Attractive and repulsive serial biases in visual cognition

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Abstract

Our eyes are the primary gates to the visible world around us. Yet, whatever we perceive involves a translation of the patterns of the photons hitting our retinas into mental representations. It could be argued that visual perception is merely an interpretation of the physical world, which raises the question of how reliable this translator is. Fischer and Whitney (2014) found that the perception of an oriented Gabor patch was influenced by the orientation of previously presented Gabor patches, a phenomenon that they called serial dependence. They argued that serial dependence reflects the visual system's assumptions about continuity: The visual world around us is generally constant from moment to moment and does not suddenly change despite large changes in viewpoint, occlusion or lighting conditions. Our perceptual systems employ this predictability to overcome potential perceptual noise and maintain perceptual stability. Subsequent research has revealed that the perception of a variety of other features, including shape, motion coherence, numerosity, facial identity, and even stimulus ensembles, is systematically biased toward recent information. Almost all of the studies mentioned above involved paradigms where the stimuli causing the serial dependence (the inducers) were attended, and therefore do not address whether items that we ignore can cause serial dependence biases. In the papers in this thesis, we studied the role of the to-be-ignored items in forming biases in our perceptual decisions. In Paper I here, we used a visual search for an oddly oriented line among distractors to demonstrate that the to-be-ignored items can form serial dependence in perceptual decisions in addition to the attended inducer. Notably, the repulsive bias occurs even when the distractors and targets are remarkably dissimilar, which distinguishes this from the well-known tilt illusion and tilt adaptation. Furthermore, our results demonstrate that explicit reports of stimulus features are not required for serial dependence. The findings in Paper I suggest that perception accounts for both attended and ignored stimuli in preserving the visual world's continuity to a greater extent than previously thought. In Paper II we demonstrated that visual search can result in serial-dependence biases in the perceived orientation of a stimulus that is unrelated to the search task. Our findings also revealed that both attention and similarity between the search stimuli (distractors and targets) and the test item play a significant role in forming serial dependence in perceptual decisions. Finally, our findings in Paper III demonstrated that similar biases to those reported in Papers I and II can occur from a single inducer line upon a set of test lines as previously observed from a set of lines upon a single test line. Secondly Paper III shows that when the inducer is similar to the test, it produces an attractive bias, but it creates a repulsive bias when these items are dissimilar. This means that the inducer creates opposing biases based on the similarity of the perceptual history content to the current stimulus. These attractive and repulsive biases can occur simultaneously when more than one test item is present. Overall, our results show that attention and proximity in feature space play a crucial role in shaping serial dependence biases. We showed that biases introduced by attended versus ignored visual search items (targets and distractors) influenced the general perceptual decisions, and furthermore, we showed that even attended items can produce repulsive biases in perceptual decisions.

Keywords:

Serial dependence, Decisional bias, Visual search, History effect, Perceptual bias.

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Contents

List of abbreviations

2AFC = Two-alternative forced choice

ANOVA = Analysis of variance

B.C. = Before christ

BF = Bayes factor

BRMS = Bayesian regression models using 'Stan'

D = Distractor

Deg = Degree

DoG = Derivative of gaussian

Exp = Experiment

FDL = Feature distribution learning

Fig = Figure

HPDI = Highest posterior density interval

Log = Logarithm

M = Mean

MS = Millisecond

PrevT = Previous target

RT = Response time

SD = Serial dependence

SD = Standard deviation

T = Target

TAE = Tilt aftereffect

VWM = Visual working memory

WAIC = Widely applicable information criterion

List of figures

Original number of figures in papers has been changed in the thesis.

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**-**III**):

I: Rafiei, M., Hansmann-Roth, S., Whitney, D., Kristjánsson, A., & Chetverikov, A. (2021a). Optimizing perception: Attended and ignored stimuli create opposing perceptual biases. *Attention, Perception, & Psychophysics, 83,* 1230–1239. https://doi.org/10.3758/s13414-020-02030-1

II: Rafiei, M., Chetverikov, A., Hansmann-Roth, S., & Kristjánsson, Á. (2021b). You see what you look for: Targets and distractors in visual search can cause opposing serial dependencies. *Journal of vision*, 21(10), 3. https://doi.org/10.1167/jov.21.10.3

III: Rafiei, M., Chetverikov, A., Hansmann-Roth, S., & Kristjánsson, Á. (Submitted) The influence of the tested item on serial dependence.

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Declaration of contribution

Mohsen Rafiei designed the experiments, collected the data, analyzed the data, and wrote the papers and thesis.

Árni Kristjánsson, Andrey Chetverikov, and Sabrina Hansmann-Roth helped design the experiment, analyze the data, and write the papers and thesis.

1 Introduction

We see the world around us through our eyes that are part of a sensory system that receives sensory input (light) and transmits this information to the brain. But what happens in our brain during this transition from light to perception? Do we see the visual world around us as it is, or does what we see from moment to involve a distorted version of reality? There is, in fact good evidence that our visual system presents to us an interpreted version of reality, where unconscious assumptions about the world are made, as in Helmholtz' famous proposal of unconscious inference (von Helmholtz, 1867). This idea can, in fact, be traced back to Plato, through the Arab scientist Alhazen, and Immanuel Kant's concept that our perceived world is strongly influenced by native mechanisms that influence the interpretation of reality (see Palmer, 1999 for a review).

Our understanding of vision has evolved over the ages. A comprehensive theory of vision must describe how information flows between the viewer and the perceived item. Early theories of vision from philosphers in ancient Greece advanced three distinct perspectives on this subject. According to one school of thought, the eye projects rays onto objects, which provide information about their low-level visual features such as color and shape to the observer, so-called extra-mission theories. These rays were assumed to travel out from the eyeballs and into the world, collecting information about the objects they encounter (Palmer, 1999). Among the most well-known proponents of this viewpoint were the Pythagoreans (followers of Pythagoras' philosophical and theological philosophy). According to another school of thought, sight is dependent on an interaction between emitted images from the eye and the rays from the sun with input from the perceiver's intellect (or soul), Socrates and Plato are two of the most well-known advocates of this theory (Lindberg, 1967). Finally, a third school of thought maintained that when humans perceive, they make physical contact with the items they see or with duplicates of those objects (so-called intromission theories). Democritus, a Greek philosopher from the fifth century B.C., held the belief that objects in the world emit copies of themselves, that he called *Eidola* (singular: eidolon). Eidola are constantly emitted by everything in the universe. According to this view, these replicas of the original are projected towards the observer and land on their eyes. According to this theory, you can only perceive a thing if one of its eidola has found its way into your eye. Several findings were assumed to support this idea, such as when someone can see their reflection in water or a mirror, this was said to prove that they are themselves emitting eidola (Palmer, 1999).

For a long time, two competing intromission theories about vision sought to explain how we see things: one proposed that objects released copies of themselves (Democritus' eidola theory), in contrast, the other suggested that vision was dependent on light rays emitted by the sun, reflected from the objects to the eyes (Palmer, 1999). Abu Ali Mohammed Ibn Al Hasn Ibn Al Haytham, also known as Alhazen, was a brilliant medieval researcher who developed remarkably modern ideas of light and vision and was a starch supporter of the intromission theory of vision and assumed that light rays from the sun enter the eyes and are then interpreted. Alhazen employed approaches to answering questions about perception that are remarkably similar to the ones currently being used (Lindberg, 1967). Aristotle's theories had been transmitted from generation to generation, but Alhazen insisted on testing them out for himself instead of depending on what he had been taught. He investigated for example, the aftereffects of staring at bright objects for long periods of time. Furthermore, he showed how objects that seem to be visible in certain lighting conditions could become invisible in other conditions. Alhazen published one of the greatest works on visual perception; his *Optics* published in 1039 was remarkable both in approach to the problem of understanding vision and in the approach taken to answer these questions.

Alhazen's approach to vision may certainly be called what many years later became known as (cognitive) *constructivism* (Palmer, 1999). One interpretation of constructivism as applied to visual perception has had a significant influence on the development of perception theory and concepts. This approach assumes that incoming sensory information is cognitively interpreted and that the brain *constructs* the visual world. The construction involves the combination of visual input through the eye and input from multiple sources such as previous knowledge and experiences, and innate interpretation processes. According to this approach, higher-order thinking or cognitive processing is critical for perception to work correctly. Perception involves more than the direct stimulation from the incoming light rays. It is comparable to inferential reasoning in that perception extends beyond sensory information, which is often distorted and ambiguous. Individuals generate and test several theories, which are composed of three factors: Sensory input or data (what is sensed), followed by former knowledge (what is kept in memory), and last, a mental process for perceptual inference. Perception is a fundamental notion that occurs due to sensory data being processed by brain activity (Gordon, 2004). According to constructivism, humans make (mostly) accurate inferences about visual sensations as a result of unconscious assumptions that reflect how the brain automatically combines data from various disparate sources, resulting in perception. Successful perception needs cognitive processes integrating thought, intelligence, and information from the visual senses with previous experience (Gordon, 2004).

The constructivist philosophy is often attributed to Hermann von Helmholtz. Helmholtz's *Physiological Optics* is undoubtedly a landmark in the field, but credit must be given to Alhazen, who proposed similar ideas more than 800 years before Helmholtz. Constructivism involves the assumption that people perceive things in ways that go beyond simply registering sensations and that other experiences and stimulation have an effect on perception (Gordon, 2004). Helmholtz suggested that there must be constructive transition mechanisms connecting sensing and perception. It is believed that perception occurs as a result of indirect, inferential processes. Rock (1983) expanded on Helmholtz's core philosophy by claiming that the perceptual system understands visual stimuli through inference. He even proposed that reasoning may have originated from perception. According to Palmer (1999) the constructivist model for visual perception is currently the dominant theory of visual perception. But what is the nature of the algorithms and tricks that the visual system uses to construct the visual world? While this question will not be comprehensively answered here, I will focus on one aspect of this construction that has received a lot of interest in recent years, which is how the visual system uses perceptual information from the recent past to predict the present state of the world.

Recent studies in visual perception have shown that our previous experiences strongly influence what we see, and that the ways in which these interpretative processes operate are therefore strongly influenced by our previous perceptions. These studies indicate that our visual system is not a passive recipient of sensory information but that perception involves an interpretation of the visual input, involving a combination of the perceiver's expectations, prior knowledge, and the information available in the stimulus itself. For example, Richard Gregory (1970), argued for a “top-down” theory of perception, arguing that perception is constructive and depends highly on top-down interpretative processing to make sense of new information. Gregory’s approach is mostly synonymous with the constructivist theory of perception, discussed above. He argued that sensory information alone cannot, on its own be the sole source of input for perceptual processing. He claimed that much of the sensory inputs would be missed due to external and internal noise in our cognition. He argued that we use the contextual knowledge from preceding information and experiences to enhance our perceptual processes and help us construct a meaningful and understandable picture of the environment from the massive visual input.

In fact, by adopting a top-down processing strategy to interpret new information, instead of draining vast amounts of energy to perceive each sensory input individually, we can combine our new incoming information with preceding knowledge and past experiences to make decisions about them and shape our perception into a more optimized form. In another influential approach, David Marr (1980) considered vision as a problem-solving exercise. While mapping brightness is a bottom-up process, he asserted that at the level of the first primal sketch, we also consider hidden patterns of field organization, even though most of this process is still mostly stimulus-driven. Another influential theorist, Irvin Rock also considered perception as the result of an unconscious inference process, problem solving, and the construction of structural representations of the surrounding environment (Rock, 1983) In this way, the brain can draw on pre-existing information to construct the visual world instead of having to make sense of the momentary input, afresh, at any given time.

According to the top-down processing model of perception, the brain adapts and incorporates prior knowledge with the visual input to create a reasonable hypothesis about a new stimulus without the need to evaluate its every single characteristic. Therefore, top-down processing involves integrating information coming from our senses with contextual information from items we already know or have experienced previously to comprehend new information. Overall, based on the top-down model of perception, what we perceive is derived from individual frameworks that assist us in perceiving and evaluating information; these frameworks are usually built on our previous experiences, prior knowledge, emotions, expectations, and perceptual history (Rauss and Pourtois, 2013) in addition to the way evolution has molded our interpretations of the environment (e.g. Pinker, 1997).

But, in what way does this previous information interact with our current perceptions? A very influential study by Fischer and Whitney (2014) showed that our perception is partially determined by what we have seen in the recent past (inducers); their results revealed that after observing an oriented line, the orientation of the following line was biased toward the inducer orientation. Hence, biases produced by preceding stimuli play a crucial role in forming our current perception. In their study, they presented an oriented Gabor and once it disappeared, they instructed the participants to adjust a response bar to report the observed Gabor orientation. Stimuli were displayed on the screen for 500 milliseconds and separated by approximately five seconds in time. While subjects' error patterns indicated that responses were consistently centered on the observed orientations throughout the experiment, on a trial-by-trial basis, the reported orientation was typically skewed in the direction of the orientation observed on the preceding trial. For example, when the Gabor on the prior trial was orientated more clockwise than the Gabor on the current trial, respondents judged the current Gabor to be slanted more clockwise than its true orientation.

Further research has revealed that the perception of a variety of other features, such as shape (Manassi, Kristjánsson & Whitney, 2019), numerosity (Fornaciai & Park, 2018), eye gaze (Alais, Kong, Palmer, and Clifford, 2018), motion coherence (Suarez-Pinilla, Seth, & Roseboom, 2018), facial identity (Liberman, Fischer & Whitney, 2014) or even emotional expressions (Libermann, Manassi, & Whitney, 2018) are all serially dependent on perceptual history.

This begs the question of what the usefulness of such biases in perception that do not provide a correct picture of our environment might be, at first glance, these biases appear to be design flaws rather than examples of practical engineering because they deviate from logic and accuracy requirements. But do they serve an adaptive purpose? To answer this question, we first need to discuss different types of biases from perceptual history. In the following paragraphs, some of the most important types of biases from history will be discussed in detail.

1.1 Aftereffects

Biases are not all misleading, or to put this more plainly, these biases can serve evolutionary functions, such as assisting humans in making faster decisions. In fact, we process a large amount of data every day, and in moments of crisis with high emotions and stakes, we might experience cognitive overload. Through compartmentalizing and generalizing, complex concepts are more manageable and provide stability in times of danger, stress, and anxiety.

One of the most well-known types of biases in perception, the visual aftereffects are the systematic changes in the perception of visual stimuli after adapting to a previous stimulus (Gibson and Radner, 1937). In the following paragraphs, various types of aftereffects will be discussed.

1.1.1 Motion Aftereffect

The motion aftereffect refers to a strong illusion of visual motion caused by exposure to a moving image (Anstis et al., 1998; Mather et al., 2008). To illustrate, if you stare at a waterfall for a while without shifting your gaze and later look at stationary rocks next to the waterfall, the rocks appear to be moving slightly in the opposite direction to the water in the waterfall. There is physiological evidence showing how this occurs: Barlow and Hill (1963) reported adaptation-induced changes in the response of individual cells in the rabbit retina. Subsequent findings of adaptation effects in animal models have supported the idea that the origin of the motion aftereffect is probably adaptation in motion-selective cells in the early visual cortex; in fact, neural adaptation occurs when neurons that code for a particular movement decrease their response rates over time when exposed to a constantly moving stimulus. Additionally, neural adaptation lowers these neurons' spontaneous, baseline activity while responding to stationary input (Srinivasan & Dvorak, 1979; Glasser, Tsui, Pack, & Tadin, 2011).

Indeed, cortical neurons in visual regions are adapted to detect and comprehend distinct directions of motion, such that some neurons are only sensitive to upwards motion while others are responsive to downward motion. However, when we observe a stationary item, the responses of neurons sensitive to different directions are usually balanced, or they cancel out, and hence we perceive the item as stationary. Therefore, motion signals arise as a result of competitive interactions among neurons outputs even though there is actually no motion in the visual input.

1.1.2 Tilt Aftereffect

The tilt aftereffect (see illustration in Figure 1) is defined as a visual illusion in which, after watching an oriented stimulus for a long time, the perceived orientations of subsequently presented oriented stimuli are changed (Mitchell and Muir 1976; Magnussen and Johnsen 1986; He and MacLeod 2001) so that they are perceived as being tilted away from the adapting stimulus. Neural models of the tilt aftereffect have argued that the aftereffect reflects the suppression of the response of neurons tuned to the previously observed orientation (Coltheart, 1971; Wainwright, 1999; Clifford et al., 2000). Accordingly, the tilt aftereffect represents the visual system's continuous recalibration to optimize our ability to distinguish visual input (Clifford et al., 2000; Krekelberg et al., 2006; Kohn, 2007; Kristjánsson, 2011).

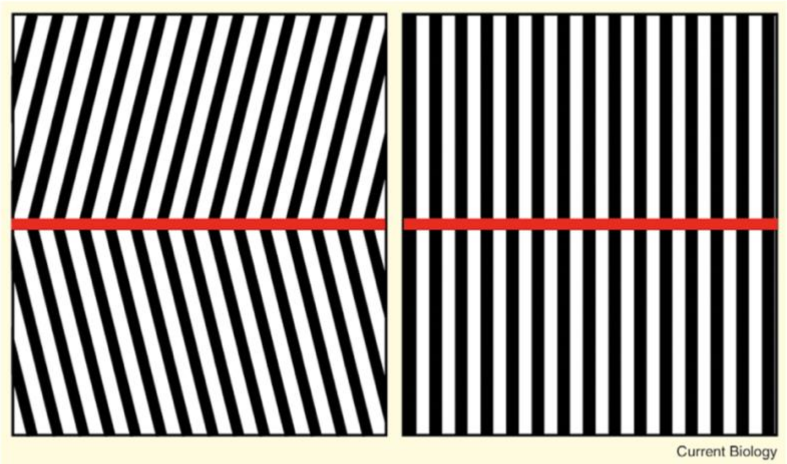

Figure 1. Illustration of the tilt aftereffect (TAE). After prolonged inspection of the left grating pattern, the perceived orientation of the grating on the right side of the illustration can appear tilted away from the orientation of the grating in the left side of the illustration. Image reproduced from Thompson and Burr (2009).

1.1.3 Negative and Positive Afterimages

As the name suggests, an afterimage is a perception that remains in our visual system after prolonged exposure to a certain image that has disappeared, and it can both be negative or positive (Virsu and Laurinen, 1977; Suzuki and Grabowecky, 2003; Tsuchiya and Koch, 2005). For example, in one example of a negative aftereffect, rods and cones in the retina become desensitized when overstimulated (see Figure 2). Those cells that process the brightest part of the image show the strongest desensitization. In contrast, those that are exposed to the darkest part of the image have the weakest one, and when you look away, the cells that are the least depleted react the strongest, and vice versa, resulting in an image with opposite brightness (see Figure 2). For example, if you see a red image for a long time, you will observe a green afterimage. On the other hand, when you see an image with the same colors as the original, it is called a positive afterimage (Virsu and Laurinen, 1977). Positive afterimages, unlike negative afterimages, are thought to occur when your rods and cones do not receive any stimulation, such as when the lights suddenly go off.

Figure 2. Negative afterimage. After looking at the cross-point for a while and later shifting eyes to a white backgrounded image, the inverse of this image should be visible. Image reproduced from Thakkar et al. (2019).

Overall, aftereffects are a group of events that influence how our nervous system operates. Aftereffects all involve a decaying time-course following the inducing stimulus (they gradually fade away, in other words). They are produced by presenting a particular type of stimulus for an extended period, and after that, perception of the already observed stimulus is distorted. Studying these aftereffects in visual perception can help us build up a picture of our brain's internal structure, and in fact aftereffects have been called the psychophysicists' electrode (Frisby, 1979), since they can provide us with insight about the operational principles of perceptual neurons. However, the aftereffects are not the only phenomenon that affects our perception based on our previous experiences; in the following paragraphs, history effects known as priming, will be discussed.

1.2 Priming

The priming effect is an implicit memory phenomenon in which one's response to a stimulus is influenced by previous stimulus exposure (Kahneman and Tversky, 2013). In other words, if you have previously been exposed to a visual object, you will process it more quickly and easily when you see it again, regardless of whether you remember seeing it previously. This process, known as 'priming,' indicates that earlier knowledge or exposure to an object alters its representation in the brain (Kristjánsson and Campana, 2010). Priming is typically considered to be an example of implicit memory (Schacter & Buckner, 1998). Studies have shown that displaying a priming stimulus for a short period of time produces positive priming; on the other hand, presenting the same stimulus for a more extended period of time might introduce negative priming effects upon perception. (Zago and Lacquaniti, 2005; Faivre and Kouider, 2011; Miyoshi and Ashida, 2014). There are numerous examples of how priming works. For example, seeing the word "red" will elicit a faster response to the term "rose" than unrelated words such as "lamp". People react faster when the second word is shown because red and rose are more closely linked in memory. In the following paragraphs, I will discuss different types of priming.

1.2.1 Negative priming

Negative priming is a phenomenon that increases the reaction times and the error rates when observers have to respond to a stimulus that had to be ignored previously or was presented for a while (Tipper, 1985; Miyoshi and Ashida, 2014). The earliest systematic investigations into this phenomenon were probably conducted by Dalrymple-Alford and Budayr (1966). Negative priming investigations suggest that there are two different types of cognitive processes linked with the negative priming phenomenon. The first is inhibition because previously ignored stimuli tend to be cognitively represented as "blocked" and irrelevant to the task that we are engaged with at a given moment; therefore, it takes longer for the brain to recognize them or react to them. The second process involved is an erroneous recall of memory since the ignored stimuli are still linked to the memory of how to behave when encountered; our memory systems are inclined to ignore these stimuli.

As an example of negative priming, in Experiment 1 in Tipper (1985) a prime display with two overlaid objects was presented. Later, a probe display including an item to be named was displayed on the screen. When the ignored item in the first display was similar to the succeeding probe, naming latencies were longer than otherwise; this phenomenon has been referred to as negative priming.

1.2.2 Positive priming

Positive repetition priming is a phenomenon in which the presence of an item facilitates the processing of the same item on successive presentations. Positive repetition priming is characterized by faster and less error-prone responses to previously presented stimuli when compared to novel stimuli. According to the positive priming literature, positive priming has two main components: short-term and long-term components. The short-term component is obvious in the masked form priming paradigm, in which the prime is exhibited very briefly before a mask and immediately followed by a target probe, rendering it unidentifiable. Forster and Davis (1984) argued that positive priming causes the prime and target to be combined into a unified representation and they also showed that priming would disappear when more than a few intervening items appear between the prime and the target. On the other hand, positive priming can be long-lasting when the prime and target are viewed as independent occurrences.

1.2.3 Attentional priming

In a recent review, Kristjánsson and Ásgeirsson (2019) argued that humans have a memory system for attention deployments that enables rapid reallocation of visual attention to previously presented stimuli, an argument originally introduced by Kristjánsson & Nakayama (2003). A prime example of such effects was demonstrated by Maljkovic and Nakayama (1994), who showed in their investigations of “priming of pop-out” that when observers searched for a uniquely colored diamond (unpredictably either red or green) between 2 other diamonds of a different color, and performed a discrimination on the target diamond, their responses were faster when the color or location of the target was repeated. Among other things, attentional priming may play an essential role in what has been referred to as top-down effects.

Theeuwes and van der Burg (2011) provide a good example of how priming can account for top-down guidance. In their study (2011), observers were instructed to search for one of two color singletons and to report the orientation of a line segment included within the segment (cued by a word). The line orientation segment inside the target singleton could be congruent (both horizontal) or incongruent (one horizontal and one vertical), depending on the orientation of the line segment inside the opposite color distractor singleton. Their findings demonstrated that when two similarly salient singletons are simultaneously present in the visual field, a top-down attentional set cannot adjust the attentional weights so that observers attend exclusively to the target singleton without interference from the distractor singleton. These attentional weights can be adjusted only through automatic intertrial priming, which is not a top-down controllable process.

On the other hand, the findings of Ásgeirsson and Kristjánsson (2019) cast some doubt on the argument that priming can comprehensively explain the top-down effects in visual search. Observers were asked to indicate the orientation of the bar inside the target circle after being given either a colored circle or a color word as a cue. The study's major goal was to see if there was a congruence effect between the bars in the target and the irrelevant distractor. Their findings contradict the results of Theeuwes, and van der Burg's discussed above. In fact, their results cast doubt upon the idea that priming effects are able to explain top-down effects in visual search. Ásgeirsson and Kristjánsson discussed that priming effects are mostly featural, while they can sometimes be episodic.

All in all, priming is one type of bias in our perceptual system whereby exposure to a stimulus will affect responses (reaction time and accuracy) to a following stimulus. Moreover, interestingly, priming can occur in various scenarios, including perceptual, conceptual, repetitive, contextual.

1.3 Serial dependence

So far, we have discussed various types of history effects, including aftereffects and priming. In the following paragraphs, we will discuss another type of biases in perception and perceptual decisions that helps us filter out the noise in our sensory inputs by biasing our perceptual decision based on what we have seen in the recent past. In 2014, Fischer and Whitney revealed that the perception of an oriented line was biased towards the orientation of previously presented stimuli, an effect they called serial dependence (SD). They used the design depicted in Figure 3, and their results showed that after showing a Gabor to participants (inducer), the perception of a test Gabor that followed it was biased towards the inducer. They discussed that their results indicated that such SD results from a spatio-temporal integration window (the continuity field) which operates as a spatiotemporally tuned, orientation-selective operator, where recently seen items interact with the perception of current stimuli so that what is perceived involves a combination of the two.

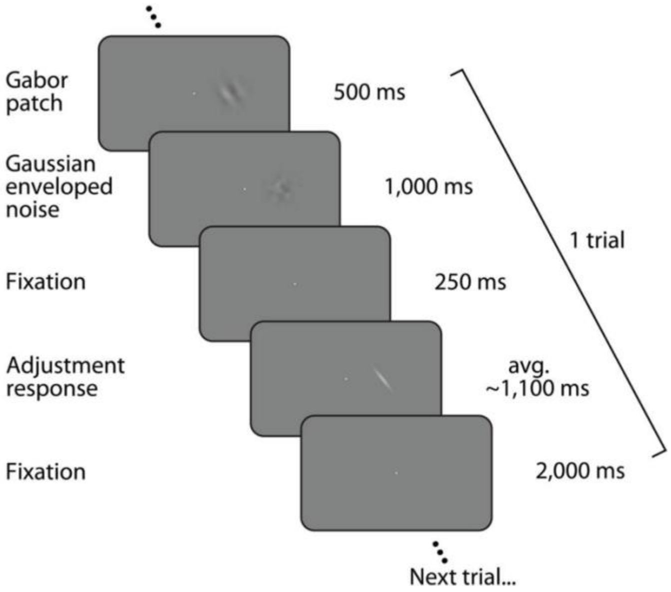

Figure 3. The design of Experiment 1 in Fischer and Whitney's (2014) study. Participants adjusted the orientation of a response bar to report the perceived orientation. Image reproduced from Fischer and Whitney (2014).

Later studies showed that this dependence in perception is not only limited to the orientation; other visual features such as shape (Manassi, Kristjánsson & Whitney, 2019), motion coherence (Suarez-Pinilla, Seth, & Roseboom, 2018), numerosity (Fornaciai & Park, 2018), facial identity (Liberman, Fischer & Whitney, 2014) and even stimulus ensembles (Manassi et al., 2017), are also systematically biased towards information from the recent past (see Kiyonaga, Scimeca, Bliss, & Whitney, 2017 & Pascucci et al., 2019, for review).

Since these initial studies of Fischer & Whitney (2014) many studies have been published on SD, showing how SD is quite ubiquitous but also a number of papers have found results that seemingly contradict one another. Some of these developments are discussed below.

1.3.1 The role of attention in serial dependence

It is still unclear how preceding sensory input must be processed to induce a serial-dependence bias upon subsequent perceptual decisions. Fischer and Whitney (2014) showed that SD is dependent on spatial attention to the previous stimulus location. In their study, they showed a test line in the same location of the inducer and their results showed that when the line was displayed on the same spot, the inducer produced robust SD, but when the following line was shown at another location on the screen, they did not find strong evidence for SD created by the inducer (they assumed that attention was deployed at the same location as the inducer).

However, SD has also been found to occur when inducers were task-irrelevant (Fornaciai & Park, 2018), implying that attention is not required for SD to occur, and in fact, Fischer & Whitney (2014) had suggested that SD might be *modulated* by attention but perhaps not required as such. In Fornaciai and Park (2018), a sequence of three dot arrays were shown on the screen: on the first screen, an inducer with either 100 or 400 dots appeared, then on the next screen a reference array with 200 dots appeared, and lastly, a probe with a variable number of dots (80–400), and participants were asked to ignore the inducer array and report whether the reference or probe array had more dots. The results in Fornaciai and Park (2018) suggest that SD occurs in the absence of an explicit task.

The results of Kim et al., 2020 demonstrated that simply presenting a stimulus does not seem to be sufficient for biasing later perception: the stimulus must be actively perceived in order to exert serial dependence. During binocular rivalry, a suppressed grating seems not to affect subsequent perception, positively or negatively. Fritsche and de Lange (2019) also indicated that feature-based attention strongly modulates attractive SD in orientation estimations but not repulsive biases for large orientation differences.

1.3.2 Role of proximity in feature space

As has been mentioned before, our visual environment is full of various sources of noise, yet the visual world that we perceive is reliable, continuous and smooth. The noisy input can be due to us moving around or moving our eyes, due to occlusion or changes in lighting. How does our brain use previous information to translate these distorted sensory inputs into reliable representations? Previous studies showed that the positive SD only happens when the inducer and the following stimuli are similar in feature space. One hypothesis could be that positive SD indicates that the visual system believes the inducer and the test are the same, whereas negative SD suggests that the system considers them as different. For example, Fischer and Whitney's (2014) study showed that the inducer would produce an attractive bias only when the inducer and the following line are similar (close in feature space). As shown in Figure 4, their results showed that SD is at its strongest when the distance between the inducer and the following line is about 25 degrees.

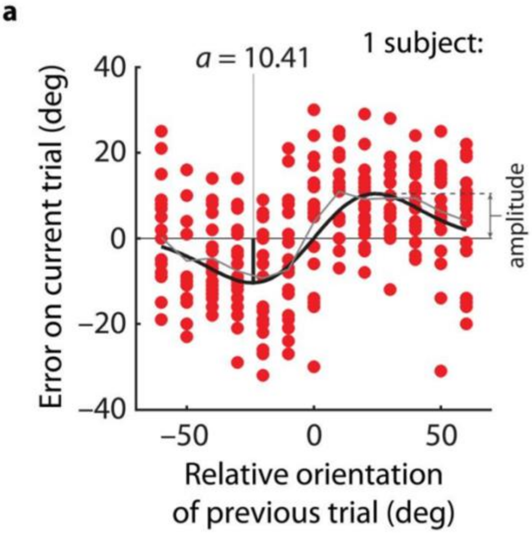

Figure 4. Error plot from Experiment 1 in Fischer and Whitney's (2014) study. Results showed that the inducer would produce a stronger attractive bias when the inducer and the following line are close in feature space. The red dots represent the estimation error in the adjustment task (the estimation error is calculated based on the difference between the reported orientation and the actual orientation of the Gabor). The gray line represents the average error; the black line represents a derivative of Gaussian (DoG) curve fitted to the data. The peak of the DoG fit determines the amplitude of SD. Image reproduced from Fischer and Whitney (2014).

On the other hand, Fritsche et al. (2017; 2019) showed that when the inducer and the test Gabor shown later are not similar (far from each other in feature space), the inducer produces a repulsive bias upon the perceived orientation of the following line. In their experiment, they tested a wide range of distances between the inducer and the test. Their results (Figure 5) showed that when the inducer and the following line are similar, they will attract each other (cause positive SD), but in which they are not similar (their distance in feature space is more than 45 degrees), the inducer would produce a repulsive bias (causing negative SD).

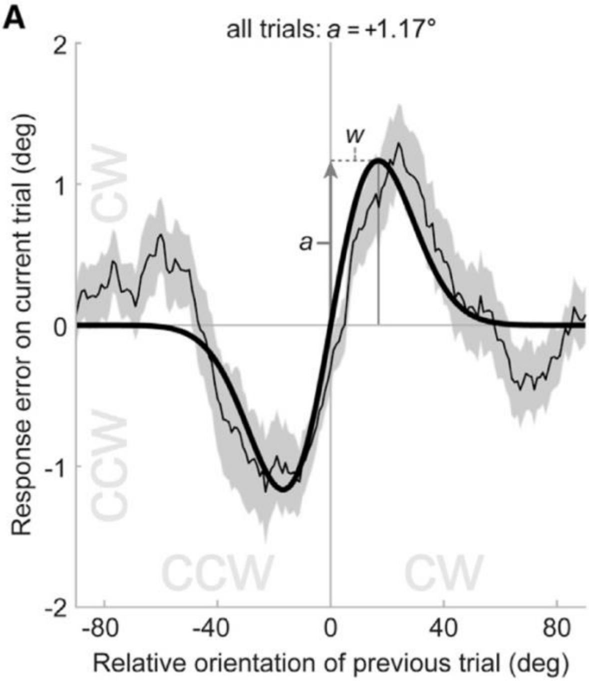

Figure 5. Error plot from Fritsche et al. (2017). The results were close to what Fischer and Whitney (2014) reported: when the inducer is similar to the following line, it would produce an attractive bias. However, the results of the Fritsche et al's. 2017 study showed that when they are not similar (far away from each other in feature space), the inducer will produce a repulsive bias. Image reproduced from Fritsche et al. 2017.

1.3.3 Serial dependence, decisional bias, or perceptual bias?

Although there is increasing evidence for serial dependency and its implications, it is still unclear at what step of perceptual processing SD occurs. Is it present in the early phases of visual cognition, later stages of decision-making, or both? The original findings of Fischer and Whitney (2014) strongly suggested that SD had a direct impact on perception. In Experiment 3 of their paper, they displayed two Gabors on the screen, one of which was cued with a dot. Following that, they showed two lines at identical positions and asked participants to choose the more clockwise-oriented Gabor (using a 2AFC method). According to their findings, the inducer created a visual illusion and changed the perception of the Gabor that appeared at the inducer position. Subsequent research has also revealed that the stimulus that creates SD (the inducer) acts directly on the perception of the next item and occurs at the early stages of visual cognition (Chopin & Mamassian, 2012; Burr & Cicchini, 2014; Taubert, Alais, & Burr, 2016; Cicchini, Mikellidou, Burr, 2017). In Cicchini et al. (2017), the results were that when response orientation was separated from the stimulus, the motor response showed minimal serial dependency, but Cicchini et al. also suggested that SD likely affects both perceptual and post perceptual processes.

On the other hand, other studies (Fritsche, Mostert, and de Lange, 2017; Pascucci et al., 2019; Ceylan, Herzog, & Pascucci, 2021) have revealed that SD could be produced at post-perceptual stages in higher levels of cognition. For example, Ceylan and colleagues (2021) reported serial dependency between Gabors with different spatial frequencies, or Gabors intermingled with dot patterns. These stimuli are considered to reflect different processes at various stages of visual processing. Ceylan et al. (2021) found that these perceptually different objects generated substantial serial dependency, contradicting low-level perceptual explanations, and indicating that SD occurs at the decisional level. It seems likely that serial dependence can actually occur at various stages of perceptual processing: according to Pascucci et al., 2019, each perceptual decision is permeated by opposing biases derived from a network of serially dependent processes: Low-level adaptation tends to repel perception away from earlier stimuli, whereas decisional traces tend to attract perceptual reports to the recent past. In this serial dependency hierarchy, continuity fields are generated by the inertia of decisional templates, not by low-level sensory processes.

Overall, SD is a form of biases produced by previously observed stimuli. Studies have shown that SD helps us to maintain a smooth and reliable representation of the visual world by ignoring negligible differences between the items we have seen before, and we still see in the present. SD also helps us to exaggerate the difference between what we have recently seen and what we see if two sequential items are different. However, it is not completely clear at what stage of visual cognition SD happens and how it is modified by attention.

2 Aims

What we see is a combination of the sensory inputs that we receive through our eyes and prior information about the stimuli. Nevertheless, it is not clear how our previous knowledge and perceptual history modulate our perception and perceptual decisions in the present. In the studies included in the current thesis, we investigated the role of attention and proximity in feature space on attractive and repulsive biases in visual perception. We firstly studied how the attentional role of previous stimuli shapes biases in perceptual decisions. Later, we tested how the similarity between what we have seen and what we see affects perceptual decisions related to what we see at a given moment. In addition, we tested how an inducer (in the context of a serial dependence study) can modulate perceptual decisions related to more than one test object.

2.1 Paper I: *Optimizing perception: Attended and ignored stimuli create opposing perceptual biases*

Previous studies (Manassi, Kristjánsson & Whitney, 2019; Suarez-Pinilla, Seth, & Roseboom, 2018; Fornaciai & Park, 2018; Liberman, Fischer & Whitney, 2014; Fischer & Whitney,2014) have shown that, after seeing a stimulus (inducer), perceptual decisions related to the following item are influenced by the inducer. Fischer and Whitney (2014) showed that seeing an attended item (inducer) produces an attractive bias in perceptual decisions related to the upcoming test item. However, it is not completely clear how a to-be-ignored item like a distractor would bias perception and perceptual decisions. On the other hand, Chetverikov et al. (2016) showed that subsequent to completing several visual search trials, participants could learn the probability distribution of the distractors shown in the search array. Hence, our first study tested how learned distractor distributions (as in Chetverikov et al.) can affect the perceptual decisions related to a target in a search array. To summarize, in our first study, we investigated the role of to-be-ignored items in forming SD biases on perceptual decisions related to a target in a visual search array.

2.2 Paper II: *You see what you look for: Targets and distractors in visual search can cause opposing serial dependencies.*

In the Paper II, we wanted to examine if the repulsive bias reported in Paper I would affect perceptual decisions in general or if its effective domain is restricted to the perceptual decision of visual search targets. In other words, we aimed to test if biases produced by a target and distractors could alter the perceptual decisions of an independent stimulus that is neither a target nor a distractor. Moreover, some recent studies had shown that proximity in feature space plays an important role in shaping the biases related to perceptual decisions (Fritsche et al. 2017; Fritsche & de Lange, 2019; see also earlier work reviewed by Hsu, 2021). Therefore, in our second study, we manipulated the distances in feature space between the independent line (test line) and target and distractors in the visual search to investigate how proximity in feature space between the inducer and current stimulus would modify the serial dependence biases. All in all, in our second study, we tested the role of proximity in feature space between the inducer and a test item in the biases introduced by inducers upon our perceptual decisions in a more general sense than in Paper I (In Paper I, we tested the effect of target and distractors on perceptual decisions related to the last target, however in the Paper II we tested these effects upon an independent stimulus).

2.3 Paper III *The influence of the tested item on serial dependence.*

In the earlier studies mentioned above, we found out that after seeing an inducer, based on its attentional role and also its similarity to the following stimulus, the inducer could introduce opposing biases upon the perceptual decisions. But in the visual world around us, we encounter various objects at the same time. For example, after seeing a stimulus as an inducer, we might see several stimuli simultaneously, and some of them might be similar, and others might be dissimilar. Therefore, in our third study, we wanted to know how an inducer would change the perception of several different items at the same time. In other words, we tested whether an inducer can produce several opposing biases at the same time.

3 Materials and methods

The methods of the studies decribed here are explained in detail in the papers attached to the thesis. All of the participants in our studies had normal or corrected-to-normal vision. Before starting the study, they provided written informed consent that briefly described the experimental procedure. The studies described below were performed at a viewing distance of 70 cm on a 24-inch Asus monitor with 1920×1080 pixel resolution.

3.1 Paper I: *Optimizing perception: Attended and ignored stimuli create opposing perceptual biases*

Twenty participants participated in the experiment. The experiment was programmed using MatLab (2016a) with Psychtoolbox-3 (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007). Participants looked for a target (irregularly oriented line) in an array of 36 lines shown in a 6x6 matrix in the middle of the screen on search trials (using the design from Chetverikov et al., 2016). When the target (an oddly oriented line) was in the top three rows, participants were instructed to hit the E key, and when it was in the lower three rows, they were asked to press the D key. On visual search trials, the distractor orientations were chosen from a truncated Gaussian distribution with a standard deviation of 15 degrees or a uniform distribution with a range of 60 degrees. Within a block, the mean and type of distribution were maintained unchanged.

On each trial, the target orientation was chosen pseudo-randomly. The target orientations were clockwise (T>D) relative to the distractor mean on half of the trials and counter-clockwise (T<D) on the other half of the trials. The distances between the target and distractor mean on trial N (last trial) were counterbalanced with the distances between the target on trial N and the target on trial N-1 in feature space. To achieve this, the target on trial N-1 was either +10 (T>PrevT) or -10 (T<prevT) degrees away from the target on trial N.

Targets were positioned 60 to 120 degrees away from the mean of the distractor distribution on the remaining learning trials in each block. Finally, participants were asked to match the orientation of a line to the target orientation on trial N at the end of each block.

3.2 Paper II: *You see what you look for: Targets and distractors in visual search can cause opposing serial dependencies.*

Twenty participants were recruited for each of the four experiments in this study, and before beginning the first test session, any participants who had never participated in our previous experiments attended a training session that was exactly similar to the test session with the same number of experimental blocks. Following the completion of the training session, participants took part in the main part of the experiment. The training and the main sessions were done on separate days. The experiments were designed and conducted in MatLab 2016a using Psychtoolbox-3. The FDL technique (Chetverikov et al., 2016) was used, in which participants were instructed to perform 4 to 5 visual search trials in each experimental block to ensure that they had learned the distractor distribution. In the visual search trials, participants looked for a target among 36 lines placed in a 6x6 matrix on a gray background. Participants were asked to hit the E key if the target was in the top three rows and the D key if the target was in the lower three rows.

After completing the search trials, the test line (a single orientated line) was presented on the screen for 500 milliseconds. The participants were required to adjust a bar at the center of the screen to report the orientation of the Test line. Participants used the "M" or "N" keys to rotate the line.

Each block's average distractor orientation on search trials was chosen randomly from between 0 to 180. The distractor distribution mean was held constant throughout each block to allow viewers to learn the distractor distribution. Each trial's target orientation was chosen pseudo-randomly from between 60° and 120° relative to the distractor distribution's mean.

Furthermore, the distances in feature space between the orientation of the test line and the last target and between the test line and the distractor mean were selected differently throughout experiments 1-3. In experiment 1, the distances between test line to target and distractors were selected randomly from within feature space; in experiment 2, the test line orientation was close to the target orientation and far from the distractors' average orientation. In experiment 3, the test line orientation was close to distractors and far from targets in feature space. In experiment 4, we cued the target and the distances in feature space between test line, target, and distractors orientation were selected in a similar way to experiment 2. Detailed information about the methods and design of the experiments are provided in Paper II attached to the thesis.

3.3 Paper III *The influence of the tested item on serial dependence.*

We recruited twenty participants to take part in this study. The stimuli were generated and presented using Psychopy 3 (Peirce et al., 2019). In total, 350 trials were displayed under the four different conditions (One-Similar, One-Dissimilar, Two-Similar, and Two-Dissimilar conditions) for each participant. Each trial was divided into four parts. First, participants were asked to pay attention to the orientation of a line shown at the screen center (inducer). Following that, the test display was shown, which consisted of either two lines on either side of the fixation point or one line on one side of the fixation point (randomized across trials).

In the One-Similar and One-Dissimilar conditions, only one line was displayed during the test display, and its orientation was similar (One-Similar) or dissimilar (One-Dissimilar) to the inducer's orientation. Two lines were displayed on the left and right sides of the screen for 500 ms in the Two-Similar and Two-Dissimilar conditions. The orientation of one of the lines was similar to the inducer's orientation, while the other line's orientation was dissimilar to the inducer's orientation (as in the One-Dissimilar condition). Later, a mask was shown for 500 ms in the center of the screen to cover the previously shown lines. Finally, participants were instructed to use the response circle to report the orientation of one the lines from the previously viewed display by matching the two disks with the test-line’s orientation (by using the 'left' or 'right' keys). The response circle indicated which line should be reported by its placement, either on the left or right, either a similar line (Two-Similar) or a dissimilar line (Two-Dissimilar).

4 Results

The studies' results are explained in more detail in the papers attached to the thesis, and here we briefly describe the most important results of each of the studies and the main conclusions from each.

4.1 Paper I: *Optimizing perception: Attended and ignored stimuli create opposing perceptual biases*

In this study, we excluded blocks with incorrect answers on the previous search trial to ensure that we tested only blocks where participants had learned the target orientation and distractor distribution. In addition to the analysis described in Paper I, we estimated the effects of the previous target and distractors' average orientation on perceptual decisions related to target orientation judgments using a hierarchical Bayesian model which is described in detail in the supplementary section of Paper I.

We found that at least two opposite biases from preceding visual search stimuli influence our current perception. Our results showed that an attractive bias caused by a previously seen target pulls our perceptual decisions related to the target toward the previously seen target. In contrast, a negative bias induced by the to-be-ignored distractors in the search task pushes the perceptual decisions related to the target away from the distractor distribution. Our findings are the first to show that as observers scan their visual environment, they experience two simultaneous biases that pull perceptual decisions related to the target in opposite ways and how these opposing biases optimize our perception and the related perceptual decisions. We also showed that the biases produced by targets and distractors are not response related biases.

4.2 Paper II: *You see what you look for: Targets and distractors in visual search can cause opposing serial dependencies.*

In this study, to ensure that we only examined blocks where we could be reasonably confident that participants had learned the target orientation and distractor distribution, we again dropped the blocks with incorrect answers on the previous search trial. We employed a hierarchical Bayesian model to estimate the effects of the last target and distractor in the visual search array on test line orientation judgment. This approach integrates all of the participants' data into a single model and accounts for the uncertainty of parameter estimations.

4.2.1 Experiment 1

The results showed that the target on the last trial introduced an attractive bias upon the perception of the test line. The visual search distractor sets resulted in repulsive serial dependence, while the target had an attractive influence on the perceived direction of the test line. And most importantly, these biases were observed for a task-irrelevant test stimulus that was neither a target nor a distractor.

4.2.2 Experiments 2 and 3

The results of Experiment 2 were similar to the results of Experiment 1; an attractive bias was introduced upon perceptual decisions related to the test line by the targets (the test line was similar to the target in feature space), while in contrast, a repulsive bias occured upon the perceptual decisions related to the test line by the distractors (the test line was dissimilar to the distractors in feature space).

However, in Experiment 3, the test line orientation was similar to distractors' orientation and dissimilar to the target orientation in feature space, and the results revealed that the distractors introduced an attractive bias while the target-produced bias was close to zero.

To summarise, the results of Experiments 2 and 3 indicate that the direction of biases induced by distractors and targets is determined by the proximity in feature space between what we have already perceived (induce) and what we observe (the test item). This suggests that the biases produced by targets and distractors are determined not only by attention (or whether an item is a target or a distractor) but also by their similarity to the test item.

4.2.3 Experiment 4

In Experiment 4, the target was cued by a dot, and participants were asked to report if the displayed dot was above or below the target. In Experiment 4, similar to Experiment 2, test line orientation was close to the target orientation and far from the average orientation of distractors. The targets induced an attractive bias upon the test line's perceived orientation. The distractors, on the other hand, caused a small repulsive bias that was close to zero. The findings in Experiment 4 reveal that proximity in feature space and the role of attention both play a significant role in forming biases upon perceptual decisions. The distractors still caused a repulsive bias in perceived test line orientation even when they became "neutral" through the use of a pre-cue. We hypothesize that some of the biases we observe are due to stimulus-based rather than due to attentional mechanisms; in other words, even when the "distractors" do not distract, their very presence on the screen influences subsequent perceptual judgments, perhaps through some automatic segmentation processing in early vision.

Overall, the findings from paper II suggest that serial dependence biases from visual search act on perceptual decisions in general, not specifically on decisions about search relevant items such as attended targets. We also showed that to-be-ignored items produce a bias that co-occurs with the attractive biases caused by attended objects. The latter is commonly referred to as serial dependence, and it is thought to stabilize and preserve the spatiotemporal region over which current object features, are pulled by previously observed items, what Fischer & Whitney (2014) (see also Liberman, Zhang & Whitney, 2018) call the continuity field. Our results also showed that in addition to the attentional role, proximity in feature space modifies the direction and amplitude of the biases produced by the inducers.

4.3 Paper III *The influence of the tested item on serial dependence.*

In paper III we tested the influence of one inducer upon more than one subsequent test lines (instead of the infuence of multiplie inducers upon a single test line as in Papers I & II).

We used a Bayesian hierarchical linear model to test if the proximity in feature space between the orientations of the inducer and test-lines produced opposing serial dependence biases upon perceptual decisions related to the test line. Our results showed that when the test line and the inducer were similar in feature space, there was an attractive bias upon perceptual decisions of the orientation of the test-line from the inducer. Next, we tested the condition where the inducer and test-line(s) orientations were dissimilar. The results revealed that the inducer produced a repulsive bias upon perceptual decisions related to the current item.

Overall, the results of this study showed that perceptual decisions related to different stimuli, that are presented simultaneously, can be biased differently, depending on the similarity in feature space between the test stimulus and inducer. Furthermore, the results show that the two biases co-exist until we determine which stimulus (close or far in feature space) needs to be reported.

5 Discussion

The studies presented in the current thesis investigated the role of attention and proximity in feature space in forming attractive and repulsive serial dependence biases in visual perception. We first looked at how the attentional role of preceding (or inducing) stimuli (whether they are attended targets or distractors to be ignored) affects biases in perceptual decisions. We also looked at how the similarity in feature space between what we have seen (inducer) influences our perceptual decisions about what we see in the present (test items). Finally, we investigated how an inducer can modulate perceptual decisions involving multiple test objects (in the context of a serial dependence study), where observers only know, following the presentation of a post-cue, which item is to be reported.

5.1 The role of attractive and repulsive biases from previously viewed items upon perceptual decisions

To begin with, our findings demonstrate that visual search-induced serial dependence biases affect perceptual decisions in general. They are not confined to the task-relevant stimuli in a given case. Biases in the perceived orientation of a search target as a function of the previous trial target and current distractors were reported in Paper I. In Paper II we raised the question whether these results may reflect that observers report their search template rather than the search target. However, the findings in Paper II indicate that this is highly improbable. Due to the fact that the search task introduced biases upon neutral items, responding according to a template rather than the neutral item makes little sense. Nonetheless, we cannot rule out that search templates may play a moderating role in the observed biases.

Secondly, the to-be-ignored stimuli (such as distractors in a visual search task) generate a bias in addition to the attractive biases induced by attended items. The attractive bias is commonly referred to as serial dependence and is considered to stabilize and preserve perceptual continuity (Fischer and Whitney, 2014). Serial dependence is assumed to assist us in dealing with familiar situations by allowing us to ignore slight changes in previously experienced items and maintaining perceptual continuity through time (Cicchini & Kristjánsson, 2015; Liberman, Zhang, & Whitney, 2016).

Recently, Pascucci et al. (2019) suggested that perception is formed by two opposing historical biases at any given moment: sensory adaptation and previous decisions. They argued that repulsive biases (such as those shown in various low-level negative aftereffects) push perception away from previously perceived stimuli. On the other hand, attractive biases influence human vision during sequences of perceptual decisions, distorting current sensory data to appear more similar to previous visual input than it actually is, compensating for sensory adaptation. This mechanism could account for the observed repulsive biases. However, this similarity effect (similar distractors produce attractive biases, whereas dissimilar distractors produce repulsive biases) does not correspond to the typical pattern of sensory adaptation (stronger repulsive biases for similar inducers, weak, often attractive, or no biases for dissimilar ones). Nonetheless, this hypothesis may be challenged in future studies on the many functions that play a role in serial dependence effects.

Our findings could be related to what has been referred to as target template tweaking throughout the history of both distractors and targets. Visual search templates can be optimally modified by perceptual history to assist us in locating items that are similar to the target. Bravo and Farid (2016) demonstrated that guidance templates are adapted to the task at any given moment, and here we argue that recent perceptual history is critical in determining this bias. The representations (or templates) are dynamic – they change according to the context – and our findings may shed light on the process through which the templates are biased. Notably, our results imply that search patterns can alter how irrelevant items are perceived and that these biases serve the objective of making the objects of interest more salient in each case. Manassi et al. (2019) demonstrated that visual classification of a stimulus is serially dependent on previously observed items but only within a narrow spatial frame, demonstrating the three features outlined for continuity fields: (temporal, spatial, and featural tuning).

5.2 The role of attention and proximity in forming biases in perceptual decisions

Our findings indicate that when feature space distances between test line orientation and the target and between target orientation and distractor orientation were randomly chosen (Paper II, Experiment 1), the target induced attractive biases, whereas distractors induced repulsive biases. Experiments 2 and 3 from the same study subsequently demonstrated that proximity in feature space plays an essential role in determining the direction of the biases.

In Experiment 2, when targets were oriented similarly to the test line, attractive biases were observed; however, no significant bias was observed when the same targets were oriented very differently from the test line. In contrast, when the distractors were dissimilar to the test line in feature space (Paper II, Experiment 2), they induced a repulsive bias upon the perceived test line orientation but an attractive bias was produced by distractors when they were close to the test line in feature space (Paper II, Experiment 3). However, while the distractors were close to the test line orientation in feature space, they produced an attractive bias (Paper II, Experiment 3). Thus, even while the distractors and target's attentional roles remained constant in Experiments 2 and 3 in Paper II, changing the proximity in feature space between the test line to distractor and the test line to target altered the direction and strength of the biases. This demonstrates an interaction between the proximity in feature space between the targets and distractors and the status of stimuli as attended targets or to be ignored distractors.

Recent studies have demonstrated attractive biases in orientation perception when preceding (inducing) stimuli had comparable orientations to the present (test) stimuli in a serial dependence experiment containing an inducer and a test stimulus (Bliss et al., 2017, Fritsche et al., 2017; Samaha et al., 2019). Additionally, Fritsche et al. (2017) found that repulsive biases occurred when the inducer and the test stimulus were dissimilar. Later, Fritsche and de Lange (2019) reported that when observers focused on a different aspect of the prior stimulus than orientation, the attractive bias was significantly reduced, demonstrating a role for feature-based attention in producing perceptual biases. This is consistent with earlier results that serial dependency is modulated by attention (Fischer & Whitney, 2014, Zhang & Whitney, 2016). On the other hand, feature-based attention did not affect Fritsche & de Lange's (2019) repulsive biases.

Our findings concur in part with these findings but contradict them in other ways. As with Fritsche et al. (2019), we observed attractive biases when items comparable to the test were used and repulsive biases when items dissimilar to the test were used. Furthermore, we found that attention strengthens the attractive biases associated with similar items. In sum, our data suggest that attention affects both attractive and repulsive biases, but in different ways.

5.3 Serial dependence; perceptual or post perceptual bias

Despite mounting evidence for serial dependence and its effects, there is still lively debate about the stage of perceptual processing at which serial dependence occurs. Does it occur during the early phases of visual processing, the later stages of decision-making, or both? Fischer and Whitney's 2014 findings made the case that SD affects perception directly; in Experiment 3 of their study, they displayed two Gabors on the screen, one of which was cued by a dot. Following that, they displayed two lines in the same locations and asked participants to choose the Gabor line that was oriented more clockwise (using a 2AFC method). Their findings indicated that the inducer created a visual illusion and affected how the Gabor that appeared at the inducer site was perceived. Subsequent studies have established that the inducing stimulus in serial dependence studies can directly affect the perception of the next item and serial dependence can therefore occur during the early stages of visual cognition (Burr & Cicchini, 2014; Cicchini et al., 2017).

But this does not appear to be the whole story. Several studies seem to indicate that serial dependence also arises at higher phases of visual cognition (Fritsche, Mostert, and de Lange, 2017; Ceylan, Herzog, & Pascucci, 2021). Serial dependence between Gabors with different spatial frequencies and Gabors blended with dot patterns, for example, was observed by Ceylan and colleagues (2021). They argued that serial dependence occured at a late processing stage given its generalization across different stimuli produced by a variety of brain systems at different levels of visual processing. According to Ceylan and colleagues, the fact that these perceptually distinct items induced serial dependence argues against low-level perceptual accounts and suggests that SD happens at the decisional level.

Our findings in papers I and II indicate that when participants are required to report the orientation of a line similar to the inducer, an attractive bias occurs for their perceptual decisions associated with the test line. On the other hand, when participants are asked to report the orientation of the dissimilar line to the inducer, the inducer introduces a repulsive bias into the dissimilar line's perceptual decisions. Our findings in Paper II could then be interpreted to suggest that the inducer's biases occur when observers are required to report the orientation of one of the shown lines, implying that this particular serial dependence occurs during a decision-making stage. As a result, one could assume that the inducer's biases arise at late levels of perceptual processing or even decision-making. Further studies are, however, needed for a conclusive answer with regard to this.

In sum, we believe that there is substantial evidence in the field that perceptual representations are serially dependent on earlier visual input and that this represents changes in the perceptual form of stimuli (Morai & Whitney, 2021; see also Cicchini et al., 2017), but the evidence for serial sependence at later stages is also strong. We claimed in Paper II that serial dependence may be a general characteristic of perceptual processing occuring at all levels of the hierarchy of visual perception, from low-level sensory processing to higher-level decision-making. Morai and Whitney (2021) made a similar point when discussing their findings of serial dependence in classification images, stating that their findings do not rule out the possibility of serial dependence in higher cognitive processes, such as decision and memory, and argued that even if serial dependence affects templates for perceptual detection, this does not mean that it is purely a low-level perceptual effect. Morai and Whitney claimed that serial dependence could reveal itself in various mechanisms, including perception, decision-making, and memory (Cicchini, Benedetto, and Burr, 2021). We might add that serial dependence could manifest in a variety of ways across these processing levels. Serial dependence has been shown to require conscious awareness of preceding stimuli in a binocular rivalry paradigm (Kim et al., 2020) and attention to previous inducing stimuli (Fischer & Whitney, 2014), indicating that a low-level explanation is improbable on its own.

6 Conclusions

Our results have shown for the first time how serial dependece in visual perception does not only reflect the attended items as we organize the environment, but that to-be-ignored items also play an essential role in producing serial dependence and by extenstion in optimizing perception and perceptual decisions (Papers I and II). We reach this conclusion since serial dependence is assumed to play a role in maintaining perceptual continuity from one moment to the next. Additionally, we showed that explicit reports of stimulus features are not necessary in order to form serial dependence in perceptual decisions. Furthermore, our findings reveal that both attention and proximity in feature space between the inducer and current stimulus play a crucial role in forming serial dependence and repulsive bias. Finally, our results in Paper III show that a single inducer can bias the orientation judgments of two items simultaneously (a single inducer simultaneously could produce both attractive and repulsive serial dependence biases). While many questions remain with regard to how percptual continuity is maintained in visual perception the results from the three papers presented in this thesis provide important information about the role of serial dependence in this continuity, and the most parsimonious explanation of serial dependence is that they are ubiquitous in perception occuring at many different levels of the perceptual hierarchy.

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8 Original publications

This Thesis has been written based on the following papers:

Paper I: Rafiei, M., Hansmann-Roth, S., Whitney, D., Kristjánsson, A., & Chetverikov, A. (2021a). Optimizing perception: Attended and ignored stimuli create opposing perceptual biases. *Attention, Perception, & Psychophysics, 83,* 1230–1239. https://doi.org/10.3758/s13414-020-02030-1

Paper II: Rafiei, M., Chetverikov, A., Hansmann-Roth, S., & Kristjánsson, Á. (2021b) You see what you look for: Targets and distractors in visual search can cause opposing serial dependencies. *Journal of vision*, *21*(10), 3-3. https://doi.org/10.1167/jov.21.10.3

Paper III: Rafiei, M., Chetverikov, A., Hansmann-Roth, S., & Kristjánsson, Á. (Submitted) The influence of the tested item on serial dependence.

Paper I

Optimizing perception: Attended and ignored stimuli create opposing perceptual biases

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9.1 Abstract

Humans have remarkable abilities to construct a stable visual world from continuously changing input. There is increasing evidence that momentary visual input blends with previous input to preserve perceptual continuity. Most studies have shown that such influences can be traced to characteristics of the attended object at a given moment. Little is known about the role of ignored stimuli in creating this continuity. This is important since while some input is selected for processing, other input must be actively ignored for efficient selection of the task-relevant stimuli. We asked whether attended targets and actively ignored distractor stimuli in an odd-one-out search task would bias observers’ perception differently. Our observers searched for an oddly oriented line among distractors and were occasionally asked to report the orientation of the last visual search target they saw in an adjustment task. Our results show that at least two opposite biases from past stimuli influence current perception: A positive bias caused by serial dependence pulls perception of the target toward the previous target features, while a negative bias induced by the to-be-ignored distractor features pushes perception of the target away from the distractor distribution. Our results suggest that to-be-ignored items produce a perceptual bias that acts in parallel with other biases induced by attended items to optimize perception. Our results are the first to demonstrate how actively ignored information facilitates continuity in visual perception.

Keywords: Feature Distribution Learning, Serial Dependence, Attention, Visual Search, Perception

9.2 Introduction

Imagine searching for an apartment for your dream vacation. After looking at a throng of ramshackle flats that are little more than distractions, even a half-decent room would look nice. However, when you see a few places that match your target criteria, each one you look at affects how the next one is perceived. Such contextual and sequential presentation effects are ubiquitous in social psychology (Simonsohn & Loewenstein, 2006; Simonson & Tversky, 1992). But can what we look for be affected by distractors and previously seen targets in *visual* search within ensembles of visual stimuli?

Perception is noisy and ambiguous, both due to external noise (e.g., differences in illumination, blur, and occlusion) and due to internal noise in the brain. The visual system might therefore utilize multiple sources of information to make correct inferences in the presence of noise. For example, knowledge of the statistics in natural images can help in perceptual decisions about visual ensembles, such as about orientation (Girshick, Landy, & Simoncelli, 2011), motion speed (Sotiropoulos, Seitz, & Seriès, 2011; Weiss, Simoncelli, & Adelson, 2002) or the color of objects (Allred, 2012; Brainard & Gazzaniga, 2009). The same knowledge, however, leads to biases in perception – for example, perceived orientation is biased towards cardinals (Girshick et al., 2011; Wei & Stocker, 2017). Similarly, knowledge that the visual input is mostly constant over time might help to optimize perception in the real world (van Bergen & Jehee, 2019), but leads to biases from recently seen stimuli in the lab – an effect coined serial dependence by Fischer and Whitney (2014).

Here we ask if the visual system utilizes multiple sources of information to optimize perception of visual ensembles such as when we search for targets among distractors. A search task is particularly interesting since it involves ensembles that involve attended stimuli (targets) and to-be-ignored stimuli (distractors). For example, a radiologist might look for signs of tumor on an X-ray image while ignoring salient distractors, such as bones. While many studies have demonstrated how attended items create perceptual biases (see below), the potential role of to-be-ignored items has not been addressed in the same way. Natural environments often involve situations involving distracting stimuli that need to be actively ignored rather than simply not attended. We may need to select targets that meet our goals, that may be hard to distinguish from others, that must then be actively rejected. Active inhibition of irrelevant items is observed for example during visual search (Arita, Carlisle, & Woodman, 2012; Beck & Hollingworth, 2015; Cunningham & Egeth, 2016). The biases created by such to-be-ignored items have not been studied to the same degree as target-based effects (but see Gaspelin, & Luck, 2018; Noonan, Crittenden, Jensen, & Stokes, 2018; Chelazzi, Marini, Pascucci, & Turatto, 2019; Geng, Won, & Carlisle, 2019)

In the context of visual search, previous studies have assessed biases in *templates* that observers use for search. Geng and colleagues (Geng, DiQuattro, & Helm, 2017; Geng & Witkowski, 2019; Won & Geng, 2018; Yu & Geng, 2019) showed that the target template, that is, the representation of the target used for search assessed through analysis of search times for different targets, can be gradually biased away from distractors. Due to noisy and unstable visual input (for example, because of occlusions or eye movements as well as noise inherent in the nervous system), the potential function of such biases from ignored distractors could be to generate a predictive code in order to correct possible errors and to stabilize perception. However, it is not clear to what extent such effects might cause biases in target perception in visual search.

The effect of distractors on perception might be especially strong when the distractor representation can be used to facilitate search on following trials. We have previously shown that the visual system can implicitly learn the feature distributions of a set of to-be-ignored items (Chetverikov, Campana, & Kristjánsson, 2016, 2017b, 2017c, 2017d, 2020; Hansmann-Roth, Chetverikov, & Kristjánsson, 2019; for review see Chetverikov, Hansmann-Roth, Tanrıkulu, & Kristjánsson, 2019 and Chetverikov, Campana, & Kristjánsson, 2017a). Our *feature distribution learning* (FDL) paradigm shows that observers learn remarkably intricate details of distributions of distractor features, not only their mean and variance, but the probability distributions of the distractors, be it a Gaussian, uniform, skewed or bimodal distribution (Chetverikov et al., 2016). The particular kind of a search task utilized in these studies – an odd-one-out search – ensures that observers have to analyze both target and distractors, because otherwise the target identity cannot be determined. While the target defining feature is not known in advance, the target can often be easily found because of the similarities among the distractors. In addition, the distractor distribution remains constant for a few trials. Observers are therefore implicitly prompted to encode the distractors to facilitate search, making this an ideal task to test whether representations of ignored items bias perception.

In addition to currently present distractors, information about previous targets can also help with identifying the current target. Fischer and Whitney (2014) found that the judgment of the orientation of a Gabor patch can be strongly biased towards the previously perceived Gabors (see Kiyonaga, Scimeca, Bliss, & Whitney, 2017, for review). Such serial dependence has been shown to occur for stimulus dimensions as varied as shape (Manassi, Kristjánsson & Whitney, 2019), position (Bliss, Sun, & D'Esposito, 2017; Manassi, Liberman, Kosovicheva, Zhang, & Whitney, 2018), eye gaze (Alais, Kong, Palmer, & Clifford, 2018), body size (Alexi et al., 2018), or perceived motion coherence (Suarez-Pinilla, Seth, & Roseboom, 2018). Fischer and Whitney (2014) found that serial dependence was produced by attended items only and suggested that attention serves as a "gating" mechanism for serial dependence (see also Fornaciai, & Park, 2018; Fritsche, & de Lange, 2019). We therefore expect that previously attended items will bias the perception of the current target in the context of visual search as well, further optimizing target perception.

In sum, our aim was to study the simultaneous effects of previously attended (targets) and ignored (distractors) items on perceived orientation of a line presented in isolation. After searching for an odd-one-out line among distractors for several trials, observers were presented with a single line and were asked to adjust its orientation to the orientation of the target seen on the last trial. Given that targets on consecutive trials varied, we were able to measure any serial dependence from preceding targets. But importantly, we additionally assessed whether the to-be-ignored items can also cause a bias in the line orientation judgements.

9.3 Method

9.3.1 Participants

20 participants (eleven females and nine males, mean age = 31.55 years) participated in the experiment. They signed a consent form that included a brief description of the experimental procedure. Each test took about 1 hour. All participants had normal or corrected to normal vision.

9.3.2 Stimuli and procedure

The design of the experiment is shown in Figure 6. All stimuli were presented on a grey background on a 24 inch Asus monitor with a 1920×1080-pixel resolution at a viewing distance of approximately 70 cm. MATLAB (2016) with Psychtoolbox-3 (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007) was used to program and run the experiment.

The experiment contained 264 blocks. Each block had 4-5 search trials (1188 trials per participant) followed by an adjustment task. On search trials (following the design of Chetverikov et al., 2016), participants searched for an oddly oriented line in an array of 36 lines displayed in a 6×6 matrix at the center of the screen. The length of each line was 1 degree. The positions of the lines on the screen were jittered by randomly adding values between ±0.5 degrees to both the vertical and horizontal coordinates. Participants were asked to press the E key when the target (an oddly oriented line) was among the three upper rows and press the D key when the target was located in the lower three rows. If the response was incorrect, the word "Error" appeared for one second on the screen. To encourage participants to be as fast and accurate as possible we used a scoring system based on the formula: Score = 10+(1-RT) *10 where the RT is the response time in seconds, while for errors: Score = -|10+(1-RT) *10| - 10. This equation results in positive scores for correct responses faster than 2 seconds and negative scores otherwise. The score for each trial was shown on the screen following each response.

The orientations of the distractors on learning trials were drawn from either a truncated Gaussian distribution with a standard deviation of 15 degrees or from a uniform distribution with a range of 60 degrees. The mean and the type of the distribution were kept constant within a block. The orientation of the targets on each trial was selected pseudo-randomly. On the last trial in each block (i.e. series of learning trials, trial *N*), the target orientation was selected from a range of -70 to +70 degree distance to the distractor distribution mean in 4-degree steps, so that targets were clockwise (T>D) relative to the distractor mean on half of the trials and counter-clockwise (T<D) on the other half. The distances in orientation space between target and distractor mean on trial *N* were counterbalanced with the distances between the target on trial *N* and target on trial N-1. To this end, on trial *N*-1 the target had either a +10 (T>PrevT) or -10 (T<prevT) degree distance from the target on trial *N*. On the rest of the learning trials in each block, targets were oriented 60 to 120 degrees away from the mean of the distractor distribution.

At the end of each block (after the last trial *N*), participants were asked to match the orientation of a single test line to the target orientation on trial *N*. The initial orientation of the test line was selected randomly. The test line was always presented at the center of the display. Participants were encouraged to respond as quickly and accurately as possible. The response time was limited to 6 seconds.

9.4 Data analysis

To filter out trials with exceedingly long response times, trials with log-transformed RT's outside of the mean ± 3 *SD* were removed. We also excluded trials with incorrect responses. Since many studies (Appelle, 1972; Li, Peterson, & Freeman, 2003; Nasr, & Tootell, 2012) have shown that human vision is more sensitive to cardinal (horizontal and vertical) than oblique orientations, the adjustment responses were corrected for cardinal biases by fitting a fourth-degree polynomial on distance to cardinal orientations for each participant and taking the residuals (the analysis of uncorrected data yielded the same results). The fourth-degree polynomial was fit using the robust regression procedure (*rlm* function from the *MASS* package in *R*) that fits the model by applying an iteratively reweighted least squares approach.

The parameters of the adjustment response distributions were then estimated by fitting a mixture of uniform and von Mises distributions (Zhang & Luck, 2008) to the observers' responses. The fitting was done separately for each observer and each condition included in a particular analysis. For example, for our main analysis of interest, we fitted a mixture of uniform and von Mises distributions for each participant and each combination of target and distractor conditions (i.e., 20x2x2). For the analysis of effects of N-2 and N-3 targets, the fitting was done for each participant and each target condition (i.e., 20x2 for N-2 and 20x2 for N-3), and so on. The mixture of von Mises and uniform was fit using maximum likelihood estimation with ten different starting points for the mixture proportion (from 0.01 to 0.91 in steps of 0.1; the starting points for the mean and precision of von Mises were chosen from randomly from $[-\pi,\pi]$ and [0,10] range, respectively). After running ten MLE optimization runs with the aforementioned starting points, the one with the highest likelihood was used in the following analyses. The mean of the von Mises part of the fitted distribution provides information about systematic shifts in target perception while random responses (e.g., from attention lapses) are reflected in the uniform part.

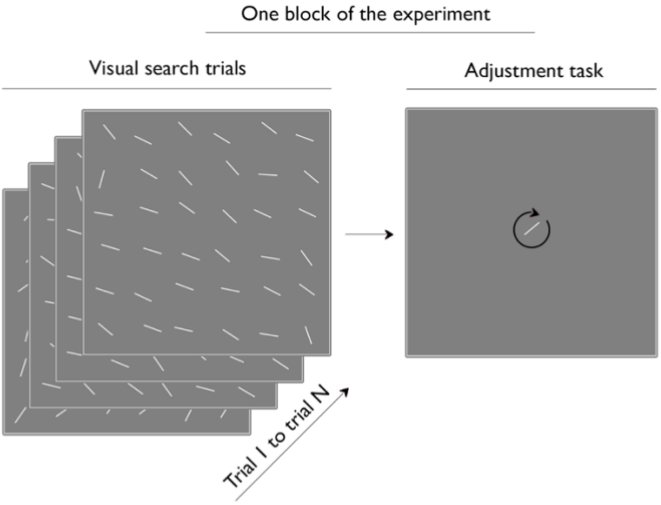

Figure 6. Design of the experiment. In each block, participants were asked to perform a visual search task that had 4 to 5 trials (learning trials), they searched for an oddly oriented line in a search array of 36 lines shown in a 6*6 matrix in the middle of the screen and subsequently they had to adjust the orientation of a single randomly oriented line to the orientation of the target that was presented on trial *N*.

9.5 Results

9.5.1 Judgements of target orientation

A repeated-measures ANOVA with the mean of the von Mises part of the fitted distribution as the dependent variable, was used to study the effects of the previous target and distractor distributions on orientation judgments for the target[1]. The estimated orientation of the target on the last trial was pushed away from the distractors, *F*(1, 19) = 4.93, *p* = .039, η^2_G = .07 (*M* = -0.59 degrees, *SD* = 2.34 degrees for T<D and *M* = 0.38 degrees, *SD* = 2.37 degrees for T>D). In contrast, it was pulled towards the preceding target, *F*(1, 19) = 36.88, *p* < .001, η^2_G = .45 (*M* = 1.45 degrees, *SD* = 1.76 degrees for T<PrevT and *M* = -1.66 degrees, *SD* = 1.88 degrees for T>PrevT), similar to previously observed serial dependence effects (Figure 7A and 7B). Both effects were observed for 19 out of 20 participants as shown in the slopes in Figures 7C and 7D. Interestingly, there was no interaction between the orientation of the previous target and current distractors, *F*(1, 19) = 0.26, *p* = .614, η^2_G < .01.

Although our main question involved the distractor and target repetition effects, for completeness we also assessed any effects of the distractor distribution type (Gaussian and uniform) on previous target and distractor distribution effects with a 2×2 (distractors relative orientation × distractor distribution type) repeated measures ANOVA. As in the previous analysis, the mean part of the fitted distribution was used as the dependent variable. The results showed that neither the main effect of distribution type, *F*(1, 19) = 0.05, *p* = .820, η^2_G < .01, nor the interaction with the target-distractor relationship, *F*(1, 19) = 4.08, *p* = .058, η^2_G = .03, were significant.

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[1] These analyses were performed on the parameters of fitted distributions rather than the raw data. We therefore present hierarchical analsyses performed on the raw data in supplimentary information, that lead to similar results.

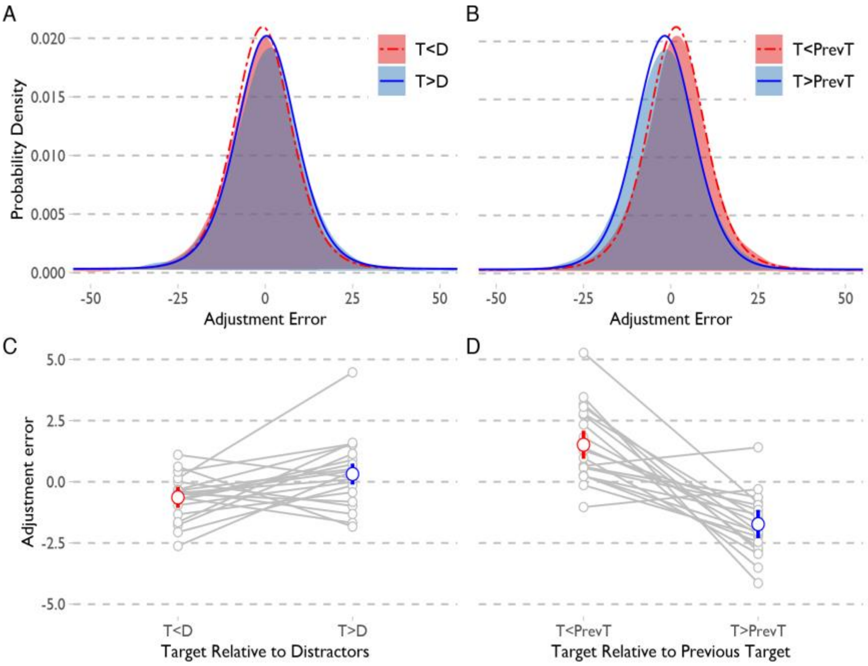

Figure 7. Effects of preceding distractor distribution and previous target on perceived orientation. A) and B) Shaded areas show the raw response error distribution. The lines show the fitted mixture model that combined the Gaussian and uniform distributions. C) and D) the mean adjustment error by participants (gray lines) and the average across participants with a 95% confidence interval (blue and red bars). T<D means that the target was oriented counterclockwise to distractors, while T>D indicates that it was oriented clockwise to distractors. T<PrevT and T>PrevT indicate the same relative to the previous target. Note that in panels A&C, the shift in the means of the response probabilities is away from the distractors (repulsion effect) while in panels B&D it is toward the previous target (attraction effect).

9.5.2 Temporal effects and target and distractor distance

It is well known that history effects upon visual perception can last for a long time (Brascamp, Pels, & Kristjánsson, 2011; Fischer & Whitney, 2014; Maljkovic & Nakayama, 1994; see review in Kristjánsson & Ásgeirsson, 2019). For example, Fischer and Whitney (2014) found that their serial dependence effect lasted for at least 3 trials. We therefore analyzed cumulative effects of the target[2] (one back, two back and three back targets) during the learning trials after excluding the adjustment responses identified by the mixture model as belonging to a uniform component with probability > 0.5 (8.7% of trials). Figure 8 shows the results. Similarly to the main analyses, the mean parts of the mixture distribution (dependent variable) were estimated for trials where preceding targets were clockwise or counterclockwise relative to the probed target, controlling for the distractor-to-target orientation difference. We found that N-2 targets created a significant bias in adjustment response (*M* = 1.16 [0.60, 1.73], *t*(19.0) = 4.32, *p* < .001), which was weaker than the bias created by the immediately preceding target (*M* = 3.23 [2.26, 4.19], *t*(19.0) = 7.01, *p* < .001), while the target on the N-3 trial did not create a significant bias (*M* = 0.22 [-0.56, 1.00], *t*(19.0) = 0.59, *p* = .564). We also performed a control analysis using the N+1 target, and, as expected, it did not create any bias (*M* = -0.55 [-1.17, 0.07], *t*(19.0) = -1.86, *p* = .078).

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[2] We could not estimate the effect from distractors on previous trials with the current design as distractor mean was kept constant during learning.

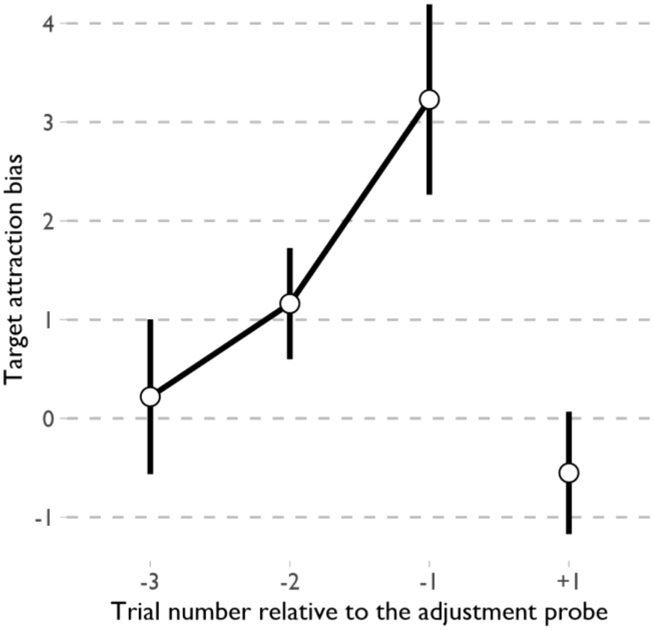

Figure 8. Attraction bias created by targets in preceding trials and in a control analysis using the next trial. Bars show 95% confidence intervals.

Additionally, we studied the role of the mean distance between the target and distractors in feature space on adjustment error using the same mixed effects approach as described above. The results revealed that the bias away from the distractor mean was similar for different distractors, non-significantly increasing with distance between the target and distractors, *B* = 0.37, *SE* = 2.53, *t*(14.98) = 0.15, *p* = .886.

9.5.3 Performance on search trials and the effect of search performance on reported orientation

We also measured the effects of the different distributions, with response times (RT) and accuracy on the search trials as dependent variables, using repeated measures ANOVAs. As Figure 9 shows, visual search accuracy was higher when the distractor distribution was Gaussian than when it was uniform, *F*(1, 19) = 21.62, *p* < .001, η^2_G = .05 (*M* = 96.0, *SD* = 2.4 for Gaussian and *M* = 94.6, *SD* = 2.4 for Uniform) and changed over the learning trials, *F*(4, 76) = 4.42, *p* = .008, η^2_G = .04. Response times were also affected by distractor distribution, *F*(1, 19) = 66.81, *p* < .001, η^2_G = .02 (*M* = 868.5, *SD* = 261.8 for Gaussian and *M* = 962.4, *SD* = 308.1 for Uniform) and by trial number, *F*(4, 76) = 9.04, *p* = .002, η^2_G = .03. We then ran a polynomial mixed effect regression to assess the effect of trial repetition in more detail. For accuracy, only the linear effect on trial number was significant, *B* = 22.95, *SE* = 3.47, *Z* = 6.61, *p* < .001, while for RT there was a quadratic relationship, *B* = 5.27, *SE* = 1.31, *t*(19.02) = 4.03, *p* < .001. This pattern of results suggests that while observers benefitted from repetitions (resulting in decreased RT after the first trial), they also spent more time analyzing the stimuli towards the end of the learning trials blocks, possibly preparing for the upcoming adjustment task.

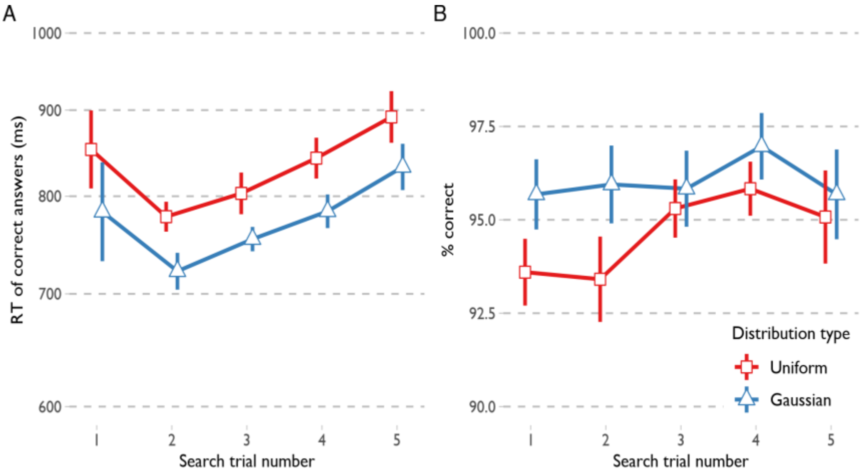

Figure 9. Performance on the search trials. Response times on the left and accuracy on the right. Bars show 95% confidence intervals.

We then analyzed the time course of distractor and target effects using search times on the last search trial and adjustment times. First, we aimed to see if the amount of time spent searching for a target (and, potentially, memorizing it) affects the observed bias magnitude. To account for differences in search time distributions between observers, we used RT percentiles for each observer. For statistical tests, we used a mixed model that included the interaction of RT percentile and the effect of interest. As Figure 10 shows, the effects of both previous target and distractors were similar across search times (*B* = 0.87, *SE* = 1.13, *t*(45.13) = 0.77, *p* = .444 for the interaction of RT with the previous target effect, and *B* = 0.47, *SE* = 1.18, *t*(25.75) = 0.40, *p* = .696 for the interaction with the distractor effect). Similarly, adjustment time did not significantly interact with the effects of interest (*B* = 0.24, *SE* = 1.04, *t*(130.92) = 0.23, *p* = .820 for the interaction of RT with the previous target effect, and *B* = -1.03, *SE* = 1.10, *t*(81.40) = -0.93, *p* = .353 for the interaction with the distractor effect).

This suggests that the amount of time observers spent searching for the target or memorizing it as well as how deliberate they were in their adjustment responses was not crucial for the biases we observed.

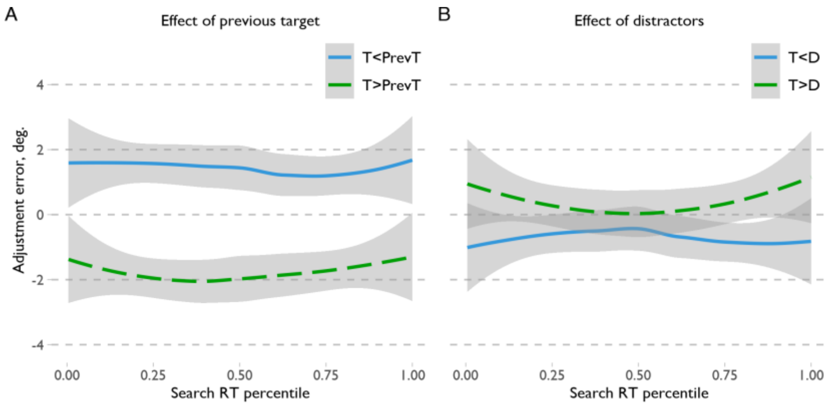

Figure 10. The time course of target and distractor effects as a function of search RT. Shaded areas show 95% confidence intervals.

9.6 Discussion

Our results are the first to show that when observers scan their visual environment, two simultaneous biases occur that pull the judgment of the orientation of a line in different directions. Firstly, our results show that orientation judgments of a single line can be biased towards a recently attended target line, consistent with findings on serial dependence (Fischer & Whitney, 2014). This occurs even though observers did not have to decide, on preceding trials, what the target orientation was. Secondly, we show for the first time that the judgement of the orientation of a line can be biased away from an ensemble of to-be-ignored items, in our case distractors in a visual search task. We propose that these two parallel effects serve a similar purpose in reducing noise and preserving continuity in perception, biasing perception towards important stimuli and away from items that should be ignored. Although the effects of previous target and distracters on target perception were not particularly large, they were stable for the vast majority of participants and such biases can nevertheless affect perception in important ways.

Studies on visual attention have shown that by selecting and limiting the information that is available at different levels of perceptual processing, attention can optimize perception, selecting stimuli of importance (Driver, 2001; Kristjánsson & Egeth, 2019). Interestingly, serial dependence is observed for attended items but not for unattended ones (Fischer & Whitney, 2014; Fornaciai & Park, 2018; Fritsche & de Lange, 2019; Liberman, Zhang, & Whitney, 2016). However, ignored items differ categorically from unattended ones. Recent studies suggest that we are remarkably good at picking up intricate patterns over time from ignored stimuli (Chetverikov et al., 2016, 2017b, 2017c; Chetverikov et al., 2019; Hansmann-Roth et al., 2019). The results of the present study further show the importance of ignored items. To-be-ignored objects, in addition to the ones selected by attention filtering systems, can bias perception.

Fischer and Whitney (2014) introduced the concept of the *continuity field*, that integrates consecutive stimuli to promote perceptual stability and continuity. They argued that serial dependence from targets was due to the operation of this continuity field, which in turn reflects constant attempts of our brain to infer the present based on the past. This is consistent with the behaviour of an optimal observer in a Bayesian framework (Burr & Cicchini, 2014; Cicchini et al., 2017; Kalm & Norris, 2018; van Bergen & Jehee, 2019). However, in preserving continuity, ignored stimuli might be no less important than attended ones. Our results highlight that the continuity field concept will need to encompass effects upon perception from the stimuli that we actively try to ignore.

Our paradigm also opens up the avenue of testing serial dependencies for visual ensembles where ignored and attended items can be contrasted. Manassi and colleagues (2017) have previously shown serial dependencies for ensembles of oriented Gabor patches and that this effect occurred at the level where a group of objects was perceived as ensembles, but our results argue that such dependencies may differ depending on the role particular items play within visual ensembles.

In a serial dependence study, the items can be treated as multiple observations coming from the same source. We may, in other words, assume that as in the real world, sequential observations are likely to originate from the same object (Kiyonaga et al., 2017). Under that assumption, it makes sense to merge the incoming sensory inputs to obtain a more precise percept. However, in the visual search task that we tested, targets and distractors clearly do not belong to the same source. This is especially evident in odd-one-out search where the target is defined as the item that stands out, the item that is different from the other items (the distractors). Under the assumption that the target comes from a different source than distractors, a negative bias from distractors might in fact be optimal. Consider the case with categorically defined distractors in an odd-one-out color search. When you know from previous experience that the target is anything but red (a prior, using the ideal observer framework language), and your sensory information tells you that it is between red and yellow (a likelihood), it is likely that the target is actually yellow and the part of the sensory information that suggests red color is just noise. This is similar to the negative biases sometimes observed in multisensory integration with high stimulus disparities that are explained by a causal inference model (Körding et al., 2007; Wallace et al., 2004).

Target representations might also become tuned during retention or decision-making to avoid interference from distractor memory. This is in line with previous findings in visual working memory (VWM) studies, where distractors were found to affect target representations as well. However, the specific pattern of results in our study is different. Rademaker, Bloem, De Weerd, and Sack (2015) found that when observers have to remember the first of two sequentially presented stimuli, memory is biased towards the second, irrelevant stimulus. When both stimuli have to be remembered, the bias is severely reduced. This is similar to a positive serial dependence effect. In contrast, Golomb (2015) found that for two simultaneously presented items, the memory of the target is biased away from the distractor when they are similar but towards it when they are dissimilar. Similar results were also reported by Chunharas, Rademaker, Brady, and Serences (2019) for hue memory, but they found that repulsion turns to attraction under high memory load. Bae and Luck (2017) also found that when two sequentially shown motion directions are to be remembered, high similarity leads to repulsive biases but low similarity to attractive ones. These studies suggest that dissimilar distractors, such as the ones used in our odd-one-out search task, should create attractive rather than repulsive biases. Thus, while we cannot reject the possibility that distractors affected target representations, the mechanisms are likely to be different from those observed in visual working memory (VWM) studies. It is important to note, however, that the extent to which serial dependence reflects perception and to what degree it reflects VWM, is a hotly debated topic, that cannot be addressed with the current data (see Kiyonaga et al., 2017 for review).

The observed repulsion bias cannot be explained by well-known adaptation and simultaneous contrast effects in orientation perception. The tilt illusion and the tilt aftereffect are known to produce repulsive biases in perceived orientation (Gibson, 1937; Gibson & Radner, 1937). However, these biases occur when the target stimulus is relatively similar to inducers and changed into attractive biases when the two are distinct (see, e.g., Clifford, 2014, for a review). In contrast, we did not observe any dependence on target-to-distractor similarity and in the range of orientation difference we studied (70 to 90 degrees) both the tilt illusion and tilt aftereffect should create positive rather than negative biases.

9.6.1 Is serial dependence a perceptual or decisional bias?

Serial dependence in visual search is especially interesting because by itself visual search does not require explicit judgments of target features. Serial dependence studies typically involve sequential decisions on stimulus features, leading some researchers to conclude that serial dependence occurs post-perceptually (Bliss et al., 2017; Fritsche, Mostert, & de Lange, 2017) while others have argued that perception is affected (Cicchini, Mikellidou, & Burr, 2017; Fornaciai & Park, 2018; Gekas, McDermott, & Mamassian, 2019;

Manassi et al., 2018, 2019). Recently, Pascucci et al. (2019) further developed the idea of decisional biases suggesting that even without an explicit task, observers might continuously make implicit decisions about target orientation, applying the same “decisional template”. Our findings, however, argue that decision-making is not necessary for serial dependence, even in this implicit form. In the odd-one-out search task, on the majority of trials observers need to analyze orientation but only to find a target but not to report the orientation itself and the target is defined as the item that differs most from the others. It is unlikely that on each trial of the search task observers make an implicit decision about target orientation. Instead, they utilize the perceived orientation of different stimuli to decide which one is most likely to be the target (Ma, Shen, Dziugaite, & van den Berg, 2015; Schoonveld, Shimozaki, & Eckstein, 2007). That is, while they have information about target orientation, the "decisional template” involves the target location. Thus, given that we are able to observe serial dependence in the context of a search task, it is likely to be caused by representations of previously presented stimuli rather than by decisions about them. Note however, that serial dependence may of course arise at many stages of processing (Cicchini & Kristjánsson, 2015; Kiyonaga et al., 2017).

9.6.2 Accuracy and response times during learning trials

Before discussing response time and accuracy for our so-called learning trials, we must note that the task was a tool toward assessing history effects upon orientation judgments, rather than being thought of as a measure in this study. The results for performance accuracy (Fig. 4B) are in agreement with previous studies (Chetverikov et al., 2016, 2017b, 2017c, 2017d), suggesting that participants learned the probability distribution of the distractors, resulting in more accurate visual search in the last trials within a block than the first trials. However, the RT analysis (Fig. 4A) showed that response times did not improve during the learning trials in contrast with the previous studies. A possible explanation for this RT pattern is that since participants did not know how many search trials would occur in each block, after the second trial they may have started to prepare for the later adjustment task, perhaps causing delays in responding.

9.6.3 Conclusions

Our results show that perception reliably reflects not only what is attended in each case (serial dependence) but for the first time our results reveal strong serial dependencies from ignored information, in this case distractors in a search task. Importantly, the bias arises even when distractors are very dissimilar to targets, distinguishing it both from the well-known tilt illusion and tilt adaptation. Additionally, our results show that explicit reports of stimulus features are not necessary for serial dependence. The results suggest that perception takes both attended and ignored stimuli into account in preserving the continuity of the visual world to an even larger degree than previously found.

9.7 Acknowledgements

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9.8 Open Practices Statement

A preprint of this paper is available at https://psyarxiv.com/m79nu. The data from the experiment reported in this paper and scripts for simulations and analyses are available at https://osf.io/zgkn9/.

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9.10 Supplementary information

9.10.1 Bayesian hierarchical model analysis

This supplement aims to demonstrate that the main results obtained in the experiment are not due to the noise introduced by fitting a mixture of von Mises and uniform distributions separately for each observer and in each condition. Here, we use a hierarchical Bayesian model instead, that combines the data from all observers in a single model and accounts for uncertainty in parameter estimates.

9.10.2 Modeling approach

The model was built using *brms* package in *R* (Bürkner, 2017, 2018) that translates the regression models given the user-provided specifications to Stan probabilistic programming language. We used the standard recommended priors for all parameters except for the uniform distribution (see below).

9.10.3 Modes parameters

The full model consisted of a mixture of two distributions following the relatively standard architecture described by Zhang and Luck (2008). The first distribution, which represents relatively accurate answers, was modeled as a normal distribution ($\mathcal{N}(\mu, \sigma^2)$). Although a von Mises distribution (or a wrapped normal) would be more appropriate, within the observers' error range (excluding guesses), a von Mises distribution can be approximated by normal as the former approaches the latter when its precision is high. This approximation drastically improves model convergence as it avoids the issues associated with circularity. The second distribution represented observers guesses and was modeled as uniform with -90 to 90 degrees range

($\mathcal{U}(-90{,}90)$). The distributions were mixed with the probability θ of an observation y coming from a normal distribution:

$$p(y|\theta, \mu, \sigma^2) = \theta \ \mathcal{N}(\mu, \sigma^2) + (1-\theta) \ U(-90{,}90)$$

The mean of the normal distribution was further modeled in line with the ANOVA analysis described in the main text. Namely, it was modeled in a mixed linear model fashion as a function of the target to distractor relationship (clockwise vs. counterclockwise) and target to previous target relationship (clockwise vs. counterclockwise) at a population level (“fixed effects”) with the additional by-observer variation in these effects and the intercepts (“random effects”). The correlations between the random effects were left free to be estimated. In addition, the weights of each distribution in a mixture (θ) were also modeled including a between-participant variation term.

In short, the full model was equivalent to a typical hierarchical linear model with the exception that the distribution of the dependent variable was defined as a mixture.

Several models were used as a comparison. One control model was a non-mixture model with the same hierarchical modeling of the dependent variable (that is, only a normal distribution part of the mixture was included). Three other control models restricted the full model by excluding different effects: either a target to distractor relationship, a target to previous target relationship, or both of them.

The code for all models is provided along with the data and the analysis scripts at https://osf.io/zgkn9.

9.10.4 Results

For model comparison, we estimated a widely applicable information criterion (wAIC) value (Vehtari et al., 2016). The effects estimation was done by computing the mean of the posterior distribution and the 95% highest posterior density interval (Kruschke, 2014).

The full model provided a dramatically better fit than a non-mixture model, supporting our approach to model the dependent variable as a mixture (ΔwAIC = 10788, logBF = 1700.92). Indeed, as Figure 11 shows, the full model provided an adequate account of the presence of “guesses” in the data.

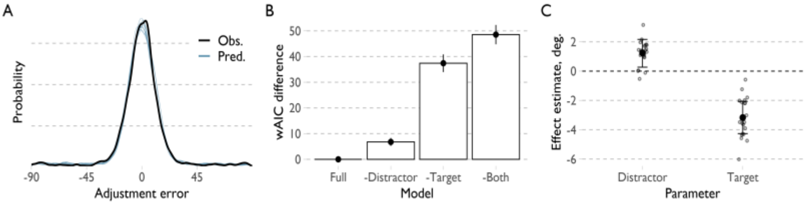

Figure 11. The results of the Bayesian hierarchical model analysis. A: A comparison of the observed data distribution (“Obs.”) with the distribution predicted by the model (“Pred.”) shows that the model adequately accounted for the “guesses” in the data. B: A comparison of the full model with the restricted models that excluded one or both of the predictors. C: The effects of the target to previous target (Target) and distractor to previous target (Distractor) on observers’ adjustment errors. Small dots show individual observers, large dot shows the population-level effect and the lines show 95% credibility intervals.

The full model also provided a better fit than the restricted models (compared to the model without distractor effect: (ΔwAIC = 7, logBF = 7.28, see Figure 11 for wAIC differences with the other models). Crucially, the effect of the previous target was attractive (*b* = -3.17, 95% HPDI = [-4.28, -2.09]) and the effect of the distractors was repulsive (*b* = 1.24, 95% HPDI = [0.31, 2.19]) matching the results observed using by-subject analyses in the main text.

9.10.5 Supplemental References

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Paper II

You see what you look for: Targets and distractors in visual search can cause opposing serial dependencies

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10.1 Abstract

Visual perception is, at any given moment, strongly influenced by its temporal context – what stimuli have recently been perceived and in what surroundings. We have previously shown that to-be-ignored items produce a bias upon subsequent perceptual decisions that acts in parallel with other biases induced by attended items. However, our previous investigations were confined to biases upon a visual search target's perceived orientation, and it is unclear whether these biases influence perceptual decisions in a more general sense. Here we test whether the biases from visual search targets and distractors affect the perceived orientation of a neutral test line, which is neither a target nor a distractor. To do so, we asked participants to search for an oddly oriented line among distractors and report its location for a few trials and next presented a test line irrelevant to the search task. Participants were asked to report the orientation of the test line. Our results indicate that in tasks involving visual search, targets induce a positive bias upon a neutral test line if their orientations are similar, while distractors produce an attractive bias for similar test lines and a repulsive bias if the test line's orientations and the distractors' average orientation are far apart in feature space. In sum, our results show that both attentional role and proximity in feature space between previous and current stimuli determine the direction of biases in perceptual decisions.

10.2 Introduction

Our visual system needs to process a large amount of complex visual information at any given moment. To make this task easier, the brain uses various heuristics based on knowledge about the environment. For example, we know that an object's appearance typically does not change dramatically from one moment to the next. This means that our visual system may ignore negligible changes in the visual input to promote stability. However, when objects do indeed change, the same heuristic might lead to biases. One example of this is serial dependence (see, e.g., Fischer & Whitney, 2014; Pascucci et al., 2019). In Fischer and Whitney (2014), observers viewed an inducer line, followed by an oriented line whose orientation had to be reported. They found that orientation estimates for this second line were biased towards the inducer orientation, concluding that perception is tuned towards previous stimuli that have similar features and appear in the same locations and proposed that serial dependence promotes perceptual stability in the visual environment (see also Burr & Cicchini, 2014; Cicchini & Kristjánsson, 2015; Kiyonaga, Scimeca, Bliss, & Whitney, 2017 for review). Further investigations have since revealed that the perception of many other features, such as shape (Manassi, Kristjánsson & Whitney, 2019), motion coherence (Suarez-Pinilla, Seth, & Roseboom, 2018), numerosity (Fornaciai & Park, 2018), facial identity (Liberman, Fischer & Whitney, 2014) and even stimulus ensembles (Manassi et al., 2017; Pascucci et al., 2019), is systematically biased by information from the recent past.

Serial dependence in perception is thought to help us keep perception stable against minor changes that might arise due to internal or external noise. But the stimuli we encounter are not all equally important, and some can be ignored to enable us to concentrate on the object of interest at a given moment. For example, during visual search we need to pay attention to items similar to the potential target while simultaneously ignoring stimuli dissimilar to the target. This raises the question of whether and how these dissimilar items that need to be ignored affect our perceptual decisions[3].

Fritsche and colleagues (Fritsche et al. 2017; Fritsche & de Lange, 2019; see also earlier work reviewed by Hsu, 2021), have suggested that proximity in feature space between the test stimulus and the inducer may determine whether biases from serial dependence are repulsive or attractive. According to Fritsche et al., an attractive orientation bias occurs when preceding targets and/or distractors have similar orientations. In contrast, a repulsive bias occurs when they have dissimilar orientations.

In a recent paper, we studied the effect of distractors upon perceptual decisions about the attended items (targets) during visual search for an oddly-oriented line among distractors (Rafiei et al., 2021). In visual search, observers can surprisingly quickly learn the probability distributions of distractor sets (Chetverikov, Campana & Kristjánsson, 2016, 2017a, 2017c, 2020; Hansmann-Roth et al. 2019, 2021, 2020a; Tanrikulu, Chetverikov & Kristjánsson, 2020). They can learn which distractor features are more probable than others in surprising detail, and importantly, unlike the items typically used in serial dependence studies, observers learn to ignore them. Following this approach, in Rafiei et al. (2021) we employed repeated distractor presentations over several trials to ensure that participants learn the

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[3] Note that we choose to remain neutral at this point on the question of whether serial dependence causes biases upon perception, decisional processes or both. The observed bias in perceptual decisions could reflect a change in appearance or decision but a direct measure of this is not available in the present work. We therefore use the term perceptual decisions. Broadly defined, perceptual decision-making involves using sensory information from the environment to guide behavior.

distractor features while judging an oddly oriented target's location. After a few search trials, participants were asked to report the target orientation on the last visual search trial. We found that the target's perceived orientation was *pushed away* from the mean orientation of the distractors. Additionally, the search targets induced an *attractive* bias upon the perceived orientation of a subsequent visual search target, a result in line with serial dependence findings. Our study demonstrated that the search task creates conditions for two simultaneous perceptual biases: a repulsive bias from distractors and an attractive bias from targets.

While our findings in Rafiei et al. (2021) show how to-be-ignored items produce a perceptual bias that acts in parallel with another bias induced by attended items, our investigation was confined to biases upon the perceived orientation of the visual search target. We did not address whether the biases influence perceptual decisions more broadly. Here we address the question whether the biases from visual search targets and to-be-ignored distractors reported by Rafiei et al. (2021) can alter perceptual processing in a more general sense, or specifically whether the biases affect the perceived orientation of a neutral test line, which was neither a target nor a distractor. To do so, we asked our participants to search for an oddly oriented line among distractors and report its location for several adjacent trials. The specific targets and distractors varied from trial to trial, but their respective probability distributions remained stable within each block of search trials to ensure that the distractor feature distribution (and the targets) were well encoded. Next, participants were asked to report the orientation of a briefly presented test line in an adjustment task. We aimed to assess the biases induced by targets and distractors on the test line's perceived orientation that was, crucially, unrelated to the visual search task.

Rafiei et al. (2021) proposed that the role the stimuli in the visual field play in attentional tasks determines whether any biases from presented stimuli are attractive or repulsive. They suggested that to-be-ignored objects (like distractors) lead to repulsive biases upon the target's perceived orientation, while attended stimuli (such as the previous targets) yield attractive biases upon subsequent perceptual decisions. In Experiment 1, we tested whether similar effects would occur for a task-irrelevant line. The distance in feature space (orientation) between the target and distractors on the one hand, and the test line on the other, was random. In Experiments 2 and 3, we therefore addressed the role of distance in feature space between the test line on the one hand and the target and distractors on the other more systematically in light of the findings of Fritsche et al., (2017) and Fritsche & de Lange, (2019). Finally, in Experiment 4, we tested the biases induced by neutral stimuli (which are neither search targets nor distractors). We cued the target location, while keeping the task the same in all other aspects, so that participants did not need to search for the target. Therefore, the lines around the cued line did not serve as distractors anymore but were neutral within the task. If their role as distractors is crucial for determining the direction of the biases, the biases should be eliminated or strongly diminished when the search is no longer required.

In sum, we had three aims in the current project. In Experiment 1, we studied biases produced by visual search upon a neutral test object. In Experiments 2 and 3, we investigated the effect that distance in feature space between the visual search targets and distractors and the task-irrelevant test line has on these biases. Finally, in Experiment 4, we tested how cueing the target location (presumably eliminating the need for a search) would affect the biases from targets and distractors in the display upon the perceived orientation of the task-irrelevant test line.

10.3 Experiment 1

In Experiment 1, we tested whether the orientation of a target and distractors in a visual search task leads to biases upon perceptual decisions about the orientation of a task-independent test line presented following a series of visual search trials. In each block, participants were asked to perform a series of visual search trials (learning trials) to ensure that they had a representation of distractors (as in studies involving the feature distribution learning (FDL) method, Chetverikov et al., 2016; see Chetverikov et al. 2019 for review). Next, a randomly oriented test line was shown on the screen for 500 milliseconds. Finally, participants had to report the test line's orientation by adjusting a subsequently presented line located at screen center (see Figure 12).

10.3.1 Method

10.3.1.1 Participants

Twenty participants (eleven females and nine males, mean age = 32.35 years) were recruited for Experiment 1. All participants had normal or corrected-to-normal vision and provided written informed consent that described the experimental procedure before starting the study. For all the experiments here, before starting the test sessions, any participants who had never participated in our similar experiments underwent a training session, which was similar to the test session with the same number of experimental blocks. After completing the training session, participants performed the test trials. The training and test sessions were held on two different days.

10.3.1.2 Stimuli and procedure

The stimuli were displayed at a viewing distance of 70 cm on a 24-inch Asus monitor with 1920×1080 pixel resolution. The experiment was programmed and carried out using Psychtoolbox-3 (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007) in MATLAB 2016a.

We employed the FDL method (Chetverikov et al., 2016), where participants were asked to complete 4 to 5 visual search trials in each experimental block to ensure that they had learned the distractor distribution.

On these visual search trials, participants searched for an oddly oriented line in the center of the screen in an array of 36 white lines (length = 1° of visual angle), arranged in a 6×6 matrix (16° × 16° at the center of a screen) on a gray background. We randomly added ±0.5° to both the vertical and horizontal coordinates of the line positions to introduce some irregularity to the search array. If the target was in the upper three rows, participants were required to press the E key (on a standard keyboard) and the D key when the target was in the lower three rows (see Figure 12).

We used both feedback and a scoring system to encourage participants to respond as quickly and accurately as possible on the search trials. If the provided response was incorrect, the word "*Error*" appeared in red on the screen for 1 second. The score on the last trial was presented in the top-left corner of the screen during the search trials, and a cumulative score was shown during the breaks. We employed the following formula to calculate the scores for correct answers: $\text{score} = 10+(1-RT) *10$ where RT stands for the response time in seconds, and the following equation determined the scores when responses were incorrect: $\text{score} = - |10+(1-RT) *10| - 10$. If the given response was correct and made in less than 2 seconds, the score was positive; otherwise, the score was negative.

After completing the search trials, the test line (a single oriented line) was presented on the screen for 500 milliseconds. In half of the blocks, the test line was shown at the last search target position, and in the rest of the blocks, it was displayed at a randomly chosen distractor position. The participants were asked to report the test line orientation by adjusting a bar located in the middle of the screen. Participants had 6 seconds to press the "M" or "N" keys to rotate the adjustment line clockwise or counterclockwise, respectively.

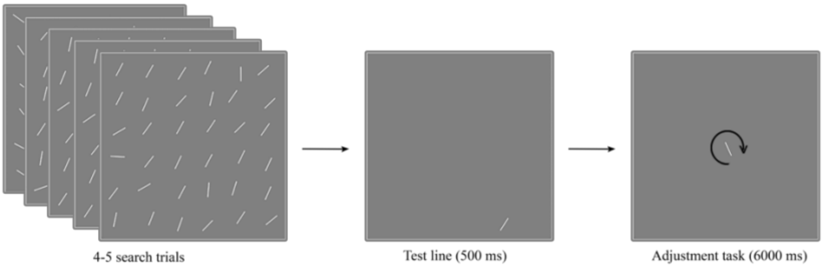

Figure 12. The design of Experiment 1. The figure shows one block consisting of the search display, the task-irrelevant test line, and the adjustment task. Firstly, participants were required to complete 4 to 5 visual search trials. They searched for an oddly oriented line (in the example shown above, the last trial's target is located in the first column, the fourth row) in the search array of 36 lines displayed in a 6×6 matrix. Next, a quasi-randomly oriented line (test line) was shown at a quasi-randomly chosen location. Finally, participants had to report the perceived test line orientation by adjusting a single bar presented at the screen center.

The mean distractor orientation on search trials was selected randomly for each block. The distractors were taken from a Gaussian distribution with a standard deviation of 15 degrees or a uniform distribution with a range of 60 degrees (the distribution type remained constant within a block; its effect is not analyzed here). Within each block, the distractor distribution mean was kept constant to allow observers to learn the distractor distribution (as shown in previous experiments; see Chetverikov et al., 2019, for review). The target orientation was selected pseudo-randomly for each trial within 60° to 120° relative to the mean of the distractor distribution.

As shown in Figure 13, the distances in orientation space between the test line and the last search target and the test line and the distractor mean were selected randomly (so the test line orientation was also selected randomly). Accordingly, in half of the blocks, the test line orientation was clockwise relative to the mean orientation of the distractors and counterclockwise in the rest of the blocks. Similarly, the test line was clockwise relative to the target on half of the trials and counterclockwise otherwise.

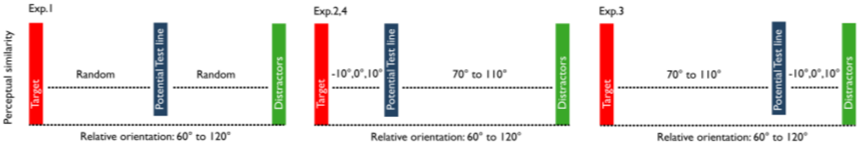

Figure 13. Proximity in feature space between test line, distractors, and target orientation in the experiments. In Experiment. 1, the distance in feature space between test line to target and test line to distractors was selected randomly. In Experiments 2 and 4, the test line was close to the target and far away from the distractors. In Experiment 3, the test line was close to distractors and far from the target.

10.4 General data analysis

We excluded blocks with incorrect answers on the last search trial to ensure that we only investigated blocks where we could be reasonably sure that participants had learned the orientation of the target and the distractor distribution. So, in Experiment 1, 313 blocks (6.13% of all of the blocks), 501 blocks (6.32%) in Experiment 2, 524 blocks (6.61%) in Experiment 3 and 860 blocks (8.14%) in Experiment 4 were excluded from the data before analyses. To estimate the effects of the previous target and distractor on the test line orientation judgment, we employed a hierarchical Bayesian model that integrates all of the participants' data in a single model and accounts for the uncertainty of parameter estimates. The model consisted of a mixture of two distributions of behavioral responses, x, each reflecting different types of responses on the adjustment task. The Gaussian distribution (with probability density $f_N(x; \mu, \sigma^2)$) represents variability and biases in adjustment errors, while the uniform distribution (spanning orientation space with probability density $f_U(x) = \frac{1}{180}$) maps the participants' random guesses (Zhang & Luck, 2008). The two distributions are mixed with the λ probability of an observation coming from a Gaussian distribution:

$$f(x;\theta,\mu,\sigma^2) = \lambda f_N(x;\mu,\sigma^2) + (1-\lambda)\, f_U(x)$$

Note that the Gaussian distribution is used here because the errors were relatively small so that the circularity of orientation space was not a concern.

We modeled the mean of the Gaussian distribution (systematic biases) with a Bayesian hierarchical linear model as a function of the relationship between the distractors and the test line (clockwise vs. counter-clockwise; in the later experiments, we also added “no difference” or “orthogonal” conditions to the model as dictated by the experimental design) and the target to the test line relationship (clockwise vs. counter-clockwise; again, in the later experiments, we added “no difference” or “orthogonal” conditions where appropriate) as fixed effects. The differences between participants in terms of the overall mean error (the intercept in the model), the effects of targets and distractors (the slopes in the model), and the mixture proportions (λ) were modeled as random effects.

Furthermore, to test how much the results depend on using the Zhang & Luck model (mixture of Gaussian and uniform), we repeated the analyses using a simple repeated-measurements ANOVA, in which the adjustment error was the dependent variable and the distractor to test line conditions, and the target to test line conditions were the independent variables, and the results were almost identical (check the supplementary section for more detail).

10.4.1 Results and discussion

Observers visual search performance followed the expected pattern. Response times (RT; *M* = 895 ms, *SD* = 270) decreased within the block, *F*(4, 76) = 18.52, $p < .001$, $\eta^2_G = .02$, while accuracy (*M* = 94.0% correct, *SD* = 3.3) remained relatively constant, *F*(4, 76) = 0.79, $p = .494$, $\eta^2_G = .01$, reflecting a typical attentional priming effect (Kristjánsson & Ásgeirsson, 2019). This suggests that observes obtained information about probable target and distractor features during the search.

We then analyzed the role of observed distractors and targets on the judgements of the orientation of an independent test line. In the adjustment task, observers were relatively precise, *M* = -0.004°, *SD* = 12.16°. As shown in Figure 14, the previous target had an attractive effect (*b* = -1.08, 95% HPDI = [-2.01, -0.14], where HPDI denotes the highest posterior density interval, a form of credibility interval defining the plausible range within which the unobserved parameter might vary) and the distractor effect was numerically repulsive (*b* = 0.54, 95% HPDI = [-0.43, 1.51]). To further test the effect of distractors and the target, we compared the full model with the restricted distractors-only (dropping the target effect) and target-only (dropping the effect of the distractors) models. The full model provided a better fit than both the distractors-only (logBF = 7.05; logBF stands for log-transformed Bayes factor with positive values here indicating evidence in favor of the full model) and target-only models (logBF = 0.74). So, as seen before in Rafiei et al. (2021), the distractor sets led to a repulsive serial dependence effect while the target caused an attractive effect upon the test line's perceived orientation. Importantly here, these biases were observed for a task-irrelevant test line, which was neither a target nor a distractor. However, the credibility interval for the distractor effect includes zero, and the logBF factor for the target-only model is small, indicating that we cannot draw strong conclusions from it.

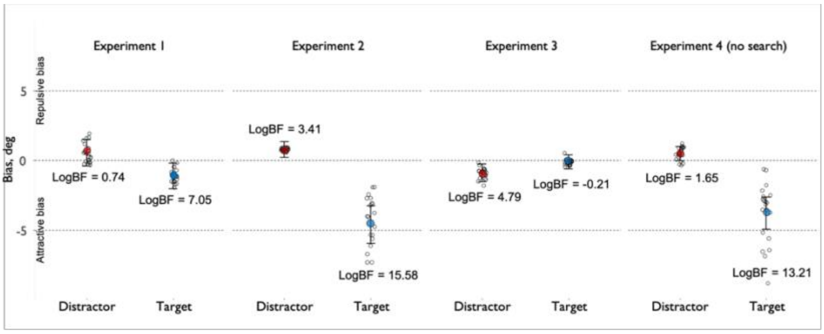

Figure 14. The target and distractor effects on adjustment error in the reported test line orientation for experiments 1 to 4. Small gray dots represent the individual observers, and large colored dots represent the population-level effects. The lines display 95% credibility intervals. Effect estimates (y-axis) show the magnitude of the biases (in degrees) produced by distractors and targets, while the x-axis shows the sources of the biases (distractors and targets).

Additionally, we ran an exploratory analysis of target- and distractor-to-test distances as continuous variables without splitting trials into clockwise/counter-clockwise groups (shown in Supplementary Fig. 1). The results suggest that the target effect is similar to what we observed in Rafiei et al. (2021), positive biases created by test lines relatively similar to the targets, and no bias from test lines dissimilar to the targets. For distractors, in contrast, the biases were repulsive and became stronger with decreasing similarity. However, due to the nature of the task, the orientations of targets and distractors are not fully independent, and therefore also the effect of their similarity to the test line (the target must be dissimilar to distractors). Therefore, we treated this analysis as exploratory and further addressed tested effects of similarity in the following experiments.

10.5 Experiments 2 and 3

The results of Experiment 1 indicate that while to-be-ignored objects (in our case distractors during visual search) lead to repulsive serial dependence effects upon perceptual decisions, the attended items (targets) casued an attractive bias. Importantly, this occurs not only for visual search targets but also for a task-irrelevant test line, indicating that this is not simply a task-based bias but causes general biases upon perceptual decisions. Yet, the evidence for the distractor effect was not significant. In Experiments 2 and 3, we looked at proximity in feature space as a potential moderating factor for both target and distractor effects.

Some recent studies have shown that proximity in feature space between what we have recently perceived and what we are currently observing can determine the direction of serial dependence produced by preceding items (whether the biases are attractive or repulsive). Fritsche et al. (2017) showed that two stimuli could induce opposite biases, depending on their distances in feature space. In Experiments 2 and 3, we therefore manipulated the distances in feature space between the distractors and test line and between the target and the test line to investigate the effect of proximity in feature space on the biases produced by our visual search stimuli (see Figure 13).

10.5.1 Method

10.5.1.1 Participants

Twenty participants (thirteen females and seven males, mean age = 31.3 years for Experiment 2, and seventeen females and three males, mean age = 28 years for Experiment 3) were recruited. All had normal or corrected-to-normal vision and provided written informed consent before starting the tests, which briefly explained the experimental procedure.

10.5.1.2 Stimuli and procedure

The methods in Experiments 2 and 3 were overall similar to Experiment 1. In Experiment 2, the test line orientation was close to the target orientation and far away from the mean of the distractor distribution. The mean distractor orientation for each block was picked randomly (from 0° to 180°), and the test line orientation was selected so that it ranged from 70° to 110° (in 4° steps) away from the distractor distribution mean with an equal number of trials within each distance bin. On the last visual search trial within each block, the target orientation had either a 10°, 0° or -10° distance to the test line (counterbalanced). On trials preceding this last trial, the target was selected from a uniform distribution with 60° to 120° distances from the distractor mean. So, to ensure that the biases produced by target and distractors are not confounded, all the distances in feature space between the test line orientation and the mean distractor orientation, and target orientation were counterbalanced.

Since our aim was to address the role of relations in feature space between targets and distractors on the one hand and the test line on the other, in Experiment 3, in contrast with Experiment 2, the test line orientation was close to the mean of the distractors and far from the target (see figure 13). The mean distractor orientation was selected randomly from 0° to 180°, as in Experiment 2. Next, the test line orientation was picked from 10°, 0°, or -10° distances to distractors. The distractors were, therefore, close to the test line in feature space. The target orientation was also chosen from 70° to 110° (in 4° steps) from the test line orientation.

10.5.1.3 Results and discussion

In both Experiments 2 and 3, priming effects were observed, suggesting that observers learned target and distractor characteristics within each block. In

Experiment 2, the RT (*F*(4, 76) = 6.11, *p* = .016, η^2_G = .02, *M* = 825 , *SD* = 200) decreased and accuracy (*F*(4, 76) = 2.94, *p* = .045, η^2_G = .02, *M* = 93.4 , *SD* = 3.9) increased significantly over the visual search trials. In Experiment 3, the priming effects for accuracy (*F*(4, 76) = 3.66, *p* = .015, η^2_G = .01, *M* = 92.7 , *SD* = 4.5), and RT were also significant (*F*(4, 76) = 9.41, *p* = .002, η^2_G = .02, *M* = 729, *SD* = 160).

The target and distractor effects on adjustment error for Experiments 2 and 3 are shown in Figure 14. Overall, the adjustment error was similar to Experiment 1 (*M* = 0.17°, *SD* = 14.28° for Exp. 2 and *M* = 0.004°, SD = 10.38° for Exp. 3). Both attention and proximity in feature space between the inducers (targets and distractors) and the test line clearly affected the direction and magnitude of the serial dependence effects (Figure 14). In Experiment 2, the targets (close to the test line in feature space) caused an attractive bias (*b* = -4.61, 95% HPDI = [-5.96, -3.22]), and the distractors (far away from the test line) caused a repulsive bias (*b* = 0.78, 95% HPDI = [0.24, 1.35]). Comparing the restricted models (dropping the target or distractor effect) against the full model, we found that the full model provided a better fit in both comparisons (full model vs. target-only: logBF = 3.41; full model vs. distractors-only: logBF = 15.58).

In contrast with Experiment 2, in Experiment 3, where the test line was similar to distractors and differed from targets, the direction of serial dependence for distractors was reversed – the distractors induced an attractive bias (*b* = -0.92, 95% HPDI = [-1.56, -0.27]), while the target-induced bias was close to zero (*b* = -0.12, 95% HPDI = [-0.63, 0.39]). The full model provided a slightly worse fit than the distractors-only model (logBF = -0.21) but predicted the data better than the target-only model (logBF = 4.79). Therefore, the results for Experiment 3 indicate, in contrast with Experiment 2, that the distractors played a larger role in shaping the adjustment error than the targets and created attractive and not repulsive biases.

Overall, the results of Experiments 2 and 3 show that proximity in feature space between what we have already perceived and what we observe determines the direction of the biases from visual search distractors and targets. This means that attention (or whether an item is a target or distractor) is not the only factor determining the direction of the biases. In Experiment 2, the targets induced an attractive bias and the distractors a repulsive bias (as in Experiment 1), while in Experiment 3, this was reversed; the distractors produced an attractive bias upon perceptual decisions of the orientation of the test line even though they were to be ignored. On the other hand, the attended stimuli (the targets) did not affect the test line's perceived orientation. Therefore, Experiments 2 and 3 argue strongly that feature-space proximity plays a large role in determining bias direction.

10.6 Experiment 4

The results of Rafiei et al. (2021) showed how attention plays a role in shaping biases from serial dependence. Distractors that must be ignored led to a repulsive bias, while attended targets introduced attractive biases. This conclusion was supported in Experiments 1 and 2 here. However, the results of Experiment 3 complicate this story since they show that proximity in feature space between what we have perceived previously (targets or distractors) and what we currently perceive modulates the direction of the biases. In Experiment 4, we aimed to assess the role of attention in forming perceptual biases by converting the distractors from to-be-ignored stimuli to neutral ones by cueing the target location.

10.6.1 Method

10.6.1.1 Participants

As in the preceding experiments, we recruited twenty participants (twelve females and eight males, mean age = 30.95 years). All had normal or corrected to normal vision and signed informed consent where the experimental procedure was outlined briefly.

10.6.1.2 Stimuli and procedure

In Experiment 4, the methods were similar to Experiment 2, where the targets were close to the test line orientation, and the distractors were far from it. However, in this experiment, the crucial difference is that the target location was cued by a small dot presented for a short period (500 milliseconds) before the visual search trial started. The size of the light-gray dot was 3 pixels, shown 30 pixels (0.54° visual angle) above or below the target line center for 500 milliseconds. We reasoned that if participants were cued to the target location, they would not need to search for the target among the distractor lines, which would therefore not need to be actively rejected as nontargets. The task was to report the target position relative to the cueing dot, so participants were to press the "D" key if the target appeared below the cue and "E" if the target appeared above it. After completing 4-5 such trials in each block, an irrelevant test line was presented, followed by the adjustment line like in previous experiments.

10.6.1.3 Results and discussion

In Experiment 4 adjustment errors were similar in magnitude to previous experiments (*M* = 0.25°, *SD* = 9.93°). The targets produced an attractive bias in the perceived orientation of the test line (b = -3.76, 95% HPDI = [-4.89, -2.57]; see plot for Experiment 4 in Figure 14). In contrast, the effect of distractors was repulsive but close to zero (b =0.48, 95% HPDI = [-0.02, 1.01]). The model comparisons showed that the full model, which included both effects, fit the data better than both the distractors-only (logBF = 13.21) and targets-only models (logBF = 1.65).

The results of Experiment 4 suggest that the role of proximity in feature space may be just as important than the role of attention. When the distractors were converted to "neutral" stimuli with a pre-cue, the distractors still produced a repulsive bias in perceived test line orientation. We speculate that parts of the biases that we see reflect stimulus-based, not attentional factors; in other words, that even though the distractors do not play a distracting role, they nevertheless bias subsequent perceptual decisions through merely being present on the screen.

10.7 General Discussion

In Rafiei et al. (2021), we demonstrated for the first time how attended and ignored stimuli in visual search create perceptual biases. We argued that at least two opposite biases influence perceptual decisions of a search target. Positive serial dependence pulls the target toward previous target features, and a negative bias pushes targets away from distractors. Here, we set out to address three questions regarding biases created by targets and distractors during visual search, this time upon perceptual decisions of a neutral test object. Our main conclusions are:

1) There were biases from both preceding targets and distractors upon perceptual decisions of a neutral, task-irrelevant test line. Overall, attended items (targets) produce stronger serial dependence than ignored ones (distractors).

2) Both attention and proximity in feature space play important roles in determining the perceptual biases from serial dependence.

3) We tested how cueing the target location (presumably eliminating the need for search) affected serial dependence biases. Even when the distractors were not "to-be-rejected" items anymore but were irrelevant to the task (and dissimilar to the test item), they still produced repulsive biases. These results show that even if their attentional role is weakened, distractors still cause biases, arguing for a lower-level bias from the repeated distractors.

10.7.1 What functional role do the biases play in perceptual decisions?

The first thing to note is that the current results show that serial dependence biases from visual search operate on perceptual decisions generally, not just on the search relevant items. Rafiei et al. (2021) reported similar biases on the perceived orientation of a search target as a function of the previous trial target and current distractors. However, those original results could reflect the fact that observers report their search template instead of the search target. Our current results suggest that this is unlikely, however. The biases created by the search task affect neutral items and reporting the search template instead of the neutral item would make little sense in this scenario. Search templates may nevertheless play a mediating role in the observed biases (see below).

Secondly, the to-be-ignored items induce a bias acting in parallel with positive biases induced by attended items. The latter is often described as serial dependence and is assumed to stabilize and preserve continuity in perception in the spirit of the continuity field proposed by Fischer & Whitney (2014). Serial dependence is thought to help us deal with familiar conditions by ignoring minor changes in already perceived items and maintaining continuity in perception over time (Cicchini & Kristjánsson, 2015; Liberman, Zhang & Whitney, 2016).

Pascucci et al. (2019) argued that perception is at any moment shaped by two contrasting history-based forces: sensory adaptation (as in classic after-effects such as the tilt or motion after-effects; Gibson, 1937; Wohlgemuth, 1911) and past decisions. According to their account, repulsive forces (such as those seen in various low-level negative after-effects) push perception away from recently perceived stimuli. Conversely, attractive forces dominate human perception during sequences of perceptual decisions, biasing the present sensory input so that it appears more similar to past visual input than it actually is, serving as compensation for sensory adaptation. This mechanism might explain the repulsive biases we observed. However, this similarity effect (similar distractors create attractive biases while dissimilar ones create repulsive biases) does not fit the typical pattern of sensory adaptation (stronger repulsive biases for similar inducers, weak, often attractive or no biases for dissimilar ones, see reviews in Clifford, 2014; note, however, that Solomon et al., 2004, observed a pattern of results that is more similar to what we found). This explanation can nevertheless be tested in future research into the effects of different roles that items play in this interdependence.

We speculate that our findings may be related to what has been called tuning of target templates through the history of both distractors (Chetverikov et al., 2020; Geng, Won, & Carlisle, 2019) and targets (Hansmann-Roth, Geng, & Kristjánsson, 2020b; Manassi, Kristjánsson & Whitney, 2019; see Geng & Witkowski, 2019 for review and see Fischer, Czoschke, et al., 2020 for evidence of context-based serial dependence). Visual search templates can be optimally tuned through perceptual history to help us find items similar to the target. As Bravo and Farid (2016) put it: “rather than being a faithful, unbiased representation of the target, the target template is a biased representation that reflects the information necessary to perform the search task.” Bravo and Farid (see also Navalpakkam & Itti, 2007) argued that the template is adapted to the task at hand, and we propose that recent perceptual history plays a crucial role in determining this bias. The representations (or templates) are dynamic – dependent on the context, and our current findings may cast light on how the templates are biased. Importantly, our results suggest that the search templates can bias perceptual decisions of irrelevant items and that these biases serve the purpose of making the objects of interest in each case more salient (assuming that the biases can influence relatively early visual processing so identifying items matching the biased search templates becomes easier during later processing). Manassi et al. (2019) reported interesting findings with respect to this in a visual classification task. They found that visual classification of single objects was serially dependent, biasing classification towards previously perceived objects, but only between similar objects and within a limited spatial window, showing the three characteristics proposed for continuity fields (featureal, temporal and spatial tuning). We speculate that this reflects the biasing of templates. The intriguing question is, therefore, whether parallel template biases can be found for distractor-based repetition effects.

10.7.2 Effects of attention and proximity in feature space

In Experiment 1, where feature space distances between test line orientation and the target on the one hand and target orientation and distractor orientation on the other, were selected randomly, the target caused attractive biases while there were hints of a repulsive bias from distractors. Experiments 2 and 3 then indicated that feature space proximity plays a crucial role in determining bias direction. In Experiment 2, where target orientation was close to the test line orientation, the targets caused attractive biases, but when the same targets in Experiment 3 were far from the test line, there was no significant bias. Conversely, the distractors produced a repulsive bias upon perceived test line orientation when they were far from each other in feature space (Experiment 2) but produced an attractive bias when they were close to the test line orientation in feature space in Experiment 3. Thus, even though the distractors and targets roles in Experiment 3 were the same as in Experiment 2, a change in how similar they are to the test item affected the direction and strength of the biases. This shows an interactive relationship between feature space proximity and whether items are attended targets or distractors to be ignored.

Bliss et al. (2017, see also Fritsche et al., 2017; Samaha et al., 2019) reported attractive biases upon orientation estimations when preceding stimuli had similar orientations to the current ones in a serial dependence paradigm involving an inducer and a test stimulus. Additionally, Fritsche et al. (2017) reported repulsive biases when the inducer and the test were dissimilar. Later, Fritsche and de Lange (2019) found that the attractive bias was strongly reduced when observers attended to a different feature of the previous stimulus than orientation, arguing for a role of feature-based attention in determining perceptual biases. This is similar to previous findings suggesting that serial dependence is gated by attention (Fischer & Whitney, 2014; Forniciai & Park, 2018; Liberman, Zhang & Whitney, 2016). In contrast, repulsive biases in Fritsche and de Lange (2019) were not affected by feature-based attention. Our results partly agree with these findings but, in other ways, go against them. As in Fritsche et al. (2019), we found attractive biases from items similar to the test and repulsive biases from items dissimilar from the test. Furthermore, we also found that attention strengthens the attractive biases from similar items. However, in our experiments, the repulsive biases were not observed for dissimilar targets, only for dissimilar distractors. Additionally, Experiment 4 suggests that the bias from distractors is weakened when they are not directly a part of the task. In sum, our findings suggest that both attractive and repulsive biases are affected by attention but in different ways.

10.7.3 Context effects and ensembles

Previous results have revealed strong effects upon response times in visual search (see Kristjánsson & Ásgeirsson, 2019 for a recent review), both from targets (Maljkovic & Nakayama, 1994) and distractors (Kristjánsson & Driver 2008; Saevarsson et al., 2008). The current results add a crucial component to such visual search effects in showing how they affect perceptual decisions of a task-irrelevant item. While we speculate that similar mechanisms facilitate search and cause the perceptual biases we see here, mapping their connection requires further research.

Our results also add to our understanding of these processes by demonstrating how both attended items and items that need to be ignored influence perceptual decisions. The distractor effect here is interesting in light of the finding that perception of a visual ensemble (e.g., a set of Gabor patches) is sequentially dependent on previously perceived ensembles (Manassi et al., 2017; see Pascucci et al., 2019, Experiment 7, for related findings). Our current findings reinforce this, suggesting that not only attended but also distracting ensembles create perceptual biases.

10.7.4 Potential relations with visual working memory

Whether serial dependence reflects working memory function is hotly debated (see, e.g., Lorenc, Mallet & Lewis-Peacock, 2021 and Kiyonoga et al., 2017 for reviews). Interestingly, Rademaker, Bloem, De Weerd, and Sack (2015) showed that when observers have to remember the first of two sequentially presented Gabor patches, the remembered orientation of the Gabor was biased towards the second irrelevant stimulus. Similar to our conclusions here, Rademaker et al. argued that both attended and ignored information (in their case in working memory) is used to maintain continuity within the visual environment. Golomb (2015) found that for two simultaneously presented stimuli, memory is biased away from a distractor when it is similar to the test item but towards it when it is dissimilar (see also Chunbaras et al., 2019; Bae & Luck, 2019). What is interesting about these findings is how feature space and attentional role are both critical for the biases of the representations as is the main finding here.

10.7.5 Serial dependence as a general feature of perceptual mechanisms?

The wide-ranging spectrum of findings on serial dependence effects that we scratch the surface of here raises the intriguing question of whether serial dependence is a general characteristic of perceptual mechanisms or whether there is a specific mechanism devoted to promoting serial dependence. Serial dependence is unlikely to solely reflect low-level activity. For example, areas of the prefrontal cortex show activity modulations from serial dependence in working memory (Barbosa et al. 2020; although there is also evidence for serial dependence in earlier visual areas, John-Saaltink et al., 2016; van Bergen & Jehee, 2019). Cicchini, Benedetto & Burr (2020) have recently proposed that the priors that presumably play a crucial role in serial dependence arise in higher-level visual processing, propagating information down to earlier sensory processing levels. This interesting possibility invites speculation that the detailed characteristics of SD may differ depending on particular circumstances, for example, whether the effects are positive or negative, large, or small (see Murai & Whitney, 2021 for similar speculation). Also, their temporal profiles may differ depending on the network involved in analysing particular aspects that SD is seen for. Our results are consistent with this general scenario since they show how two separate aspects, feature proximity and attention, lead to serial dependence. In sum, serial dependence might be a general characteristic of perceptual processing at different levels of the cognitive hierarchy, from low-level sensory processing to higher-level decision-making. A similar proposal regarding the nature of potentially related history effects (attentional priming) has recently been made (Kristjánsson & Ásgeirsson, 2019).

10.7.6 Summary and Conclusions

The most important result here is that visual search can induce biases in the perceived orientation of a test line that is unrelated to the search task. Our results also indicate that these biases are strongly determined by both attention and similarity between the search stimuli and the test item. Overall, we speculate that our results provide a glimpse of the bag of tricks that the visual system uses to optimize perceptual decisions over time. These tricks may be diverse, depending on the context and may not always follow simple operational principles but can be highly task-dependent. Biases from previous stimuli may be a general feature of perceptual mechanisms and their diverse manifestations may reflect the operational characteristics of the particular neural mechanisms involved in each case.

10.8 Open Practices Statement

A preprint of this paper is available at https://psyarxiv.com/sah9n. Additionally, the experiment's scripts and the code that we use to analyze the collected data in our experiments are available at https://osf.io/ndmju/.

10.9 References

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Paper III

The influence of the tested item on serial dependence

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11.1 Abstract

Serial dependence in vision reflects how perceptual decisions can be biased by what we have recently perceived. While these studies have typically involved single stimuli, our visual world at any given moment contains a multitude of objects. We recently demonstrated how serial dependence from large arrays of visual search items affects the perceived orientation of a single test-line. Visual search targets caused positive serial dependence while the to-be-ignored distractors caused negative serial dependence. Secondly, repulsive serial dependence occurred from dissimilar items and attractive serial dependence from similar items. Here we asked the complementary question: What effect does a single item have when there is more than one subsequent test item? We first displayed a single line (inducer) on the screen and subsequently, either a single test-line or two simultaneous test-lines appeared, varying in similarity in orientation space to the inducer and test. Next, participants reported the orientation of the test-line using a response circle located either at the left or the right (to indicate which test-line should be reported). A single inducer caused serial dependence biases upon two stimuli presented simultaneously that was modulated by distance in feature space between the inducer and test items where distant items caused repulsive serial dependence and close items caused attractive serial dependence.

11.2 Introduction

Despite all the noise in our sensory input, we perceive a seamless and stable visual world around us whenever we open our eyes. How does the visual system achieve this stability? Serial dependence studies (Fischer & Whitney, 2014; Cicchini, Mikellidou, & Burr, 2017, 2018; Fornaciai & Park, 2018) suggest that perceptual history is used to construct a continuous visual world and to compensate for noise in the visual information from factors such as changes of viewpoint from eye movements or self-motion, changes in lighting or shading or because of occlusion.

Fischer and Whitney (2014) showed that following an oriented Gabor patch inducer, perceptual decisions related to the orientation of a subsequent test Gabor were serially dependent upon the inducer's orientation (see Burr & Cicchini, 2014; Cicchini & Kristjánsson, 2015; Kiyonaga, Scimeca, Bliss, & Whitney, 2017 for review). Fischer & Whitney (2014) argued that such serial dependence results from a spatiotemporal integration window that they called the continuity field, where stimuli seen a few seconds ago interact with the perception of current visual stimuli (Collins, 2019; Gekas, McDermott, & Mamassian, 2019; Fritsche, Spaak, & de Lange, 2020). Further studies have shown that judgments of numerosity (Fornaciai & Park, 2018), eye gaze (Alais, Kong, Palmer, and Clifford, 2018), shape (Manassi, Kristjánsson & Whitney, 2019), motion coherence (Suarez-Pinilla, Seth, & Roseboom, 2018), facial identity (Liberman, Fischer & Whitney, 2014), gaze direction (Alais, Kong, Palmer, & Clifford, 2018), or emotional expressions (Liberman, Manassi, & Whitney, 2018) are also serially dependent on perceptual history.

These serial dependence studies were typically performed on single objects. However, our visual world at any given moment contains a multitude of objects. Rafiei et al. (2021a) used attended targets and ignored distractors in a visual search task as inducers finding that the attentional role of the inducers played a crucial role in determining the direction and amplitude of serial dependence. Utilizing the feature distribution learning (FDL) method (Chetverikov, Campana & Kristjánsson, 2016, 2019, 2020; Hansmann-Roth et al., 2019; 2020a; 2021; Tanrikulu, Chetverikov & Kristjánsson, 2020) to ensure sure that participants learned the distractor distributions, participants completed a few odd-one-out visual search trials. At the end of each block, participants were asked to report the orientation of the last target in the block (target on trial N). The target on trial N-1 caused an attractive bias upon decisions about the target orientation on the last trial (trial N), while the distractors produced a repulsive bias. Later, Rafiei et al. (2021b) tested serial dependence effects of visual search items upon a task-irrelevant test-line, with similar results, showing that the effectiveness of these biases is not limited to the perception of a visual search target.

Notably, the attractive serial dependence effect found in Rafiei et al. (2021b) decreased in amplitude with decreasing similarity of the test and inducer. The orientation difference between the inducer and test affected the direction of the bias (see also Fritsche et al., 2017; Fritsche & de Lange, 2019). In four experiments, participants in Rafiei et al. (2021b) completed 4-5 odd-one-out visual searches, locating an oddly oriented target among distractors; followed by a briefly presented test-line, and participants then reported the orientation of the test-line by rotating a line located in the middle of the screen. The proximity in orientation space between the target orientation, the distractors' average orientation, and the orientation of the test-line was manipulated. The distractors produced an attractive bias when the test-line orientation was close in feature space to the distractor orientation. However, when the target orientation was far from the test-line orientation, it did not produce any serial dependence upon the test-line. Rafiei et al. argued that both proximity in feature space and the attentional role of a particular item (whether it is a visual search target or distractor) both play a crucial role in determining the direction and the amplitude of biases in perceptual decisions.

11.3 Current aims

In these previous studies, we investigated the influence of a set of items upon the perception of a subsequent single item. In the current study, we addressed the opposite question – what serial dependence biases are induced by a single item upon more than one item when observers only learn after the items disappear, which one is relevant. We compare this with the case when only one test item appears. This question is also crucial from the perspective of the issue of proximity in feature space since unlike in the studies in Rafiei et al. (2021a; 2021b) the inducer does not have an explicit task role (a target or a distractor). Our observers viewed an inducer (an oriented line) on the screen, and subsequently, two lines with different orientations appeared, where one of them was similar to the inducer's orientation (close in feature space), and the other dissimilar (far in feature space).

To summarize, our previous investigations revealed that inducers (visual search targets and distractors) produce attractive or repulsive bias upon perceptual decisions depending on their attentional role. Here we asked whether similar biases upon a set of lines would occur from a single inducer and whether a single inducer simultaneously causes both attractive and repulsive biases. We also assessed the effects of proximity in feature space between the inducer and the visual search items.

11.4 Method

11.4.1 Participants

Twenty students or members of staff at the University of Iceland participated (11 Females, average age = 26.31 years; 9 Males, average age = 25.75) signing informed consent forms. All participants had normal or corrected to normal vision. All participated in a training session which was held at least one day before the experimental session. The training and experimental sessions were identical.

11.4.2 Stimuli and procedure

The stimuli appeared on a grey background on a 24-inch Asus monitor with a 1920×1080-pixel resolution at a viewing distance of approximately 70 cm, and Psychopy 3 (Peirce et al., 2019) was used to generate the stimuli and control their presentation. Trials were defined by the combination of the number of lines on the test screen (One or Two) and the similarity of the tested line to the post-cued inducer (Similar or Dissimilar): One-Similar, One-Dissimilar, Two-Similar, and Two-Dissimilar conditions, see Figure 15). There were 350 trials in each session, selected randomly from the four conditions.

Each trial had four parts (Figure 15). Firstly, participants were asked to pay attention to the orientation of a 2.5 deg line presented at the screen center for 500 ms (inducer, orientations selected randomly from 0-180). Subsequently, the test display was presented, which involved either one line on the left or right side of fixation or two 2.5 deg lines on either side of fixation (10 degrees away from the fixation point displayed for 500 ms) . The main manipulation was how the orientation of these test-lines differed relative to the inducer's orientation. There were four different test displays: In the *One-Similar* condition, only one test line appeared either on the left or right side of the screen, oriented similarly as the inducer (-15 to 15 in 5-degree steps, excluding 0 degrees). In the *One-Dissimilar* condition, the orientation of the presented line on the left or right side of the screen was ± 50 to 80 degrees, away from the inducer's orientation. In both these conditions the orientations were randomly clockwise (CW) or counter-clockwise (CCW) relative to the inducer. Two lines were displayed on the left and right sides of the screen for 500 ms in the *Two-Similar* and *Two-Dissimilar* conditions. The orientation of one of the lines was similar to the inducer's orientation (as in the One-Similar condition), while the other line's orientation was dissimilar to the inducer's orientation (as in the One-Dissimilar condition).

A mask was then presented in the middle of the screen for 500 ms (covering the locations of the lines). Finally, participants were asked to report the orientation of the line from the previously seen display using the response circle by aligning the two disks with the orientation of the test-line (by pressing the 'left' or 'right' keys). They confirmed their response with the "Up" key and moved on to the next trial. The response circle was located either on the left or the right, and its location served as a post-cue about which line should be reported. Therefore, participants did not know which line from the Two-Similar and Two-Dissimilar conditions should be reported until the response screen appeared. In the one-similar and one-dissimilar conditions, the response circle always appeared behind the presented test-line.

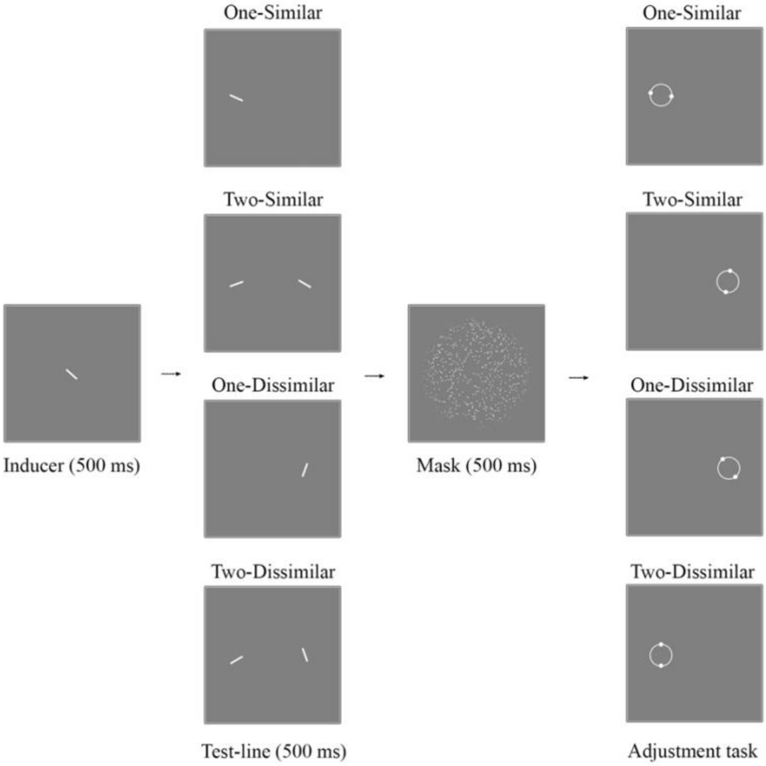

Figure 15. Design of a single trial in the experiment. Participants were asked to pay attention to the inducer's orientation and the test-line(s) presented on the following screen in each trial. Subsequently, participants had to report the orientation of the line from the previously viewed screen (second screen), using the response circle positioned either on the left or right side (to indicate which line should be reported), where they used the "Right" and "Left" keys to rotate the answer circle.

11.5 Data analysis

A hierarchical Bayesian model was used to estimate the effects of the inducer's orientation on the judgment of the test-lines. The hierarchical Bayesian model integrates all the data in a single model and evaluates the uncertainty of parameter estimates. We modeled the biases with a Bayesian hierarchical linear model as a function of the number of lines and the similarity between inducer and test-line(s). However, before starting analyzing the data, we removed the outliers from the data, and to do that, we first determined the direction (being attractive or repulsive) of the biases for each participant. To accomplish that, we compared the fits of the two models. The first model assumes an attraction for cardinal orientations and that the mean error for each observer is a function of two fourth-degree polynomials centered on cardinal orientations (0,90), with each polynomial spanning a 90-degree range (so one is from -45 to 45 and another is at 45 to 135). The second model presupposes repulsive biases and comprises two polynomials with their centers in oblique orientations (45, 135). Both models presuppose that the response variance can change linearly as a function of the distance to the polynomial's center. Whichever model fits the data better is chosen for the subsequent analyses. Following that, the best-fitting model is used to compute the bias-corrected responses by removing the mean predicted error, or in other words, computing the model's residuals. Finally, bias-corrected errors greater than or equal to +/- 3 predicted standard deviation are considered outliers and excluded from subsequent analyses.

After excluding the outliers, to assess how proximity in feature space between the inducer and current stimulus orientations affected the biases produced by the inducer, we calculated the adjustment error for the reported orientation by subtracting the actual orientation from the reported orientation.

11.6 Results

We modelled the bias caused by the inducer by employing a Bayesian hierarchical linear model as a function of the proximity in feature space between the inducer and the test line, the number of line(s) presented on the screen and the intercept as fixed effects. The number of line(s), the proximity in feature space between the inducer and the test line, and the intercept were also modeled as random effects. As shown in Figure 16, when the orientations of the test-line and the inducer were similar, there was a strong attractive bias upon the test-line, (*b* = -0.71, 95% HPDI = [-1.01, -0.40], BF = 3999, the calculated BF is for both the One-Similar and Two-Similar conditions).

We next tested the condition where the orientations of the inducer and test-line(s) were dissimilar. The results showed that the inducer produced a repulsive serial dependence bias upon the current item (*b* = 0.29, 95% HPDI = [0.54, 0.03], BF = 24.64, for both One-Dissimilar and Two-Dissimilar together), independently of the number of lines shown on the test-line screen (see figure 16).

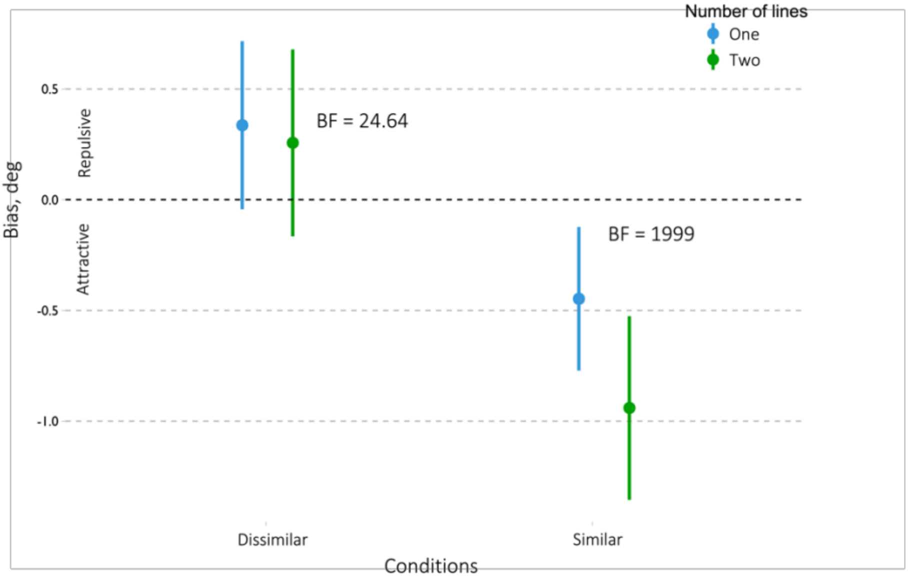

Figure 16. The biases produced by the inducer upon similar and dissimilar test-lines as a function of whether one or two test-lines were presented. The results showed that based on the similarity between the inducer and the test-line, the inducer caused opposing serial dependence. When the inducer and test-line(s) were dissimilar, the inducer produced a repulsive bias. However, the inducer produced an attractive serial dependence bias when they were similar. The bars here represent the confidence interval of the biases produced by the inducer.

To test how the number of simultaneous test-lines affected the serial dependence, we compared the biases in the trials where one line was shown on the screen against trials with two lines presented on the screen in the "Similar" condition. To do that, we used a Bayesian paired t-test, and the results showed that the number of lines presented on the screen did not affect the bias produced by the inducer (BF = 0.90). We also adopted a similar analysis for the "Dissimilar" trials and compared the biases on the trials where one line was presented on the screen versus the trials where two lines were displayed on the screen; the results showed that the number of lines presented on the screen did not affect the serial dependence (BF = 0.38).

11.7 Discussion

Here we investigated whether similar biases from a single line upon a set of test-lines would occur as we found from a set of lines upon a single test-line in Rafiei et al. (2021a; 2021b). Secondly, we further assessed the effects of proximity in feature space between the inducer and the test items. Thirdly, we assessed whether a single inducer could cause both attractive and repulsive serial dependence upon a subsequent test item.

We first presented a single inducer and later showed either one or two oriented test-lines on the screen. On half of the trials, participants needed to report the orientation of the only test line, while on the rest of the trials, they were asked to report the orientation of one of two test lines (they did not know which one to report until the report display appeared). This question is interesting from the perspective of the proposal of the continuity field in perception (Fischer & Whitney, 2014; Liberman et al., 2016) since when two potential tests appear the continuance is uncertain, a version of the well-known correspondence problem seen in many contexts in visual perception (e.g., Ullman, 1979). The results showed that a single inducer introduced opposing serial dependence biases upon the two items, depending on their relations in feature space.

11.7.1 Is serial dependence altered by having two potential test-lines?

Serial dependence is thought to help us make sense of noisy visual input from our environment (like when we move our eyes, we blink, or we see unwanted items like distractors) by using previous information about items in the visual environment and making the assumption of continuity (Fischer and Whitney, 2014; Cicchini, Mikellidou, & Burr, 2017; Liberman et al., 2016; Rafiei et al., 2021a, 2021b). For example, our earlier studies (Rafiei et al., 2021a and 2021b) showed that distractors and targets could act as two sources of biases in perceptual history, introducing opposing biases upon the perception of a single test item. Most SD studies have investigated the role of a single preceding stimulus on the perception of a subsequent single item. In the real world, however, we usually perceive many stimuli simultaneously, raising the question of how information from our perceptual history affects the multitude of items we see at a given moment.

The role of serial dependence has been assumed to *smooth* perception to maintain perceptual continuity to deal with noise in the visual input from sources such as shifts in gaze, occlusion or change in lighting (Burr & Cicchini, 2014; Cicchini & Kristjánsson, 2015; Collins, 2019; Gekas, McDermott, & Mamassian, 2019; Fritsche, Spaak, & de Lange, 2020). But how does the visual determine what follows what? While our results do not directly address this question, they show that a single inducer item can introduce serial dependence biases upon more than one item simultaneously. Note that Fischer et al. 2020 (experiments 3 and 4): presented two differently colored dot fields simultaneously at different spatial positions, finding serial dependence between trials modulated by the color of the dots. They did not, however, try to address the question that we address here of differences between one and two items, nor did they assess effects of a single task-irrelevant inducer line upon subsequent test-lines.

11.7.2 The effects of proximity in feature space

Proximity in feature space between the inducers and test item has been found to affect the direction of the serial dependence biases (Rafiei et al., 2021a, 2021b; as shown previously by Fritsche et al. 2017; 2019). However, in previous studies, two factors potentially affected the biases; their attentional role (whether they were a target or a distractor), or the proximity between the inducer and the current stimulus. Here, the inducer did not have any differential attentional role (it was not attended like a target among distractors or actively ignored like a distractor) and our results therefore confirm that when the inducer and the current item are similar (close in feature space), there is an attractive bias from the inducer line upon the test-line (in line with Fischer and Whitney, 2014, and Rafiei et al., 2021a, 2021b). But if the inducer and the current item are dissimilar (far from each other in feature space), the inducer introduces a repulsive bias. These results align with our previous findings in Rafiei et al., (2021a, 2021b) and Fritsche and colleges (2017, 2019). Proximity in feature space is one of the main factors determining whether biases produced by an inducer line are attractive or repulsive, but importantly this bias is not specific to a single test-line but occurs for two potential test items, where which one to report is only revealed after they were presented.

11.8 Conclusion

In Rafiei et al. (2021a,b) we showed how serial dependence from arrays of visual search stimuli affects the perceived orientation of a single test-line. But what is the effect of a single item upon more than one subsequent test item? Our results show that a single inducer can bias the orientation judgments of two items simultaneously. Secondly, we assessed the effects of proximity in feature space between the inducer and the visual search items finding that proximity in feature space affects the direction of the biases produced by the inducer. The same inducer causes an attractive bias if it is similar to the test but a repulsive bias if they are dissimilar. This means that a single inducer simultaneously produces both attractive and repulsive serial dependence biases.

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