The role of feature-based attention in visual serial dependence

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Perceptual decisions about current sensory input are biased toward input of the recent past—a phenomenon termed *serial dependence*. Serial dependence may serve to stabilize neural representations in the face of external and internal noise. However, it is unclear under which circumstances previous input attracts subsequent perceptual decisions, and thus whether serial dependence reflects a broad smoothing or selective stabilization operation. Here we investigated whether focusing attention on particular features of the previous stimulus modulates serial dependence. We found an attractive bias in orientation estimations when previous and current stimuli had similar orientations, and a repulsive bias when they had dissimilar orientations. The attractive bias was markedly reduced—to less than half of its original magnitude—when observers attended to the size, rather than the orientation, of the previous stimulus. Conversely, the repulsive bias for stimuli with large orientation differences was not modulated by feature-based attention. This suggests separate sources of these positive and negative perceptual biases.

Introduction

Humans often form perceptual decisions based on ambiguous and unstable sensory input. In vision, this instability is exacerbated by several factors such as eye movements, blinks, and temporary occlusions of the visual scene. Moreover, further instabilities are introduced in the form of biological noise during neural processing. Yet despite all these instabilities, we exhibit a remarkable capacity for making successful perceptual decisions. A key question is therefore how our brains maintain stable neural representations for perceptual decision making.

Importantly, our environment is relatively stable over short timescales and thus exhibits temporal continuity (Dong & Atick, 1995). Theoretically, this temporal continuity could be exploited to stabilize neural representations. In particular, by leveraging information from the recent past, neural representations could be smoothed in time to compensate for perturbations which are not caused by genuine changes in the physical world (Burr & Cicchini, 2014). In line with this idea, recent studies have found that perceptual decisions about a large variety of visual stimulus features are biased toward features encountered in the recent past. Such features include orientation (Cicchini, Mikellidou, & Burr, 2017; Czoschke, Fischer, Beitner, Kaiser, & Bledowski, 2018; Fischer & Whitney, 2014; Fritsche, Mostert, & de Lange, 2017), numerosity (Cicchini, Anobile, & Burr, 2014; Corbett, Fischer, & Whitney, 2011; Fornaciai & Park, 2018a), spatial location (Bliss, Sun, & D'Esposito, 2017; Manassi, Liberman, Kosovicheva, Zhang, & Whitney, 2018; Papadimitriou, White, & Snyder, 2017), visual variance (Suárez-Pinilla, Seth, & Roseboom, 2018), face identity (Liberman, Fischer, & Whitney, 2014), emotional expression (Liberman, Manassi, & Whitney, 2018), and attractiveness (Xia, Leib, & Whitney, 2016). Such serial-dependence biases may arise at different stages during the perceptual decision-making process (Bliss et al, 2017; Cicchini et al., 2017; Fornaciai & Park, 2018a; Fritsche et al, 2017; Pascucci et al., 2019) and could perhaps jointly occur at multiple levels of stimulus processing (Kiyonaga, Scimeca, Bliss, & Whitney, 2017). Generally, the ubiquity of serial dependencies in perceptual decisions is striking and suggests that they might arise from a general computation of the brain, potentially reflecting the stabilization of neural representations.

Although serial-dependence biases have been observed in perceptual decisions about a variety of stimulus features, the conditions under which they arise are still elusive. Consequently, the precise boundaries within which a stabilization of neural representations could take place are not known. In particular, it is unclear how a previous stimulus needs to be processed in

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order to exert a serial-dependence bias in subsequent perceptual decisions. While serial dependence has been shown to depend on spatial attention toward the previous stimulus location (Fischer & Whitney, 2014), it has also been reported to occur when previous stimuli were task irrelevant (Fornaciai & Park, 2018a, 2018b), suggesting that attention to a particular stimulus feature is not necessary for serial dependence to occur. In a similar vein, serial dependence is often thought to arise on the level of objects (Liberman et al., 2014; Liberman et al., 2018), suggesting that attention to a particular stimulus feature might not be necessary as long as the object is spatially attended. Conversely, one recent study showed that serial dependence in judgments about visual variance occurred only when observers attended and reported the variance of a previous motion stimulus and not its direction (Suárez-Pinilla et al., 2018). While this result calls into question the independence of serial dependence from feature-based attention, it is unclear whether this would generalize to perceptual decisions about lower level visual features such as orientation or numerosity. Furthermore, Suárez-Pinilla et al. used different response methods for visual variance and direction reports, permitting the possibility that their results were influenced by serial dependencies in decisions about particular response adjustments rather than about the stimulus feature itself. The current study, therefore, aims to elucidate the role of feature-based attention in serial dependence. To this end, we measured serial dependence in orientation estimations about gratings, while participants attended to either the orientation or the size of a previous grating stimulus. Importantly, to isolate the effects of feature-based attention we tightly controlled the difficulty and the visual input in the two attention conditions.

Besides attractive serial-dependence biases, previous studies have observed concurrent repulsive biases when subsequent stimuli differed markedly (Bliss et al., 2017; Fritsche et al., 2017; Samaha, Switzky, & Postle, 2019). Currently, it is unclear whether attractive and repulsive biases originate from the same underlying neural process or whether they are two distinct phenomena, concurrently observed in behavioral responses. To shed light on this question, we also assessed whether repulsive biases for stimuli with large orientation differences are modulated by feature-based attention. Different modulations of concurrently observed attractive and repulsive biases by feature-based attention would indicate that these biases arise from at least partially independent processes.

To preview: Serial-dependence biases in orientation judgments were strongly modulated by feature-based attention. That is, orientation estimations were biased toward the previous stimulus orientation, and this bias was twice as strong when participants attended the orientation versus the size of the previous stimulus. Strikingly, repulsive biases for stimuli with large orientation differences were also robustly present but not modulated by feature-based attention, suggesting that they may arise from an independent process, potentially akin to classical repulsive tilt aftereffects (Gibson & Radner, 1937). Overall, the current study provides important insights into the conditions under which serial dependencies arise and demonstrates crucial boundaries within which stabilizations of neural representations through serial dependencies take place.

Methods

Participants

Thirty-eight participants (27 female, 11 male; age range: 19–34 years) who were unaware of the goals of the study took part in the experiment. All participants reported normal or corrected-to-normal vision and gave written, informed consent prior to the start of the study. The study was approved by the local ethical review board (CMO region Arnhem-Nijmegen, the Netherlands) and was in accordance with the Declaration of Helsinki. Our target sample size was $n = 34$. This sample size was chosen to obtain 80% power for detecting a medium effect size ($d = 0.5$) with a two-sided paired t test at $\alpha = 0.05$. Four participants were excluded after the first experimental session due to insufficient performance and were not invited to the main experimental sessions. These participants were replaced with new participants to obtain 34 complete data sets. The experiment and analyses were preregistered on the Open Science Framework (https://osf.io/q7gj3/).

Apparatus and stimuli

Visual stimuli were generated with the Psychophysics Toolbox (Brainard, 1997) for MATLAB (MathWorks, Natick, MA) and were displayed on a 24-in. flat-panel display (Benq XL2420T, resolution: 1,920 × 1,080, refresh rate: 60 Hz). Participants viewed the stimuli from a distance of 53 cm in a dimly lit room, resting their head on a table-mounted chin rest.

A central white fixation dot with a diameter of 0.25° visual angle was presented on a midgray background throughout all experiment blocks. Participants were instructed to maintain fixation at all times. A cue stimulus in the form of a white disc windowed by a Gaussian envelope ($SD = 0.4°$) was presented 9° visual angle to the left or right from fixation. Reference stimuli were formed by a dark-gray disc of variable size (radius 3°–3.5°) and two smaller, opposing discs (radius 0.2°) of the same color that were offset 7° from the

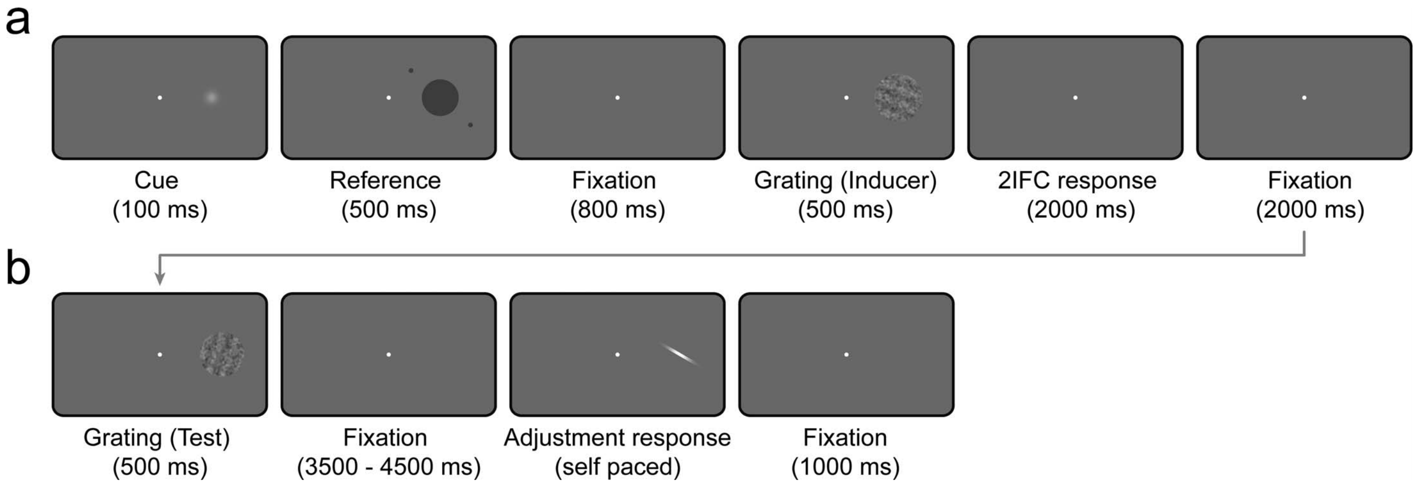

Figure 1. Sequence of events in the (a) two-interval forced-choice (2IFC) and (a–b) main-experiment tasks. In the 2IFC task, participants judged either the orientation or the size of a grating stimulus against a prior reference stimulus. The reference orientation was defined by a virtual line that connected the two outer discs of the reference stimulus, while the reference size was defined by the diameter of the inner disc. In separate blocks, participants had to indicate either whether the grating was oriented more clockwise or counterclockwise or whether it had a larger or smaller size than the reference. This task was used in a staircase procedure to titrate the orientation and size differences between grating and reference to a set level of difficulty for the main experiment. In each trial of the main experiment, participants first performed either the orientation or size 2IFC judgment on the first grating stimulus (inducer), separated in different sessions. After the 2IFC response, participants saw a new grating stimulus (test) and subsequently reproduced the orientation of this test grating by adjusting a response bar. Stimulus presentation in the left or right visual field was pseudorandomized across trials.

center of the reference stimulus. These smaller discs formed a reference orientation, which was defined as the orientation of a virtual line connecting the two small discs. We chose to indicate the reference orientation via these orientation discs—which were perceptually very different from the subsequent grating stimuli and did not contain any physical orientation information at the location of subsequent gratings—in order to minimize any positive or negative sequential biases exerted by the reference stimulus itself, as those biases are generally dependent on the similarity of successive stimuli and spatial overlap (Fischer & Whitney, 2014; Georgeson, 1973; Knapen, Rolfs, Wexler, & Cavanagh, 2010; Liberman et al., 2014). Grating stimuli consisted of a sine-wave grating (spatial frequency: 0.5 c/°, random phase, 8% Michelson contrast) with additive white noise smoothed with a Gaussian kernel with *SD* 0.1° (16% contrast). Stimuli were masked with a circular aperture of variable size. The response-bar stimulus was a white bar (width 0.4°) windowed by a Gaussian envelope with *SD* 1.2° and was presented at the same horizontal eccentricity as the cue and grating stimuli (Figure 1a and 1b).

Procedure

The experiment consisted of three separate sessions, each conducted on a different day, with consecutive sessions no more than 2 days apart. In the first session, we first measured each participant's individual thresholds for the orientation and size two-interval forced-choice (2IFC) tasks. In the remainder of the first session, participants practiced the serial-dependence task, which they performed in the second and third sessions. Participants were not invited to the second and third sessions if their orientation or size threshold for the 2IFC tasks exceeded previously defined maximum thresholds, thereby excluding those who were unable to perform the 2IFC tasks.

Threshold estimation

The sequence of events within each trial of the orientation and size 2IFC tasks is illustrated in Figure 1a. At the beginning of each trial, a cue was presented to the left or right of fixation for 100 ms. After a further 400 ms of fixation, a reference stimulus was presented on the same side as the cue for 500 ms. The inner disc of the reference stimulus had a radius randomly drawn from a uniform distribution on the interval [3°, 3.5°]. The two outer discs of the reference stimulus formed a reference orientation, defined as the orientation of a virtual line connecting the two discs. On each trial, the reference orientation was randomly drawn from a uniform distribution on the interval of all possible orientations (0°, 180°]. After 800 ms of fixation, a grating stimulus was presented on the same side as the cue and reference stimulus for 500 ms. The grating stimulus was oriented slightly more clockwise or counterclockwise with respect to the reference orientation and was slightly smaller or larger than the inner disc of the reference stimulus. After the offset of the grating stimulus, there was a fixed 2,000-ms response period and an intertrial interval of 2,000 ms. Participants performed one of two tasks, separated into different blocks. In the orientation 2IFC task, they judged whether the grating stimulus was oriented more clockwise or counterclockwise than the reference orientation. In the size 2IFC task, they judged whether the grating stimulus was smaller or larger than the reference disc. Responses were given via the arrow keys on a standard keyboard, and if no response was given within 2,000 ms after the offset of the grating, the fixation dot briefly turned red and a new trial began. In order to avoid participants focusing on a subpart of the grating stimulus to solve the tasks, the spatial position of the grating stimulus was randomly jittered by a maximum of 1.5° visual angle on every trial.

The difficulty of the 2IFC tasks could be varied by changing the relative orientation $\Delta\theta$ (during the orientation task) and size Δs (during the size task) of the grating with respect to the reference stimulus. For each participant, we estimated their individual thresholds $\Delta\theta$ and Δs for performing at an accuracy of 75% on both tasks using the QUEST staircase algorithm (Watson & Pelli, 1983). The resulting thresholds presented average thresholds for clockwise and counterclockwise rotations and size decrements and increments, respectively.

We first estimated the size threshold Δs, while holding $\Delta\theta$ constant at $\pm 10°$ orientation difference. Participants performed blocks of 48 trials. After each block, the convergence of the Δs threshold estimate was visually inspected by the experimenter, and estimation was terminated after Δs converged to a stable value. Subsequently, we employed the same procedure to estimate the orientation threshold $\Delta\theta$, while holding Δs constant at $\pm 0.15°$ visual angle change in radius. Prior to each threshold estimation, participants performed one or more practice blocks with fixed values of $\Delta\theta = 15°$ and $\Delta s = 0.3°$, respectively, until they felt comfortable with the tasks. During the practice blocks, participants received feedback about the correctness of their response via brief color changes of the fixation dot to green (correct) or red (incorrect).

Serial-dependence task

The sequence of events within each trial of the serial-dependence task is illustrated in Figure 1a and 1b. The first part of each trial was identical to the 2IFC task already described, with the exception that $\Delta\theta$ and Δs were now set to the individually estimated thresholds for each participant. Depending on session, participants performed either the orientation or the size 2IFC judgment. After the 2IFC response and 2,000 ms of fixation, a second grating stimulus was presented for 500 ms at the same side as the cue, reference, and first grating stimulus. This second grating had a relative orientation ranging from −90° to +90° in steps of 10° with respect to the first grating, and all relative orientations occurred equally often in pseudorandomized order. After a variable delay ranging from 3,500 to 4,500 ms, a response bar with a random initial orientation appeared at the same location as the grating. Participants were asked to reproduce the orientation of the second grating by adjusting the response bar with the left and right arrow keys. The response was submitted by pressing the space bar. The response was followed by a 1-s intertrial interval before the next trial began. The role of the first grating stimulus, which was always compared in orientation or size to the reference stimulus, was to induce biases in adjustment responses to the subsequent second grating stimulus on each trial. Therefore, we term the first grating the *inducer* grating and the second one the *test* grating. Since for the orientation 2IFC judgment participants had to focus on the orientation of the inducer and could neglect its size, we refer to the serial-dependence task with the orientation 2IFC judgment as the *orientation* condition. Likewise, the serial-dependence task with the size 2IFC judgment is termed the *size* condition, as participants had to focus on size and could ignore the inducer orientation.

Participants completed a total of 576 trials in the second and third sessions, each split into eight blocks. Whether they first performed the session with the orientation or size condition first was counterbalanced across participants. The horizontal location of the stimuli, the rotation and size change of the inducer grating with respect to the reference stimulus, and the relative orientation of the test grating with respect to the inducer grating were pseudorandomized across trials. Importantly, we used the exact same stimuli, trial parameters, and trial sequence in both the second and third sessions, with the only difference being that participants judged either the orientation or size difference of the inducer grating with respect to the reference.

Data analysis

Outlier exclusion

We did not invite participants to the serial-dependence tasks in the second and third sessions if their estimated orientation or size threshold in the first session exceeded $\Delta\theta = 20°$ or $\Delta s = 0.4°$ visual angle, respectively. Furthermore, participants were excluded from data analysis if their thresholds for the orientation or size 2IFC task were more than three standard deviations above the group mean thresholds. Participants were also excluded if their mean 2IFC accuracy in either the orientation or the size condition of the serial-dependence task was below 60%. Finally, participants were excluded if their average response error in the orientation reproductions was more than three standard deviations above the group mean response error. According to these criteria, four participants were excluded after the first experimental session, because their $\Delta\theta$ threshold in the orientation 2IFC task exceeded 20°.

For the analysis of serial-dependence biases, we excluded individual trials for which the absolute adjustment error was more than three standard deviations away from the average adjustment error of that participant. Furthermore, we excluded trials in which no 2IFC response was given within the 2,000-ms response period. Prior to further analyses, we removed each participant's mean adjustment response error from the adjustment data, separately for each attention condition, to remove general clockwise or counterclockwise response biases that are independent of biases due to stimulus history. On average, we rejected 5.62 of 576 trials per participant due to outlier adjustment responses (orientation condition: $M = 2.79$, $SE = 0.35$; size condition: $M = 2.82$, $SE = 0.31$). Furthermore, we rejected an average of 8.26 trials per participant because no 2IFC response was given within the 2,000-ms response period (orientation condition: $M = 3.88$, $SE = 0.90$; size condition: $M = 4.38$, $SE = 0.66$).

Accuracies and response times

We statistically compared the 2IFC accuracies and the mean adjustment errors in the orientation and size conditions of the serial-dependence task with a two-sided paired *t* test and a Bayesian undirected paired-sample *t* test with a Cauchy prior with a default scale of 0.707 (Rouder, Speckman, Sun, Morey, & Iverson, 2009). Similarly, we assessed potential differences in response times in both the 2IFC and adjustment responses across the two conditions.

Serial dependence on inducer grating

In order to quantify systematic biases in adjustment responses about the test grating toward the orientation of the inducer grating—that is, serial dependence—we first expressed the adjustment response errors as a function of the orientation difference between inducer and test gratings. For positive values of this orientation difference, the inducer grating was oriented more clockwise than the test grating. Similarly, positive response errors denote trials in which the response bar was adjusted more clockwise than the test grating. Next, we pooled the response errors of all participants, in the orientation and size conditions respectively, and fitted derivative-of-Gaussian curves (DoGs) to the group data in both conditions (Fischer & Whitney, 2014). The DoG is given by $y = xawce^{-(wx)^2}$, where x is the relative orientation of the inducer grating, a is the amplitude of the curve peaks, w is the width of the curve, and c is the constant $\sqrt{2}/e^{-0.5}$. The constant c is chosen such that a numerically matches the height of the curve peak. The amplitude parameter a was taken as the strength of serial dependence, as it indicates how much the response to the test orientation could be biased toward the inducer orientation for the maximally effective orientation difference between stimuli. For all model fits, the width parameter w of the DoG curve was treated as a free parameter, constrained to a range of plausible values ($w = 0.02$–0.07, corresponding to curve peaks between 10° and 35° orientation difference).

We used permutation tests to statistically assess serial-dependence biases in the orientation and size conditions. A single permutation was computed by first randomly inverting the signs of each participant's response errors (i.e., changing the direction of the response errors). This is equivalent to randomly shuffling the labels between the empirically observed data and a distribution of no serial dependence (a flat surrogate response-error distribution) and subtracting the two conditions from each other per participant. Subsequently, we fitted a new DoG model to the pooled group data and collected the resulting amplitude parameter in a permutation distribution. We repeated this permutation procedure 10,000 times. As *p* values, we report the percentage of permutations that led to equal or more extreme values for the amplitude parameter than the one estimated on the empirical data. The significance level was set to $\alpha = 0.05$ (one-sided permutation test) for testing serial dependence in the orientation condition, as we expected to find attraction biases in line with previous studies. The significance level for the size condition was set to $\alpha = 0.025$ (two-sided permutation test), since due to the lack of previous experimental evidence we regarded both attraction and repulsion biases as possible. The exchangeability requirement for permutation tests is met, because under the null hypothesis of no serial dependence, the labels of the empirically observed data and a flat surrogate response-error distribution of no serial dependence are exchangeable.

In order to assess the difference in serial dependence between the orientation and size conditions, we used a permutation test as well. For each permutation, we randomly shuffled the condition labels of the orientation and size conditions of each participant. We then fitted DoG models to the permuted conditions, pooled across participants, and recorded the difference between the amplitude parameters. We repeated this procedure 10,000 times. As p values, we report the percentage of permutations that led to an equal or more extreme amplitude difference than the one we observed in the experiment. The significance level was set to $\alpha = 0.025$ (two-sided permutation test). The exchangeability requirement for permutation tests is met, because under the null hypothesis of no difference in serial dependence between the orientation and size conditions, the condition labels are exchangeable.

In addition to this analysis in which we pooled data across participants, we conducted a second analysis in which we fitted DoG models to the data of each participant, thereby obtaining estimates of serial-dependence biases for each individual. We compared the group's mean bias in each condition to zero using one-sample t tests. As with the permutation tests, we used a one-sided t test in the orientation condition and a two-sided t test in the size condition. To assess a difference in biases across conditions we used a two-sided paired t test. All significance levels were set to $\alpha = 0.05$. Furthermore, for all classical null-hypothesis significance tests we conducted the analogous Bayesian t tests with default Cauchy priors (scale 0.707).

Repulsive biases for large orientation differences

Next to positive attraction biases for subsequent stimuli with similar orientations, we expected to observe negative repulsive biases for stimuli with large orientation differences beyond 60° (Bliss et al., 2017; Fritsche et al., 2017). In order to test whether such repulsive biases also occurred in the current experiment, we averaged each participant's adjustment response errors in a negative and a positive bin. The negative bin comprised trials with orientation differences of −80°, −70°, and −60° between inducer and test grating, whereas the positive bin comprised trials with orientation differences of 60°, 70°, and 80°. For each participant, we computed a bias by subtracting the average response error in the negative bin from the error in the positive bin and dividing the resulting value by two. Negative values for this bias reflect repulsive biases of adjustment responses away from the inducer grating. We statistically compared the biases in the orientation and size conditions against zero using one-sample t tests. Analogous to the tests of positive serial dependence, we used a one-sided test in the orientation condition and a two-sided test in the size condition at significance levels of $\alpha = 0.05$. Moreover, we were interested whether the repulsive biases for large orientation differences were modulated by feature-based attention toward the orientation or size of the inducer grating. To this end, we compared the biases in the orientation and size conditions using a two-sided paired t test. Similar to the analyses already described, we conducted Bayesian t tests with default Cauchy priors (scale 0.707). Additionally, to statistically assess whether feature-based attention differentially modulated the magnitude of attractive and repulsive biases, we conducted a further analysis not preregistered in the original analysis plan. In this analysis, we quantified the attractive biases for stimuli with small orientation differences as the average response bias in the orientation bins of ±10°, ±20°, and ±30°, in the same manner as for the repulsive biases. We then entered these attractive biases for stimuli with small orientation differences together with the repulsive biases for stimuli with large orientation differences (computed over ±60°, ±70°, and ±80°) into a repeated-measures analysis of variance, with factors of relative orientation difference (small, large) and attention (orientation, size). Importantly, since attending to the size of the inducer grating and ignoring its orientation was expected to reduce both positive attractive and negative repulsive biases toward zero, in this analysis we inverted the negative sign of the repulsive biases computed for large orientation differences in order to assess the interaction between feature-based attention and the magnitude of attractive and repulsive biases.

Serial dependence on previous test grating

The current experiment was primarily designed to measure orientation estimation biases toward or away from a preceding inducer grating, which was attended in terms of either its orientation or its size. However, previous studies have found attractive biases toward not only immediately preceding stimuli but also stimuli seen further in the past (Fischer & Whitney, 2014; Fritsche et al., 2017). Two interesting questions derive from these previous findings in the context of the current study. First, we wondered whether we could replicate the finding of attractive serial-dependence biases toward temporally more distant stimuli. Second, we asked whether feature-based attention on the inducer grating would modulate the attraction bias toward not only this inducer but also to stimuli that were presented further in the past. In other words, is the serial-dependence bias toward the recent stimulus history modulated by how intervening information is processed? To shed light on this question we conducted a further exploratory analysis that was not part of the preregistered analysis plan. In this analysis, we investigated whether adjustment responses were biased toward not only the inducer grating on the same trial but also the test grating presented on the previous trial (Fritsche et al., 2017). To this end, we repeated the serial-dependence analysis already described, with the exception that response errors were now expressed as a function of the orientation difference between the test gratings presented on the previous and the current trial, respectively. Since we expected the attraction biases toward the previous trial's test grating to be weaker and more variable, potentially resulting in problems with model fits to single-subject data, we focused on fitting the DoG models to the group data and statistically assessed the amplitude estimates with the random-effects permutation test already described. Notably, the orientation and size conditions of the experiment were similar in the sense that participants always attended to the orientation of each test grating, as they had to reproduce its orientation. However, the conditions differed in the processing of the inducer grating, which was presented in between the previous and current test gratings and was attended in terms of either orientation or size. Importantly, if information from different stimuli encountered in the recent past were integrated independently with the current stimulus representation, then this differential processing of the intervening inducer grating should not impact biases between test gratings of successive trials. Conversely, if stimulus information from different moments in the recent history were to interact or interfere, attending to the orientation or size of an intervening inducer grating could influence serial dependencies between successive test gratings.

Results

Overall task performance

The accuracies of the 2IFC judgments in the main task were close to the target accuracy of 75% (orientation condition: $M = 74.70\%$, $SE = 0.81\%$; size condition: $M = 77.03\%$, $SE = 0.81\%$), and the average thresholds were $\Delta\theta = 10.17°$ ($SE = 0.64°$) and $\Delta s = 0.13°$ visual angle ($SE = 0.006°$), respectively. While a paired t test revealed that participants performed significantly more accurately in the size 2IFC task, $t(33) = -2.33$, $p = 0.03$, a Bayesian t test indicated only anecdotal evidence for a difference in 2IFC performance across conditions ($BF_{10} = 1.93$). Similarly, the average error in adjustment responses was slightly but significantly lower in the size compared to the orientation condition (orientation condition: $M = 8.99°$, $SE = 0.30°$; size condition: $M = 8.61°$, $SE = 0.31°$), $t(33) = 2.41$, $p = 0.02$, while a Bayesian t test again indicated only anecdotal evidence for a difference across conditions ($BF_{10} = 2.27$). We observed that participants gave significantly faster 2IFC responses in the size than in the orientation condition (orientation condition: $M = 0.60$ s, $SE = 0.03$ s; size condition: $M = 0.49$ s, $SE = 0.03$ s), $t(33) = 4.40$, $p < 0.001$, $BF_{10} = 240$. We note that despite this difference in responses times, the response period was always 2,000 ms, and therefore there was no difference in interstimulus intervals between inducer and test gratings across conditions. Finally, there was no significant difference between adjustment response times across conditions (orientation condition: $M = 2.45$ s, $SE = 0.10$ s; size condition: $M = 2.45$ s, $SE = 0.08$ s), $t(33) = 0.04$, $p = 0.97$, $BF_{01} = 5.44$.

Serial dependence on inducer grating is modulated by feature-based attention

Adjustment responses to test gratings were systematically attracted toward the orientation of the preceding inducer grating when it was of similar orientation (Figure 2a and 2b), in both the orientation condition ($a = 2.36°$, $p < 0.0001$, permutation test) and the size condition ($a = 1.01°$, $p < 0.0001$, permutation test). Crucially, however, this serial-dependence bias was significantly stronger when people attended to the orientation of the inducer grating compared to when they attended to its size ($p < 0.0001$, permutation test). Furthermore, the peak locations of the DoG model were significantly narrower in the size compared to the orientation condition (±13.74° vs. ±17.88°, $p = 0.01$, permutation test, not preregistered). These results were corroborated by a second analysis in which we fitted DoG models to the individual-participant data. This complementary analysis revealed significant serial dependence both when participants attended to the orientation of the inducer (a: $M = 2.60°$, $SE = 0.38$), $t(33) = 6.73$, $p < 0.0001$, $BF_{10} = 2.6 \times 10^5$, and when they attended to its size (a: $M = 0.81°$, $SE = 0.29°$), $t(33) = 2.77$, $p = 0.009$, $BF_{10} = 4.64$. Similar to the first analysis, serial dependence was significantly stronger when participants attended the orientation of the inducer, $t(33) = 4.74$, $p < 0.0001$, $BF_{10} = 578$.

Since participants responded slightly but significantly faster when judging the size rather than the orientation of the inducer stimulus, one might be worried that the difference in serial dependence between attention conditions could stem from a difference in the overall processing time of the inducer stimulus per se rather than differences in feature-specific processing of its size or orientation information. To investigate such a relationship between response times and the strength of serial dependence, we correlated response times within the orientation and size conditions with the individual serial-dependence estimates from the single-participant DoG model fits. There was no significant correlation in the orientation condition ($r = 0.16$, $p = 0.37$) or the size condition ($r = 0.15$, $p = 0.41$), and Bayes factors indicated moderate evidence for the null hypothesis of no correlation ($BF_{01} = 3.20$ and 3.39, respectively). This indicates that individuals with longer response times did not show stronger serial dependencies, and alleviates the concern

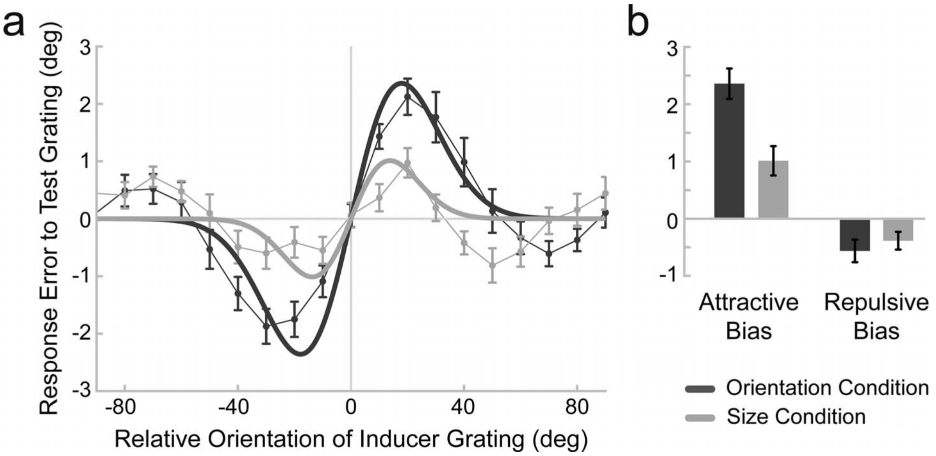

Figure 2. Systematic attractive and repulsive biases of adjustment responses to the inducer grating. (a) Serial-dependence error plot of trials in which participants attended to the orientation (dark gray) or size (light gray) of the inducer. We expressed the adjustment response errors (*y*-axis) as a function of the orientation difference between inducer and test grating (*x*-axis). For positive *x* values the inducer was oriented more clockwise than the test grating, and for positive *y* values the current response error was in the clockwise direction. Responses to test gratings with orientations similar to the inducer were systematically biased toward the inducer, as can be seen from the group average response errors (dark- and light-gray data points; data points were smoothed by averaging with the respective neighboring data points). This bias follows a derivative-of-Gaussian shape (model fits shown as thin dark- and light-gray lines). Crucially, the magnitude of this attractive bias was significantly weaker when participants judged the size instead of the orientation of the inducer grating (b, left), as indicated by a reduced amplitude parameter of the derivative-of-Gaussian model (error bars show bootstrapped standard error of the mean). Additionally, alongside the attractive bias between inducer and test grating with similar orientations, adjustment responses were repelled from the inducer when the inducer and test grating had very different orientations (difference $\geq$ 60°). Notably, unlike the attractive bias, this repulsive bias appeared not to be modulated by attending to either the orientation or size of the inducer (b, right). Error bars depict standard error of the mean.

that differences in serial dependencies across the two attention conditions were due to differences in response times.

To summarize, while adjustment responses were biased toward the inducer orientation, even when the inducer orientation was not attended, the attraction bias was more than twice as strong when the inducer orientation was attended. Therefore, positive serial dependence is strongly modulated by feature-based attention toward previous stimulus features.

Repulsive biases for large orientation differences are not modulated by feature-based attention

Along with the attraction bias toward previous inducer gratings with similar orientations, adjustment responses were repelled away from inducer gratings with large orientation differences (Figure 2b). This held true when participants attended both the orientation of the inducer grating, $t(33) = -2.81$, $p = 0.004$, $\mathrm{BF}_{10} = 10$, and its size, $t(33) = -2.43$, $p = 0.02$, $\mathrm{BF}_{10} = 2.33$. However, there was no significant difference in repulsion biases across the two conditions, $t(33) = -0.74$, $p = 0.46$, and a Bayesian *t* test revealed moderate evidence for the null hypothesis of no difference across conditions ($\mathrm{BF}_{01} = 4.22$). Moreover, a repeated-measures analysis of variance directly comparing the influence of attention on the magnitude of repulsive and attractive biases revealed a significant interaction between the relative orientation difference between inducer and test gratings and the attention condition, $F(1, 33) = 7.605$, $p = 0.009$. That is, whereas attending to the size of the inducer strongly reduced the attraction bias for stimuli with similar orientations (analysis of averaged response errors), $t(33) = 4.879$, $p < 0.001$, $\mathrm{BF}_{10} = 852$, the magnitude of the repulsive bias remained unaffected (see earlier). This indicates that unlike the positive serial dependencies between stimuli with similar orientations, the repulsive biases for successive stimuli with large orientation differences are not modulated by feature-based attention. This suggests that the attractive and repulsive biases measured in adjustment responses may originate, at least partly, from separate underlying processes and be superimposed in the final behavioral response.

One may wonder whether the current finding, that repulsive biases for successive stimuli with large orientation differences are not modulated by feature-based attention, might critically depend on the preregistered analysis choice of bin widths from ±60° to ±80° over which the repulsive biases were computed. This concern is strengthened by the observation that feature-based attention appears to modulate not only the amplitude of the positive serial-dependence bias but also its width (Figure 2a). As a consequence, manipulating positive biases in the center of the serial-dependence plot may have a systematic impact on the repulsive biases expressed in the periphery. For instance, a narrower tuning of the central positive biases might be accompanied by a shift of the repulsive biases toward the center of the error plot. In this case, computing the repulsive biases within fixed peripheral bins might underestimate the actual magnitude of the repulsion. Consequently, comparing the repulsive biases over the same orientation differences in both attention conditions might lead to a biased estimation of the repulsive biases. In order to overcome this potential issue, we conducted an additional exploratory control analysis of the repulsive biases, following a multiverse analysis approach (Steegen, Tuerlinckx, Gelman, & Vanpaemel, 2016). This control analysis was similar to our original analysis, with the exception that we allowed the bin widths for which we computed the repulsive biases to vary independently in the orientation and size conditions. Specifically, we varied the number of bins included in the analysis by including or excluding bins toward the center of the serial-dependence plot—that is, computing biases over the range [$\pm X°$, ±80°], where X was varied between 40° and 80° in steps of 10°. As a result, we could compare biases in the orientation condition that were, for instance, computed over a range of orientation differences from ±60° to ±80° to biases in the size condition that were computed from ±40° to ±80° orientation difference, thereby investigating the robustness of the current result in light of different analysis choices for bin widths (see Supplementary Figure S1). The analysis revealed significant repulsion biases for $X \geq 60°$ in the orientation condition and for $40° \leq X \leq 60°$ in the size condition (all ps < 0.05). Moreover, for those values of X for which there were significant repulsion biases in both conditions, there was no significant difference between biases across conditions (all ps > 0.25). Similarly, Bayesian t tests revealed moderate evidence for the null hypothesis of no difference across conditions for all but one comparison (all $BF_{01} > 3$, except $X_{\text{ori}} = 80°$, $X_{\text{size}} = 40°$: $BF_{01} = 2.91$). To conclude, even when we computed repulsive biases over a wide range of variable orientation differences, there was no evidence that feature-based attention modulates these repulsive biases.

Serial dependence on previous test grating is modulated by attention to intervening inducer

In an additional exploratory analysis, we investigated whether adjustment responses to the current test grating were also systematically attracted toward the previous test grating, as has been reported before (Cicchini, et al., 2017; Fritsche et al., 2017). Of particular interest, we explored whether this attraction bias was modulated by *how* the intervening inducer grating was processed, in terms of feature-based attention. Although there was always an inducer grating presented between test gratings of subsequent trials, previous studies have reported that serial dependencies can exist for stimuli seen up to 10–15 s in the past (Fischer & Whitney, 2014). In the current experiment, the onset of a new test grating occurred on average ~13.4 s after the offset of the previous test grating and ~6.9 s after the offset of the previous adjustment response. Indeed, we found that adjustment responses were significantly biased toward the test grating on the previous trial (Figure 3), in both the orientation condition ($a = 1.38°$, $p < 0.0001$, permutation test) and the size condition ($a = 2.18°$, $p < 0.0001$, permutation test). Surprisingly, the bias was significantly stronger in the size than in the orientation condition ($p = 0.0003$, permutation test). That is, although the previous test grating was processed similarly in both conditions, serial dependence was stronger when participants attended to the size of an intervening inducer grating compared to when they focused on its orientation. Crucially, one would not expect such an influence of the processing of intervening stimuli if representations of recently encountered stimuli were independently integrated with the current stimulus representation. In turn, to a first approximation this may suggest that representations of the recent

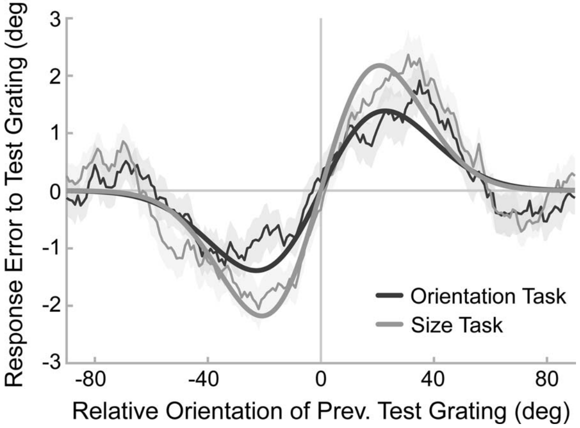

Figure 3. Serial-dependence bias toward test grating on the previous trial is modulated by attention to the intervening inducer. We assessed serial dependence toward the previous test grating similarly to in Figure 2a, but conditioned on the relative orientation of the previous test grating instead of the current trial's inducer. Intriguingly, the attraction bias toward the test grating of the previous trial was stronger when participants judged the size instead of the orientation of the intervening inducer grating ($p = 0.0003$).

perceptual history interact or interfere when maintained in memory and integrated with new information. This finding could inform computational models of serial dependence. Unfortunately, however, the current experimental design, with interleaved adjustment and 2IFC responses, is not ideally suited to quantitatively assess computational models of serial dependence, such as a recently proposed mixture model of internal representations (Kalm & Norris, 2018). Furthermore, more experiments will be required to confirm the current exploratory finding and shed light on the aspects of intervening stimulus processing which may modulate the influence of the more remote perceptual history on current estimation responses.

In contrast to the attraction bias for successive similar test gratings, adjustment responses were repelled away from previous test gratings with large orientation differences (difference $\geq 60°$, peripheral regions in Figure 3)—orientation task: $t(33) = -2.162$, $p = 0.04$; size task: $t(33) = -2.318$, $p = 0.03$. This repulsive bias was not modulated by how the intervening stimulus was processed, $t(33) = -0.124$, $p = 0.9$, $BF_{01} = 5.40$. In line with the results of our main analysis, this differential modulation of attractive and repulsive biases again suggests that attractive and repulsive biases measured in adjustment responses may in part be driven by different neural mechanisms.

Discussion

We have shown that attractive serial-dependence biases in orientation estimation are strongly modulated by feature-based attention. That is, orientation estimations of a stimulus are more strongly attracted to the orientation of a previous inducer grating when observers attended to the inducer's orientation rather than its size. This finding is consistent with a previous study showing that positive serial-dependence biases in orientation estimation are modulated by spatial attention (Fischer & Whitney, 2014). Importantly, observers in the current study always attended the same object at the same spatial location, precluding a difference in serial dependence due to differences in object-based or spatial attention. Integrating the current results regarding feature-based attention with previous findings on the modulatory role of spatial attention in positive serial dependence (Fischer & Whitney, 2014; Kiyonaga et al., 2017) suggests a selective smoothing operation of perceptual representations. Furthermore, the current finding that serial dependence can selectively smooth attended features of an object over time while leaving unattended features of the same object relatively unsmoothed suggests that it may, in part, operate below the level of object representations.

Interestingly, attractive serial-dependence biases in orientation estimation did not completely disappear when observers attended to the size of the inducer grating. It is possible that the remaining small but robust attraction bias reflects a distinct bias, which is attention independent, potentially arising from different processes than the attention-dependent bias. However, a perhaps more plausible explanation is that even though observers were asked to focus only on the size in the size 2IFC task, they might have nevertheless paid some attention to orientation as well, leading to small attraction biases in the size condition. To minimize inadvertent attention to the task-irrelevant feature dimension, we held the attention task constant across blocks in a session. Nevertheless, since attention is likely not a binary all-or-none process, it is difficult to rule out the possibility that the attractive bias in the size condition could have occurred due to residual attention toward orientation. Moreover, it has been previously shown that feature-based attention itself can be serially dependent (White, Rolfs, & Carrasco, 2013), and thus the orientation reproduction of the test stimulus on each trial might have facilitated the allocation of attentional resources to orientation information of the next trial's inducer even when that orientation was task irrelevant. In a similar vein, previous findings of serial dependence to task-irrelevant stimulus features could be explained by residual attention to the feature dimension for which serial dependence was assessed (Fornaciai & Park, 2018a, 2018b).

A natural question that arises from the current finding that feature-based attention modulates positive serial dependencies concerns the precise mechanisms which underlie this modulation. Feature-based attention has been found to enhance the representation of attended features within the visual system (Jehee, Brady, & Tong, 2011). In the context of the current experiment, attending to the size of the inducer grating and ignoring its orientation may have led to a weaker, less reliable representation of the inducer's orientation compared to when the orientation was actively attended. Importantly, if serial dependence arises from optimal integration of previous and current stimulus representations, the brain should integrate these representations weighted by their respective reliability (Cicchini et al., 2018). Consequently, unattended and therefore less reliable orientation information may exert a weaker influence on subsequent orientation estimations, leading to a reduced serial-dependence bias as observed in the current experiment. This would complement a recent finding that serial-dependence biases are modulated by changes in bottom-up reliability of the current stimulus (Cicchini et al., 2018).

It is worthwhile to note that in the current experiment, attractive serial dependence in orientation reproductions occurred even though the inducer orientation was never reproduced, only judged with respect to a reference stimulus. Importantly, this judgment of the inducer's orientation with respect to the reference was independent with respect to the orientation of the subsequent test grating. This provides corroborating evidence that an adjustment response, or the covert preparation thereof, is not necessary for inducing serial-dependence biases, and serial dependence of visual features can occur when these features are embedded within two entirely different tasks and decisions, confirming previous claims (Fischer & Whitney, 2014; Suárez-Pinilla et al., 2018). Notably, in contrast to these previous findings, a recent study reported a switch from attractive to repulsive biases in orientation estimations when no active decision, in the form of an estimation response, was made on the previous trial (Pascucci et al., 2019, experiments 3 and 5). This was taken as evidence that attractive serial dependencies arise at a decisional rather than a sensory stage, consistent with a previous proposal (Fritsche et al., 2017). However, the precise reasons for the divergence of findings between these two lines of research remain elusive, as the differences in experimental manipulations appear minor. While further research is required to understand this discrepancy, the current results corroborate the claim that serial dependencies occur even in the absence of previous adjustment responses and extend these findings by showing that they occur even between stimuli that require different types of decisions about the same stimulus feature (discriminative orientation judgment against reference versus orientation estimation).

Related to these points, a recent study found that attractive serial-dependence biases in successive orientation estimations were boosted by the confidence in the previous trial's estimation response, even when confidence was experimentally dissociated from task performance (Samaha et al., 2019). This intriguing finding suggests that the strength of serial dependencies might be modulated by a subjective, rather than objective, estimate of sensory uncertainty pertaining to the recent past. However, in the context of the current study it is important to note that subjective confidence estimates concerning the perceptual decision about the inducer stimulus likely reflected the certainty about the discriminative judgments of the difference between inducer and reference stimuli, not the certainty about the overall orientation or size of the inducer stimulus. At this point, it is not clear how such confidence estimates about discriminative decisions would affect subsequent decisions of orientation estimations. It is, however, possible that observers formed implicit confidence estimates about the overall orientation and size of the inducer grating. In this case, one would expect higher confidence in the inducer's overall orientation when orientation was attended rather than size, which should boost attractive serial dependence, consistent with the current results.

Apart from the attraction biases for inducer and test gratings with similar orientations, we found that adjustment responses were repelled when inducer and test gratings had markedly different orientations (Bliss et al., 2017; Fritsche et al., 2017, Samaha et al., 2019). Strikingly, we found no evidence for modulation of these repulsive biases by feature-based attention. This asymmetric influence of attention on attractive and repulsive biases suggests that the two might originate from at least partially independent neural processes, and cautions against devising computational models of serial dependence in which positive and negative biases are codependent. These observations are also in line with a previous finding that the repulsive biases for successive stimuli with large orientation differences disappeared when stimuli were presented at different spatial locations, whereas the attractive bias remained of identical magnitude (Fritsche et al., 2017). Together, these findings suggest that the repulsive biases might occur at an early, retinotopic stage, which is not strongly modulated by attention, while the attraction bias might occur at a later, more spatially invariant stage, which is strongly affected by feature-based attention. However, the exact nature of the repulsive biases remains elusive. While this is reminiscent of classical negative perceptual adaptation (Webster, 2015), classical tilt aftereffects predominantly occur for orientation differences between 0° and 45° and can turn into attractive biases for larger differences (Gibson & Radner, 1937). Furthermore, perceptual adaptation effects have been found to be modulated, albeit weakly, by feature-based attention (Kreutzer, Fink, & Weidner, 2015; Spivey & Spirn, 2000). Thus, it appears unlikely that the repulsive biases we observed reflect classical perceptual adaptation. However, perceptual adaptation effects can occur even when inducer stimuli are rendered invisible by crowding (He, Cavanagh, & Intrilligator, 1996), binocular rivalry (Wade & Wenderoth, 1978), and continuous flash suppression (Maruya, Watanabe, & Watanabe, 2008), and neural adaptation can be observed in anesthetized animals (Kohn & Movshon, 2003), suggesting that adaptation can occur in the absence of attentional selection. Therefore, whether the present repulsive biases reflect a form of classical adaptation or a distinct phenomenon will be an interesting topic for future research.

To conclude, we have demonstrated that attractive serial dependence in orientation estimations is strongly modulated by feature-based attention, while repulsive biases for large orientation differences are not. This presents a distinguishing feature for positive and negative biases that are concurrently observed in perceptual estimations. Furthermore, our findings

provide important insights into the conditions under which attractive serial dependencies occur, indicating a selective smoothing operation which stabilizes representations of successively attended features of the same kind. The current study therefore contributes to understanding the boundaries within which stabilization of neural representations through serial dependence can take place.

Keywords: serial dependence, feature-based attention, perceptual decision making, visual perception, adaptation

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