing us in this information rich environment is the following: how do we most effectively select the correct pieces of information?

As we are continuously experiencing the environment around us on our walk, we will also perceive changes, we walk past a tree, we reach a new tree; suppose we are looking for a tree whose branches are facing in a certain direction, the orientation of the branches will be our guide for decisions on our next turn. Here, we are faced with a second problem, where the smooth flow of visual experience and changes in the environment is achieved by the perceptual system taking advantage of regular similarities in the visual scene. However, this means that different pieces of information are bound together, which gives us history-driven biases in our perceptual decision making. Our judgment of the orientation of the branches will be drawn towards the orientation of a previous set of branches on the trees we saw: We might end up deciding the orientation is incorrect and continue walking straight when we should have turned! But this should not be concerning, for reasons we shall get into later, since the alternatives, without this seamless integration of past and present information, make us much more likely to make these types of mistakes.

The sensory information that we receive is not perfect but is filled with noise and uncertainty: our eyes are not perfect (perhaps it is time to visit the ophthalmologist for a new pair of glasses), objects are overlapping, lighting and shadows are confusing, the weather is raining and foggy, and we might not feel confident in our decisions. Temporally and spatially smoothing perception enables us to integrate previous and current percepts, allowing compensation for when sensory noise, or our uncertainty is high (Ceylan et al., 2021; Gallagher & Benton, 2022; van Bergen & Jehee, 2019).

This slightly elaborate example touches on the core subjects that will be explored in this thesis, which involves continuity in perception, serial dependencies in vision and behavior, how these processes are guided by attention and attentional selection in space, selection of certain features, or certain objects. In the thesis, history-driven biases, mainly serial dependence, will be our primary tool to investigate perceptual decision making, how attentional selection of information relevant to our task guides behavior, and also addressing the question of what becomes of the information deemed unusable. Does this ignored information leave a trace? Does it get integrated with our selected information? Or is it simply ignored with no trace remaining? In short, in the thesis, the phenomenon of serial dependence will be used to investigate how attention affects decision making and integration of past and present events.

First, I will continue the introduction of the relevant concepts to the studies presented here: history-driven biases such as the motion aftereffect, the tilt aftereffect and finally serial dependence, the attraction to previous stimuli and decisions and its connection with other aftereffects. Following this, I will elaborate on the concept of attention, specifically attentional selection, priming effects, statistical learning of the spatial and temporal characteristics in each scene or sequence of stimuli, followed by a brief elaboration of the aims with each paper. Then, I will give a short overview of the most common methods, their strengths and weaknesses, and elaboration of the methods chosen for this project. Finally, the results of the three papers will be summarized and their contribution to the questions currently asked in the scientific fields of visual attention and serial dependence discussed.

1.1 History-driven biases

History-driven biases in visual perception have recently experienced a resurgence as a topic after a number of studies revealed that our estimates of visual stimuli are not made independently, but are affected by recent experience, in a manner, that bias our estimates more towards previously seen stimuli (Cicchini et al., 2014; Corbett et al., 2011; J. Fischer & Whitney, 2014). However, this is not the only type of history-driven bias of which there are several, some with much older history, which overlap and must be disentangled. Such disentanglement has proved to be difficult, however, as recent work has suggested that they occur concurrently, such that our perception can be both attracted towards and repulsed away from previous visual experience in the same moment (Moon & Kwon, 2022; Pascucci et al., 2019; Sheehan & Serences, 2022). This repulsion from previously seen features is an older and, in isolation, a well understood phenomenon.

1.1.1 Visual aftereffects – Motion aftereffect

First described by Aristotle, who noted that turning your gaze away from objects in motion like a river, the visual stimulation remains present and things at rest are perceived as moving (Sekuler, 1965). Much later, in 1819, Purkinje described a parade of horse riders eliciting the same effect, and speculated that eye movements and fixations had become accustomed to following each rider passing by and thus repeating the movements even when all the riders are gone (Purkyn, 1819; Sekuler, 1965). Later, a chemist and lecturer described the same curious phenomenon from his trip to the Loch Ness, gazing at the waterfall, and recreated the phenomenon upon his return to his laboratory, proposing an eye movement account similar to Purkinje's (Addams, 1834; Sekuler, 1965).

While their idea of getting accustomed to the visual input turned out to be somewhat correct, they were incorrect that the aftereffect was due to eye movements. It is instead a phenomenon of *adaptation* in cells in the visual cortex tuned to respond to motion direction (Anstis et al., 1998). The exact neural interactions are still unknown; one proposal is when we then turn our gaze away from the adapting stimulus, the adapting cells lose in competition with the opposite motion direction cells, creating this visual sensation of flowing motion while watching still objects (Anstis et al., 1998). While repeated stimulation of the targeted neurons suppresses their activity, it is unlikely that this is due to neural fatigue. Instead, these types of adaptation effects are more likely a result of the perceptual system optimizing resource and energy usage. (Anstis et al., 1998). This strategic use of resources is theorized to start at early stages of visual processing in primary visual cortex (V1) and move towards higher processing areas. More recent accounts propose an attractive shift in the tuning curves of neurons from an interaction between adapted feedforward input and recurrent excitatory and inhibitory connections. Importantly, adaptation can be captured by efficient sensory encoding coupled with Bayesian decoding models (Clifford et al., 2007). Here we can argue that there is an instance of our perception being directly affected by our recent sensory experience, an example of a bias driven by viewing history. Motion can be relatively complex with several brain areas and processing steps included. However, there are similar perceptual aftereffects and adaptation that can occur even when we are just watching an oriented line.

1.1.2 Visual aftereffects – Tilt aftereffect

A similar, yet more subtle, effect was demonstrated in much simpler stimuli. Termed the tilt-aftereffect, it is a simple phenomenon: When we perceive an oriented grating, upon viewing a subsequent grating we will perceive and estimate its orientation 4-5 degrees in the opposite direction of the previous grating (Gibson & Radner, 1937). It was further shown to follow a similar adaptation when viewing colors, and was proposed to be a general retinotopic sensory adaptation phenomenon occurring within the space occupied by the stimulus within the visual field (J. J. Gibson, 1937).

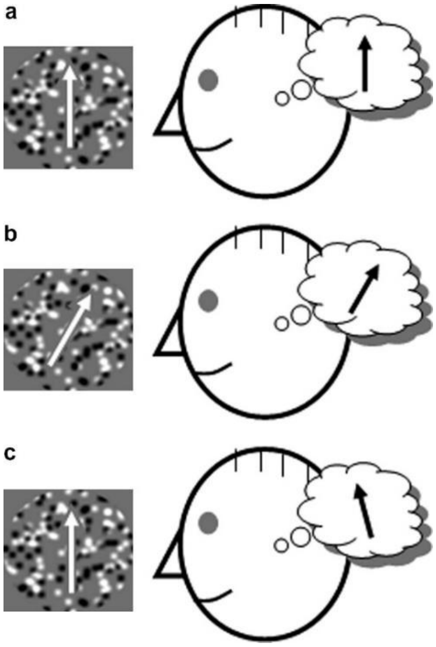

Figure 1. Visual adaptation – tilt aftereffect.

Demonstration of the repulsive effects of adaptation during motion and tilt aftereffects. a) Participants are viewing a pattern of dots moving in the direction of the arrow. b) After prolonged exposure to a previous oblique direction of motion, c) perception of the following horizontal stimulus is perceived as moving in the opposite direction of the previous stimulus. Figure taken from (Levinson & Sekuler, 1976).

Similar to the motion aftereffect, neural models of the tilt aftereffect suggest that the effect occurs as a result of suppression of the neurons sensitive to the orientation of the previously seen stimulus (Clifford et al., 2000). Adaptation has been shown to benefit discrimination around the adapting stimulus, and overall serves a functional purpose to the visual system proposed as a continuous calibration optimizing the distinction of visual inputs (Clifford et al., 2000; Kristjánsson, 2011). Serial dependence studies, as we will demonstrate later, have typically been performed with orientation adjustment tasks. The repulsive effects of adaptation are inextricably linked to the attractive effects of the serial dependence literature, and much work still remains to disentangle the two (Pascucci et al., 2023).

1.1.3 Serial dependence

In an experiment by Corbett and colleagues (2011), participants had to estimate the number of dots displayed in one out of four quadrants on the screen. The number of displayed dots varied randomly between 25 to 45. They then computed the independence between pairs of estimates by calculating improvement in estimation accuracy through averaging participants' responses relative to considering them separately. Specifically, in their approach they evaluated how much more accurate people become by taking a second glance at the same set of stimuli, and how independent are the first and second glances from each other over time. Counter-intuitively, with increased independence between estimates, the improvement in accuracy by simply averaging also increases. Corbett and colleagues (2011), also found high autocorrelations between estimations, concluding that sequential visual percepts are serially dependent, meaning that they are dependent on what preceded the current percept, with some retinal specificity.

Following an influential article by Fischer and Whitney (2014), serial dependence became the widely adopted term for this attraction to the past, which happens not just with numbers, it happens across all levels of vision: low-level stimuli like orientation or color, mid-level stimuli like ensembles and shapes, and high-level features such as faces or even emotional expressions on faces (Collins, 2022a, 2022b; J. Fischer & Whitney, 2014; Fornaciai & Park, 2018b; Liberman et al., 2018; Manassi et al., 2017).

Fischer & Whitney (2014) performed five experiments to elaborate on previous findings, in the first experiment, participants viewed an oriented Gabor (a grating pattern tilted at a particular orientation) presented to the left or the right of a fixation dot in the middle of the screen. Afterwards, a patch of random noise was presented in the same location, which 1) removes the afterimage on the retina and 2) helps prevent visual aftereffects from adaptation. Afterwards participants then reproduced the orientation of the Gabor by adjusting the orientation of a line. In experiment two, to rule out effects of motor performance, participants carried out the same task except that on 25% of trials there was no required response. The experiments demonstrate that participants' error in the task (reported orientation – correct orientation) systematically displayed bias towards the orientation of the stimulus in the previous trial, and that such bias did not require memory recall of the biasing stimulus, nor was it a result of motor execution during the response (J. Fischer & Whitney, 2014).

In a third experiment, participants performed a two-alternative forced-choice task, where two Gabors were displayed, and participants had to report whether the cued Gabor was tilted more clockwise than the uncued stimulus. This prompted a shift in the point of subjective equality towards the orientation of the previously cued Gabor of the previous trial (PSE, when the two Gabors are perceived as having the same orientation). Participants' perception of the present Gabor was thus influenced by the cued Gabor from the previous trials with a slight reduction in the ability of observers to discriminate orientations. Importantly, this point separates serial dependence from priming, which facilitates processing and increases discriminability of repeated stimuli (J. Fischer & Whitney, 2014; Galluzzi et al., 2022).

In a fourth experiment, they proceeded to demonstrate that attention towards the stimulus is required for serial dependence. They cued a location to be reported before displaying a circular array of 8 Gabors, only observing serial dependence when the location of the previous trial and current trial cues matched. This point has further been solidified by a binocular rivalry study, where serial dependence only occurred towards the dominant percept (J. Fischer & Whitney, 2014; Kim et al., 2020). Finally, following upon the results with a fifth experiment, Fischer & Whitney put forward the notion of the perceptual continuity field. They argued that we are only attracted to previous stimuli within a certain spatial distance within 15-20 deg. of visual angle and within a 10-15 second time window (Figure 2.C).

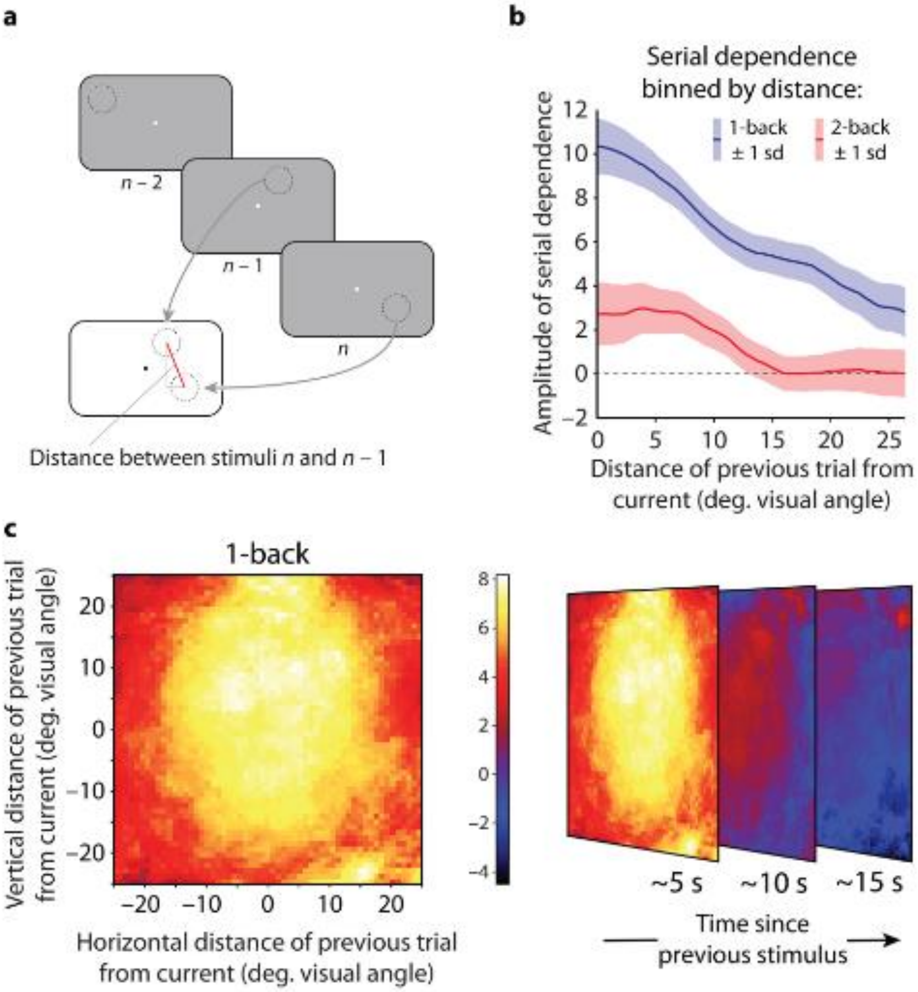

Figure 2. Spatiotemporal continuity field.

Experiment five from Fischer and Whitney (2014). The experimental design can be seen in (a) where they investigate the spatial tuning of serial dependence by randomizing the location of the Gabor. Amplitude of the bias (b) elicited from previous stimulus (blue line) and the stimulus two trials back (red line) is calculated in a rolling window. Attraction to the 2-back stimulus was significantly smaller than for the previous trial. Afterwards (c), they computed a rolling window within a two-dimensional space over the relative positions of the current and previous stimuli and expands it over points of time.

1.1.3.1 *Serial dependence and after-effects.*

So, which is it? Serial dependence or after-effects? Attraction or repulsion? The answer seems to be both: The two apparently opposing processes seem to be distinct mechanisms serving different purposes and following slightly different sets of rules. Nevertheless, these contrasting processes are constantly interacting (Moon & Kwon, 2022; Pascucci et al., 2019; Schwiedrzik et al., 2014; Sheehan & Serences, 2022). For instance, adaptation effects are retinotopically highly specific, while attractive effects are observed within a wide spatial window (J. Fischer & Whitney, 2014). Furthermore, adaptation builds up through elongated exposure to the stimulus to accommodate when change happens in the visual environment (Kohn, 2007). However, in situations where quick changes occur, these might not be associated with inherent changes in the object, but rather an external event or internal sensory noise (J. Fischer & Whitney, 2014). To further support this, investigations of the functional role of serial dependence indicate that, not only does it improve accuracy and decrease reaction times, attractive effects are strongest when stimulus information is noisy and less precise (Ceylan et al., 2021; Cicchini & Burr, 2018; van Bergen & Jehee, 2019).

The neural origin of adaptation is relatively well understood, although the exact neural mechanisms are still debated (see the visual aftereffects section). The origin of attractive serial dependence is still not clear: Does it reflect low-level perceptual vision or higher-level decisional areas that relate to perceptual decisions? Tied into this debate, does serial dependence act directly on our perception in a behavioral sense, in the same sense as a motion aftereffect, which leaves a very salient percept of motion? Or is it an effect which only affects our decisions when we are prompted for an estimate – in other words, forced to make a decision? This is still actively debated, and while the research described here will not address this question, it is an effective segway towards the recent modelling work of history-driven biases in vision.

Some recent work found behavioral as well as some neuroimaging evidence that we do perceive stimuli as being more similar to previously occurring stimuli and it is not just the measured estimate that is biased towards the previous percept or response (Cicchini et al., 2017; Collins, 2020; Fischer & Whitney, 2014). One fMRI study observed activation in primary visual cortex (V1) evoked by previous stimuli, potentially suggesting a perceptual nature of serial dependence (St. John-Saaltink et al., 2016). However, another fMRI study using bistable stimuli found separable effects and networks for adaptation and hysteresis, attraction towards previous stimuli. They found that adaptation effects were restricted to early visual areas. Serial dependence, or hysteresis, effects were mediated through a wider distributed network of high-level visual and frontoparietal areas (Schwiedrzik et al., 2014. See Pascucci et al., 2023 for review). As noted earlier, studies that followed this one supported this view (Moon & Kwon, 2022; Sheehan & Serences, 2022; van Bergen & Jehee, 2019).

An influential paper proposed a late-to-early model, or in other words, a high-to-low level processing model, where the high-level distributed network would affect the early low-level sensory areas. The basic idea being that previous high-level visual processing would affect subsequent low-level processing. In this view, perceptual decisions are mediated by a two-process model where readout weights of decision units compensate encoding and sensory adaptation (Pascucci et al., 2019). Some models of hysteresis thought the attractive bias to be the signs of an ideal observer (Cicchini et al., 2018). However, later works demonstrating the role of uncertainty, either in terms of a noisy sensory signal or low observer confidence, were inconsistent with the notion of an ideal observer (Ceylan et al., 2021; Samaha et al., 2019).

The main concern was that serial effects are strongest when uncertainty is high in the current trial, regardless of the uncertainty on the previous trial, i. e. previous uncertainty does not affect the extent of serial dependence (Ceylan et al., 2021; Gallagher & Benton, 2022). Bayesian models were advocated by van Bergen & Jehee (2019) after their fMRI study suggested that probability distributions decoded from early visual areas (V1-V3) reflected the uncertainty informing the decisions the observer makes. Fritsche et al., (2020) proposed a model using efficient encoding with a mixture prior, accounting for regularities in the environment over extended timescales, and Bayesian decoding of visual information, reflecting the two-process model proposed earlier. This model effectively captured attractive and repulsive effects over time, suggesting that visual information of stimuli is encoded efficiently, and that Bayesian decoding of the encoded information is used to take advantage of stability in the visual environment by making predictions based on visual history. While this current modelling work has given a better understanding of how adaptation and serial dependence interacts, it remains unclear why uncertainty only matters in the current trial independent of the previous trial.

1.2 Attention

Early studies suggest that serial dependence is gated by attention since unattended stimuli do not affect our perceptual decisions on following stimuli (J. Fischer & Whitney, 2014; Kim et al., 2020). However, this notion of uncertainty presents a conundrum. Attention typically facilitates encoding of stimuli, meaning that closely attended stimuli should be more strongly encoded and associated with less uncertainty. As such, the idea that attention only gates serial dependence seems unlikely: attention should also modulate uncertainty and serial dependence by extension in more subtle ways.

1.2.1 History driven effects in attentional selection – priming

Attention also has effects driven by recent visual history, often referred to as attentional priming, where visual objects are processed differently dependent on their role. One example, referred to as 'priming of pop-out', is that reaction times are faster when a target item is of the same color or on the same location as the previous trial (Maljkovic & Nakayama, 1994, 1996). Another type of priming effect is positive repetition priming, where the repeated presence of a target stimulus facilitates processing of this stimulus in the following trials, thus participants react quicker and with less error in such repeated instances (Kristjánsson & Campana, 2010). The reverse effect also exists, negative priming, where a stimulus to be ignored in the previous is processed slower and less accurately when the same stimulus is to be reported in the current trial (Frings et al., 2015). Whether such attentional effects on the encoding and processing of stimuli affect attraction or repulsion of previous stimuli is still poorly understood. It could be hypothesized that positively primed stimuli will elicit a lesser serial bias due to stronger encoding of stimulus features and less perceptual noise. Another possibility is that negatively primed stimuli elicit a stronger bias. However, there are more complex factors to consider first. Recently, with regard to attentional priming, the case has been made that there is a memory system for recent attentional deployments which allows for quick reorientation and deployment of attention to stimuli which are relevant to our task at any given time (Kristjánsson & Ásgeirsson, 2019). Attentional selection, an act of selecting certain stimuli relevant to solve a task at hand, is supported by such a system which rapidly learns from recent experience in order to better select relevant stimuli and maintain stability during switches in the visual environment and task demands (Kristjánsson, 2006).

For selecting relevant targets, this can be very useful. But how do we deal with stimuli to be ignored, when negative priming suggests such a shift impairs performance when they switch to become relevant? When this has been studied using classic cuing paradigms the problem of the white bear occurs: if we are asked to not think of a white bear, our thoughts will jump to a white bear. If participants are informed of which stimuli will be a distractor in a display with multiple targets, it will impair their performance as they will theoretically attend to the distractor before the target (Tsal & Makovski, 2006). A subsequent study revealed that this is true, however, over time and with consistent practice and repetition of the same task, the distractor is ignored and the target is selected faster (Cunningham & Egeth, 2016). This has led to the notion that, in attentional selection, target facilitation and distractor suppression (ignoring irrelevant information), are distinct processes (Noonan et al., 2016).

To better understand distractor suppression, we must explore the notion of statistical learning: Over time we develop a probabilistic representation of the visual environment ad develop expectations towards it (Slagter & Van Moorselaar, 2021; Wang & Theeuwes, 2018b). We form attentional templates of relevant and irrelevant stimuli which reflect probabilities of the features or locations of stimuli. This is demonstrated in an odd-one-out search, where participants search for a target which is the odd stimulus amongst an ensemble of stimuli. Here search slows when target features approximate the feature distribution of previously seen irrelevant stimuli (Chetverikov et al., 2020).

Statistical learning both facilitates processing of relevant information and guides attention away from irrelevant information (Geng & Behrmann, 2002; van Moorselaar & Slagter, 2019). A study directly tested active top-down suppression against implicit suppression derived from statistical learning of distractor location probabilities. They found that when adding an explicit arrow-shaped cue indicating distractor location probability no suppression occurred, on the contrary, search became faster in the trials where the target randomly appeared in the cued location (Wang & Theeuwes, 2018a). Indicating that distractor filtering occurs as an implicit process, which can be hindered by top-down attentional selection, further underlining the findings of Noonan and colleagues (2016).

Attentional selection of relevant information while successfully suppressing distracting information seems to occur as an implicit process, where we implicitly observe statistical regularities of distractor features or location to form expectations and attentional priority maps which guide attention around irrelevant information (Failing et al., 2019; Ferrante et al., 2018; Gao & Theeuwes, 2020, 2022). However, such an implicit operation does not seem to come without a cost: when a distractor is present we locate the target quicker, but when the distractor is absent baseline search speed is slowed (Marini et al., 2013).

To summarize, on short timescales, a memory system tracks previous attentional deployments primarily to facilitate processing of relevant information, while maintaining stability during changes in visual environment and task context. When a previous distractor becomes a target search reaction time will be increased and accuracy reduced, for example. Complete filtering of distractor information seems to occur implicitly on longer timescales, where expectations about distractors are built through previous experience creating attentional templates or priority maps guiding us towards targets, once we have learned what information is irrelevant and can be safely ignored.

1.2.2 Three forms of attention; Feature, Space, Object

If we think of attentional selection as a highlighter of visual information, it seemingly works through three primary methods of highlighting. As discussed above, there are many cases of spatial and feature-based attention. Spatial attention highlights information at a specific location where relevant information is expected to appear. Feature-based attention will highlight a task relevant feature in visual space: If we are looking for green apples, green will be given attentional priority across space. Finally, there is object-based attention, which could be described as a combination of the previous two.

Attention is allocated to information within a space defined by a conjunction of features, which can for example be lines forming a rectangular object, or a group of stimuli sharing a feature like color or motion direction, though whether the last example constitutes feature-based or object-based attention is still debated (Cavanagh et al., 2023). In, Egly, Driver & Rafal (1994), the authors drew two horizontal or vertical rectangles on the left and right sides, or above and below, a fixation dot. A cue would then highlight the end of one rectangle where the target will most often appear. Importantly, the cue was not always valid, and crucially there were two cue-invalid conditions, in which the target could appear at an equidistant location from the cue either within the same or within the different rectangle. Their results showed that participants were significantly faster at reporting the cue-invalid target when it appeared at an equidistant location within the same object compared to the different object. This suggests that the 'highlighted' space from the cue extends to the entire object (Egly et al., 1994) and not uniformly across space.

Later studies have shown that it does not only operate in a goal-directed manner, but that features forming the bounds of an object can elicit object-based effects in a stimulus driven manner as well (Kimchi et al., 2007; Yeshurun et al., 2009).

All of these processes interact to organize our perception of a visual scene and create a scene-wide pattern of attentional facilitation of said scene (Kravitz & Behrmann, 2011).

1.2.3 Serial perception: Vision goes for novelty, decisions for perseverance

Before we return to serial dependence, now that some aspects of attention have been introduced, let me briefly introduce Inhibition of Return, which underlines a sentiment also recently brought up in serial dependence literature, in the proposal that vision goes for novelty (Pascucci et al., 2019; Posner & Cohen, 1984). Briefly returning to our opening example, we are walking through the woods conducting a visual search for a target in the visual environment which indicates where to turn. As we are orienting our gaze from one point to another in the visual scene, a relative suppression of the processing of stimuli previously subject to our attentional focus occurs. This inhibition of return discourages orienting towards previously inspected locations and objects, which facilitates search and encourages seeking novelty in the visual scene (Itti & Koch, 2001; Posner & Cohen, 1984). This effect has shown not only that search slows when returning to a previously viewed location or object, but also reduces our perceptual sensitivity towards stimuli at these locations (Ivanoff & Klein, 2006). Our ability to discriminate stimuli or the signal we receive from stimuli is subject to more noise, and it may be speculated whether this might tie in with the spatial window observed in serial dependence studies, since attraction is strongest at the same location.

1.3 Serial dependence, attention, features, and object identity

The curious reader might ask at this point, is serial dependence just priming? Indeed, this question has been raised at conferences by people aware of the phenomenon but not experts on the literature. But notably, priming and serial dependence operate in some cases similarly enough to warrant a special investigation confirming that they are indeed mediated by two distinct mechanisms (Galluzzi et al., 2022). Serial dependence has however shown to affect spatial attention: detection of an oriented stimulus increased or decreased depending on whether attraction or repulsion from irrelevant stimuli on the screen occurred (Collins, 2020). Similar to the spatial findings of Fischer & Whitney (2014), in a visual search for the odd-one out oriented line amongst an ensemble of oriented distractors, it was found that reproduction of the target lines was biased away from the orientation distribution of the distractors (Rafiei, Hansmann-Roth, et al., 2021). Not only has spatial attention been shown to affect serial dependence, feature-based attention has also been shown to be important. In a study published by Fritsche & de Lange (2019), they demonstrated that if participants are attending to the size of a previous oriented stimulus, attraction towards its orientation is significantly reduced. Similarly, if participants are presented with two differently colored Gabors and asked afterwards via post-cue to reproduce one Gabor of a specific color, attraction only occurs towards the previous Gabor of the same color (C. Fischer et al., 2020).

This touches on a couple of key issues in serial dependence, working memory, task-dependency, and object identity. Since the task involves visual working memory when reproducing stimulus features, it has been shown that serial dependence occurs independently of any explicit memory of prior stimuli (J. Fischer & Whitney, 2014). However, a few studies show that if the retention interval is elongated before reproducing a stimulus feature, attraction towards previous stimuli increases, suggesting that working memory can at least modulate the effect, even indirectly such as by affecting the observers' state of uncertainty (Bliss et al., 2017; Fritsche et al., 2017). Similarly to other findings of task irrelevant or distractor stimuli, similar effects were observed in working memory. Displaying two stimuli followed by a post-cue to determine which is to be reported, there was a repulsive bias from the non-reported stimulus within a trial and attraction towards the previously reported (Czoschke et al., 2019). Following this finding another study suggested this is caused by active removal from working memory in contrast with passive removal (Shan & Postle, 2022). This indicates that serial dependence can be affected by task-relevance and contextual factors such as location or features indicating task relevance. Working memory can be one of several top-down processes affecting serial dependence.

Some studies have shown that serial dependence can occur without any explicit task indicating that while top-down processes can affect history-driven biases, these effects can also be caused by bottom-up driven processes (Fornaciai & Park, 2018a; Murai & Whitney, 2021). But task driven factors can determine where attention is directed, which objects or features are relevant and which are irrelevant and can be ignored or discarded. It has been shown that when solving tasks, representations are not fixed, they can be simplified for utility, efficiency, and optimal use of limited cognitive resources (Ho et al., 2022). C. Fischer and colleagues (2020) suggest that the modulations observed in their study, attraction only towards the cued contextual feature when relevant, reflect that single features of objects as bound together and that working memory items as a combination of content and context features closely match object-files. In order to discriminate objects, we must bind features correlated in time and space together, and such a representation must also remain stable over time despite transient changes in the environment (C. Fischer et al., 2020; Kahneman et al., 1992; A. M. Treisman & Gelade, 1980).

However, this notion of the role of serial dependence is at odds with the findings from Ceylan and colleagues (2021), where participants were found to be equally attracted towards the previous Gabor stimulus when they were judging the direction of motion of a dot kinematogram or vice versa. One possibility could be that object features are bound in visual working memory, and serial dependence selectively operates on representations of objects. Another possibility, is that serial dependence functions on elementary task features, where similar features that overlap spatiotemporally are assumed to belong to the same object (Collins, 2022a; Pascucci et al., 2023). Both explanations fit the idea of the spatiotemporal continuity field, however under the second option, where representations of elementary features are maintained as representations in working memory, serial dependence is not hinged on the continuity of objects. Instead, serial dependence may occur between similar features across objects (Ceylan et al., 2021; Kwak & Curtis, 2022; Pascucci et al., 2023). Another study had participants reproduce the orientations of Gabors on a moving trajectory through an occluder (Liberman et al., 2016). They observed only attraction towards the previous stimulus when it matched the same movement trajectory, thus providing evidence for operation on object representations when they mimic properties of the real world. Furthermore, they found that when judging more complex stimuli, such as emotional expressions on a face, attraction is object dependent (Collins, 2022a). However, the possibility remains that this is contingent on task demands and that complex visual objects such as faces cannot easily be reduced to low-level features and other task demands such as responding to a certain color cue.

Serial dependence is not only tuned to space and time, but is additionally argued to be tuned to a window of feature-space (Kiyonaga et al., 2017; Manassi et al., 2019), i. e. the similarity in features between the prior and current stimuli. Often serial dependence is mostly quantified as the amount of degrees behavior is attracted toward the previous stimulus at its peak. However, some studies have noted that at increasing dissimilarity between previous and current stimulus features, attraction becomes repulsion (Bliss et al., 2017; Fritsche et al., 2017; Fritsche & de Lange, 2019). Perplexingly, one prior stimulus can elicit both effects on two simultaneous stimuli determined by their feature similarity (Rafiei et al., 2023). This further interacts with attentional effects of a task, such that the repulsive effect typical of distractors becomes attractive when they are systematically similar to the reported stimulus (Rafiei, Chetverikov, et al., 2021). One proposal is that these effects can be a way for the perceptual system to attribute ‘objecthood’ based on feature similarity between stimuli: when they become sufficiently dissimilar they might be treated as different objects (Liberman et al., 2016; Pascucci et al., 2023). A study proposed that autocorrelation of features in time had considerable impact on serial dependence, where stimuli subject to drastic changes (low temporal autocorrelation) can promote more repulsive bias inducing higher sensitivity to changes in features (Kiyonaga et al., 2017; Taubert et al., 2016). In such a view, objecthood by feature similarity could be a measure to compensate for situations of volatility in the visual environment when distinguishing different stimuli.

In sum, we are thus dealing with a complex phenomenon with many aspects. Serial dependence interacts with visual adaptation effects, and it is affected at various stages of processing: early low-level vision as well as higher level processing such as attention, working memory, decisions, and potentially object-level processing.

2 Aims

When we are making consecutive perceptual decisions, these are affected by history-driven biases. If we have been looking at something for an extended time and shift our gaze, we will judge the next stimulus more unlike the previous one than it actually is. If transient changes happen in the environment or our gaze, or under circumstances of uncertainty, we judge subsequent stimuli more like those preceding. Much research has initially been done judging a single stimulus in a vacuum without taking temporal context into account. However, recently many studies have examined the effects of multiple stimuli, whether they be task relevant or irrelevant. There are still many pieces of the puzzle to solve. Does attention gate serial dependence and in what way? What happens to the surrounding objects and features in the visual environment? Does the nature of the task change the nature of serial dependence, for example whether there is attraction or repulsion to previous stimuli? Primarily, we investigated the role of attention and nature of the task in serial dependence. By utilizing attentional tasks and paradigms, we examined the role of spatial, object and feature-based attentional selection and suppression in order to further understand if there are differences between non-attended or actively suppressed stimuli. Secondarily, these methods allowed us to further investigate the intricacies of uncertainty, feature and object representations of stimuli.

2.1 Paper I: The effects of visual distractors on serial dependence

Notably, research on serial dependence and attention have typically manipulated attention via explicit instructions regarding what to attend and what to ignore (J. Fischer & Whitney, 2014). Distractors in everyday visual experience will mostly be unexpected and compete with visual targets for attention, and these distractors will have to be actively ignored to prevent them interference with our goals (Chelazzi et al., 2019). Whether and how the brain integrates such unexpected distractors and whether suppression will remove their interference is still relatively unknown. Previous studies have provided mixed evidence. Working memory studies suggest active removal of no-longer-relevant information causes repulsion (Shan & Postle, 2022). There are mixed findings showing some evidence towards repulsion from distractors, however the role of task-relevance and attention is still unclear (Czoschke et al., 2019; J. Fischer & Whitney, 2014; Rafiei et al., 2021). Thus, we investigated whether truly task irrelevant distractors would interfere with perceptual decisions of target stimuli, and further, by manipulating distractor location probability between conditions, we investigated whether attentionally non-suppressed or suppressed distractors would interfere differently with perceptual decisions.

2.2 Paper II: The role of secondary features in serial dependence

In the second paper, we wanted to further investigate the effect of attention and task-demands by employing a feature-based attention task. As described in the introduction, visual features are combined within a spatiotemporal window, demonstrated by serial dependence. Some studies argue that this bias combines features of sequential stimuli while promoting and maintaining the continuity of object representations (Collins, 2022a; C. Fischer et al., 2020; Liberman et al., 2016). However, to what extent serial dependence can be related to object processing, and the role that task-demands play, remains unclear. For example, in an experiment where participants attended the size of a stimulus, attraction towards the orientation of the previous stimulus was significantly reduced, suggesting that the attended feature or the task feature plays an important role (Fritsche & de Lange, 2019). While the work of Collins (2022) confirms this finding, they additionally argue that for more complex task stimuli (judging the emotion of a face), serial dependence occurs only between the same face, operating on combinations of features at the object level. Further, when a secondary feature like color is task relevant, serial dependence occurs for stimuli that share color, however, when a secondary feature is task irrelevant, attraction occurs towards previous stimuli regardless of the secondary feature (Ceylan et al., 2021; C. Fischer et al., 2020). This suggests that when a secondary feature can be ignored it has no effect on serial dependence. However, it remains unclear whether it occurs when more than one secondary feature—a certain color for example—is task relevant. Here we investigated whether making all color features (red and green) task relevant would modulate serial dependence consistent with object-level processing or if it would be modulated by what is attended and task-relevant.

2.3 Paper III: Object-based attention widens the window of serial dependence

As mentioned previously the relationship between serial dependence and object representations is complex. Serial dependence can occur despite changes in secondary features and between stimuli with different secondary features, suggesting that it is not contingent on object processing and continuity (see Pascucci et al., 2023). Previous studies investigating spatial and feature-based attention have found dramatic changes when secondary features or certain locations are to be ignored or become task irrelevant. The temporal and spatial tuning of serial dependence does suggest it may play a role in how we maintain stable representations of objects over time. There is ample evidence that the brain operates on so-called 'object-files' and tends to form representations of objects which are maintained and drive our perception and attention (Kahneman et al., 1992; Kimchi et al., 2007; A. Treisman, 1988; Yeshurun et al., 2009). However, it remains unclear how we perceive variations within an object's features, and it is still unknown if object-based attention modulates serial dependence. In the third paper we further attempt to investigate the tuning of serial dependence to object representations by employing an object-based attentional paradigm.

3 Materials and Methods

Before we continue, we will first delve a bit deeper into the experimental methods used in the three papers. These are general methods points and see individual papers for further details and variations within individual experiments. All participants had normal or corrected-to normal vision, and they were provided with spoken word instructions about the experiment before being provided with a written informed consent form. Before the experiments started, they were additionally provided with written instructions and a short practice session supervised by the experimenter, to ensure that instructions were understood, before starting the experiment. All studies were conducted in a dimly lit experimental booth, at a viewing distance of 57 cm on a 24-inch Asus monitor with a 1920x1080 pixel resolution, a refresh rate of 60hz, connected to a windows-based machine running custom made scripts from MATLAB version 2019b and the Psychophysics Toolbox (Brainard, 1997). All stimuli were presented on a grey background.

3.1 Paper I: The effects of visual distractors on serial dependence

Thirty-five healthy observers (age 20-42, 15 female) from the University of Iceland community participated in two experiments for a monetary reward (1500 ISK per hour). Fifteen (one excluded from the final analysis, six female, age 18-42) participated in experiment one, and twenty (two excluded from the final analysis, nine female, age 22-42) in experiment two. Participants had normal or corrected-to-normal vision and were naïve about the purpose of the experiments. Written informed consent was collected from all participants.

3.1.1 Paper I: Stimuli and procedure

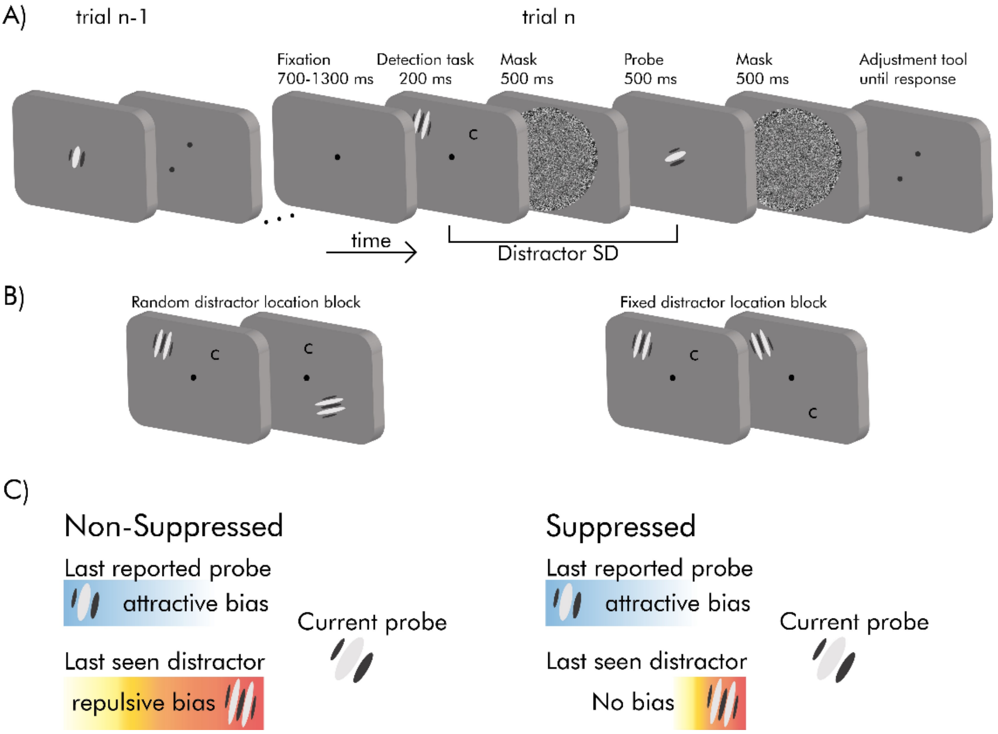

Figure 3. Experimental design of paper I

The paradigm in experiments 1 and 2 of paper I. A) Example of a trial sequence: An orientation adjustment task was interleaved with a discrimination task. In the discrimination task, participants had to report whether the gap in a Landolt C was on the left or the right. On 50% of trials, a distractor (an oriented Gabor) was presented together with the target. Following a noise mask, the central Gabor of the adjustment task was presented, and participants had to reproduce its orientation by rotating a response tool. B) In two different blocks, the distractor appeared either in a random location or at fully predictable locations ('random' and 'fixed' conditions, respectively). C) Based on previous studies, we expect to find interference from the non-suppressed distractor and no interference from the suppressed distractor.

The experiment consisted of a series of trials where observers performed two sequential tasks (see figure 3A). At the beginning of each trial, participants were presented with a fixation dot for 700-1300 seconds. Afterwards they had to solve a quick discrimination task, locating a regular or flipped 'Landolt' c and report if the c was facing left or right as quickly and accurately as possible by pressing the corresponding arrow key. In half of the trials a high-resolution Gabor was presented at a separate location as a distractor (peak Michelson contrast = 75%, spatial frequency of 1 cpd, sigma of 2.75°), stimuli were presented briefly for 200 ms before being replaced by a 500 ms mask. After participants reported the target stimulus, a similar high-resolution (experiment one) or a low-resolution Gabor (experiment two, peak Michelson contrast = 10%, spatial frequency of 0.25 cpd, sigma of 2.75°) was presented at central fixation. After another 500 ms mask, a response tool appeared, and participants were instructed to reproduce the orientation of the second Gabor by rotating two dots at the end of an imaginary and invisible line and confirming when they thought that the tool matched the orientation of the perceived orientation of the last Gabor. The starting orientation of the response tool was selected randomly. Participants had no time limits and confirmed their response by pressing the left mouse button, after which the next trial would proceed. In order to investigate the interference of a non-suppressed and suppressed distractor participants alternated between two types of blocks, a block where the probability of the distractor location was random (25%), and a block where location probability was 100% essentially fixing the distractor to a location for the duration of the block. Participants were informed that a distractor would appear in half of the trials and were further instructed that it was irrelevant and to ignore it. The Landolt C did not appear in the fixed distractor location. Participants were not informed about the locational probabilities in the two different blocks.

The two experiments were performed on two independent samples. Any differences between the experiments were minimal except for critical manipulations: In experiment one participants reproduced the orientation of a Gabor identical to the distractor stimulus, whereas in experiment two, the Gabor to be reported was lower resolution thus increasing uncertainty in the second experiment. Both experiments were performed over two separate sessions lasting approximately one hour each and comprising 1000 trials in total. Participants were instructed to maintain their gaze on the fixation dot at fovea during for the entire duration of each trial (breaks and between trials excluded).

3.1.2 Paper I: Analysis

Before the main analyses, trials were removed in the following cases: 1) reaction times (RT) in the discrimination task were outside the 200-1000 ms range; 2) adjustment errors detected as outliers in a two-step procedure, first excluding errors larger than ±45°, then excluding errors more than 1.5 interquartile ranges above the upper quartile or below the lower quartile; 3) responses slower than 10 seconds. By these exclusion criteria, 4.3% and 3.7% of the total trials were removed from experiment 1 and 2 respectively. We also employed the following criteria for participant exclusion: 1) more than 25% of the trials were marked as outliers; 2) a circular correlation between the reported and presented orientation lower than 0.4; 3) accuracy and reaction times during the detection task three standard deviations away from the group mean. In experiment 1, one participant was excluded for adding 90° to every response. In experiment 2, one participant was excluded because of poor performance on the discrimination task (accuracy = 51%), and one participant exceeded the 25% of trials marked as outliers in the orientation adjustment task. The main analysis was conducted on trials with correct responses during the discrimination task.

To analyze reaction times (RT) in the discrimination task, we used a general linear mixed-effects (GLM) regression (Matlab *fitglme*, distribution: inverse gaussian, link: identity), with RT as the dependent variable. The main predictors were the intercept plus the slope and the interaction associated with effect of the location condition (random vs. fixed, coded as binary variable) and distractor presence (absent vs. present, coded as a binary variable). In the GLM, we modelled the individual intercept as a random effect and excluded trials with incorrect discrimination responses.

For the serial dependence analyses, we used a novel approach. Serial dependence patterns typically contain a combination of repulsive and attractive effects due to prior stimuli (Pascucci et al., 2023). For example, several studies have shown attractive effects when prior stimuli are attended and reported, but repulsion, or a combination of the two otherwise (Pascucci et al., 2019; Pascucci & Plomp, 2021). Because the Gabor stimulus in the discrimination task was a distractor, and therefore not attended, previous studies may therefore suggest a repulsive effect, or a combination of repulsion and attraction. However, the common approach of fitting the 1st derivative of a Gaussian function (DoG; (J. Fischer & Whitney, 2014) can only capture the effect that dominates (irrespective of whether it is repulsive or attractive). So, to provide a more exhaustive description of the bias, we developed a method based on model comparison.

Adjustment errors from all participants were aggregated into a pooled dataset and modelled with a set of linear regression models (see Table 3 in Paper I), including 1) a model with only an intercept (Δ0), 2) a model with an intercept and one variable accounting for the effect of the difference (Δ) between prior and current orientations (Δ1), 3) a model including a second variable accounting for an additional effect of Δ, which can model the combination of repulsive and attractive effects (Δ2), 4) a variant of Δ1 including the interaction between Δ and the random vs. fixed location condition (Δ1∗loc), and 5) a variant of Δ2 including the interaction between both components related to Δ and the location condition (Δ2∗loc). Since the effect of Δ on adjustment errors is typically non-linear (i.e., it follows the shape of the DoG), the Δ variables used in each model were first transformed by multiplying Δ with a Gaussian function of variable width (from 10° to 80°) and choosing the best-fitting width (the one with the highest r-squared; Barbosa & Compte, 2020).

We then performed model comparison using the Bayesian Information Criterion (BIC; Kass & Raftery, 1995; Raftery, 1995), selecting the model with the lowest BIC as the best. For further comparison we calculated the ΔBIC by subtracting the largest BIC from all the BIC values. ΔBIC can be considered as an approximation of the Bayes factor where a difference of 2 ΔBIC between models indicates positive evidence in support of the model with the lower BIC, and a value of 6 ΔBIC or above can be considered as strong positive evidence. This procedure was applied to analyse the errors as a function of both the distractor orientation on the immediately preceding discrimination task (distractor present trials) and the orientation of the last probe stimulus one trial before.

3.2 Paper II: The role of secondary features in serial dependence

Using a sequential no-report task, forty-one observers (age range of 18-52 years, 9 females; 19 in Experiment 1, 22 in Experiment 2) performed an attentional task as a sequence of Gabors of green or red color, randomly selected, were presented displayed on the screen. After the sequence they reproduced the last Gabor in the sequence.

3.2.1 Paper II: Stimuli and procedure

Each trial started with a fixation dot shown for 1000 ms. A sequence of Gabors (peak contrast of 100%, spatial frequency of 0.75 cpd, and a Gaussian envelope of 25°) was then presented. Each Gabor was presented for 250 ms and followed by a 250 ms inter-stimulus interval. On a single trial, there could be 4, 6, or 8 Gabors, presented at random locations, with their center positioned on the circumference of an imaginary circle (radius of 8° from the fixation dot). The length of the sequence was randomly determined on each trial. The fixation dot remained on the screen for the entire duration of each trial and its color varied between experiments 1 and 2 (Figure 1B). In experiment one the fixation dot acted as a cue for target color, being either red or green. In experiment two the fixation dot was gray and had no relationship with the task. During the sequence participants performed an attentional task, in experiment one participants performed a detection task, pressing a key as quickly and accurately as possible, whenever a Gabor of the same color as the fixation dot was displayed. In experiment two, observers performed a discrimination task, pressing a key whenever a green Gabor appeared and a different key whenever a red Gabor appeared on screen (see figure 4B). At the end of a sequence the same response tool as in paper I appeared on the screen and participants followed the same response procedure (See Paper I: Stimuli and procedure for details).

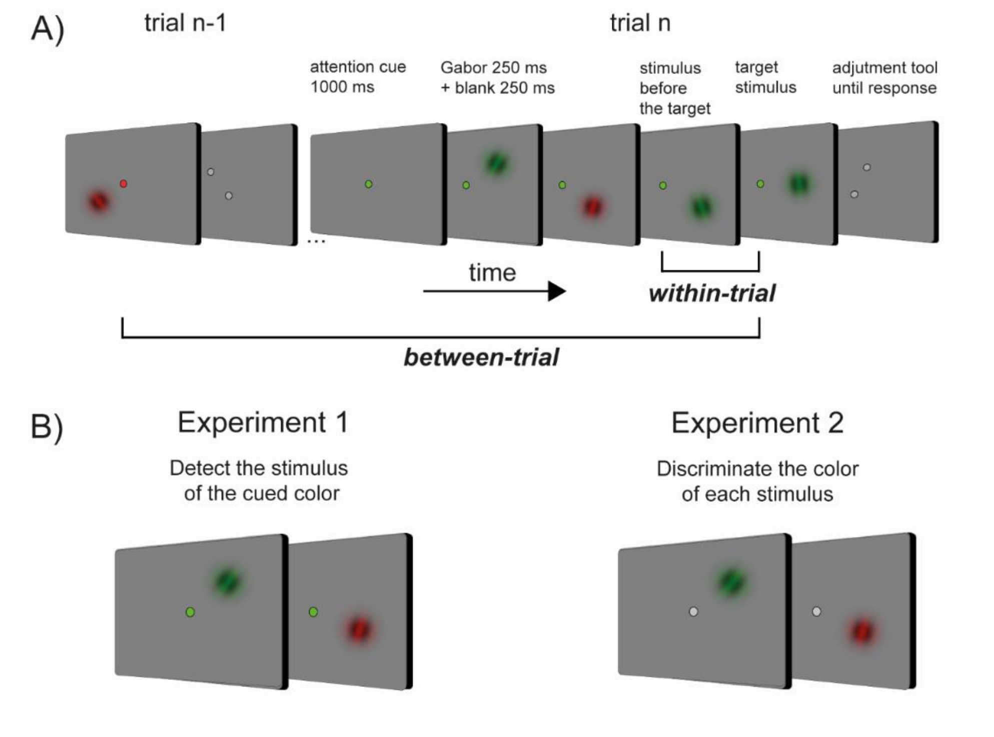

Figure 4. Experimental design of paper II

The paradigm and the main experimental manipulations (stimuli are not drawn to scale). A) Each trial contained a sequence of oriented Gabors whose color, red or green, was randomly assigned. Observers were asked to perform a task during the sequence (see B) and to reproduce the orientation of the last stimulus when the sequence ended. The orientation reproduction was made by rotating an imaginary line connecting two dots. B) In Experiment 1, the task during the sequence was to detect and quickly report the occurrence of a stimulus with the same color as the fixation dot. In Experiment 2, the task was to discriminate whether the present stimulus was red or green, by pressing two corresponding keys. The fixation dot had a neutral color in Experiment 2.

Participants were instructed to reproduce the orientation of the last Gabor in the sequence which in experiment one was always the target color and random in experiment two. Colors within sequence were selected randomly. In experiment one observers were instructed to ignore (not respond) to stimuli of irrelevant color, in experiment two they were instructed to attend and respond to both colors. Like Paper I, participants were instructed to maintain their gaze on the fixation dot for the duration of each trial (breaks excluded). Participants were free to take breaks between each block.

3.2.2 Paper II: Analysis

Before the main analysis two major preprocessing steps were performed on the data, first, exclusion of outlier trials and observers, second, orientation bias removal was performed on participants' error in the orientation reproduction task (for specific details see paper II in the appendix). Trials were marked as outliers and removed in the following cases: 1) accuracy in the within-trial detection or discrimination tasks was lower than 50%; 2) absolute adjustment errors were larger than 30° (Cicchini et al., 2018) or adjustment times slower than 10 seconds. Trials at the beginning of each block were also removed, leading to a total proportion of trials removed of less than 9% for Experiment 1 and 12% for Experiment 2. For subject exclusion, we applied the following criteria: 1) more than 25% of their trials were marked as outliers; 2) a value of circular correlation between the reported and presented orientation was lower than 0.5. Ten subjects were excluded by these criteria (4 in Experiment 1, and 6 in Experiment 2).

Orientation space is not perceptually uniform and notable biases have been documented (Appelle, 1972; Balikou et al., 2015; van Bergen & Jehee, 2019). This is particularly relevant for the analysis of serial dependence, and previous work has recommended corrections for these biases to avoid unwanted noise (Sheehan & Serences, 2023). To remove such biases, orientation adjustment responses were first demeaned and then residualized from oblique effects and orientation biases. Sinusoidal (Pascucci et al., 2019) or polynomial (Manassi et al., 2018; Rafiei, Hansmann-Roth, et al., 2021) fits have been used in previous work to capture systematic orientation biases, but there is no standard procedure. Here we used a non-linear mixed model with fixed and random effects estimated on the whole group of subjects. We started from the assumption of a sinusoidal trend in orientation biases (Balikou et al., 2015; Pascucci et al., 2019; Sheehan & Serences, 2023; van Bergen & Jehee, 2019) and fitted a cumulative sum of sinusoidal functions. The individual residuals obtained from this model were used for the rest of the analyses.

For the serial dependence analyses, we used a single-trial non-linear mixed-effects model following the same approach as in Pascucci et al., (2019). Briefly, individual and single-trial residualized adjustment errors were fitted to the first derivative of a Gaussian (δoG) function, $y = x\alpha wce^{-(wx)^2}$, where x is the relative orientation of the previous stimulus, and with curve amplitude (α) and curve width (w) as free parameters. Finally, c is the constant $\sqrt{2}/e^{-.5}$ rescaling the α parameter to match the height of the positive peak of the curve (J. Fischer & Whitney, 2014). In the *within-trial* analysis, we modeled serial dependence as a function of the inducer color, that is, whether the Gabor stimulus before the last one was of the *target* or *non-target* color. In doing so, the mixed-effects model included two δoG functions multiplied by a dummy variable coding for the condition (Pascucci et al., 2019), for a total of four parameters (two amplitudes and widths per condition). All parameters were included as fixed and random effects. The statistical significance of individual parameters and comparisons between parameters were computed employing T-tests and Z-tests, respectively (Pascucci et al., 2019). A separate model with a similar structure was used in the analysis of *between-trial* serial dependence, with the dummy variable coding whether the color of the previously reported stimulus was the *target* as on the present trial or a *non-target*. In this latter analysis, responses following trials marked as outliers were also excluded. All mixed-effects models were estimated using *nlmefit.m* (with *'fminunc'* as the optimization function) from the Statistics and Machine Learning Toolbox (Matlab R2021a). Initial parameter guesses were $\alpha = 2°$, $w = 0.05$.

3.3 Paper III: Object-based processing reduces feature-tuning in serial dependence

Twenty-two healthy human participants (age range of 21-39 years, 12 females) from the University of Iceland, voluntarily took part in the study. Participants had normal or corrected-to-normal vision and were naïve as to the purpose of the experiments. Written informed consent was collected from all participants beforehand.

3.3.1 Paper III: Stimuli and procedure

In order to investigate the tuning of serial dependence to object representations, observers performed a classic orientation reproduction task adapted to the object-based attention paradigm of Egly and colleagues (1994). At the start of each trial a fixation dot and two vertical or horizontal rectangle objects placed left and right or above and below from the fixation dot were drawn on the screen, and they remained on the screen throughout the duration of the trial. After a brief fixation period of 500 ms, a Gabor (peak Michelson contrast of 10%, spatial frequency of 0.33 cpd, and a Gaussian envelope of 25°) was then presented at a random location at the four ends of the rectangles (25% chance per location) for 250ms. A mask stimulus was then drawn in the same location remaining on screen for 500ms. At the end of the presentation sequence, a response tool appeared at the location where the fixation point had appeared. The response tool consisted of a dark-grey bar that participants had to rotate in order to reproduce the perceived orientation of the Gabor. The initial orientation of the response tool, as well as the orientation of all the Gabors, were selected randomly. Before the experiment, participants were provided with written and verbal instructions and performed twenty practice trials under the supervision of the experimenter. The experiment was divided into 4 blocks of 100 trials and lasted approximately 40 minutes. Participants were instructed to maintain their gaze on the fixation dot at the center of the screen for the entire duration (breaks excluded).

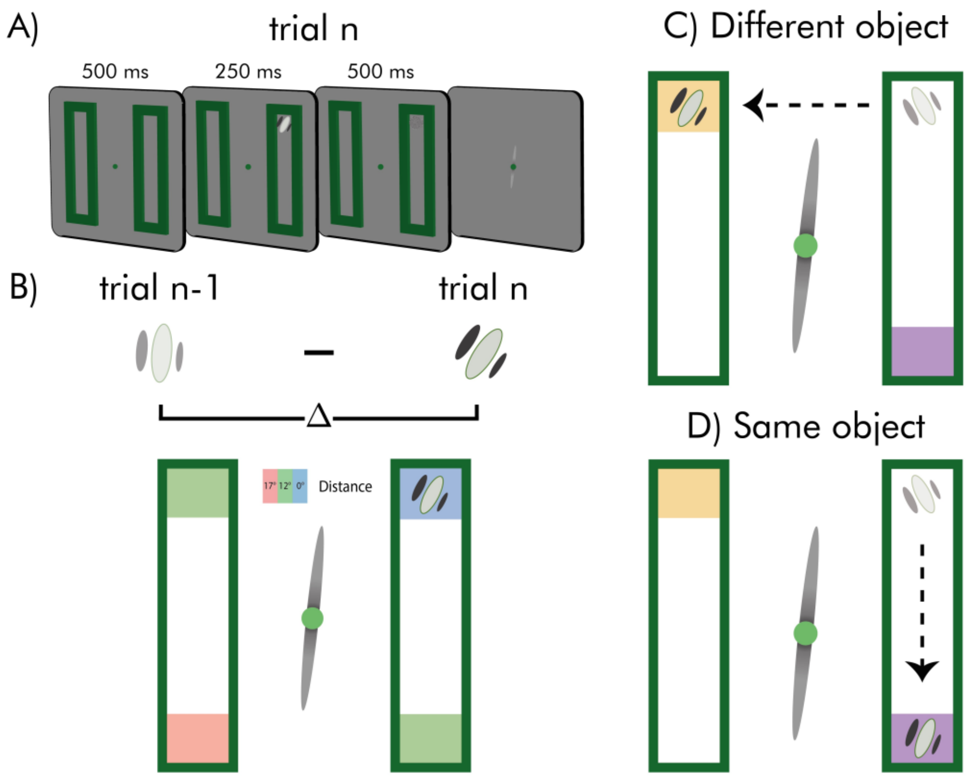

Figure 5. Experimental design of paper III

The paradigm and main experimental manipulations of paper III (not drawn to scale). A) the procedure of the experiment. After fixation a Gabor was briefly presented followed by a mask in the same location. Afterwards observers reproduce the orientation of the Gabor by rotating the bar. B) A Gabor was drawn at one of four possible locations at the ends of either rectangle (colored squares), the colored squares denote spatial distance at the same location (blue, 0°), close distance (green, 12°), and at a far distance in the diagonal location (red, 17°). C) & D) The primary conditions investigated where participants must either (C) switch attention to a different object from the preceding trial or (D) switch attention to the same object as the previous trial.

3.3.2 Paper III: Analysis

Before the main analysis, trials were marked as outliers and removed in the following cases: 1) absolute adjustment errors were larger than 45° (Samaha et al., 2019), or adjustment times were slower than 5 seconds or faster than 0.5 seconds. Trials at the beginning of each block were also removed, leading to a total proportion of trials removed of 3.4%. For subject exclusion, we applied the following criteria: 1) more than 25% of their trials were marked as outliers; 2) a value of circular correlation between the reported and presented orientation was lower than 0.5. No subjects were excluded by these criteria.

To prevent any effects of orientation bias or other low-level perceptual biases, orientation adjustment responses were first demeaned and then residualized. Following the procedure of previous works, a six cycles sinusoidal function was fitted to the data of each participant over the entire orientation range. The individual residuals obtained from this model were then used for the rest of the analyses (Balikou et al., 2015; Pascucci et al., 2019; Sheehan & Serences, 2023; van Bergen & Jehee, 2019). The main results were consistent even when orientation bias removal was not applied.

For the serial dependence analyses, individual and single-trial residualized adjustment errors were fitted to the first derivative of a Gaussian (δoG) function, $y = x\alpha wce^{-(wx)^2}$, where x is the relative orientation of the previous stimulus, with curve amplitude (α) and curve width (w) as free parameters. Finally c is the constant $\sqrt{2/e}$-.5 rescaling the α parameter to match the height of the positive peak of the curve (J. Fischer & Whitney, 2014). The statistical significance of individual parameters and comparisons between parameters were computed employing permutation tests. To test significance of serial dependence in each of individual conditions, a distribution of amplitude (α) and width (w) was built by randomly sampling the data 5000 times with replacement and fitting a δoG function. The mean of the distributions of α and w was then compared to a surrogate null distribution where the sign of the adjustment error was randomly switched. Comparisons between conditions were conducted in a similar manner, where the surrogate distribution was built by randomly switching the conditions between observations. We then fit a one-term gaussian model collecting the amplitude of the gaussian curve. We then performed similar between conditions permutation tests as for serial dependence. To validate our fitting analysis, we conducted corresponding model-free analyses. Serial dependence was calculated by averaging each participants' error within a defined bin of delta. Errors were first averaged for the positive (1-to-40-degree range) and the negative (-1 to -40 degree range) orientation differences, then, the average error in the positive range was subtracted from the average error in the negative range, leading to an estimate of the 'bias'. Average error being positive (positive bias) indicates an attraction towards the previous stimulus, whereas being negative (negative bias) indicates a repulsion away from the previous stimulus.

4 Results

The detailed results and statistics can be found in the papers, in this section there will instead be a summary without the numbers and tests detailed. Here I will briefly describe the most important results and conclusions from each paper; for details please visit the appendix.

4.1 Paper I: The effects of visual distractors on serial dependence

In this study we excluded trials with incorrect responses in the discrimination task, to ensure that participants were attentive during the trial. We split the data into the 25% distractor location probability (random) and 100% distractor location probability (fixed) blocks. Additionally, we further split the data when the distractor orientation was similar to the previous reported Gabor ($\Delta < 45°$) and when it was dissimilar ($\Delta > 45°$). By performing this split, we were able to investigate whether distractor similarity to previously reported stimuli change its interference with current stimuli. We estimated the effects of distractor and last reported Gabor orientation on perceptual decisions in the orientation reproduction task using a novel approach, modeling error as a function relative orientation difference and performing model comparisons (see Materials and Methods). This manipulation allowed us to perform comparisons of both positive and negative peaks of serial dependence.

Importantly, we found that the attentional suppression did not influence serial dependence. Participants were faster in the discrimination task during 100% distractor location probability blocks when the distractor was present in both experiment one and two. Attentional capture was further found to be significantly lower in the high location probability block. Notably, this suppression came at a preparation cost. This proactive suppression reflected how observers proactively filtered the predictable distractor, leading to slower reaction times in its absence (Marini et al., 2013). In both experiments we found attraction towards the last reported Gabor when the relative difference in orientations were small, we found significant repulsion when previous and current reported Gabor differed greatly in orientation. We did not consistently find direct effects on perceptual decisions from the distractor: In experiment one we found a negligible repulsion from the distractors' orientation, and in experiment two we surprisingly found no serial effects from the distractor. Model comparison revealed that in all scenarios location probability of the distractor did not play any role despite the distractor having reduced attentional capture.

This result may suggest that attentional filtering of task information might be an important factor in deciding when serial dependence occurs. Further, we found increased interference of perceptual decisions from the distractor when its orientation was similar to the previously reported Gabor. Overall, we found that distractors interfered with perceptual decisions related to the reported Gabors regardless of attentional suppression; however, repulsion towards the distractor was either weak or absent. The distractor did still have strong attentional capture in both conditions, which may explain the effect. It is hard to conclude whether the presence or absence of the effect is due to between-experiment variability.

4.2 Paper II: The role of secondary features in serial dependence

In this study, we investigated object processing and feature-based attentional filtering of task information. Participants performed a detection task as they were viewing a sequence of randomly selected red or green Gabors. To ensure participants were attentive throughout the sequence, trials with less than 50% correct responses were excluded from analysis. We investigated attraction towards the previously seen stimulus within-trial (the penultimate stimulus in the sequence) and between-trials attraction towards the previously reported stimulus when the colors did or did not match. We fit a first derivative of gaussian function to the data for each condition (same or different color within or between trials) and used the α and w parameters in a non-linear mixed effects model as fixed and random effects.

4.2.1 Experiment one

In the first experiment a target color was cued by the color of the fixation dot. Our conditions were therefore labeled *target* and *non-target* color. We found that perceptual decisions were only attracted within-trial towards stimuli of target color. However, perceptual decisions between-trials were attracted towards the previously reported Gabor regardless of being *target* or *non-target* color. The results are on the surface consistent with the notion of serial dependence on object level put forward by C. Fischer and colleagues (2020), such that secondary features can be considered task irrelevant between trials when participants are reproducing the orientations of stimuli. However, it is unclear whether this result occurs as a result of attentional filtering of task information or serial dependence occurring at the 'object-level' of representations.

4.2.2 Experiment two

To test the possibility that the results of experiment one reflected attentional filtering of task features, we had observers perform a color discrimination task during the sequence of red and green Gabors, the idea being to make secondary feature always task relevant within trial as this has yet to be tested. If results mirror the previous experiment and there is only attraction towards the stimuli of the same color, this would be more consistent with object-file processing. If, however, attraction occurs within trial regardless of color, an attentional account of task information would be more appropriate.

The results of experiment two revealed attraction towards previous stimuli both within and between trials. When both primary and secondary features are task-relevant serial dependence does not adhere strictly to object-file like processing, at least in tasks involving simple low-level features like orientation.

We propose an account of parsimony, in which representations of feature conjunctions or holistic objects are maintained when required by the task while the complexity of representations is reduced to the simplest dimensional format possible, i.e., the complexity of processing during a task determines the complexity of the information which is carried forward to the next trial. In our case, low-level features like orientation can be reduced into a simple abstract representation of a tilted line regardless of other secondary features which are not needed to solve the orientation reproduction task (Kwak & Curtis, 2022).

4.3 Paper III: Object-based attention widens the window of serial dependence

In the third paper we investigated the tuning of serial dependence to object representations by employing an object-based attention paradigm. Data was split into factors of spatial distance (0°, 12°, 17°) between the previous and current stimulus, and when the previous stimulus was presented in the same or different object at an equidistant location to rule out spatial effects.

We found a linear decrease in attraction towards the previous Gabor with increasing distance, in line with the spatial continuity field proposed in recent papers. As expected from the results in paper II, as the task involves perceptual decisions on an elementary feature such as orientation, observers’ judgment was attracted to the previous stimulus whether it was presented in the same or in a different object.

We further found an increase in serial dependence within the same object by a widening of the window of feature space in which attraction happens. Feature tuning is in other words decreased when the stimulus reappeared within the same object, compared to a different object. This demonstrates that serial dependence is influenced by object-level processing. We speculate that objects influence internal priors related to temporal changes in visual features. Overall, we found differential effects of spatial and object-level processing on serial dependence.

5 Discussion

The purpose of the studies presented in this thesis was to investigate the role of attentional selection and filtering of task relevant or irrelevant information in forming serial dependence biases in perceptual decisions. In each paper we specifically examined how various forms of attentional selection, spatial (paper I), feature-based (paper II), and object-based attention (paper III) affected history-driven biases in perceptual decisions. The role of spatial attention has been relatively clear in the literature: Attraction decreases with increasing distance between attended stimuli. There is a strong trend towards repulsive biases at irrelevant stimuli at irrelevant locations in current research, however whether interference from such stimuli persists when they are being attentionally suppressed is still unclear (J. Fischer & Whitney, 2014; Rafiei et al., 2021). Next, the attended feature has shown to be important for serial dependence, such that a cued secondary feature to be attended like size or color drastically reduces attraction towards the reported feature (C. Fischer et al., 2020; Fritsche & de Lange, 2019). There is plenty of evidence that the perceptual system will bind conjunctions of features correlated in space and time into representations of objects or object-files, a few studies propose that serial dependence operates on these object representations (Collins, 2022a; C. Fischer et al., 2020). However, it still remains unclear whether this is an intrinsic property of serial dependence bias, or if it is by-product of attentional filtering of task information. To further investigate the tuning of serial dependence to objects—if it is attraction of an object representation towards previous and similar objects, object-based attention should modulate the bias—we used object-based attention to investigate the effect of previously attended objects.

5.1 Attentional filtering of task information and serial dependence

Our results support the notion that attention plays a key role in serial dependence perhaps in more ways than just gating it. Though some studies revealed serial dependence by just mere exposure to a series of stimuli with no task involved, attention is nevertheless important (Fornaciai & Park, 2018a; Murai & Whitney, 2021). While the presence of an explicit task might not be essential, the presence of one can strongly modulate history-driven biases. In many spatial attention tasks unattended irrelevant stimuli or stimuli to-be-ignored elicit an opposite repulsive bias in contrast to the attraction observed toward attended stimuli (J. Fischer & Whitney, 2014; Rafiei et al., 2021). Fischer & Whitney (2014), only found a trend towards repulsion away from uncued, unreported stimuli, while Rafiei and colleagues (2021) found a solid effect, though in their odd-one-out task the distractor ensemble could be argued to be relevant to solve the perceptual task, since locating the odd target out requires encoding of the orientation distribution of distractors in order to identify the target which orientation lies outside of the distribution. Serial dependence has been shown to have both a repulsive and attractive component, where repulsion is similar to that of adaptation (Pascucci et al., 2019). However, visual adaptation follows a slightly different set of rules: Most importantly, it is retinotopic, increases with viewing time of a stimulus, is reduced by backward masking, highly spatially specific, and not sensitive to task context (Boi et al., 2011; Clifford et al., 2007; Knapen et al., 2011). This is a key explanation for the attractive bias we observed in the sequential non-report paradigm employed in paper II compared to similar experiments with stimuli presented in a stable position at fovea (Pascucci et al., 2019; Pascucci & Plomp, 2021). However, these conditions do not apply to either experiment finding repulsive biases from unattended irrelevant stimuli: In one case it was unattended, with the tested location switched, and masked, whereas in another repulsion occurred away from the mean orientation of the ensemble distributed across the screen. One proposed explanation lies in the similarity in features, for example similar features cause attraction and dissimilar features repulsion, a mechanism exaggerating differences between relevant and irrelevant features to keep them distinct (Rafiei et al., 2023). Indeed, there is support of such a mechanism in working memory integrating or segregating task information depending on task context (Czoschke et al., 2019; Shan & Postle, 2022).

In paper I we set out to investigate the effects of spatial suppression on truly task-irrelevant stimuli, expecting to find interference from the non-suppressed distractor which would either reduce or vanish when suppressed. Our results showed that the distractor was successfully suppressed in blocks with high location probability, but we found no effect of suppression on perceptual decisions of orientations; however, in both conditions the distractor still had high attentional capture. Internal models of information to be ignored have been proposed to involve inhibitory mechanisms in sensory processing (Ramaswami, 2014) , while others argue that suppression is merely a byproduct of models facilitating information regarding target information such as features or probable location (Carlisle & Kristjánsson, 2018; Chelazzi et al., 2019; Woodman et al., 2013).

Paper I demonstrates and provides further evidence that having only a negative model of what to avoid can speed up search. However, distractors in our experiments were still processed to the extent that they left a trace or interfered with traces of other prior stimuli. This interference most reliably occurred when the orientation of the distractor was similar to the previous reported Gabor, increasing repulsion in cases where the previously reported orientation was dissimilar to the current orientation reported. A speculative explanation could be a strengthening of the trace left by the previous Gabor thus increasing this segregation of task irrelevant information or exaggerating the differences further. In experiment one we found direct repulsion from the distractor;

such repulsion was not observed in experiment two. Unfortunately, we cannot rule out between-experiment variability, thus we can only speculate on possible explanations. Two major possibilities come to mind: First, the increased attraction in experiment two dominated over other potential biases of perceptual decisions, and second, the physical similarity between distractor and target in experiment one increased serial effects of the distractor. Exploring the first option, history-driven biases have recently been proposed to arise concurrently and additively, the expressed attraction or repulsion depends on the dominant component (Fornaciai & Park, 2019; Moon & Kwon, 2022; Pascucci et al., 2019; Sheehan & Serences, 2022). In such a view, the weak attraction and stronger repulsion present in bias towards the previously reported stimulus in experiment one, would leave room for repulsive effects to dominate. However, the source of repulsion is unclear: Visual adaptation is possible but unlikely, as the distractor occupies a different retinotopic location and stimuli are masked; however it could possibly be a matter of active removal of a relatively stronger trace in working memory as discussed above (Shan & Postle, 2022).

Another possibility is that the physical dissimilarity between distractor and reported Gabor in experiment two caused them to be perceived as dissimilar objects thus decreasing direct interference from the distractor or increasing perceived task relevancy in experiment one. These are not mutually exclusive; however, serial dependence does not seem to require objecthood, but is instead promoted by task-relevance and active behavior as the results of Paper II suggests (Ceylan et al., 2021; C. Fischer et al., 2020; Pascucci & Plomp, 2021). As observed in the second paper, there was no serial dependence towards filtered or ignored orientation information based on a secondary feature in the first experiment. There were no tendencies of any attraction or repulsion away from these ignored stimuli. Why this difference occurs between the different paradigms is unclear.

5.2 Attentional selection: Objects and uncertainty

Another result of paper I speaks to uncertainty: the increase in attraction towards the previously reported stimulus when the signal to noise ratio decreases is becoming well understood (Ceylan et al., 2021; Cicchini et al., 2018; Gallagher & Benton, 2022). When observers are currently uncertain about a perceptual decision they rely increasingly on perceptual and decisional history. Attentional processes typically facilitate processing of target information in addition to filtering task information. This is clear from studies of spatial and feature-based attention and the traces of representation sometimes left behind after filtering. The information carried from one trial to another is task-dependent and will default toward the minimum required information. Paper III underlines that variations of features within one object will affect the perceptual decisions regarding features within another object.

Furthermore, Paper III demonstrates that object-based attention widens or narrows the feature tuning window, that is, the range of relative feature differences within which attraction occurs. While it is not entirely clear why or how feature tuning becomes wider within the same object, we speculate that this is an effect caused by how attention is employed based on previously viewed objects. One possibility is that Inhibition of return is spread from the previously attended location throughout the previously attended object (B. S. Gibson & Egeth, 1994). Such inhibition has been shown to reduce sensitivity to non-spatial features of task stimuli (Handy et al., 1999; Ivanoff & Klein, 2006).

A study by Cicchini and colleagues (2018) showed that serial dependence was affected by stimulus reliability, less precise stimuli such as low spatial frequency Gabors or even oblique orientations exhibited stronger serial dependence. This was further supported in an fMRI study conducted by van Bergen and Jehee (2019). They measured representations of sensory uncertainty using decoding techniques and compared them to serial dependence. They found that representations of sensory uncertainty decoded from early visual cortex increased the bias in behavior when uncertainty went from low to high (van Bergen & Jehee, 2019). However, only testing low-to-high and high-to-low uncertainty scenarios, the dynamics were still unclear. For example, if it is a Bayesian observer the relative strength of evidence in the previous or current trials is important, as it would be determined by previous uncertainty. Later studies tested all four combinations, albeit only behaviorally with Gabors of low or high spatial frequency and contrast, concluding that evidence indicates that only uncertainty in the current trial has a considerable effect on serial dependence (Ceylan et al., 2021; Gallagher & Benton, 2022). Such uncertainty need not be external: Internal uncertainty has shown to elicit a similar effect, and the cause and difference remains unclear (Pascucci et al., 2023; Samaha et al., 2019). If Inhibition of Return is the cause of increased serial dependence in paper III, sensitivity would be reduced in the current trial with increasing current uncertainty; our results fit within this framework. This reduced sensitivity within the same object would reduce the signal-to-noise ratio of information increasing uncertainty and serial dependence by widening the feature-tuning window of perceptual decisions in the orientation reproduction task (Ceylan et al., 2021; Gallagher & Benton, 2022).

5.3 Attentional selection: Object-representations and serial dependence

One way to frame the results in Paper II: stimuli actively responded to will attract subsequent responses, as demonstrated through feature-based attention in the two experiments. When presented with a target color cue, stimuli of non-target color will not leave a trace or interfere in the reproduction task. This is not the case when both are made task-relevant, yet discriminated: In experiment two, serial dependence occurred regardless of changes in secondary feature. It has previously been argued that a key property of serial dependence is its selective operation between objects with similar contents and that secondary or contextual features leave traces in working memory to relate corresponding object representations across memory episodes (C. Fischer et al., 2020).

To continuously perceive objects over time, multiple features closely correlated in space and time must be bound together in order to represent such objects (A. Treisman, 1996). One proposal is that such binding takes place automatically by co-occurrence of features and is heavily mediated by task content and the current attentional set (Hommel, 2004). A model of relevance filter proposes a computational account where features are weighted and integrated according to their task relevance (Bundesen, 1990; Hommel & Colzato, 2004). Whether and how serial dependence operates on object representation while maintaining and smoothing object continuity is unclear. C. Fischer and colleagues (2020) sequentially presented two clouds of moving dots of different color using a post-cue identifying which to report, such that both stimuli had to be memorized simultaneously. Under such circumstances, they only observed serial dependence when color cue matched in the previous and current trial. This could suggest that serial dependence operates on integrated features when observers must select from competing representations in working memory. This only occurred when color was the task-relevant feature and in such cases only one color needed a response; conversely, when color was task-irrelevant responses were attracted to previous stimuli regardless of color, leaving open the possibility that competing object representations can affect each other in working memory. Ultimately, the results of paper II supports the proposal that serial dependence is modulated by task context and attention, they provide further evidence that serial dependence is promoted by task relevance and active behavior (Pascucci & Plomp, 2021).

However, the role of object continuity is still contentious. In studies examining judgments of facial emotion, one study found reduced serial dependence between faces of different genders, while another study found strongly reduced serial dependence between just different faces, while further demonstrating that it can occur at both the level of features and objects (Collins, 2022a; Liberman et al., 2018). Collins (2022a) goes on to suggest that the relative level of serial dependence depends on the type of task stimulus. In line with these and previous papers which show that serial dependence occurs between different objects which can be reduced to a common representation of the judged feature (Ceylan et al., 2021; Kwak & Curtis, 2022; Pascucci & Plomp, 2021), we propose an account of parsimony (see Pascucci et al., 2023).

We propose that the perceptual system accomplishes tasks with minimal, but sufficient representations (Ceylan et al., 2021; Ho et al., 2022). Tasks such as orientation reproduction can be accomplished with an abstract representation of a tilted line and discarding irrelevant information, while emotional face expression cannot be judged without binding together all the features which constitute a face (Kwak & Curtis, 2022). In short, the information propagated from one trial to the next is determined by the representation required to perform the task. Such operation allows for efficient and sparing resource usage in everyday vision, where objects and features are continuous and spatio-temporally correlated, while hampering feature integration and causing interference between objects in experimental paradigms such as ours.

When previous studies have manipulated object-level representation, it has been done with the expectation that serial dependence is stronger when a visual feature is expected to be part of the same object. However, the results of paper III showed a different pattern. The changes to features within the same object tended to be underestimated by observers, resulting in a broader range of serial dependence effects. Attraction towards the previous stimuli persisted within the same object even with marked orientation differences between prior and current stimuli well outside of the regularly reported feature-tuning window (Bliss et al., 2017; Fritsche et al., 2017; Fritsche & de Lange, 2019).

These finding challenges conventional approaches evaluating serial dependence in terms of the peak of the bias, where width is considered an additional metric to assess the tuning of serial dependence to visual features (Fritsche & de Lange, 2019). We further demonstrate that larger peaks and narrower feature tuning do not necessarily indicate stronger integration of past and present stimuli. Reduced feature tuning can be an indicator of stronger serial dependence (C. Fischer et al., 2020); however, correctly evaluating the strength of integration based on both peak and tuning presents a challenge for future studies to consider.

The results of Paper III show that object-level processing leads to reduced feature tuning, despite observing comparable peaks of serial dependence. This could suggest that perceived objects influence internal prior expectations related to temporal changes in their visual features (Mamassian & Landy, 2001).

An object is usually safely expected to maintain its properties over time (Dong & Atick, 1995), assuming a high temporal autocorrelation promoting stronger integration within the same object (Taubert et al., 2016). Thus, almost regardless of orientation feature similarity, integration is strong between even large variations within an object's features. The attentional mechanisms discussed above could be a concrete proposal on how this insensitivity within the same object occurs. We propose that these mechanisms reflect the brain's attempt to maintain stable representations of visual features within the same object, ultimately enhancing the perceived similarity between features of an object at consecutive moments.

6 Conclusions

In sum, there are a litany of history-driven effects in vision some more well-understood than others. Serial dependence, a particular form of bias towards previous visual history, is a particularly puzzling phenomenon. In this thesis we set out to further understand attentional processes and serial effects, particularly what kind of representational traces are left present after attentional selection and filtering of task information, and how do they affect perceptual decisions? Many debates still remain open in serial dependence with many seemingly contradictory findings. Is it perceptual or decisional? What is the neurological source? Does it maintain continuity between object representations? However, serial dependence is simultaneously distinct enough with a set of diagnostic properties to be separated from the countless of other history-driven biases present in visual perception (Manassi et al., 2023). Recently viewed stimuli within a certain spatial and temporal window of each other will cause responses to be biased away from or towards their features. As discussed briefly above, the relative flexibility of this continuity field separates serial dependence, particularly repulsive effects, from other history-driven effects such as visual adaptation. Attention has shown to be of particular importance, with attended stimuli consistently eliciting serial effects, while unattended stimuli typically do not elicit any attractive biases.

The results of papers I, II, and III along with other recent research demonstrate that attentional effects on serial dependence are varied, subtle, and sensitive to task context. The results of paper I suggest that regardless of spatial suppression of stimuli, they are sufficiently processed to leave behind a trace of their representation which interfered with perceptual decisions. Furthermore, paper I and II suggest that attentional filtering of ignored information determines serial effects: we observed either no bias or a weak repulsion away from stimuli to be ignored regardless of attentional capture.

Alternatively, serial dependence occurs if the task requires an action from stimuli, regardless of their primary judged feature. In paper II we observed serial dependence in the second experiment when the task required an action in response to both secondary features. In paper I and III we further explored the role of uncertainty and attentional facilitation of stimuli. We show further evidence of the effect of external uncertainty on serial dependence in paper I, and we demonstrate that attentional facilitation via object-based attention and object-level processing modulates the feature-tuning window of serial dependence. We can conclude from all three papers, in line with other recent studies, that contextual task demands play a large role in modulating serial dependencies.

Serial dependence and its modulations have been shown to occur across at various levels of visual processing. Based on this and our results we take a stance of parsimonious use of attentional resources. They reflect observers' optimal use of minimal, but sufficient, representations to perform a given perceptual task, such that the information required is the information propagated from one instance to another. Recent papers have shown that representations can be flexibly simplified and reduced to abstract representations for efficient use of limited cognitive resources (Ho et al., 2022; Kwak & Curtis, 2022). In some tasks serial dependence is sensitive to object representations, while in others attraction towards previous stimuli occurred regardless of object type. Parsimony can account for various seemingly conflicting findings such as the above example.

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Original Publications

This thesis has been written on the basis of the following papers:

Paper I: Houborg, C., Pascucci, D., Tanrikulu, Ö. D. & Kristjánsson, Á. (2023). The effect of visual distractors on serial dependence. Journal of Vision, 23(12):1. https://doi.org/10.1167/jov.23.12.1.

Paper II: Houborg, C., Tanrikulu, Ö. D., Kristjánsson, Á. & Pascucci, D. The role of secondary features in serial dependence. Journal of Vision 2023; 23(5):21. https://doi.org/10.1167/jov.23.5.21.

Paper III: Houborg, C., Kristjánsson, Á. & Pascucci, D. (Submitted) Object-based attention in serial dependence.

Paper I

Journal of Vision (2023) 23(12):1, 1–16

The effects of visual distractors on serial dependence

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Attractive serial dependence occurs when perceptual decisions are attracted toward previous stimuli. This effect is mediated by spatial attention and is most likely to occur when similar stimuli are attended at nearby locations. Attention, however, also involves the suppression of distracting information and of spatial locations where distracting stimuli have frequently appeared. Although distractors form an integral part of our visual experience, how they affect the processing of subsequent stimuli is unknown. Here, in two experiments, we tested serial dependence from distractor stimuli during an orientation adjustment task. We interleaved adjustment trials with a discrimination task requiring observers to ignore a peripheral distractor randomly appearing on half of the trials. Distractors were either similar to the adjustment probe (Experiment 1) or differed in spatial frequency and contrast (Experiment 2) and were shown at predictable or random locations in separate blocks. The results showed that the distractor caused considerable attentional capture in the discrimination task, with observers likely using proactive strategies to anticipate distractors at predictable locations. However, there was no evidence that the distractors affected the perceptual stream leading to positive serial dependence. Instead, they left a weak repulsive trace in Experiment 1 and more generally interfered with the effect of the previous adjustment probe in the serial dependence task. We suggest that this repulsive bias may reflect the operation of mechanisms involved in attentional suppression.

Introduction

Our visual environment is a continuous stream. Information about objects and features constantly arrives at the retina in an overwhelming flow. The visual system therefore faces a major challenge in prioritizing information and tracking the history of task-relevant objects, while ignoring potential distractors and irrelevant details.

Recent research has shown that when we repeatedly attend to the same feature, such as the orientation or motion of a stimulus, our perceptual decisions become serially dependent: the stimulus features are judged as being more similar to recent past than they actually are (Fischer & Whitney, 2014; see Pascucci et al., 2023 for a review). This phenomenon has been reported in nearly all sorts of visual tasks and comes in many colors (Bliss, Sun, & D'Esposito, 2017; Ceylan et al., 2021; Collins, 2020; Collins, 2022; Fornaciai & Park, 2018b; Fritsche, Mostert, & de Lange, 2017; Fritsche & de Lange, 2019; Houborg, Kristjánsson, Tanrikulu & Pascucci, 2023; Manassi, Kristjánsson & Whitney, 2019; Murai & Whitney, 2021; Pascucci et al., 2019; Pascucci & Plomp, 2021a; Rafiei, Hansmann-Roth, Whitney, Kristjánsson, & Chetverikov, 2021a; Rafiei, Chetverikov, Hansmann-Roth, & Kristjánsson, 2021; Tanrikulu, Pascucci, & Kristjánsson, 2023). Such *attractive* serial dependence, in which decisions are biased *toward* prior stimuli, is considered to result from how the brain links together events across consecutive perceptual episodes (Corbett, Fischer, & Whitney, 2011; Fischer et al., 2020; Fischer & Whitney, 2014),

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a process that appears strongly influenced by attention (Fischer & Whitney, 2014; Pascucci et al., 2019). For instance, serial dependence is mostly evident when previous and current stimuli share a common feature that is attended to and they occur at nearby locations (Fischer & Whitney, 2014; Fritsche & de Lange, 2019). These aspects closely resemble the way attention has traditionally been considered to combine features into coherent objects, by binding together similar attended features, and only at similar attended locations (Kahneman, Treisman, & Gibbs, 1992; Treisman & Gelade, 1980).

Notably, however, research on this topic has typically manipulated attention by explicit instructions on what to attend to or not (Fischer & Whitney, 2014). Yet most of our everyday visual experience is made up of unexpected distracting stimuli that not only require no attention but also must be actively ignored to prevent interference with our current goals (Chelazzi, Marini, Pascucci, & Turatto, 2019). Whether and how the brain integrates such distractors in a sequence of perceptual episodes remains largely unknown.

Attentional suppression

When we attend to an object, we rarely view that object in isolation. Visual scenes are cluttered with similar and distinct objects dispersed in space, which often surround and interfere with the current focus of our attention (Neisser, 1967; Tiurina, Markov, Choung, Herzog, & Pascucci, 2022; Treisman, 1988, see Kristjánsson & Egeth, 2020 for review). Sudden, unexpected stimuli can then abruptly capture our attention, breaking the current stream of perceptual and attentional focus (Chelazzi et al., 2019). Hence, our attentional system is constantly challenged to overcome the impact of irrelevant stimuli.

One way to efficiently overcome distraction is to anticipate the occurrence of irrelevant stimuli, for instance, by inferring their most likely features and locations from the statistics of visual events. This is evident in typical visual search tasks, where repeating the feature or location of a target leads to speeded and more accurate responses (Geng & Behrmann, 2002; Goschy, Bakos, Müller, & Zehetleitner, 2014; Maljkovic & Nakayama, 1994, Maljkovic & Nakayama, 1996; Pascucci & Turatto, 2013; van Moorselaar & Theeuwes, 2021, see Kristjánsson & Ásgeirsson, 2019; Ramgir & Lamy, 2022 for reviews). Priming phenomena of this kind are one of the most investigated examples, but there are more complex ways in which the brain may tune itself to avoid distraction. Recent research has clearly shown that when a distractor appears at predictable locations, these locations can be discounted from attentional focus and the distractor ceases to exert its original effect (Failing, Wang, & Theeuwes, 2019; Reder, Weber, Shang, & Vanyukov, 2003, see Gaspelin & Luck, 2019). Such learning of statistical regularities occurs regardless of awareness (Gao & Theeuwes, 2020, Gao & Theeuwes, 2022; Kristjánsson & Nakayama, 2003; Leber, Gwinn, Hong, & O'Toole, 2016) and typically leads to faster search times when a distractor is present at predictable locations or with predictable features. But the learning might also come at a cost, slowing search when a distractor is not present because observers "pre-activate" a resource-demanding attentional strategy against the expected distractor —that is, proactive filtering (Marini, Chelazzi, & Maravita, 2013; Marini, Demeter, Roberts, Chelazzi, & Woldorff, 2016; Wang & Theeuwes, 2018).

A still-debated topic concerns the underlying mechanisms and whether they involve, for instance, active suppression of distractor processing (Becker, Hemsteger, & Peltier, 2015; Cunningham & Egeth, 2016), faster reallocation of attention to the target (Chang, Cunningham, C., & Egeth, 2018), or the build-up of inhibitory templates that counteract distractor-related neural activity (Ramaswami, 2014). In this context, a recent line of work suggests that the ability to anticipate distractors may instantiate "rejection templates" that act as "negative" filters to suppress distractions (Arita, Carlisle, & Woodman, 2012; Beck & Hollingworth, 2015). Under this view, the action of a negative filter could result in negative serial dependence (i.e., a repulsive bias away from the features of a distractor encountered in the recent past).

In sum, the myriad of studies on distractor suppression suggests that when the properties of a distractor can be anticipated, the brain can successfully resist distraction and maintain focus on relevant aspects of visual input. It remains unclear, however, whether distractor stimuli leave any trace on the processing of subsequent task-relevant stimuli.

Current aims

We sought to address a question that has not been considered before: does a distractor stimulus leave any discernible trace in a sequence of perceptual judgments? Previous studies have shown that attended stimuli cause serial dependence whereas unattended stimuli have no effect or even cause repulsive biases (Fischer & Whitney, 2014; Rafiei, Chetverikov, et al., 2021; Rafiei, Hansmann-Roth, et al., 2021). However, not attending to a stimulus is different from dealing with a distractor, and answering the question above can help to shed light on the neural fate of visual distractors and the mechanisms that facilitate their suppression.

To this aim, we combined an orientation adjustment task with a secondary discrimination task (see Figure 1). In the discrimination task, observers focused on a Landolt C while a distractor stimulus appeared on

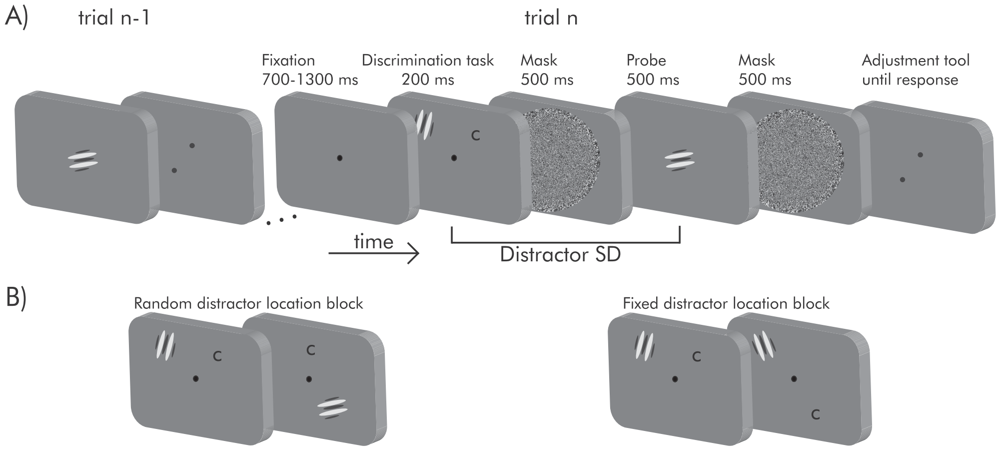

Figure 1. The paradigm in Experiments 1 and 2. (**A**) Example of a trial sequence: An orientation adjustment task was interleaved with a discrimination task. In the discrimination task, participants had to report whether the gap in a Landolt C was on the left or the right. On 50% of trials, a distractor (an oriented Gabor) was presented together with the target. Following a noise mask, the central Gabor of the adjustment task was presented, and participants had to reproduce its orientation by rotating a response tool. (**B**) In two different blocks, the distractor appeared either in a random location or at fully predictable locations ("random" and "fixed" conditions, respectively).

50% of trials. Crucially, the stimulus observers had to reproduce in the adjustment task (the probe), and the distractor in the discrimination task were both oriented Gabors. When these stimuli are attended, the orientation of the previous stimulus typically causes serial dependence in current decisions. Here, we made the previous Gabor a distractor and manipulated the probability of its location in two separate blocks. In the "random" block, the distractor could appear at one of four possible locations, randomly determined. In the "fixed" conditions, the distractor always appeared at the same location (see Methods). In the discrimination task, observers had to report the side of the gap in a Landolt C presented at one of the four locations, non-overlapping with the possible locations of the distractor. In two experiments, the distractor was exactly the same Gabor stimulus as the adjustment probe (Experiment 1) or differed in spatial frequency and contrast (Experiment 2). We measured serial dependence from the distractor as a function of its predictable or random location under the idea that predictable locations facilitate attentional mechanisms that anticipate, and therefore resist distractors more efficiently.

To investigate both the attractive and repulsive effects of the distractor on adjustment responses, we developed a novel method based on model selection, and evaluated models including attractive and repulsive components, as well as the effect of the predictability of the distractor. Furthermore, we considered serial dependence from the distractor, but also from the previously attended probe and its relation to the orientation of the distractor. Although we found no evidence for an effect of distractor predictability on neither the discrimination nor the adjustment task, our results indicate that distractors led to a weak but repulsive bias that affected current perceptual judgments and interfered with the trace of prior attended stimuli. In our paradigm, this effect appeared to be stronger when both the distractor and the probe were of high spatial frequency and low contrast (Experiment 1). We discuss these results in light of current theories of serial dependence and distractor processing, proposing that serial dependence can be a key to understanding the mechanisms of distractor suppression.

General methods

Ethics statement

The study was performed according to the requirements of the local ethics committee.

Apparatus

The stimuli were generated with custom-made scripts from Matlab (2019b) and the Psychophysics Toolbox (Brainard, 1997) and presented on a 24-inch

Asus monitor (resolution: 1920 × 1080 pixels, refresh rate: 60 Hz), on a Windows-based machine. The experiment was performed in a dimly lit room, and participants were positioned approximately 57 cm from the computer screen.

Participants

Thirty-five healthy observers (age range 18–42, 15 females) from the University of Iceland community participated in the two experiments for a monetary reward (1500 ISK). Fifteen (one excluded, six female, age range 18–37) participated in Experiment 1, and 20 (two excluded, nine female, age range 22–42) in Experiment 2. The participants had normal or corrected-to-normal vision and were naïve about the purpose of the experiments. Written informed consent was collected from all participants beforehand.

Stimuli and procedure

The experiments consisted of a series of trials where participants performed two sequential tasks (Figure 1). Each trial started with a fixation dot shown for 700 to 1300 ms. Participants then had to discriminate whether the gap in a Landolt C (peak contrast of 47%) was on the left or the right, while a distractor—a randomly oriented Gabor stimulus ranging from 0° to 180° in 20° steps—appeared on 50% of the trials, randomly determined. The distractor appeared at 8° off fixation, placed at the corners of an imaginary square. The Landolt C and distractor were presented for 200 ms and were followed by a noise mask for 500 ms (peak Michelson contrast = 75%, spatial frequency of 1 cpd, sigma of 2.75°). Participants had to report the side of the gap as quickly as possible by pressing the corresponding arrow key. After the discrimination task, a probe Gabor appeared at screen center, with a random orientation between 0° to 180° serving as the stimulus for the orientation adjustment task.

In Experiment 1 the probe and distractor Gabor stimuli were identical (i.e., same contrast and spatial frequency). In Experiment 2, both the contrast (peak Michelson = 10%) and the spatial frequency (0.25 cpd) of the probe Gabor were lower than those of the distractor stimuli. In both experiments, the adjustment stimuli had a random orientation difference with respect to the distractor, in the range between ±65° and were shown for 500 ms. The probe Gabor was followed by a noise mask, after which a response tool appeared at the center of the display. The response tool consisted of two dark-gray dots positioned at the end of an imaginary (nonvisible) line on a circle and participants had to rotate the line to reproduce the perceived orientation of the last Gabor. The initial orientation of the response tool was selected randomly. Participants could take as much time as they wanted and had to press the left mouse button to confirm their response, after which the next trial would proceed.

In both experiments, participants received verbal instructions and performed a sequence of practice trials under the supervision of the experimenter. Practice trials were not analyzed further. Participants were further instructed to ignore a distractor which appears in some trials, they were not informed about the locational probabilities in the blocked conditions. The two experiments were performed on two independent samples, and each experiment consisted of two separate sessions on separate days (one week was the maximum time allowed between sessions). Each session lasted approximately one hour and comprised of 1000 trials in total. During the experiments, participants were instructed to maintain their gaze on the fixation dot at screen center for the entire duration (breaks and between trials excluded). All stimuli were presented on the same gray background (83.33 cd/m^2).

Analysis

Before the main analyses, trials were removed in the following cases: 1) reaction times (RT) in the discrimination task outside the 200-1000 ms range; 2) adjustment errors detected as outliers in a two-step procedure, first excluding errors larger than ±45°, then excluding errors more than 1.5 interquartile ranges above the upper quartile or below the lower quartile; 3) adjustment errors slower than 10 seconds. By these exclusion criteria, 4.3% and 3.7% of the total trials were removed from Experiments 1 and 2, respectively. We also employed the following criteria for participant exclusion: 1) more than 25% of the trials were marked as outliers; 2) a circular correlation between the reported and presented orientation lower than 0.4; 3) accuracy and reaction times during the detection task three standard deviations away from the group mean. In Experiment 1, one participant was excluded for adding 90° to every response. In Experiment 2, one participant was excluded because of poor performance on the discrimination task (accuracy = 51%), and one participant exceeded the 25% of trials marked as outliers in the orientation adjustment task.

To analyze RT in the discrimination task, we used a general linear mixed-effects (GLM) regression (Matlab *fitglme*, distribution: inverse gaussian, link: identity), with RT as the dependent variable. The main predictors were the intercept plus the slope and the interaction associated with effect of the location condition (random vs. fixed, coded as binary variable) and distractor presence (absent vs. present, coded as a binary variable). In the GLM, we modelled the individual intercept

Model	Function
$\Delta 0$	$y = a$
$\Delta 1$	$y = a + b\Delta 1$ $b\Delta 1$: difference between prior and current orientations
$\Delta 2$	$y = a + b_1\Delta 1 + b_2\Delta 2$ $b_1\Delta 1$, $b_2\Delta 2$: attractive and repulsive effects
$\Delta 1$*loc	$y = a + b_1\Delta 1 + b_2\Delta 1 * b_3 Loc$ $b_3 Loc$: dummy variable coding random vs. fixed location
$\Delta 2$*loc	$y = a + b_1\Delta 1 + b_2\Delta 2 + \ b_3\Delta 1 * b_4 Loc + b_5\Delta 2 * b_6 Loc$ $b_{4/6}Loc$: dummy variable coding random vs. fixed location

Table 1. Models of serial dependence in the analysis of experiments 1 and 2. Models are named as in Figures 2D and 4D. In all equations y is the adjustment error variable, a is the intercept, $b_{1,\dots,6}$ are the coefficients associated to each additional variable included in the model.

as a random effect and excluded trials with incorrect discrimination responses.

For the serial dependence analyses, we used a novel approach. Serial dependence patterns typically contain a combination of repulsive and attractive effects due to prior stimuli (Pascucci et al., 2023). For example, several studies have shown attractive effects when prior stimuli are attended and reported, but repulsion, or a combination of the two otherwise (Pascucci et al., 2019; Pascucci & Plomp, 2021a). Because the Gabor stimulus in the discrimination task was a distractor, and therefore not attended, previous studies may therefore suggest a repulsive effect, or a combination of repulsion and attraction. However, the common approach of fitting the 1st derivative of a Gaussian function (DoG; Fischer & Whitney, 2014) can only capture the effect that dominates (irrespective of whether it is repulsive or attractive). So, to provide a more exhaustive description of the bias, we developed a method based on model comparison.

Adjustment errors from all participants were aggregated into a pooled dataset and modelled with a set of linear regression models (see Table 1), including (1) a model with only an intercept (Δ0), (2) a model with an intercept and one variable accounting for the effect of the difference (Δ) between prior and current orientations (Δ1), (3) a model including a second variable accounting for an additional effect of Δ, which can model the combination of repulsive and attractive effects (Δ2), (4) a variant of Δ1 including the interaction between Δ and the random vs. fixed location condition (Δ1*loc), and (5) a variant of Δ2 including the interaction between both components related to Δ and the location condition (Δ2*loc). Since the effect of Δ on adjustment errors is typically nonlinear (i.e., it follows the shape of the DoG), the Δ variables used in each model were first transformed by multiplying Δ with a Gaussian function of variable width (from 10° to 80°) and choosing the best-fitting width (the one with the highest r^2; Barbosa & Compte, 2020).

We then performed model comparison using the Bayesian Information Criterion (BIC; Kass & Raftery, 1995; Raftery, 1995), selecting the model with the lowest BIC as the best. For further comparison we calculated the ΔBIC by subtracting the largest BIC from all the BIC values. ΔBIC can be considered as an approximation of the Bayes factor where a difference of 2 ΔBIC between models indicates positive evidence in support of the model with the lower BIC, and a value of 6 ΔBIC or above can be considered as strong positive evidence. This procedure was applied to analyze the errors as a function of both the distractor orientation on the immediately preceding discrimination task (distractor present trials) and the orientation of the last probe stimulus one trial before. Model comparison enabled the identification of effects caused by previous stimuli, their direction, the presence of multiple components of the opposite sign, and the interaction of these effects with the experimental conditions of interest while controlling for model complexity, thus providing a more exhaustive description of the data than the typical approach of fitting DoG functions.

Results

Experiment 1

Fourteen observers participated in Experiment 1, performing the discrimination task with a mean accuracy of 97% and mean RT of 498 ± 54.5 ms. The mean absolute error in the adjustment task was 9.29° ± 2.61° and response times were 1630 ± 310 ms.

For the discrimination task analyses, we modeled RT as a function of the presence/absence of a distractor and of the distractor location condition (fixed vs. random). The GLM results (see Methods) revealed a significant slope associated with the effect of a distractor, as well as with the effect of the distractor location and the interaction between the two (see Table 2). Observers were overall slower in the presence of a distractor, but the difference in RT varied as a function of whether the distractor location was fixed or random (Figure 2A). Although this pattern led to an apparent reduction of attentional capture (RT difference between distractor-present and distractor-absent trials) in the fixed location condition (Figure 2B), the interaction resulted from (1) a reduction of RT for distractor present trials in the fixed location condition and (2) an increase of RT for distractor absent trials in the fixed location condition (Figure 2A).

Together these results suggest that the fixed location condition adds a cost on distractor absent trials, which could be interpreted as a form of “proactive suppression” where observers expected and proactively filtered the distractor at the fixed location, leading to

Variable	Estimate	SE	*t*-test	DF	*p* value	Lower	Upper
Intercept	489.29	13.93	35.13	13374	<0.001	461.99	516.59
Location	4.128	1.731	2.385	13374	0.0171	0.735	7.521
Distractor	18.53	1.786	10.38	13374	<0.001	15.029	22.03
Interaction	−10.97	2.517	−4.36	13374	<0.001	−15.90	−6.032

Table 2. GLM summary. Location refers to the random versus fixed location of the distractor (coded as a binary variable with random = 0). Distractor refers to the absence or presence of a distractor (coded as a binary variable with absent = 0). *Notes:* SE = standard error; DF, degree of freedom.

slower RT even when no distractor was present (Marini et al., 2013).

Effect of distractor orientation on adjustment responses

After the discrimination task, observers performed an adjustment task on the same trial, with a new stimulus (probe) presented at the center. To examine the impact of the distractor orientation on the adjustment task, we used model comparison to assess various models predicting repulsive and attractive effects, as well as their interaction with fixed versus random distractor location conditions (see Methods). Our objective was to evaluate how the distractor influenced current perceptual decisions and whether this influence was affected by the predictability of the distractor location. The results of our RT analysis indicated that the distractor interfered with the discrimination task and that the predictability of its location also played a role, supporting the hypothesis that these effects may also manifest in serial dependence for the subsequent adjustment stimulus.

However, as revealed by the model comparison, although we found an overall effect of the distractor orientation, this effect was not modulated by the distractor location conditions. More precisely, when comparing models including no effect of the distractor ($\Delta 0$), a single effect (e.g., either attractive or repulsive, $\Delta 1$), a mixture of two effects (both attractive and repulsive, $\Delta 1 + \Delta 2$), and the interaction of these effects with the distractor location variable ($\Delta 1$ * loc, $\Delta 2$ * loc, see Figure 2, and Methods for details), the model with a single effect $\Delta 1$ was preferred over all the others (see Table 3). Model evidence was in favor of $\Delta 1$ against the model with the second smallest BIC (evidence in favor of $\Delta 1$ against $\Delta 0$, quantified by the $\Delta \text{BIC} = 2.20$). Crucially, the effect fitted by the winning model was repulsive (i.e., a peak bias of −0.49°), indicating that observers were slightly biased away from the orientation of the distractor but independently of the location condition of the distractor. Similar repulsive effects of distractor stimuli have been reported in different contexts (Fischer & Whitney, 2014; Rafiei, Chetverikov, et al., 2021; Rafiei, Hansmann-Roth, et al., 2021).

Effect of the previous probe on adjustment responses

To ensure that the observed repulsive effect of the distractor was indeed specific to the distractor, we conducted an analysis using the same model comparison as above, but with the aim of examining the impact of the previous probe (i.e., the stimulus presented on the preceding adjustment trial) on current adjustment errors. This served as a control to verify the presence of attractive serial dependence in our paradigm.

As expected, adjustment errors were systematically biased by the orientation of the previous probe, revealing a combination of attraction and repulsion, with the model predicting two components ($\Delta 2$) resulting in the best fit (see Table 3, Figure 4D). The best model ($\Delta 2$) was preferred over the second-best model, which included the distractor location effect ($\Delta 2$*loc, $\Delta \text{BIC} = 15.03$). The attractive peak (0.76°) was evident for small Δ whereas the repulsive peak (−0.49°) occurred for larger Δ, as in typical patterns dominated by attractive serial dependence (Fritsche & de Lange, 2019).

Interference between the distractor and the previous probe effect

The results presented above suggest that adjustment errors were influenced by both the orientation of the distractor and the one of the previous probes, but in opposite ways. With additional analyses, we evaluated whether the two effects interacted with each other, specifically whether the impact of the previous probe changed depending on the similarity between its orientation and that of the distractor. If this were the case, it would suggest that the effect of prior stimuli, which are normally integrated with current ones, is diminished when prior stimuli are similar to irrelevant

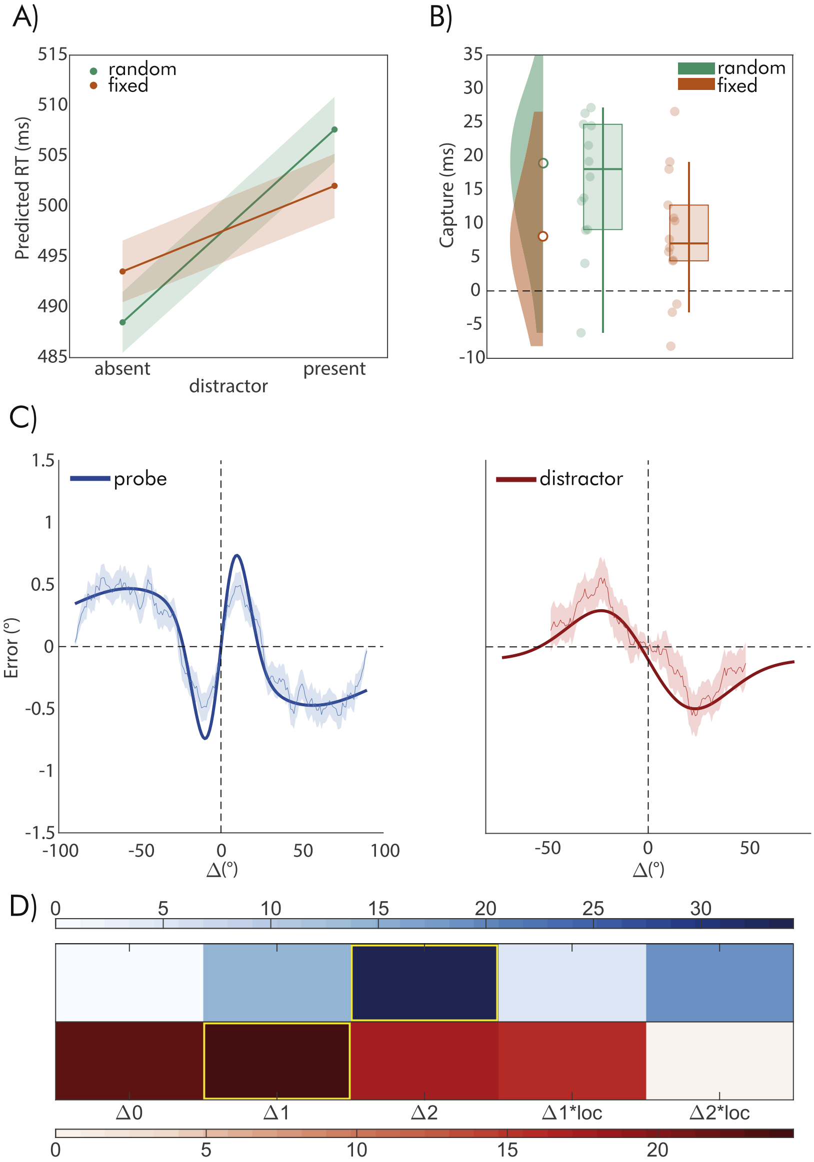

Figure 2. Results of Experiment 1: (**A**) Predicted RT mean and 95% CI from the GLM model estimating the effect of the distractor presence and location condition on RT. (**B**) Box plots, distributions, and individual datapoints of the capture effect on RT, computed as RT in distractor present minus absent trials, separately for the random (green items) and fixed (orange items) location conditions. (**C**, left plot) Errors (y axis) in the adjustment task as a function of the difference in orientation between the probe adjustment stimulus on the current and on the previous trial (Δ, x axis). (**C**, right plot) Errors as a function of the Δ between the current probe stimulus and the distractor in distractor-present trials. Data in C are moving averages of the group mean with 1 standard deviation smoothed in a 21° moving window, the fitted line is the predicted pattern from the best-fitting model (see Methods and Results). Models were fitted to the unsmoothed single-trial data. (**D**) Results from the model comparison applied to both the effect of prior probes (red color scale), and distractors (blue color scale). Values in the color scale reflect the difference in BIC values (ΔBIC) of each model from the one with the largest BIC (the one with the largest BIC has a value of 0, larger values indicate better fits, see Methods for the description of each model). The best-fitting models are highlighted in yellow.

	Distribution			
	Experiment 1		Experiment 2	
Model	Previous probe BIC	Distractor BIC	Previous probe BIC	Distractor BIC
Δ0	89322 ΔBIC = 0	44432 ΔBIC = 22.30	117487 ΔBIC = 0	58533 ΔBIC = 29.38
Δ1	89305 ΔBIC = 14.77	44429 ΔBIC = 24.50	117364 ΔBIC = 117.31	58539 ΔBIC = 23.39
Δ2	89286 ΔBIC = 34.29	44436 ΔBIC = 17.46	117336 ΔBIC = 151.46	58544 ΔBIC = 17.58
Δ1 * loc	89314 ΔBIC = 5.50	44438 ΔBIC = 15.79	117374 ΔBIC = 107.96	58548 ΔBIC = 14.74
Δ2 * loc	89300 ΔBIC = 19.27	44454 ΔBIC = 0	117355 ΔBIC = 132.56	58562 ΔBIC = 0

Table 3. The set of models used in the serial dependence analysis and their associated BIC values for experiments 1 and 2. The results include models applied separately to the effect of the previous probe and the distractor. ΔBIC is reported for each model and computed as the difference between the model with the largest BIC (indicated as ΔBIC = 0) and all the other models. Larger ΔBIC values are indicative of better models.

and distracting stimuli that are presented in between. To investigate this possibility, we divided the dataset into two halves based on the similarity between the previous probe and the distractor orientation (i.e., whether it was smaller or larger than 45°), and conducted a separate model comparison for the effect of the probe on each half. The model comparison results revealed no difference in the preferred model as a function of the similarity between the previous probe and the distractor, still favoring the Δ2 model with attractive and repulsive components (similar condition, ΔBIC = 14.5, dissimilar condition, ΔBIC = 18.80). For the condition in which the previous probe and distractor were dissimilar, the Δ2 was strongly favored over the second-best model (evidence in favor of Δ2 against Δ1, quantified by the ΔBIC = 10.38). However, for the condition where the probe and distractor orientation were similar, there was no conclusive evidence favoring the Δ2 model over the simplest Δ1 model (evidence in favor of Δ2 against Δ1, quantified by the ΔBIC = 0,74), suggesting that a single effect of Δ, characterized only by a repulsive component, provides a more parsimonious description of the data. In line with this, a direct comparison between the estimated coefficients of the two components from the Δ2 model, revealed that repulsion increased when the previous probe and the distractor had similar orientations ($z = 3.51$, $p < 0.001$, z-test for comparing coefficients between models, see Figure 3), whereas the attractive effect remained the same ($z = 0.58$, $p = 0.56$).

Experiment 2

The serial dependence effects observed in Experiment 1, whether repulsive or attractive, were relatively small compared to previous studies (Fischer et al., 2020; Fritsche & de Lange, 2019; Kiyonaga, Scimeca, Bliss, & Whitney, 2017; Tanrikulu et al., 2023), with bias peaks of less than 1°. This could be because the high-spatial frequency stimuli used did not have enough uncertainty in their orientation content, an aspect that plays a key role in serial dependence (Ceylan, Herzog, & Pascucci, 2021; Cicchini, Mikellidou, & Burr, 2018; Tanrikulu et al., 2023; see review in Pascucci et al., 2023). It is therefore unclear whether the results of Experiment 1 can be applied to a broader context or if they may vary with modifications of the stimulus parameters.

In Experiment 2, the same paradigm was used, but with a reduction in contrast and spatial frequency of the probe Gabors. However, all other aspects of the experiment, including the contrast and spatial frequency of the distractor, remained the same as in Experiment 1. It is worth noting that the adjustment response bias caused by the distractor could potentially increase as a result of making the distractor more noticeable and less ambiguous than the probe.

Eighteen observers participated in this experiment, performing the discrimination task with a mean accuracy of 96% and a mean RT of 526 ± 86 ms. The mean absolute error in the adjustment task was 9.41° ± 2.10° and response times were 1600 ± 270 ms. The results of the GLM model on RT revealed a pattern in line with Experiment 1, showing a significant slope for the effect of distractor (absent vs. present), location (random vs. fixed), and their interaction (see Table 4).

Effect of the distractor orientation on adjustment responses

In contrast to the findings of the model comparison conducted in Experiment 1, the results of this experiment indicated no influence of the distractor on

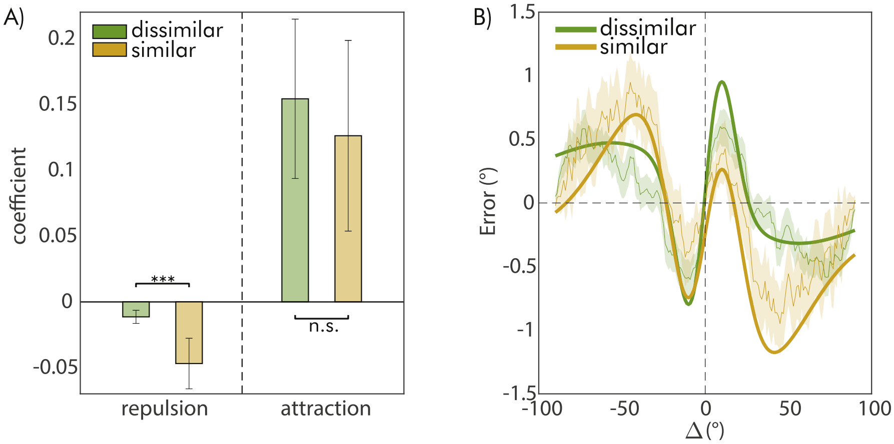

Figure 3. (**A**) Comparison of the effects of the previous probe as a function of whether the previous probe orientation was similar (within 45°, dark yellow bars) or different from the orientation of the distractor (above 45°, green bars). The two sets of bars refer to the attractive and repulsive components of the Δ2 model. Error bars are 95% CI, asterisks denote significant differences (*$p = 0.05$, **$p = 0.01$, ***$p < 0.001$). (B) Serial dependence curves and Δ2 model fit from the previous probe effect, represented with the same color coding as in A).

Variable	Estimate	SE	*t*-test	DF	*p* value	Lower	Upper
Intercept	517.35	19.44	26.61	16903	<0.001	479.24	555.45
Loc. Prob.	5.437	1.646	3.30	16903	<0.001	2.210	8.663
Distractor	15.30	1.687	9.07	16903	<0.001	11.99	18.60
Interaction	−7.241	2.388	−3.03	16903	0.002	−11.92	−2.561

Table 4. GLM model summary. The effects of distractor and location probability on performance in the discrimination task in experiment two. *Notes:* SE = standard error; DF, degree of freedom.

the adjustment task. All models that incorporated an effect of Δ performed worse than the null model, which predicted no impact of Δ (as shown in Figure 4C). Furthermore, the null model was considerably favored, even when compared to the simplest model with only one component, whether it be attractive or repulsive, linked to the effect of Δ (with a ΔBIC of 5.99, as displayed in Table 4).

Effect of the previous probe on adjustment responses

When considering the effect of the previous probe, we observed a clear attractive bias, which was larger than in Experiment 1 (peak bias = 1.42°. Figure 4C). This trend, similar in shape and size to previous studies, was also accompanied by a repulsive component located at the tails (with a peak bias of −0.53°). The model comparison validated the existence of two components that accounted for the attractive and repulsive impact of Δ on adjustment errors, with evidence supporting the Δ2 model over the second-best fitting model (Δ2 * loc, with a ΔBIC of 18.90).

Interference between the distractor and the previous probe effect

As in Experiment 1, we also performed a separate model comparison dividing the data into two halves based on the orientation similarity of the distractor and the previous probe (orientation difference smaller or larger than 45°). Model choice was not affected by dividing the data, and the preferred model remained the same in both conditions (e.g., Δ2), with strong evidence relative to the second-best models (evidence in favor of Δ2 against second choice, quantified by the ΔBIC > 10 in both conditions, see Figure 5B for the model fit).

However, a comparison of the coefficients accounting for repulsive and attractive effects as in Experiment 1,

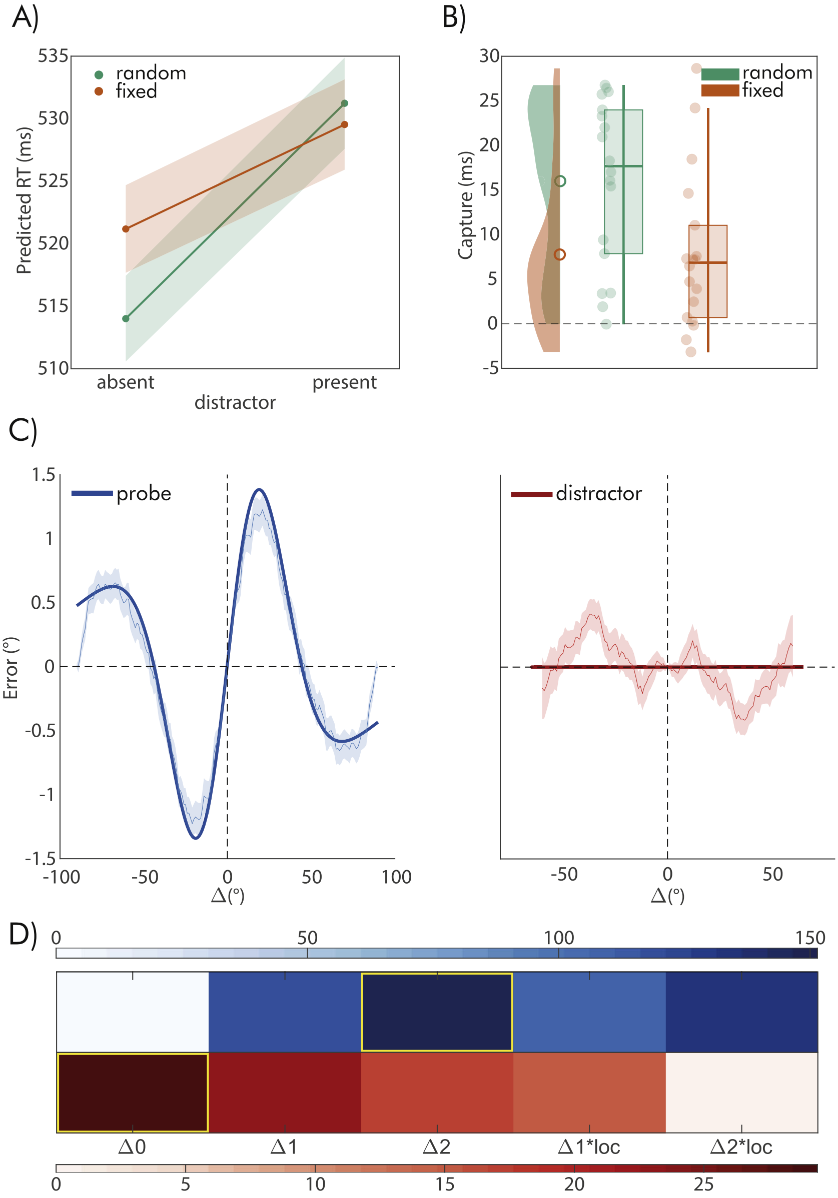

Figure 4. Results of Experiment 2: (**A**) Predicted RT mean and 95% CI from the GLM model on RT. (B) Capture effect on RT, computed as RT on distractor present minus absent trials, separately for the random (green items) and fixed (orange items) location conditions. (**C**, left plot) Errors (y-axis) on the adjustment task as a function of the difference in orientation between the probe adjustment stimulus on the current and the previous trial. (**C**, right plot) Errors as a function of the Δ between the current probe stimulus and the distractor in distractor-present trials. (**D**) Results from the model comparison applied to both the effect of prior probes (red color scale), and distractors (blue color scale). Values in the color scale are reported as in Figure 2. The best-fitting models are highlighted in yellow.

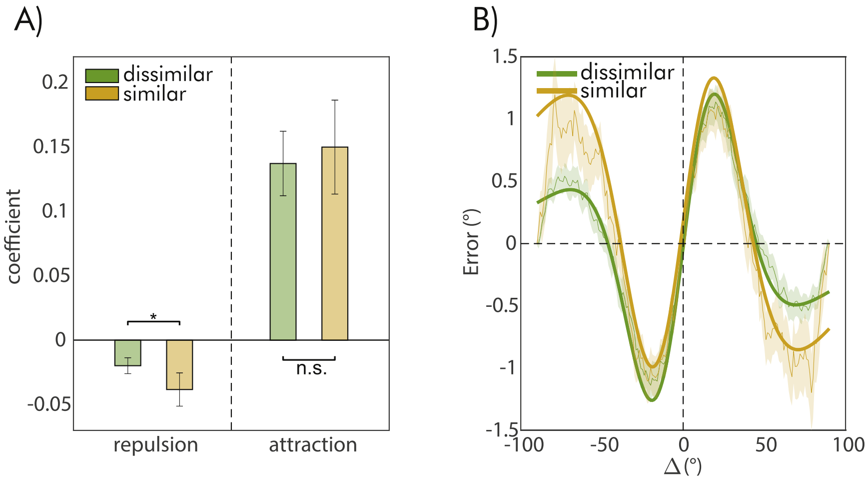

Figure 5. (**A**) Comparison of the effects of the previous probe as a function of whether the previous probe orientation was similar (within 45°, dark yellow bars) or different from the orientation of the distractor (above 45°, green bars) in Experiment 2. The two sets of bars refer to the attractive and repulsive components of the △2 model. Error bars are 95% CI, asterisks denote significant differences ($*p = 0.05$, $**p = 0.01$, $***p < 0.001$). (B) Serial dependence curves and △2 model fit from the previous probe effect, represented with the same color coding as in A).

revealed a significant increase in the repulsive effect of the previous probe when its orientation was similar to the distractor ($z = 2.53$, $p = 0.011$, Figure 5), but no changes in the attractive effect ($z = -0.57$, $p = 0.57$, Figure 5). Hence, even though the probe effect always had both attractive and repulsive components, the strength of repulsion increased when a distractor with a similar orientation appeared right after the probe.

General discussion

Our aim was to investigate the effects of visual distractors on serial dependence. While prior research suggests that serial dependence typically occurs when stimuli are attended, it remains unclear whether this effect extends to stimuli that capture attention but are ignored, or suppressed, as distractors. Additionally, we explored whether the predictability of the distractor location plays a role, as predictable distractors are typically easier for the visual system to ignore (Failing et al., 2019; van Moorselaar & Slagter, 2019; Wang & Theeuwes, 2018). To address these questions, we conducted two experiments that involved a discrimination task using Gabor stimuli as distractors, interleaved with an adjustment task involving task-relevant Gabor patches (probes). Our results show that visual distractors, exert a weak repulsive bias on subsequent decisions and interfere with the attractive serial dependence typically induced by preceding attended and task-relevant stimuli.

Previous studies do not provide a conclusive understanding of how the visual system integrates prior and current information when the preceding history includes both relevant and irrelevant stimuli. Some studies conclude that serial dependence occurs independently of the task and that the task relevance of a stimulus does not play a role (Fornaciai & Park, 2018a; Murai & Whitney, 2021). In contrast, other studies have shown repulsive effects due to stimuli that were not attended to or not reported in the recent past (Fischer & Whitney, 2014; Fornaciai & Park, 2018b; Pascucci et al., 2019; Pascucci & Plomp, 2021b; Rafiei, Chetverikov, et al., 2021; Rafiei, Hansmann-Roth, et al., 2021). However, none of these studies have examined the effect of an "irrelevant" stimulus that the visual system must suppress to prevent distraction. Here, we found that distractors are not integrated in the perceptual stream that leads to attractive serial dependence, even when they are highly similar to other stimuli in close temporal and spatial proximity. This finding is particularly relevant because distractor stimuli can capture attention and, therefore, they might be processed to some degree (Moher & Egeth, 2012), which differs from prior studies where irrelevant stimuli were simply ignored, as there was no accompanying task.

The repulsive serial dependence from distractor stimuli

In the two experiments, the repulsive effect of visual distractors was either weak (Experiment 1) or absent (Experiment 2). This could have two explanations. First, the different results may be due to between-experiment variability. Second, the modified parameters could have been the critical factor. In Experiment 2, we used more uncertain stimuli as probes in the adjustment task (e.g., Gabor of lower contrast and spatial frequencies). As attractive serial dependence increases under uncertainty (Ceylan et al., 2021; Cicchini et al., 2018; Tanrikulu et al., 2023), this might have led to an overall dominance of attractive biases due to the previous probe and a reduced measurable effect of repulsion caused by the distractor. Recent studies have suggested that attractive and repulsive components of serial dependence are additive and arise concurrently, so that in the absence of one, the other will be more dominant (Fornaciai & Park, 2019; Moon & Kwon, 2022; Pascucci et al., 2019; Sheehan & Serences, 2022). Under this view, it is plausible that repulsive effects from distractors are only seen when all the stimuli are highly reliable and any attractive bias towards prior stimuli is overall reduced. By this logic, we speculate that the lower spatial frequency of the probe in Experiment 2, which is typically associated with more uncertain stimuli (Ceylan et al., 2021; Cicchini et al., 2018; Tanrikulu et al. 2023), might have fostered attractive influences of the previous probe orientation that outweighed any potential repulsive effect of the distractor. Nevertheless, the distractor orientation interfered with the effect of the previous probe in both experiments. In particular, the repulsive effect of the previous probe, evident for large orientation differences between consecutive probes, was further increased when the previous probe was similar to the distractor, indicating an indirect effect that still supports a repulsive component related to distractor processing, which shaped the effect of previous probes.

The effect of statistical regularities on attentional suppression

Our results also speak to potential effects of manipulating the predictability of distractor locations. Specifically, RTs in the discrimination task, were reduced when the distractor appeared at a fixed and predictable location compared to a random location. However, we also observed an increase in RT in blocks where the distractor was absent, but its location was predictable. This pattern, which was consistent across both experiments, suggests that manipulating the distractor location not only affected the capture caused by the distractor, but also led to an overall change in attentional strategy. One explanation is that participants proactively expected the distractor at a fixed location and engaged anticipatory filtering mechanisms, which come at the cost of an overall increase in RT (Marini et al., 2013). It is worth highlighting that our manipulation of presenting the distractor at a fixed location for entire blocks differed from the more implicit manipulations of statistical regularities often employed in visual attention research (e.g., Leber et al., 2016), and this difference might have prompted different attentional strategies in our study. Nonetheless, our findings add to a large body of literature indicating that the attentional system is sensitive to both explicit and implicit regularities in distractor events, allowing the system to build a model of what is irrelevant and distracting, and when and where it is likely to occur (Pascucci & Turatto, 2015; Turatto, Bonetti, & Pascucci, 2018; Turatto & Pascucci, 2016).

A central question is what implications the internal model has, especially with regard to developing a model of what should be ignored, such as a distractor (Ramaswami, 2014; Turatto, Bonetti, Pascucci, & Chelazzi, 2018). There is open debate that focuses on whether the attentional system would benefit from so-called “negative models” or “rejection templates,” which, rather than facilitating specific target features, would help to prevent allocating attention to nontarget elements (Carlisle & Kristjánsson, 2018; Woodman, Carlisle, & Reinhart, 2013; see Chelazzi et al., 2019 for a review). For example, it has been proposed that negative models may involve inhibitory mechanisms in sensory processing (Ramaswami, 2014), whereas other studies argue that evidence of rejection templates is only the indirect consequence of building models of what is relevant and attended (Ferrante et al., 2018; Sauter, Liesefeld, Zehetleitner, & Müller, 2018). Our study demonstrates that knowing the location of a distractor in advance can speed up performance in the relevant discrimination task but also has a weak repulsive effect on subsequent stimuli and interferes with the effect of previous stimuli. This suggests that the occurrence of distractors leaves a negative (repulsive) trace that persists for a few seconds, in line with the notion of sensory suppression mechanisms (Ramaswami, 2014). Another debated issue is whether ignoring a distractor involves initial processing of the distractor and faster reallocation of attention away from it, or no processing at all (Cunningham & Egeth, 2016; Ferrante, Zhigalov, Hickey, & Jensen, 2023; Moher & Egeth, 2012). Our results seem to suggest that distractors, at least in our paradigm, were processed to the extent that they left a trace or interfered with other ongoing traces of prior stimuli.

Our findings show that the predictability of the distractor location did not affect serial dependence in either of the experiments. Therefore it is difficult to draw conclusions about the impact of more efficient suppression resulting from statistical regularities. Instead, the observed effects are most likely a consequence of the distractor's capture rather than its suppression, which was strong and evident in both the predictable and unpredictable location conditions. Despite this, this finding is important because it shows that distractors that capture attention are not incorporated into sequential perceptual decisions the way relevant stimuli are. Thus, the results reported here add to research showing that perceptual decisions are biased away from the features of recent distractors (Rafiei, Chetverikov, et al., 2021; Rafiei, Hansmann-Roth, et al., 2021). In a broader context, the rationale behind our study may provide a basis for future research exploiting serial dependence as a tool to understand the mechanisms implicated in distractor processing and the neural outcomes of such stimuli, by measuring the imprint left by a distractor on perceptual processing.

Conclusions

Our aim was to shed light on the role of attention in serial dependence, by revealing the effects of attentional distractors, when they can or cannot be suppressed through location suppression. We found no evidence of positive serial dependence caused by distractor stimuli but some evidence of negative serial dependence. This result may provide a starting point for future research elucidating the perceptual consequences of attentional filtering and the fate of successfully suppressed stimulus features in the context of spatiotemporal continuity in vision.

Keywords: serial dependence, attentional suppression, spatial attention, distractor inhibition

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Paper II

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The role of secondary features in serial dependence

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Recent work indicates that visual features are processed in a serially dependent manner: The decision about a stimulus feature in the present is influenced by the features of stimuli seen in the past, leading to serial dependence. It remains unclear, however, under which conditions serial dependence is influenced by secondary features of the stimulus. Here, we investigate whether the color of a stimulus influences serial dependence in an orientation adjustment task. Observers viewed a sequence of oriented stimuli that randomly changed color (red or green) and reproduced the orientation of the last stimulus in the sequence. In addition, they had to either detect a certain color in the stimulus (Experiment 1) or discriminate the color of the stimulus (Experiment 2). We found that color does not influence serial dependence for orientation, and that observers were biased by previous orientations independently of changes or repetitions in the stimulus color. This occurred even when observers were explicitly asked to discriminate the stimuli based on their color. Together, our two experiments indicate that when the task involves a single elementary feature such as orientation, serial dependence is not modulated by changes in other features of the stimulus.

Introduction

In our everyday visual environment, we are constantly exposed to a myriad of visual features. A major challenge for the visual system is to represent the history of these features in a meaningful way (i.e., determining which feature corresponds to the same stimulus at different times). Recent work on serial dependence suggests that visual features are temporally combined over an extended region of time and space, in a way that promotes the continuity of feature processing (for a review, see Pascucci et al., 2023). This notion stems from evidence of serial dependence in almost any sort of visual task, where current decisions about a stimulus feature are biased toward the features of stimuli seen before (see Cicchini & Kristjánsson, 2015; Kiyonaga, Scimeca, Bliss, & Whitney, 2017). This systematic bias has often been related to the way perception combines sequential views and promotes the continuity of object representations (Fischer, Czoschke, Peters, Rahm, Kaiser, & Bledowski, 2020; Kiyonaga et al., 2017; Liberman, Zhang, & Whitney, 2016).

However, the extent to which serial dependence can be related to object processing remains unclear. The majority of studies have, indeed, focused on investigating serial dependence on a single dimension of stimuli, when only one feature changes such as orientation. Objects are, by definition, made of combinations of features that co-occur, maintain a constant relationship, and remain stable for a certain period of time (Treisman, 1996; Treisman & Schmidt, 1982).

But, results on the effects of varying multiple features in serial dependence have been quite mixed. For example, Fritsche and de Lange (2019) showed that the feature that causes serial dependence is the one that was attended to on the previous and current

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trial. When the size of a stimulus was attended on the preceding trial, the previous stimulus orientation had a reduced effect on current judgments about orientation (Fritsche & de Lange, 2019). Similarly, Collins (2021) showed that, when the relevant feature is the stimulus shape, changes in the stimulus orientation can reduce but not prevent serial dependence in size judgments. Additionally, when the task involves the orientation of the stimulus, and a secondary feature such as color or the pattern of the stimulus is completely irrelevant, changes in the secondary feature do not affect serial dependence (Ceylan, Herzog, & Pascucci, 2021; Huffman, Pratt, & Honey, 2017; Kim, Burr, Cicchini, & Alais, 2020). Other work suggests that, when a secondary feature (e.g., color) is relevant to the primary task (e.g., motion discrimination), serial dependence occurs for stimuli that share the secondary feature (Fischer et al., 2020). Moreover, when the task involves more complex stimuli, such as judgments about faces, which are defined by a combination of local features, serial dependence may occur at the object level and, therefore, for combinations of features (Collins, 2021; Liberman, Manassi, & Whitney, 2018).

Taken together, the above studies seem to suggest that the effect of a secondary feature on serial dependence is a function of the relevance of that feature for ongoing processing. When the secondary feature can be completely ignored it has no effect, or it may only modulate but not determine serial dependence. These findings seemingly complicate a clear picture of the relationship between serial dependence and object continuity, because objects maintain the relationship between their defining features (Pascucci et al., 2023). One possibility is that, in experimental settings, the explicit instructions to focus on a single feature encourage observers to ignore other aspects of the display, thus preventing binding of multiple features across perceptual episodes.

We investigated the role of an additional task that requires the processing and discrimination of a secondary feature in serial dependence. By having observers focus on both the primary and secondary features, we evaluated whether serial dependence would be modulated by the secondary feature, in a way consistent with object-based processing. We used a variant of a classic paradigm in which multiple stimuli are sequentially presented within a single trial and only the last stimulus is reported (i.e., a “sequential no-report” task) (Pascucci et al., 2023). This paradigm has previously been used to disentangle two forms of serial dependence: one induced by the stimulus, in the absence of behavioral report, and one induced by the last reported stimulus (Pascucci, Mancuso, Santandrea, Libera, Plomp, & Chelazzi, 2019; Pascucci & Plomp, 2021). This corresponds to measuring the effect of the last stimulus within the trial sequence (within-trial) and the effect of the stimulus reported before (between-trial), terminology that we will use to distinguish the two throughout the manuscript. The within-trial sequence had variable length and consisted of a series of Gabor stimuli with varying orientations and two possible colors, red or green. Observers performed two tasks. In Experiment 1, they had to reproduce the orientation of the last stimulus at the end of the sequence and quickly detect the occurrence of stimuli of the designated target color within the sequence (by pressing a key). The target color always corresponded to the color of the last Gabor. Hence, the color defined the target dimension for both the detection task and the orientation adjustment task. In Experiment 2, observers again reproduced the orientation of the last Gabor but discriminated between the color of each Gabor during the sequence. Hence, color was relevant for the discrimination task but irrelevant for the orientation task. Our main question was whether asking observers to actively use the color feature would modulate serial dependence in a way consistent with object-level processing—that is, only the orientation of stimuli possessing the same color would be subject to serial dependence. If this were the case, serial dependence would only be observed between stimuli of the same color, in both Experiments 1 and 2. Conversely, if serial dependence is totally independent of the secondary task, then the orientation of previous stimuli would induce a bias on current judgments independently of the color tasks and manipulations, in both experiments.

Our results revealed a more nuanced picture. In Experiment 1, serial dependence was modulated by color, but this most likely occurred because color cued the orientation to attend. In Experiment 2, where both colors were attended and not informative about the relevant orientation, serial dependence occurred completely independently of color. Furthermore, in both experiments, we found strong biases toward the orientation reported on the preceding trial, independently of the color and of the fact that many additional stimuli were shown within the current trial. We discuss these results in light of the role of attention, task relevance, and object processing in serial dependence.

Methods

Ethics statement

The study was performed in accordance with the requirements of the local ethics committee.

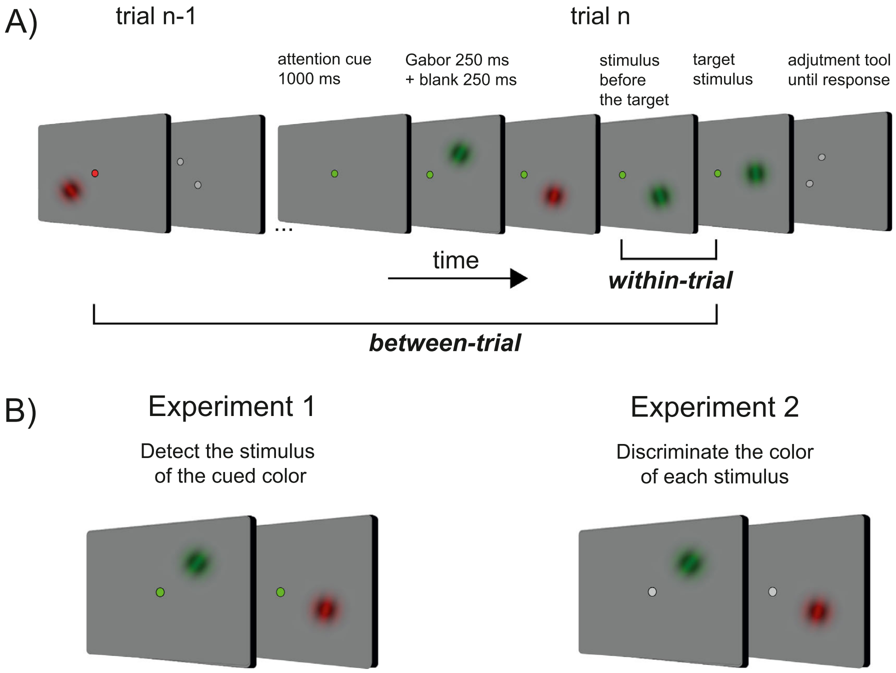

Figure 1. The paradigm and the main experimental manipulations (stimuli are not drawn to scale). **(A)** Each trial contained a sequence of oriented Gabors whose color (red or green) was randomly assigned. Observers were asked to perform a task during the sequence (see B) and to reproduce the orientation of the last stimulus when the sequence ended. The orientation reproduction was made by rotating an imaginary line connecting two dots. **(B)** In Experiment 1, the task during the sequence was to detect and quickly report the occurrence of a stimulus with the same color as the fixation dot. In Experiment 2, the task was to indicate whether the present stimulus was red or green by pressing two corresponding keys. The fixation dot had a neutral color in Experiment 2.

Apparatus

Stimuli were generated with custom-made scripts in MATLAB R2021a (MathWorks, Natick, MA) and the Psychophysics Toolbox (Brainard, 1997), and presented on a 24-inch monitor (resolution: 1920 × 1080 pixels, refresh rate: 60 Hz; Asus, Taipei, Taiwan), on a Windows-based machine (Microsoft, Redmond, CA). The experiment was performed in a quiet and dimly lit experimental booth, and participants were positioned approximately 57 cm from the computer screen.

Participants

Forty-one healthy human participants (age range, 18–52 years; nine females; 19 subjects in Experiment 1 and 22 in Experiment 2) from the University of Iceland took part in the study for a monetary reward (1500 ISK). Participants had normal or corrected-to-normal vision and were naïve as to the purpose of the experiments. Written informed consent was collected from all participants beforehand.

Stimuli and procedures

An example of a trial sequence in Experiments 1 and 2 is depicted in Figure 1. The experiments consisted of a series of trials containing a sequence of stimuli. Each trial started with a fixation dot shown for 1000 ms. A sequence of Gabors (peak contrast of 100%, spatial frequency of 0.75 cpd, and a Gaussian envelope of 25°) was then presented. Each Gabor was presented for 250 ms and followed by a 250-ms interstimulus interval. On a single trial, there could be 4, 6, or 8 Gabors, presented at random locations, with their center positioned on the circumference of an imaginary circle (radius of 8° from the fixation dot). The length of the sequence (4, 6, or 8) was randomly determined on each trial. The fixation dot remained on the screen for the entire duration of each trial, and its color varied between Experiments 1 and 2 (Figure 1B, and see below). The Gabors presented in a sequence were red or green, and the color was randomly determined. A response tool appeared at the locus of the fixation point 250 ms after the presentation of the last Gabor. The response tool consisted of two dark-gray dots positioned at the extremities of an imaginary line, and participants had to rotate the line to reproduce the perceived orientation of the last Gabor. The initial orientation of the response tool and the orientation of all of the Gabors were selected randomly, with the exception that the maximum orientation difference between Gabors in a single trial sequence was fixed at ±50°. Between trials, the orientation difference could vary within the whole ±90° angular range.

Before each experiment, participants were provided with written and verbal instructions, and they performed a sequence of practice trials under the supervision of the experimenter. Practice trials were not analyzed further. Both experiments were divided into 10 blocks of 20 trials and lasted approximately 1 hour. Participants were instructed to maintain their gaze at the center of the screen for the entire duration (breaks excluded). Participants were free to take breaks between each block. All stimuli were presented on a gray background (83.33 cd/m^2).

Experiment 1

Experiment 1 had 19 participants (four excluded, see below). In this experiment, the color of the fixation dot was red or green (Figure 1B). During the sequence of Gabors presented on each trial, participants had to press the “X” key as fast as possible whenever a Gabor of the same color as the fixation dot was detected (*target*), while ignoring (i.e., not responding to) Gabors of the irrelevant color (*non-target*). At the end of the sequence, they reproduced the orientation of the last seen Gabor with an adjustment response. The color of the last Gabor, at the end of the sequence, always matched the color of the fixation dot, so the last Gabor was always task relevant. Participants were informed at the beginning of the experiment that the fixation color also indicated the color of the stimuli relevant to the orientation adjustment task.

Experiment 2

Experiment 2 had 22 participants (six excluded, see below). In this experiment, the color of the fixation dot was gray and had no relationship with the relevant stimuli in the orientation task; therefore, all stimuli were task relevant. During the sequence, participants had to discriminate the color of each Gabor by pressing a related response key (“X” for red, “C” for green). At the end of the sequence, they reproduced the orientation of the last seen Gabor, which could equiprobably be red or green.

Data preprocessing

Outlier exclusion

Before the main analysis, trials were marked as outliers and removed in the following cases: (1) accuracy in the within-trial detection or discrimination tasks was lower than 50%, or (2) absolute adjustment errors were larger than 30° (Cicchini, Mikellidou, & Burr, 2018) or adjustment times were slower than 10 seconds. Trials at the beginning of each block were also removed, leading to a total proportion of trials removed of less than 9% for Experiment 1 and 12% for Experiment 2. For subject exclusion, we applied the following criteria: (1) more than 25% of their trials were marked as outliers, or (2) a value of circular correlation between the reported and presented orientation was lower than 0.5. Ten subjects were excluded based on these criteria (four in Experiment 1 and six in Experiment 2).

Orientation bias removal

Orientation space is not perceptually uniform, and notable biases have been documented (Appelle, 1972; Balikou et al., 2015; van Bergen & Jehee, 2019). This is particularly relevant for the analysis of serial dependence, and previous work has recommended corrections for these biases to avoid unwanted noise (Sheehan & Serences, 2023). To remove such biases, orientation adjustment responses were first demeaned and then residualized from oblique effects and orientation biases. Sinusoidal (Pascucci et al., 2019) or polynomial (Manassi, Liberman, Kosovicheva, Zhang, & Whitney, 2018; Rafiei, Hansmann-Roth, Whitney, Kristjánsson, & Chetverikov, 2021) fits have been used in previous work to capture systematic orientation biases, but there is no standard procedure. Here we used a nonlinear mixed model with fixed and random effects estimated on the whole group of subjects. We started from the assumption of a sinusoidal trend in orientation biases (Balikou et al., 2015; Pascucci et al., 2019; Sheehan & Serences, 2023; van Bergen & Jehee, 2019) and fitted a cumulative sum of sinusoidal functions with a frequency increase of one cycle. The model fitting proceeded with the recursive addition of sinusoids with increasing frequency (from one to six cycles over the 0°–180° orientation range), as both fixed and random effects. The resulting set of coefficients quantified the best-fit amplitude of each sinusoid at the population level (fixed effects) and individual level (random effects). At each step, we computed the circular correlation between the residuals of the model and the orientation variable. Sinusoidal functions with an estimated amplitude lower than 1 and providing only a negligible increase in correlation were then discarded. This resulted in the choice of four sinusoidal functions (one, two, four, and six cycles) to best model the orientation bias. The individual residuals obtained from this model were used for the rest of the analyses.

Statistical analysis of serial dependence

Following the approach of Barbosa and Compte (2020), we presented the average curves using folded errors, computed by multiplying trial-wise error by the sign of the trial-wise relative difference in orientations (Δ). The average folded errors were then plotted as a function of absolute values of Δ. For the serial dependence analyses, we used a single-trial, nonlinear, mixed-effects model following the same approach as in Pascucci et al. (2019). Briefly, individual and single-trial residualized adjustment errors were fitted to the first derivative of a Gaussian (δoG) function with amplitude (α) and width (w) as free parameters. In the *within-trial* analysis, we modeled serial dependence as a function of the inducer color—that is, whether the Gabor stimulus before the last one was of the *target* or *non-target* color. In doing so, the mixed-effects model included two δoG functions multiplied by a dummy variable coding for the condition (Pascucci et al., 2019), for a total of four parameters (two amplitudes and widths per condition). All parameters were included as fixed and random effects. The statistical significance of individual parameters and comparisons between parameters were computed employing t-tests and z-tests, respectively (Pascucci et al., 2019). A separate model with a similar structure was used in the analysis of *between-trial* serial dependence, with the dummy variable coding whether the color of the previously reported stimulus was the *target* as on the present trial or a *non-target*. In this latter analysis, responses following trials marked as outliers were also excluded. All mixed-effects models were estimated using *nlmefit.m* (with *fminunc* as the optimization function) from the Statistics and Machine Learning Toolbox (MATLAB R2021a). Initial parameter guesses were $\alpha = 2°$ and $w = 0.05$. Note that, even though the plots were made with smoothed and folded average errors for graphical purposes, the model fit and results were performed on single-trial errors; thus, the smoothing factor and folding procedure did not influence the model results.

Results

Experiment 1

Fifteen observers were presented with a sequence of four, six, or eight low-contrast Gabors on each trial. The Gabors were either green or red (randomly intermixed) and were presented briefly in the periphery of the visual field (see methods, and Figure 1A). Each trial started with a colored fixation dot that indicated the color of the *target* stimulus in the sequence, and the other color was designated the *non-target* stimulus.

Overall, participants performed the detection task with an accuracy of 98%, also showing strong inter-trial priming effects (Kristjánsson & Ásgeirsson, 2019): The detection rate increased when the color of the target stimulus was the same on two consecutive trials; for the same versus different color, $t(14) = -5.98$, 95% confidence interval $= -0.0248$ to -0.0117, $p < 0.001$ (see Figure 2A). This priming effect indicated that the memory of the target color on the previous trial persisted on the present trial.

Participants performed the orientation adjustment task with a standard deviation of errors of 8.36° ± 6.47° and an average adjustment time of 2.12 ± 1.04 seconds. The analysis of serial dependence focused on whether the last reported (*between-trial*) and last seen (*within-trial*) Gabor had the *target* or *non-target* color. In principle, if observers combine orientations depending on the stimulus color, then both within- and between-trial serial dependence should occur for stimuli of matching color, resembling the observed priming effect. Conversely, if the only feature that matters is the relevant orientation, then within-trial serial dependence should be induced by stimuli of the target color, because the target color indicates the relevant orientation, whereas between-trial serial dependence should be independent of color changes (e.g., a stimulus of a different color could be the target on the previous trial).

In the *within-trial* analysis, orientation adjustment responses showed the typical serial dependence pattern only when the previous stimulus had the *target* color (Figure 2A, within-trial, gray curve and line). In this condition, response errors were biased toward the orientation of the last seen Gabor, particularly when the difference in orientation between the previous and present stimulus (Δ) was small, leading to a significant half-amplitude of the δoG curve ($\alpha = 2.90°$, $p < 0.001$, two-tailed t-test of the nonlinear mixed-model parameter α against 0; see Methods). Conversely, previous stimuli with *non-target* colors produced no bias ($\alpha = 0.74°$, $p > 0.05$). The difference between *target* and *non-target* serial dependence was significant (*target* minus *non-target*, α difference $= 2.16°$, $p = 0.013$, z-test on the parameters' difference) (see Figure 2A).

In the *between-trial* analysis, however, the orientation reproduced on the last trial induced a strong bias on current responses, independently of whether the color attended on the previous trial was the *target* or *non-target* on the present trial (see Figure 2A). When the target color was the same on two consecutive trials, current responses were significantly biased toward the

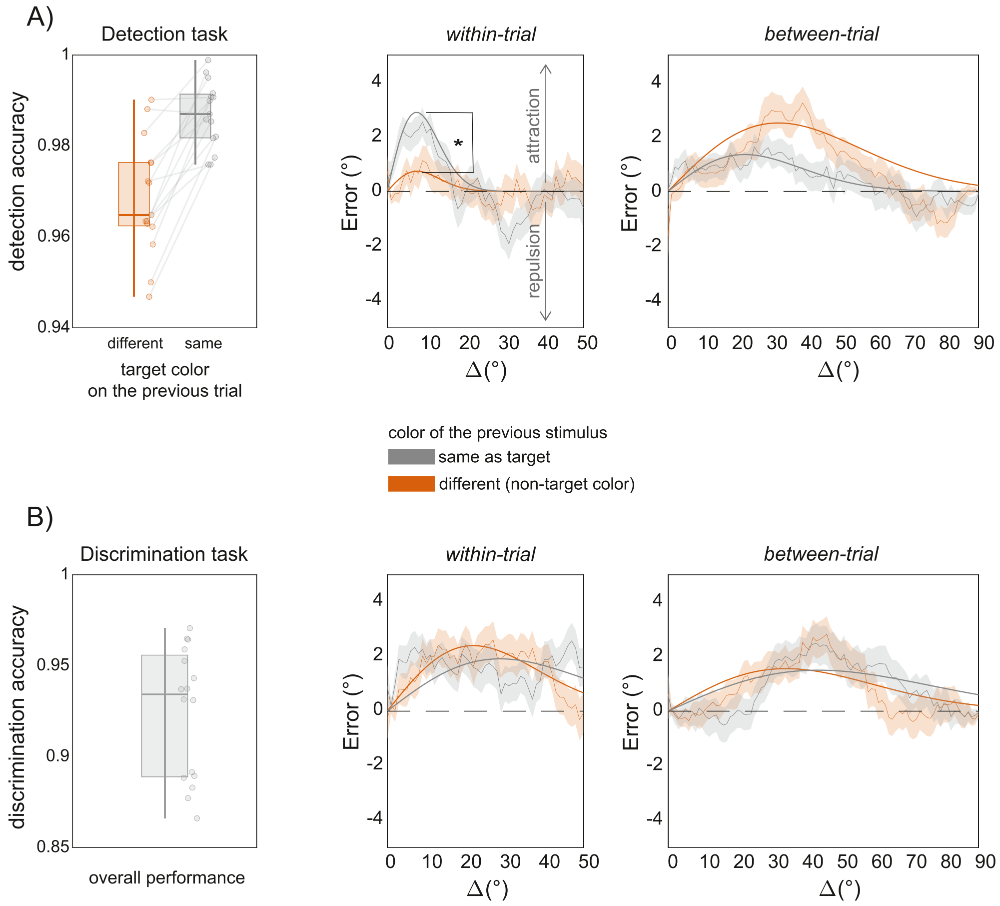

Figure 2. Main results of the two experiments. **(A)** In Experiment 1, observers detected the occurrence of Gabor stimuli with the *target* color indicated by the fixation dot, while ignoring stimuli of the *non-target* color. Performance on the detection task was strongly influenced by the repetition of the same target color—an intertrial-priming effect (left panel). *Within-trial* serial dependence was only evident when the previous stimulus in the trial sequence had the *target* color (i.e., the same color as the last stimulus to be reported), whereas *non-target* stimuli produced no effect (middle panel). *Between-trial* serial dependence occurred independently of the stimulus color (right panel). **(B)** In Experiment 2, observers discriminated the color of each stimulus in the sequence. Discrimination accuracy was well above chance (left panel). In this experiment, both *within-* and *between-trial* serial dependence were significant, independently of the color of the stimulus. Note that, in Experiment 2, *target* and *non-target* refer to whether or not the previous stimulus (within or between the trials) was of the same color as the one to be reported. Curves depict a running average ± 1 SD of adjustment errors over Δ (using a sliding window of 9° for the *within-trial* and 19° for the *between-trial* plots, for graphical purposes). Fitted lines depict the predictions of the best-fitting δoG for each condition.

previously reported orientation ($\alpha = 1.35°$, $p = 0.002$). The results were similar when the target color on the preceding trial was different from the current one, with a qualitatively larger serial dependence amplitude ($\alpha = 2.51°$, $p < 0.001$), which did not differ significantly across conditions (*target* minus *non-target*, α difference $= -1.15°$, $p = 0.103$).

Experiment 2

In Experiment 1, observers were biased by the orientation of the target color within-trial and by the orientation reported on the preceding trial, independently of the color. This finding may have two explanations. The first is that only relevant and attended stimuli cause orientation serial dependence, no matter the stimulus color. In this case, serial dependence was modulated by the target color during the sequence because the target color indicated the orientation to attend, but it was independent of the color between trials because stimuli of different colors could be targets on different trials. The second is that the effects measured within and between trials reflect different forms of serial dependence, one driven by the last stimulus (within-trial) and the other by the last report (between-trial). In this case, it is still possible that within-trial serial dependence was modulated by the stimulus color. However, because we did not test the bias in reproducing stimuli of the non-target color, the results cannot determine whether stimuli were combined depending on the color or simply because of the relevant orientation.

In Experiment 2, we therefore tested within-trial serial dependence for Gabors of both colors, making them both relevant to a discrimination task. Observers had to attend to all of the Gabors in the sequence and explicitly discriminate their color by means of a forced choice task (see Methods). If observers would combine orientation based on color, because the Gabors have to be discriminated by color, then serial dependence should only occur when the last stimulus within the trial sequence was of the same color as the one to be reported.

Sixteen observers performed the discrimination task with an overall accuracy of 92% and performed the orientation adjustment task with a standard deviation of errors of 9.47° ± 7.05° and an average adjustment time of 1.99 ± 0.99 seconds. As in Experiment 1, we considered serial dependence for *target* and *non-target* stimuli, as well as *within-* and *between-trial* effects. In the *within-trial* analysis, serial dependence was significant when the previous stimulus in the sequence had both the *target* color ($\alpha = 1.92°$, $p < 0.001$) and the *non-target* color ($\alpha = 2.40°$, $p < 0.001$), with no significant difference between the two ($p > 0.05$) (see Figure 2B). Similarly, in the *between-trial* analysis, the orientation of the stimulus reported on the previous trial induced systematic serial dependence, independently of whether the color of the stimulus reported on the previous and current trials was the same (*target* condition, $\alpha = 1.50°$, $p < 0.001$) or different (*non-target* condition, $\alpha = 1.56°$, $p < 0.001$; *target* vs. *non-target*: $p > 0.05$).

The results of Experiment 2 indicate that serial dependence for orientation is independent of changes in the stimulus color, even when observers are explicitly asked to discriminate two stimuli based on their color.

Discussion

We investigated the role of a secondary feature (color) in serial dependence for orientation. Previous research has reported no influence of a secondary feature (Ceylan et al., 2021; Kim et al., 2020), but, in these cases, the secondary feature was entirely irrelevant to the task. In contrast, we made the color feature relevant to the secondary task. In Experiment 1, observers performed a color-detection task where color also indicated the color of the relevant stimuli for the adjustment task. In Experiment 2, observers had to discriminate the color of each stimulus, but the color was not informative for the orientation adjustment task.

We hypothesized that, by explicitly asking observers to perform a task based on color, serial dependence in orientation would be affected by color, indicating that the two features were integrated, as in object-level representations. This would be even more likely to occur when observers had to discriminate the stimuli based on color. However, our two experiments confirmed previous findings showing that serial dependence in orientation is independent of changes in the stimulus color.

In Experiment 1, serial dependence was affected by the target color, but this is likely because the target color also indicated the orientation to attend during the trial sequence. Hence, stimuli that were attended to in the past were of the same color as the one tested for serial dependence. This is in line with many studies showing a clear role of attention in serial dependence, with the typical observation that previous stimuli induce a bias when they are attended to (Fischer & Whitney, 2014; Fritsche & de Lange, 2019; Pascucci et al., 2019). As mentioned, in Experiment 1, we did not test serial dependence for stimuli of the unattended color. This leaves open the possibility that within-trial serial dependence could occur separately for stimuli of both the target color and the non-target color.

The results of Experiment 2 then demonstrated that, when stimuli of both colors are relevant, serial dependence occurs independently of the stimulus color. That is, even though observers were asked to discriminate the stimulus color, the orientation of the previous stimulus within the trial caused a bias on the current response, completely independent of whether the color was the same or not. Adding to the results of Experiment 1, this finding supports the conclusion that serial dependence in orientation is largely unaffected by changes in other features.

In both experiments, we replicated serial dependence effects from stimuli reproduced far back in time and followed by an intervening sequence of new stimuli that are not reported (Pascucci et al., 2019; Pascucci & Plomp, 2021). There are two important observations to make regarding this finding. First, this and similar results may appear surprising because serial dependence is believed to be a function of time, and the last reported stimulus was far back in time, followed by several other intervening stimuli, and also considering to the typically large $n - 1$ effects reported in many studies. We believe that the sequential no-report paradigm used here and in previous works may isolate two different forms of serial dependence, one that is largely driven and strengthened by processes related to behavioral reports (e.g., memory, decision-making) and the other that is induced by the stimulus even in the absence of a report. These two forms of serial dependence may operate at different time scales and be differentially affected by the time interval and the number of intervening stimuli between the inducer and the test stimulus. The second observation is that, although previous work has typically reported repulsive biases within trials and attractive ones between trials (Pascucci et al., 2019; Pascucci & Plomp, 2021), we found attractive biases (or no effect) for both (see also Abreo, Gergen, Gupta, & Samaha, 2023). Although the nature of repulsive biases in these tasks is still a matter of debate (Pascucci et al., 2023), one potential explanation is that what determines whether repulsion or attraction is seen is the task relevance of the stimulus or the role it plays in the task (e.g., Rafiei, Chetverikov, Hansmann-Roth, & Kristjánsson, 2021; Rafiei, Hansmann-Roth, et al., 2021). In prior work where the stimuli in the trial sequence were not relevant for any additional task, observers may have expected the relevant stimulus later in the sequence and paid less attention to the rest, thus promoting repulsive effects. In the current work, the additional task may have increased the relevance and level of attention during the entire sequence. Although this remains a possibility, further work is needed to clarify the nature of repulsive and attractive biases in these particular paradigms.

The main aims and the manipulation type here are reminiscent of the literature on feature binding and integration. To perceive the continuity of objects, the brain must conjointly represent and bind together multiple visual features that lie close in space and time, combining multiple features to represent coherent objects (Treisman, 1996). There are several views on this topic. One view proposes that the integration of visual features is initiated automatically, driven by the mere co-occurrence of stimulus features, but is then strongly mediated by task context and attention (Hommel, 2004; see also Ho, Abel, Correa, Littman, Cohen, & Griffiths, 2022). In the "relevance filter" model (Bundesen, 1990; Norman, 1968), for example, individual features are weighted and integrated into persisting "object files" depending on their task relevance and the current attentional set (Hommel & Colzato, 2004). Although the relation between serial dependence and object processing is still not well understood (Pascucci et al., 2023), our results can be tentatively contextualized within this framework, suggesting that feature integration (e.g., of color and orientation) is largely mediated by task context (Fischer et al., 2020; Hommel, 2004) and is not revealed by simply adding a secondary feature in serial dependence tasks.

Recent work has, however, shown that in other conditions serial dependence can be influenced by contextual features and object-level information (Collins, 2021; Fischer et al., 2020). For example, Fischer and colleagues (2020) used a paradigm in which two clouds of moving dots with different colors were memorized at the same time. A post-cue indicated the color of the relevant clouds on each trial. In this paradigm, serial dependence in motion direction judgments occurred only when the post-cued color was the same on the previous and present trials. This suggests that, when feature binding is necessary to select between competing representations in working memory, serial dependence occurs at the level of integrated features. Similarly, when visual judgments involve complex aspects of objects, such as emotional expressions, that can only be extrapolated through the combination of elementary features, serial dependence occurs at the object level and for conjunctions of features (Collins, 2021). Hence, even if we explicitly asked observers to distinguish the stimuli based on a secondary feature, our paradigms may not have fulfilled the necessary conditions to observe serial dependence at the level of objects and integrated features.

We propose that our findings reflect an observer's tendency to use minimal but sufficiently detailed representations to perform a perceptual task—that is, the information that propagates from one trial to the next depends on the representation required by the task (Ceylan et al., 2021; Kwak & Curtis, 2022). Features such as orientation can be reduced to a compact and low-dimensional format that allows for the sparing of unnecessary perceptual and memory resources (e.g., the orientation of a stimulus can be represented as a tilted line, discarding other irrelevant features) (Kwak & Curtis, 2022). As a consequence, serial dependence in these and similar paradigms may operate mostly at the level of low-dimensional abstract "codes" that are independent of the object and the other features it contains (Ceylan et al., 2021). Although this might be beneficial in terms of resource optimization in everyday vision, where objects and features are truly continuous and temporally correlated, it prevents feature integration and leads to object-independent serial dependence when the relationship between objects and features is experimentally altered.

Keywords: serial dependence, sequential biases, object processing, attention

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Paper III

Object-based processing reduces feature-tuning in serial dependence

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Abstract

The brain relies on object-based representations to guide behavior, assuming that objects maintain their features over time. Here, we investigated how humans estimate changes in visual features within the same object versus a different one. Participants were presented with two rectangular objects and tasked with reproducing the orientation of a stimulus displayed at one end of either rectangle. Our findings revealed serial dependence, where participants' responses were biased towards the orientation of the preceding stimulus. This bias was most pronounced when the current and previous orientations were highly similar and inversely related to their spatial distance. Crucially, when spatial distance remained constant, object-based processing had a significant impact: Serial dependence was less sensitive to similar orientations when two consecutive stimuli occurred within the same object, demonstrating less precise feature tuning. We propose that object-based processing enhances the similarity of feature representations over time.

Introduction

Our perceptual system constantly faces a wealth of ambiguous and incomplete sensory data. To extract meaningful information, the brain relies on prior assumptions (Knill & Richards, 1996), such as the assumption that objects and their defining features maintain consistent physical properties and coherent behavior over time (Dong & Atick, 1995). Indeed, the brain has a remarkable ability to bind multiple features into objects (A. M. Treisman & Gelade, 1980) and use object-based representations to guide attention (A. Treisman, 1988), memory representations (Kahneman et al., 1992), and visual search (Egly et al., 1994). One key advantage of object-based representations is that they bypass the need for detailed reprocessing or integration of individual features at every moment.

But how does the visual system handle variations in object features? Recent research suggests that visual features are represented in a serially dependent way, with current stimuli judged as more similar to previous ones than they truly are (J. Fischer & Whitney, 2014; Pascucci et al., 2023). Serial dependence is typically stronger when 1) consecutive stimuli share a highly similar feature, and 2) when they occur at nearby locations, suggesting that feature similarity and space are key dimensions in the integration of prior and current stimuli (J. Fischer & Whitney, 2014; Manassi et al., 2023; Pascucci et al., 2023; Rafiei et al., 2021). Here, we investigate whether serial dependence is also tuned to object-based representations and influenced by changes in the objects to which visual features belong.

We combined an orientation adjustment task with a classic object-based attention paradigm (Egly et al., 1994). On randomly intermixed trials, an oriented Gabor appeared at one of four possible locations within two distinct rectangle objects (Figure 1). Participants were asked to reproduce the perceived orientation through an adjustment response. We then measured serial dependence —i.e., the bias in adjustment errors due to the stimulus shown on the preceding trial— as a function of the spatial distance between consecutive stimuli and of whether they appeared within the same or a different object. In line with prior work, we found clear spatial tuning, with serial dependence gradually decreasing as a function of the spatial distance. Crucially, serial dependence was more pronounced and less tuned to similar features when the stimuli appeared within the same compared to a different object, even if spatial distance was equal. These findings most likely reflect stronger priors for the continuity of visual features within the same object.

Results

Twenty-two observers were presented with a Gabor stimulus shown at one of four possible locations, randomly intermixed across trials. These locations corresponded to the four ends of two separate rectangles defining two distinct objects (Figure 1). Participants reproduced the perceived orientation by rotating a response tool (see Methods, average standard deviation of adjustment errors = 8.81° ± 1.03°, average adjustment times = 1.55 ± 0.2 s).

To quantify serial dependence, we fitted the first derivative of a Gaussian function (δoG) to predict the pattern of adjustment errors as a function of the difference (Δ) between the orientation shown on the previous and current trial (J. Fischer & Whitney, 2014; Pascucci et al., 2019), using the aggregated data for all observers (Ceylan et al., 2021; Fritsche et al., 2017; Houborg et al., 2023). The δoG has two main parameters: the half-amplitude α, quantifying the strength of serial dependence, and the width w, quantifying the tuning of serial dependence along the Δ variable, the inverse of w is reported below for easier interpretation (see Methods). Positive α values indicate that errors were attracted towards the previous orientation; smaller w values indicate that the bias mostly occurs for small Δ values (more 'feature tuning'), whereas larger w indicates broader serial dependence, extending to larger Δ values (less 'feature tuning').

First, we evaluated the effect of spatial distance, assessing serial dependence as a function of the physical distance between consecutive stimuli (0, 12, or 17°, see Figure 1). In line with prior work, serial dependence was largest when the stimulus appeared at the same location as on the preceding trial (0° distance, $\alpha = 2.03°$, $p_{\text{perm}} < .001$, $1/w = 41.66°$), and gradually decreased as the distance increased, becoming smallest when the current stimulus appeared at the farthest location from the previous one (17°, $\alpha = 0.66°$, $p_{\text{perm}} = 0.02$, $1/w = 32.26°$; same vs. far location: difference in $\alpha = 1.37$, $p_{\text{perm}} < .001$, difference $1/w = 9.4°$, $p_{\text{perm}} = .16$). A clear effect of distance was also evident when averaging the bias over the entire Δ range and fitting a linear model, predicting the bias as a function of spatial distance (effect of distance: $t(64) = -3.58$, $\beta = -0.11$, $p < .001$).

Second, we evaluated the effect of whether two stimuli occurred within the same or a different object at an equal spatial distance, that is, only considering trials in which the distance was 12° (see Methods). While the size of serial dependence was comparable (half-amplitudes: same object: $\alpha = 1.53°$, $p_{\text{perm}} < .001$; different object: $\alpha = 1.40°$, $p_{\text{perm}} < .001$; difference: $\alpha = 0.135°$, $p_{\text{perm}} = .34$), there was a significant difference in its tuning (width: same object: $w = 58.82°$; different object: $1/w = 29.41°$; difference: $1/w = -29.41°$, $p_{\text{perm}} = .01$).

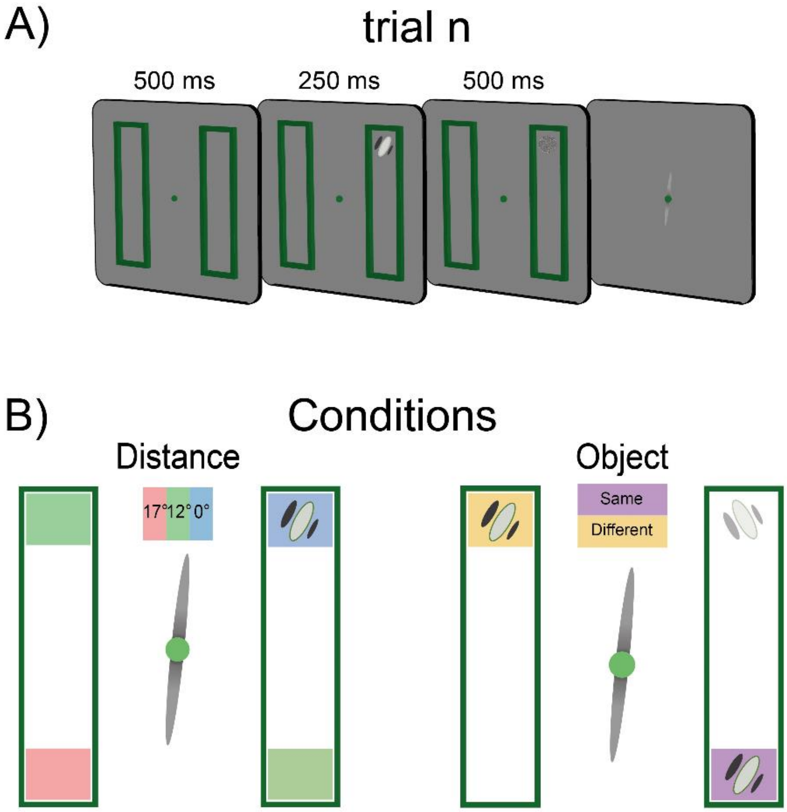

Figure 1. Paradigm and conditions. A) Each trial began with a fixation interval, after which a Gabor stimulus appeared at one of the four ends of two rectangle shapes, effectively defining two distinct objects. Subsequently, a noise mask was presented at the location of the Gabor, and participants were then tasked with reproducing the perceived orientation by adjusting a response bar displayed at screen center. B) The location of the Gabor stimulus was randomly determined on each trial, resulting in three different spatial distances between the current and prior stimuli. These distances included 0°, where the stimulus repeated at the same location (color-coded in blue); 12°, where the current stimulus appeared at an intermediate 'close' distance from the previous (color-coded in green); and 17°, where the stimulus appeared at a far distance from the previous (color-coded in red). Additionally, there were two 'objecthood' conditions. In one condition (color-coded in purple), the current stimulus could appear within the same rectangle object as the previous one. In the other condition (color-coded in yellow), the current stimulus could appear in a different object. It is important to note that when analyzing the effect of object-based processing, the spatial distance was kept constant by focusing solely on the two equidistant locations, as depicted in Panel B.

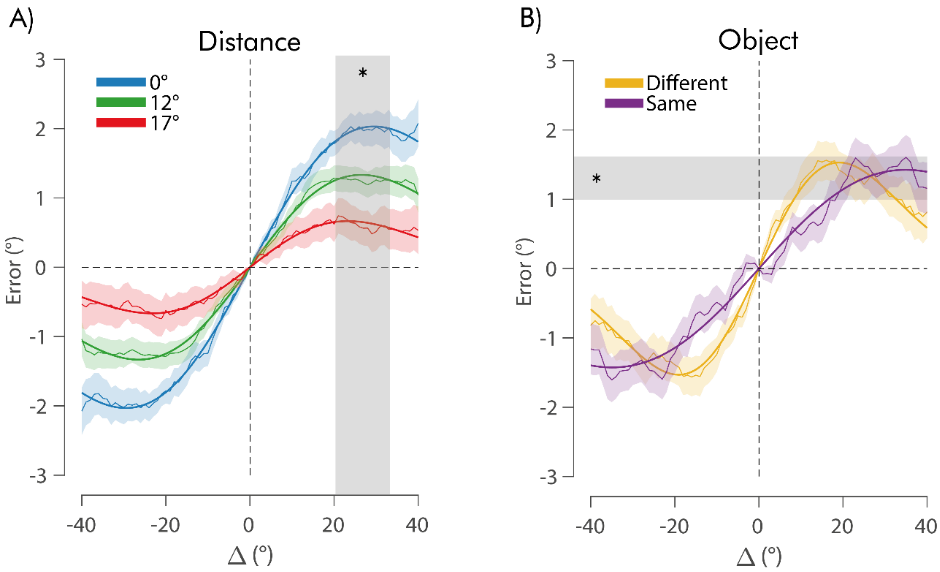

Figure 2. Results. A) Serial dependence as a function of the spatial distance between the current and the previous stimulus, with color coding consistent with Figure 1. The curves in this panel represent the group average data, including ±1 standard deviations of adjustment errors. These data are plotted as a function of the difference between the previous and current orientation (previous minus current, Δ) and have been smoothed using a running average with a sliding window of 27°. Additionally, fitted lines depict the predictions of the best-fitting δoG for each condition. Note that while the data are smoothed and folded for graphical purposes (as detailed in the Methods section), the fit itself was conducted on raw single-trial errors. B) Serial dependence as a function of whether the current and previous stimulus occurred within the same or a different object, with spatial distance being equal (color coding as in Figure 1).

Discussion

Our study demonstrates that serial dependence is not only influenced by the spatial distance between consecutive stimuli but also by object-based processing. Specifically, we observed a decrease in serial dependence in orientation judgments as the spatial distance between the current and prior stimulus increased, in line with prior work (Collins, 2019; J. Fischer & Whitney, 2014; Manassi et al., 2023). Importantly, when the stimulus reappeared within the same object, as opposed to a different object, serial dependence was less precisely tuned towards similar orientations.

Previous studies have explored aspects of serial dependence that could be linked to object processing (Ceylan et al., 2021; Collins, 2022; C. Fischer et al., 2020; Houborg et al., 2023; Liberman et al., 2016; Tanrikulu et al., 2023), but these studies involved paradigms with less direct tests of object-based effects, yielding seemingly contradictory results. For example, Liberman and colleagues (Liberman et al., 2016) associated serial dependence with object continuity, demonstrating a larger bias toward prior stimuli when the prior stimulus was in motion and subsequently occluded, but its trajectory remained coherent. Conversely, other studies have found serial dependence for basic features like orientation even when the object completely changed from one trial to the next (Ceylan et al., 2021; Houborg et al., 2023; Tanrikulu et al., 2023). However, none of these studies directly addressed whether serial dependence is tuned to object-based representations. Here, we tested a direct manipulation of object-based effects (Egly et al., 1994), finding a clear influence of object-based processing upon serial dependence.

When manipulating object-based representations, one might expect stronger serial dependence when a visual feature is expected to be part of the same object shown in the past compared to when the object changes, a hallmark of object continuity (Pascucci et al., 2023). However, our findings reveal a different pattern. Changes in features within the same objects tended to be underestimated, resulting in broader serial dependence effects. Even with marked orientation differences between current and prior stimuli, which typically lead to a reduction in attractive serial dependence or even a repulsive bias (Ceylan & Pascucci, 2023), the attractive effects of prior stimuli persisted. This suggests that objects influence internal priors related to temporal changes in visual features (Mamassian & Landy, 2001), leading to more widely tuned priors.

This finding poses challenges for conventional approaches to evaluating serial dependence, where the primary focus is on the peak of the bias, with the width considered as an additional metric for assessing how 'tuned' serial dependence is to visual features (Manassi et al., 2023). We demonstrate that larger peaks and narrower feature tuning do not necessarily indicate stronger integration of the present and the past. Object-based processing leads to reduced feature tuning, despite comparable serial dependence peaks.

In sum, serial dependence is typically assessed in terms of spatial and feature tuning (Manassi et al., 2023; Pascucci et al., 2023). Our research highlights the role of object-based processing in reducing feature tuning. We propose that these mechanisms reflect the brain's attempt to maintain stable representations of visual features within the same object, ultimately enhancing the perceived similarity between features of an object at consecutive moments.

Methods

Ethics statement

The study was performed in accordance with the requirements of the local ethics committee.

Apparatus

Stimuli were generated with custom-made scripts in Matlab (R2019b) and the Psychophysics Toolbox (Brainard, 1997), and presented on a 24-in Asus monitor (resolution: 1920 x 1080 pixels, refresh rate: 60 Hz), on a Windows-based machine. The experiment was performed in a quiet and dimly lit experimental booth and participants were positioned approximately 57 cm from the computer screen.

Participants

Twenty-two healthy human participants (age range of 21-39 years, 12 females) from the University of Iceland, voluntarily took part in the study. Participants had normal or corrected-to-normal vision and were naïve as to the purpose of the experiments. Written informed consent was collected from all participants beforehand.

Stimuli and procedures

An example of a trial and the main conditions are depicted in Figure 1. Each trial started with a green fixation dot shown at central fixation for 500 ms. Two green rectangle objects were shown with two possible configurations. In one configuration, the rectangles were horizontally oriented and placed above and below fixation. In the other configuration, the rectangles were vertically oriented and placed to the left and right of fixation. Each configuration was maintained for an entire block of trials, to promote an enduring representation of the two distinct objects. Rectangles were placed at 6° from the center in both configurations.

The relevant stimulus was a Gabor (peak Michelson contrast of 10%, spatial frequency of 0.33 cpd, and a Gaussian envelope of 25°), presented at one of the four ends of the rectangles, with the location randomly chosen on each trial (25% probability per location). The Gabor was presented for 250 ms and followed by a mask (a noise patch with peak Michelson contrast of 90%) presented for 500 ms on the same location. The fixation dot and rectangles remained on the screen for the duration of each trial. A response tool appeared at the location of the fixation point after the presentation of the noise patch. The response tool consisted of a dark grey bar that participants had to rotate to reproduce the perceived orientation of the Gabor. The initial orientation of the response tool, as well as the orientation of all the Gabors, were selected randomly, with the exception that the maximum orientation difference between current and previous Gabors was restricted to ± 40°.

Before the experiment, participants were provided with written and verbal instructions and performed twenty practice trials under the supervision of the experimenter. Practice trials were not analysed further. The experiment was divided into 4 blocks of 100 trials and lasted approximately 40 minutes. Participants were instructed to maintain their gaze on the fixation dot at the center of the screen for the entire duration (breaks excluded). Participants were free to take breaks between each block. All stimuli were presented on a grey background (83.33 cd/m^2).

Data preprocessing

Adjustment errors were computed as the angular difference between the reported and the actual orientation on each trial. Before the main analysis, trials were marked as outliers and removed in the following cases: 1) absolute adjustment errors were larger than 45°, or adjustment times were slower than 5 seconds or faster than 0.5 seconds. Trials at the beginning of each block were also removed, leading to a total proportion of trials removed of 3.4%. No subjects were excluded (we applied the following exclusion criteria: 1) more than 25% of trials were marked as outliers; 2) a value of circular correlation between the reported and presented orientation was lower than 0.5). In addition, adjustment errors were also demeaned to remove any systematic average bias, and cleaned from orientation biases by removing the fit of a six-cycle sinusoidal function (Balikou et al., 2015; Pascucci et al., 2019; Sheehan & Serences, 2023; van Bergen & Jehee, 2019). This latter step did not affect the results.

The serial dependence analyses are based on the relationship between adjustment errors and the relative difference between consecutive stimuli (previous minus current orientation, Δ). Following a similar approach to Barbosa & Compte, 2020, we presented the average curves with folded errors, computed by multiplying single-trial errors with Δ. Folded errors, when plotted over the original Δ, result in a symmetric pattern of bias.

To assess serial dependence, the aggregate single-trial residualized adjustment errors of all participants were fitted to the first derivative of a Gaussian (δoG) function, $y = \Delta\alpha wce^{-(w\Delta)^2}$, where Δ is the relative orientation of the previous stimulus, α is the half-amplitude quantifying the strength of serial dependence (i.e., the amount of deviation towards prior stimuli), w is the width parameter of the δoG curve, and c is the constant $\sqrt{2}/e^{-0.5}$ rescaling the α parameter to match the height of the positive peak of the curve (J. Fischer & Whitney, 2014). For ease of interpretation, we report the inverse of the parameter w as 1/w, which corresponds approximately to the width of the δoG in degrees.

We conducted separate δoG fits for each condition of interest, encompassing three conditions to investigate the influence of the spatial distance between previous and current stimuli (0, 12, 17°) and two conditions to investigate the impact of object-based processing (same vs. different, as illustrated in Figure 1). In the analysis specifically addressing object-based processing effects, we controlled for the effect of spatial distance. For this, we included only trials where the current and past stimuli were presented at an equal distance of 12°.

The statistical significance of individual parameters and comparisons between parameters were assessed with permutation statistics. To test serial dependence in each condition, distributions of α were obtained by randomly sampling the data 5000 times with replacement and fitting a δoG function. The mean of this α distribution was then compared to a surrogate null distribution where the sign of the adjustment error was randomly shuffled 5000 times (J. Fischer & Whitney, 2014; Fritsche et al., 2017). When comparing conditions, we tested for differences in both the α and w parameters using condition-level permutations, where the surrogate distribution was built by randomly shuffling the condition labels 5000 times. While the plots were smoothed (using a sliding circular average with a window size of 27°) using folded average errors for graphical purposes, the δoG was fit on single-trial errors without folding or averaging.

To test the spatial distance effect in a more graded manner, we computed an overall measure of the bias for each participant and spatial distance. In this analysis, serial dependence was calculated by averaging each participant's error over the entire delta range (± 40°). Errors were first averaged for the positive and the negative range, then the average error in the positive range was subtracted from the negative, leading to a 'bias' estimate, positive values indicating attraction and negative indicating repulsion (Ceylan et al., 2021; Samaha et al., 2019). To analyze this 'bias' estimate, we employed a linear mixed-effects model. This model incorporated both the intercept and spatial distance as fixed effects, with participants treated as a random effect.

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