Spontaneous repulsive adaptation in the absence of attractive serial dependence

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Despite noisy and discontinuous input, vision is remarkably stable and continuous. Recent work suggests that such a remarkable feat is enabled by an active stabilization process integrating information over time, resulting in attractive serial dependence. However, precise mechanisms underlying serial dependence are still unknown. Across three psychophysical experiments, we demonstrate that suppressing high-level modulatory signals on early cortical activity via visual backward masking completely abolishes the serial dependence effect, indicating the critical role of cortical feedback processing on serial dependence. Moreover, we show that the absence of modulatory feedback results in a robust repulsive aftereffect, as in perceptual adaptation, after only 50 ms of stimulation, indicating the presence of a local neurocomputational process for an automatic and spontaneous recalibration of the stimulus representation. These findings collectively illustrate the interplay between two contrasting cortical mechanisms at short timescales that serve as a basis for our perceptual experience.

Introduction

The fact that our conscious visual perception is usually stable and seamless in the face of noise and discontinuities in sensory input has led to the idea of an active stabilization mechanism modulating sensory representations. In recent years, there has been a renewed interest in a perceptual distortion called serial dependence, whereby a current stimulus appears similar to the one previous to it, as that phenomenon was interpreted as a byproduct of such an active stabilization mechanism (Cicchini, Mikellidou, & Burr, 2017; Cicchini, Mikellidou, & Burr, 2018; Fischer & Whitney, 2014; Fornaciai & Park, 2018a). Such attractive biases have been demonstrated to affect several visual domains, spanning from basic attributes such as orientation (Cicchini, Anobile, & Burr, 2014; Fischer & Whitney, 2014), position (Manassi, Liberman, Kosovicheva, Zhang, & Whitney, 2018), motion (Alais, Leung, & Van der Burg, 2017), or numerosity (Cicchini et al., 2014; Corbett, Fischer, & Whitney, 2011; Fornaciai & Park, 2018a, 2018b), to more complex features such as visual variance (Suárez-Pinilla, Seth, & Roseboom, 2018), face identity (Liberman, Fischer, & Whitney, 2014), attractiveness (Xia, Leib, & Whitney, 2016), gaze direction (Alais, Kong, Palmer, & Clifford, 2018), or emotional expressions (Libermann, Manassi, & Whitney, 2018), suggesting a general mechanisms affecting all aspects of perception. Although the perceptual nature of attractive serial dependence has been subject to debate (Bliss, Sun, & D'Esposito, 2017; Fritsche, Mostert, & de Lange, 2017), there is increasing evidence that it likely operates at the earliest level of visual perception (Cicchini et al., 2017; Fornaciai & Park, 2018a, 2018b; Manassi et al., 2018; St. John-Saaltink, Kok, Lau, & de Lange, 2016). However, recent studies have found that this attractive perceptual bias requires attention (Fischer & Whitney, 2014; Fornaciai & Park, 2018b), suggesting that serial dependence likely arises from high-level modulatory feedback to early visual cortex.

Previously, we have demonstrated that a task-irrelevant "inducer" dot array presented before two other dot arrays that a participant is asked to discriminate causes an attractive serial dependence (Fornaciai & Park, 2018a, 2018b). Using a similar experimental paradigm (see Figure 1), we here tested the hypothesis that serial dependence is abolished in the absence of modulatory feedback. To do so, we first exploited visual backward masking. Backward masking (i.e., involving a mask rapidly presented after a target stimulus) suppresses the awareness of the stimulus by inhibiting the reentrant feedback from high- to low-

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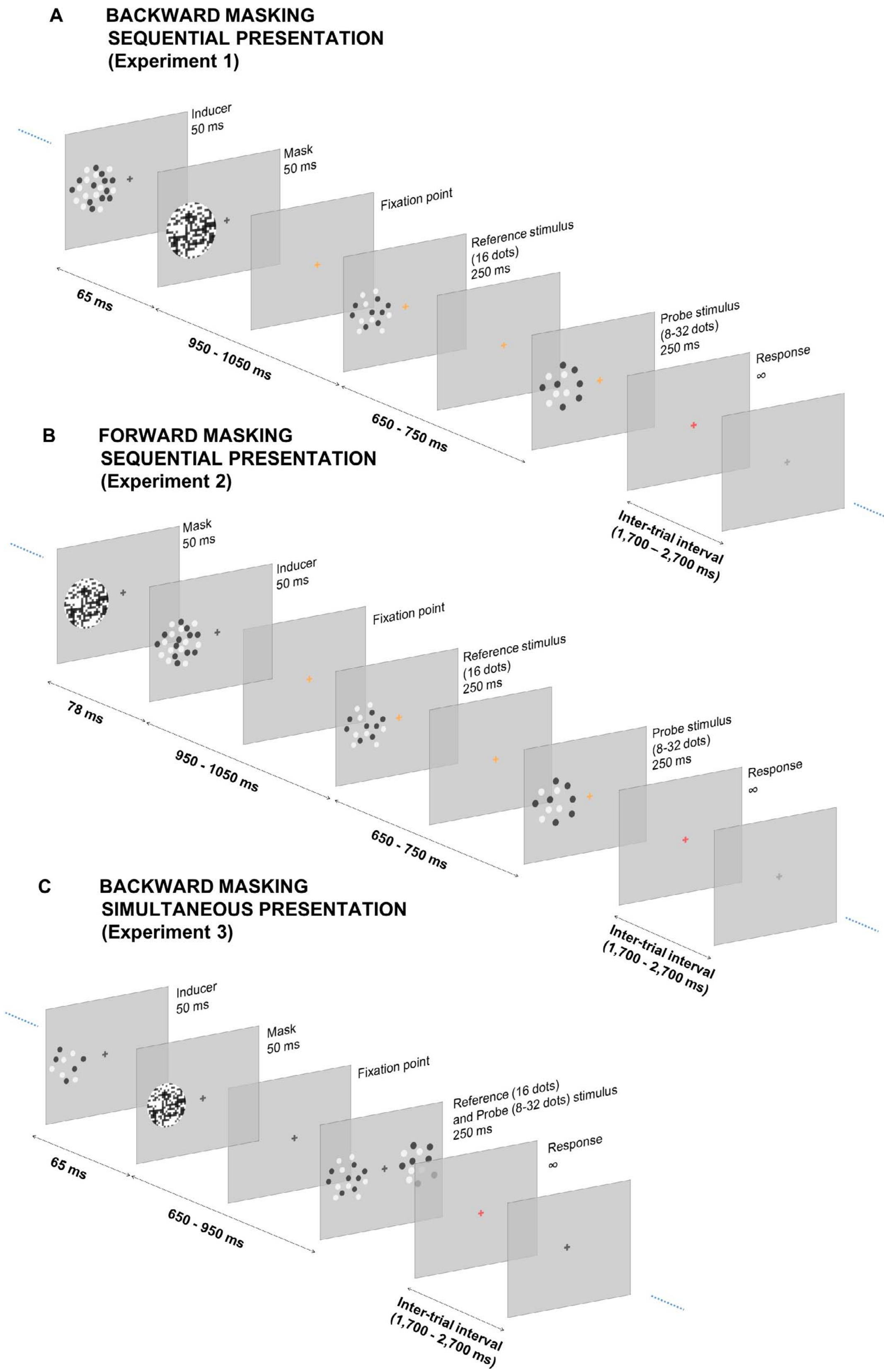

Figure 1. Graphical depiction of the paradigms in Experiments 1 through 3. (A) Experiment 1, backward-masking condition. A sequence of three arrays each containing a mixture of black and white dots was presented at either the left or right side of the central fixation cross (randomized; eccentricity = 11 dva). The three arrays were a task-irrelevant inducer (either 12 or 24 dots), a reference (16 dots), and a probe with variable numerosity (8–32 dots). A pattern mask was presented immediately after the inducer, with an →

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SOA of 65 ms. Participants were told to pay attention to the entire sequence of the stimuli, but that only the last two in the sequence were relevant for the task. To help participants recognize the two task-relevant stimuli (i.e., to avoid confusion with the inducer), a cue (orange fixation cross) was presented just before and throughout the presentation of reference and probe stimuli. At the end of each trial, participants indicated whether the reference or the probe contained more dots. (B) Experiment 2, forward-masking condition. The sequence of dot-array stimuli was identical to the backward masking, except that the mask stimulus was presented before the inducer, with an SOA of 78 ms. (C) Experiment 3, backward masking with simultaneous presentation. Unlike Experiments 1 and 2, reference and probe were presented simultaneously on the two sides of the screen (center-to-center distance = 22 dva). The inducer stimulus was always presented at the same position as the reference stimulus. To ensure that participants pay attention to the inducer stimulus, we introduced a simple secondary task. Namely, participants were asked to pay attention to the color of the inducer, as on a small proportion of trials (four trials per block) the inducer stimulus was presented in red. In those cases, participants had to press a different key, and the trial was later discarded from data analysis. Detection rate in the secondary task was 94% ± 7% (*M* ± *SD*). In all experiments, the duration of the inducer and the mask was 50 ms, while reference and probe were presented for 200 ms each. Finally, in all three experiments, in addition to the depicted masking condition, there was a condition with a much longer SOA (550 ms) before (Experiment 2) or after (Experiments 1 and 3) the inducer as well as a condition with no masking. Timing measures represent SOAs. Stimuli are not depicted in scale.

level visual areas, while sparing feedforward processing (Boehler, Schoenfeld, Heinze, & Hopf, 2008; Fahrenfort, Scholte, & Lamme, 2007). In Experiments 1 and 3, we applied backward masking to the "inducer" stimulus in order to minimize high-level modulatory feedback. If serial dependence requires feedback signals, attractive biases caused by the inducer in a numerosity discrimination task should be abolished by backward masking. In Experiment 2, on the other hand, we used forward masking in order to suppress even the initial onset responses during feedforward processing. Our results show that not only attractive serial dependence is abolished by visual backward masking, but that a systematic repulsive bias, akin to perceptual adaptation (Kohn, 2007), emerges. On the other hand, forward masking also suppresses the repulsive aftereffect, suggesting that such a bias reflects a spontaneous and local recalibration of sensory processing occurring during the initial feedforward sweep, in the absence of high-level feedback modulation.

Materials and methods

Participants

A total of 105 subjects participated across three experiments (89 females, mean age ($M \pm SD$) = 21.06 ± 1.87 years old). Participation in the study was rewarded with course credit. All participants signed a written informed consent before participating in the study, and (with the exception of the author MF who participated in the masking timing preliminary experiment) were naive to the aims of the experiment. All participants had normal or corrected-to-normal vision, and reported no history of neurological, attentional, or psychiatric disorder. Experimental procedures were approved by the Institutional Review Board of the University of Massachusetts at Amherst and were in line with the Declaration of Helsinki. Note that the sample size in the three experiments concerning serial dependence has been chosen based on previous studies using a similar behavioral paradigm (Fornaciai & Park, 2018a, 2018b).

Apparatus and stimuli

Visual stimuli across the three experiments were generated using the Psychophysics Toolbox (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997) for MATLAB (version r2016b; MathWorks, Natick, MA), and presented on a 1920- × 1080-pixel monitor screen running at 144 Hz, encompassing approximately 35 × 20 degrees of visual angle (dva) from a viewing distance of about 80 cm.

All the experimental conditions performed across the different experiments involved a task-irrelevant "inducer" stimulus followed by task-relevant reference and probe stimuli (see Procedure below). These stimuli were arrays of black and white dots (50% and 50%, with the exception of a few odd probe numerosities where the color of the exceeding dot was randomly assigned) presented on a gray background with a contrast of 90%. All the stimuli were systematically constructed to range equally in three orthogonal dimensions, corresponding to numerosity (*N*), size (*Sz*), and spacing (*Sp*). However, since the primary goal of the study concerns serial dependence on numerosity perception, the different levels of nonnumerical dimensions were collapsed together during data analysis. For a more detailed description of the stimulus construction procedure, see DeWind, Adams, Platt, and Brannon (2015) and Park, Dewind, Woldorff, and Brannon (2016). The parameters of the dot-array stimuli were set as follows. Inducer dot arrays comprised either 12 or 24 dots. The reference stimulus always comprised 16 dots, while the probe arrays comprised a variable number of dots (8, 10, 13, 16, 20, 25, or 32 dots). The area of each individual item ranged from 113 pixels^2 (0.038 dva^2), corresponding to a diameter of 0.11 dva (6 pixels), to 452 pixels^2 (0.15 dva^2), corresponding to a diameter of 0.22 dva (12 pixels). The field area of the stimuli (i.e., the virtual area within which the dots were drawn) ranged from 70,686 pixels^2 (23.9 dva^2), encompassing 5.5 dva in diameter (300 pixels), to 282,743 pixels^2 (95.7 dva^2), encompassing 11 dva in diameter (600 pixels). In all cases, the individual size of the dots was kept homogeneous within an array, and we set a minimum distance between any two dots equal to at least the radius of the dots.

In addition, in some of the conditions a mask stimulus was presented either in the temporal vicinity of the inducer stimulus (65 or 78 ms) or separated by a relatively long temporal interval (550 ms). The mask stimulus was a black/white pattern mask comprising a random composition of small squares (side = 22 pixels), randomly arranged within a circular area corresponding to the area of the inducer stimulus (depicted in Figure 1). Additionally, the mask stimulus was mildly smoothed applying a Gaussian filter ($\sigma = 0.4$).

General procedure

All the experimental conditions were performed in a quiet and dimly illuminated room, with participants sitting in front of a monitor screen at a distance of about 80 cm. In all the experiments (with the exception of the preliminary masking timing experiment), participants performed a numerosity discrimination task, choosing the stimulus containing the larger number of dots between a reference (16 dots) or a variable probe (8–32 dots). To induce serial dependence, a task-irrelevant "inducer" stimulus was presented at the beginning of each trial. In Experiments 1 and 2, the presentation procedure was entirely sequential (Figure 1A and 1B), with inducer, reference, and probe (in this order) presented on the screen for 200 ms each. Stimuli were separated by a variable interstimulus interval (ISI) of 950–1,050 ms (inducer-reference) or 650–750 ms (reference-probe). In the sequential procedure of Experiments 1 and 2, all the stimuli were presented at one side of the screen (eccentricity = 11 dva from the central fixation cross), with the presentation side randomly determined in each trial (left or right of the fixation cross). A mask stimulus (duration = 50 ms) could be presented around the timing of the inducer stimulus, 65 ms (masking condition) or 550 ms (long stimulus onset asychtony [SOA] condition) after the onset of the inducer (Experiment 1) or 78 or 550 ms before the onset of the inducer (Experiment 2). In case the mask was not presented (no-mask condition), a pause of equal duration was introduced. The three conditions (masking, long SOA, no mask) were randomly intermixed within each block. Participants were instructed to pay attention to the entire sequence of the stimuli in order to avoid getting distracted and missing some of the stimuli, but to only judge the second (reference) and the third (probe) stimulus in the sequence. To help participants recognize the task relevant stimuli and avoid getting confused with the inducer, a cue (orange fixation cross) was presented before the appearance of the reference and throughout the trial. In Experiment 3, reference and probe stimuli were always presented simultaneously on the screen for 200 ms (Figure 1C), with their position (left or right of the fixation point) randomly determined on each trial (center-to-center distance = 22 dva). With this simultaneous presentation procedure, the inducer stimulus was always presented at the same location as the reference stimulus (ISI = 650–950 ms), with its position (left or right of the fixation point) varying from trial to trial according to the position of the reference. Similarly to Experiments 1 and 2, a mask could be presented around the timing of the inducer stimulus, either 65 ms (masking condition) or 550 ms (long SOA condition) after the onset of the inducer. The conditions including a mask were intermixed with no mask trials within each block, as in Experiments 1 and 2. Participants were instructed to compare the two stimuli appearing together on the screen, and report which one contained a larger number of dots. Additionally, to ensure that participants paid enough attention to the inducer stimulus—which is crucial for the serial dependence effect to occur (Fornaciai & Park, 2018b)—participants performed an additional secondary task on the inducer stimulus (color-oddball detection task). Namely, on some trials (four trials per block) the inducer stimulus was presented in red, and in those cases participants were asked to disregard the subsequent stimuli and press a different key. The average ($M \pm SD$) detection rate in the color oddball secondary task was 94% ± 7%. Note that catch trials always corresponded to trials without masking (i.e., no mask or long SOA), to ensure that the participant could detect the red dot-array stimulus. The catch trials (including correct detection, misses, and also false alarms where participants reported a red stimulus when none was presented) were excluded from the main data analysis. In all experiments, participants performed 10 blocks of 46 trials each, and were free to take breaks between different blocks. The entire experimental session took typically around 50 min to be completed. Before starting the actual experimental session, participants performed a brief training session (14 trials) to familiarize themselves with the task and ensure that they understood the instructions.

Additionally, in a preliminary experiment, we measured the optimal masking timing. In this condition, participants were asked to rate the visibility of a briefly presented (50 ms) target dot array (with numerosities equal to the inducer stimulus used in the main experiments), in a scale from 1 to 4 (Railo & Koivisto, 2012). Namely, the scale corresponded to *no visible target stimulus* (1), *just a glimpse of the target stimulus* (2), *the target was detected but not completely visible* (3), or *the target was clearly and completely visible* (4). In most of the trials, a pattern mask stimulus (duration = 50 ms) with variable timing was presented in the temporal vicinity of the target (SOA ranging from −147 to 260 ms with respect to the onset of the target). In a minority of the trials either no target or no mask was presented (catch trials), to ensure that the participants were performing the task correctly. The timing of the mask stimulus corresponding to the lowest average visibility ratings in the range before (forward masking) and after (backward masking) the target was then used to set the masking timing in Experiments 1 through 3.

Behavioral data analysis

Numerosity discrimination performance was analyzed separately for each subject and condition, and the serial dependence effect was assessed by separating the trials according to the inducer numerosity. To obtain a measure of participants' accuracy and precision in the task, we fitted the distribution of response probabilities as a function of probe numerosity with a cumulative Gaussian curve, according to the maximum likelihood method (Watson, 1979). The point of subjective equality (PSE; the probe numerosity perceptually matching the reference numerosity), reflecting the accuracy in the task, was defined as the median of the best-fitting cumulative Gaussian curve to all the data of each participant in each condition. In other words, the PSE corresponds to the probe numerosity resulting in chance level responses (i.e., 50% "probe more numerous" responses; indicated by a dashed line in Figure 2), indicating that such a probe numerosity is perceptually indistinguishable from the reference. To assess and control the performance level in order to exclude subjects showing insufficient performance, we used the just-noticeable difference (JND), taken as the difference in numerosity between chance level (50%) responses and 75% "probe more numerous" responses. We set an exclusion cut-off at JND equal or greater than 10 dots. A total of 10 subjects was excluded from data analysis based on this criterion, across all the experiments. A finger error rate correction (2%) was applied to account for random response errors or lapses of attention (Wichmann & Hill, 2001). To ensure the quality of the data included in the analysis, individual blocks were individually checked to exclude blocks in which participants performed the task with an insufficient level of performance (i.e., too many random errors, opposite responses in the task, random responses). During this procedure, a total of 23 blocks (out of a total of 1,050 across the three experiments; 2.4%) were excluded from data analysis (no more than two blocks excluded for a single participant, leaving at least eight blocks of trials for each participant). To assess serial dependence effects, a *t* test was performed comparing the distribution of PSEs corresponding to different inducer numerosity conditions. Within each experiment, we also compared the three conditions against each other using *t* tests. To assess whether serial dependence effects are accompanied by changes in precision in the task, we used a two-way repeated-measure analysis of variance (ANOVA) to test the effects of factors Condition (no mask, long SOA, masking) and Inducer (different inducer numerosities; 12 and 24) on the JND.

Additionally, in case of a nonsignificant result of a *t* test comparing two conditions, a Bayesian test was applied to quantify the evidence for an alternative against a null hypothesis. When testing an alternative hypothesis of a positive (attractive) effect against a null hypothesis of no effect, we modeled the prior distribution as a truncated gaussian with $\mu = 1$ and $\sigma = 2$ (i.e., in terms of serial dependence effect, measured as the difference in PSE between different inducer conditions), with a lower bound of the distribution at 0 and an upper bound at 2, meaning that the prior has no probability density outside the lower and upper bound. These values have been chosen taking into account the typical range of effects observed in previous studies (Fornaciai & Park, 2018b), and particularly considering as a typical effect an under- or overestimation of around one dot, with a maximum effect not exceeding two dots (again in terms of difference in PSE between different inducer conditions). On the other hand, when testing the alternative hypothesis of a negative (repulsive) effect (in Experiment 2; see Results), the prior distribution was modeled to span negative values, with $\mu = -1$ and $\sigma = 2$, and spanning from −2 (lower bound) to 0 (upper bound). The null hypothesis, finally, always assumed an effect equal to zero. Note that the parameters used to test for a repulsive effect were chosen based on the results of the backward masking condition in Experiment 1. Indeed, Experiment 2 has been specifically designed as a control for Experiment 1, and hence the results from this latter experiment were used to model the hypothesized effect and assess the results of

Experiment 2. Finally, we performed a more comprehensive series of tests comparing the same condition across different experiments. Namely, we performed three one-way ANOVAs separately for the no mask, long SOA, and mask conditions, with factor "experiment" (Experiments 1 through 3) in order to assess the possible differences in the effect with data collected in different independent experiments and with different techniques.

Data availability

All the data generated during the experiments described in this manuscript is fully available on Open Science Framework (https://osf.io/rtwbq/).

Results

Experiment 1: Visual backward masking

We used visual backward masking in order to suppress high-level feedback processing along with the visual awareness of an inducer stimulus, which under normal viewing conditions, causes systematic attractive biases affecting subsequent stimuli (Fornaciai & Park, 2018a, 2018b). In order to set up the optimal timing parameter, the effectiveness of visual masking as a function of SOA between target and mask images was measured in a preliminary experiment ($n = 14$). Namely, participants were asked to rate (1–4 visibility rating scale; Railo & Koivisto, 2012) how well they can see a target stimulus (a dot array comprising either 12 or 24 black/white dots) presented on the screen for 50 ms, preceded (forward masking) or followed (backward masking) by a pattern mask (duration = 50 ms; SOA ranging from −147 to 260 ms). In addition to these timing manipulations, we added some catch trials where the mask was presented without the target (no target) or the target was presented without the mask (no mask). From the results of this preliminary experiment (data not shown), we selected the backward masking timing corresponding to the lowest visibility rating, which turned out to be the SOA of 65 ms.

We then tested the effect of visual backward masking on serial dependence in an independent group of participants ($n = 28$). To this aim, we employed a sequential presentation procedure previously used in other studies from our group (Fornaciai & Park, 2018a, 2018b). In this paradigm, participants were asked to discriminate between the numerosity of a reference (16 dots) and a probe (8–32 dots) array presented sequentially. Crucially, a task-irrelevant (inducer; 12 or 24 dots) stimulus was presented before the task relevant ones to induce serial dependence biases (Figure 1A), although on some trials a high-contrast mask was presented in close temporal proximity to the inducer to suppress the awareness of the stimulus and the high-level modulation resulting from its processing. More specifically, three different conditions were intermixed throughout a single session: (a) a no-mask condition, to measure the serial dependence effect; (b) a long SOA condition, to measure the effect of the mask stimulus without impairing awareness (inducer-mask SOA = 550 ms); and (c) a masking condition, where the mask was presented right after the inducer (SOA = 65 ms). Figure 1A shows a depiction of the masking condition in Experiment 1.

Figure 2 shows the psychometric curves obtained by pooling the data of all the participants in Experiment 1. In Panel A, depicting the results of the no-mask condition separately for the two inducer numerosities, the curves are shifted relative to each other consistently with an attractive effect. Namely, there is a leftward shift in the 12-dot inducer condition, and a rightward shift in the 24-dot inducer condition, indicating a relative underestimation and overestimation of the reference stimulus, respectively. Conversely, the curves in Panel B are largely superimposed, showing that introducing an additional stimulus in the sequence strongly reduces the effect of the inducer. Finally, Panel C shows the results observed in the masking condition. Here, surprisingly, the curves are shifted in the opposite direction compared to the no-mask condition. This shift is consistent with a repulsive effect, resulting in relative overestimation induced by the 12-dot inducer and a relative underestimation caused by the 24-dot inducer.

To better characterize the different patterns of effect in the different conditions, we computed the average effect by fitting the psychometric curves individually for each participant, thus obtaining individual measures of the reference perceived numerosity (PSE) and computing the average across the group. The results of Experiment 1 in terms of average PSE as a function of inducer numerosity are shown in Figure 3A. Consistent with previous studies (Fornaciai & Park, 2018a, 2018b), we observed again a systematic attractive bias as a function of inducer numerosity in the no-mask condition (leftmost panel of Figure 3A). That is, a 12-dot inducer caused the 16-dot reference to appear significantly less numerous compared to the same 16-dot reference preceded by a 24-dot inducer (paired sample t test, $t[27] = -2.27$, $p = 0.031$, $d = 0.43$). Such an attractive bias illustrates how previous stimuli are incorporated into current percepts, resulting in a shift of the numerical representation of the reference stimulus *toward* the inducer. When a mask was presented with a very long SOA after the inducer (middle panel of Figure 3A) thus not influencing its

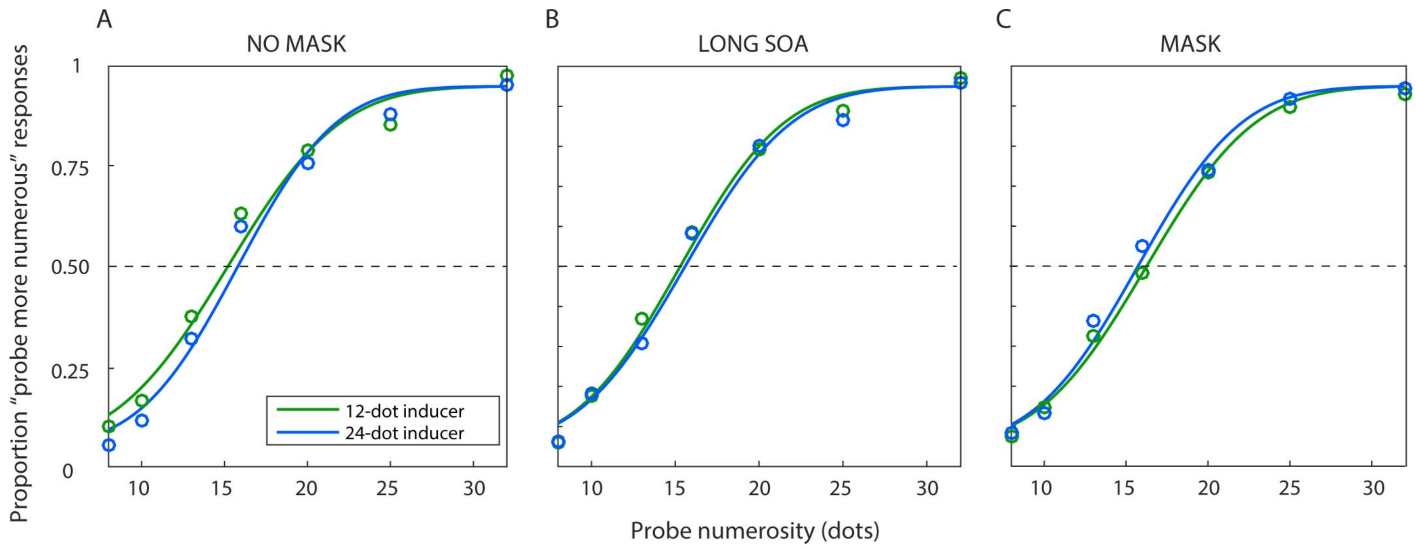

Figure 2. Psychometric curves in Experiment 1. Psychometric curves were obtained by pooling together the data from all the participants. (A) Psychometric curves in the no-mask condition of Experiment 1, for the 12-dot (green) and 24-dot inducer (blue). (B) Psychometric curves in the long SOA condition of Experiment 1. (C) Psychometric curves in the mask condition. Note that pooling the data of all participants is not equivalent to taking the average of individual results, which instead is shown in Figure 3.

visibility, only a nonsignificant attractive trend was observed, $t(27) = -0.72$, $p = 0.48$, $d = 0.13$, illustrating that the presence of the mask itself disrupts the numerosity-specific effect of the inducer. Performing a Bayesian test further confirmed that there is no evidence supporting the presence of a robust attractive effect in this condition (i.e., the test supports the null hypothesis of no effect; Bayes factor [BF] = 0.23). Crucially, when a mask was presented shortly after the inducer to suppress awareness, we instead observed something radically different: a significant repulsive effect—i.e., the opposite of attractive serial dependence, $t(27) = 2.58$, $p = 0.015$, $d = 0.49$. This repulsive effect is akin to perceptual adaptation, pulling the representation of a stimulus away from the preceding one (e.g., see Kohn, 2007 for a review). Moreover, we also compared the different conditions against each other. First, the results showed that there is a statistically significant difference between the no-mask and mask conditions, confirming that these two stimulation conditions result in radically different perceptual effects (paired t test comparing the distribution of serial dependence indexes in the two conditions; $t[27] = 3.48$, one-sided $p < 0.001$, $d = 0.66$). On the other hand, we also compared the long SOA condition versus the other two conditions. In the case of the no-mask condition, we did not find a significant difference, $t(27) = -0.85$, $p = 0.199$, $d = 0.16$, suggesting that some residual attractive effect is present also in the long SOA condition. The effect in the long SOA condition is, however, significantly different from the masking condition, $t(27) = 2.14$, $p = 0.021$, $d = 0.41$, showing that the suppressing effect of masking is likely not merely due to the presence of an additional stimulus like in the long SOA condition.

In additional analyses, we tested whether any of the experimental manipulations affected participants' precision in the task (i.e., JND; data not shown), as one might wonder if the observed attractive and repulsive biases are also accompanied by changes in the level of precision. A two-way repeated-measure ANOVA with factors Condition (i.e., the three conditions of the experiment) and Inducer (i.e., the two inducer numerosities), however, revealed no main effect of condition, $F(2, 27) = 0.459$, $p = 0.635$; no main effect of inducer, $F(1, 27) = 1.535$, $p = 0.226$; and no interaction, $F(2, 27) = 0.198$, $p = 0.821$, suggesting that the observed biases cannot be explained by perceptual precision.

Experiment 2: Visual forward masking

Backward masking suppresses high-level feedback signals to early visual cortex, while sparing feedforward activity. Thus, the repulsive effect observed in Experiment 1 indicates that spontaneous recalibration of sensory signals arises from feedforward activity. If this is correct, then suppressing the feedforward processing of the inducer stimulus should, in principle, abolish such a recalibration. We evaluated this hypothesis in Experiment 2 ($n = 25$) by using forward masking, which has been shown to inhibit even the transient responses at the onset of a masked target (Macknik & Livingstone, 1998). The procedure was identical to Experiment 1, with the only difference of presenting the mask

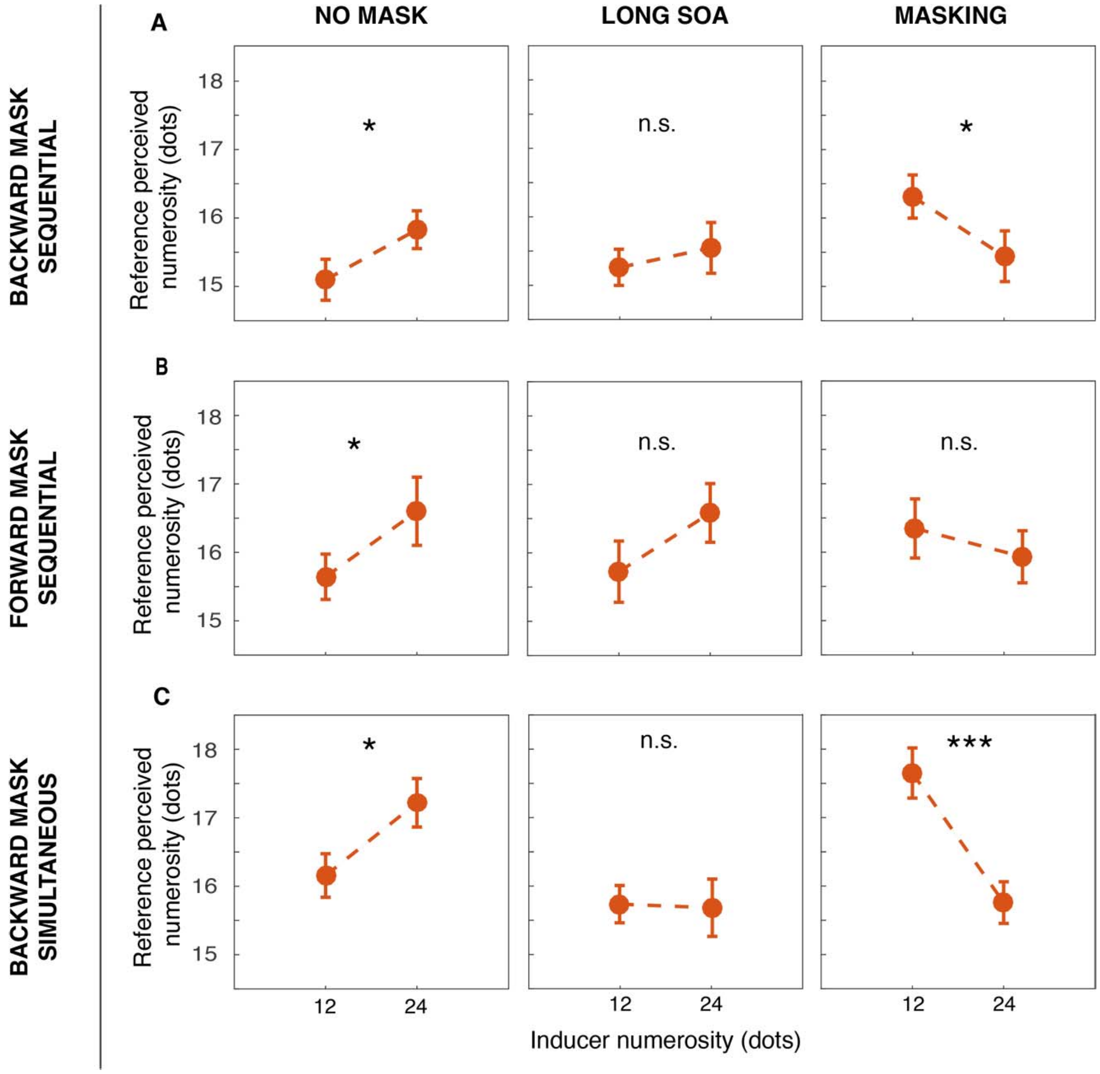

Figure 3. Results of Experiments 1 through 3. Results are reported in terms of perceived numerosity of the reference stimulus (PSE) as a function of the inducer numerosity. (A) Experiment 1. While without masking we observed a significant attractive effect (left), backward masking resulted in a significant repulsive aftereffect (right). (B) Experiment 2. Forward masking, thought to suppress the feedforward onset response to a stimulus, did not result in the same repulsive aftereffect although there was a nonsignificant trend (right). (C) Experiment 3. The results of Experiment 1 were replicated in a design involving a simultaneous presentation of reference and probe, with backward masking of the inducer again resulting in a strong repulsive aftereffect. Error bars are *SEM*. n.s. = not significant, $*p < 0.05$, $***p < 0.001$.

before the inducer (Figure 1B), with a mask-inducer SOA of 78 ms chosen as the most effective timing measured in the preliminary experiment. Again, we tested three different conditions: a no-mask condition inducing serial dependence, a long SOA condition to control for the presence of an additional stimulus without masking, and a forward-masking condition.

As in Experiment 1, a significant attractive effect emerged in the absence of masking (Figure 3B, left panel), $t(24) = -2.70$, $p = 0.013$, $d = 0.54$. With a long SOA (middle panel), we observed a nonsignificant attractive trend, $t(24) = -1.84$, $p = 0.077$, $d = 0.37$. In this context, a Bayesian analysis again provided little support for the presence of an attractive effect (BF = 1.25), suggesting that in this condition serial dependence is much weaker. In contrast, forward masking resulted in a nonsignificant repulsive trend (right panel), $t(24) = 1.06$, $p = 0.30$, $d = 0.21$. While this effect initially seemed to be due to low statistical power, a Bayesian analysis showed that the data are more in support of the null hypothesis against the alternative hypothesis, asserting that there exists a repulsive effect (BF = 0.37). Overall, these results show that any recalibration/adaptation process is strongly suppressed by forward masking, suggesting that feedforward processing is necessary for sensory recalibration. Comparing the different conditions against each other, we first found a significant difference between the effect in the no-mask and mask conditions, $t(24) = 3.03$, one-sided $p = 0.003$, $d = 0.61$, suggesting that also in this case the presence of masking strongly suppresses attractive serial dependence. The long SOA condition, instead, did not show any significant difference compared to the no-mask condition, $t(24) = -0.15$, $p = 0.44$, $d = 0.03$, again suggesting that some residual effect is still observable when the mask is presented with a long SOA. The long SOA condition is, however, significantly different from the masking condition, $t(24) = 2.06$, $p = 0.025$, $d = 0.41$, again showing that masking is the crucial factor suppressing the effect.

Similarly to Experiment 1, a two-way repeated-measure ANOVA on JNDs revealed no main effect of condition on precision, $F(2, 24) = 0.162$, $p = 0.851$; no main effect of inducer numerosity, $F(1, 24) = 0.215$, $p = 0.646$; and no interaction, $F(2, 24) = 1.415$, $p = 0.252$.

Experiment 3: Visual backward masking with simultaneous presentation

The results of Experiment 1 demonstrate that while the recent history of stimulation provides an attractive bias under normal viewing condition, such a bias is abolished when the high-level conscious processing of a preceding stimulus and the related feedback signals to visual areas are suppressed by means of backward masking. Instead, a strong repulsive bias emerges, reflecting a spontaneous recalibration of sensory signals in the absence of high-level influences mediating visual stability and continuity. However, while the sequential paradigm employed in Experiments 1 and 2 has practical advantages, previous serial dependence studies showed that having task-relevant stimuli presented simultaneously is a more robust procedure, as it minimizes the involvement of working memory encoding in the observed effect (Fritsche et al., 2017). In our previous study (Fornaciai & Park, 2018b), we demonstrated that an experimental paradigm with simultaneous presentation provides virtually identical results compared with a sequential paradigm, as long as subjects pay enough attention to the inducer stimulus. Therefore, the results from Experiments 1 and 2 are not likely to be attributed to working memory biases. Nevertheless, to achieve more robust results, we replicated Experiment 1, employing a simultaneous presentation procedure (Figure 1C), in an independent group of participants ($n = 28$). In this procedure, reference and probe were simultaneously presented at the two sides of the screen, preceded by the inducer in a position corresponding to the reference. We ensured that participants paid attention to the inducer by means of a secondary task orthogonal to the numerosity discrimination task (color oddball detection; see Materials and methods).

Figure 3C shows the results of this experiment. Again, with no masking, we replicated the attractive serial dependence effect, with perceptual estimates of the reference stimulus significantly biased towards the inducer numerosity, $t(27) = -2.62$, $p = 0.014$, $d = 0.49$. With a long SOA, the mask resulted in a disruption of the attractive effect resulting in no significant bias, $t(27) = 0.10$, $p = 0.92$, $d = 0.02$, BF = 0.10, consistent with Experiment 1. Strikingly, with backward masking, we again observed a strong repulsive aftereffect, $t(27) = 5.35$, $p < 0.001$, $d = 1$, with an even stronger effect compared with Experiment 1. These results support evidence for repulsive recalibration even in a paradigm, minimizing the involvement of working memory processes in the discrimination task. As in the previous experiments, we also compared the three conditions against each other. Doing so, we found a statistically significant difference between the no-mask condition, $t(27) = 5.65$, one-sided $p < 0.001$, $d = 1.05$, in line with the results from Experiments 1 and 2. Comparing the long SOA condition against no-mask and mask conditions, on the other hand, we found again no significant difference compared to no mask (although approaching significance), $t(27) = -1.67$, $p = 0.053$, $d = 0.31$, and a significant difference compared with the masking condition, $t(27) = 3.02$, $p = 0.003$, $d = 0.56$, in line with the previous experiments.

Similarly to the previous experiments, a JND analysis revealed no main effect of condition, $F(2, 27) = 0.111$, $p = 0.895$; no main effect of inducer numerosity, $F(1, 27) = 1.653$, $p = 0.209$; and no interaction, $F(2, 27) = 0.234$, $p = 0.792$.

Finally, we performed a more comprehensive series of tests comparing the same condition across different experiments. Specifically, we performed a series of one-way ANOVAs, with factor Experiment (Experiments 1, 2, and 3), separately for the no-mask, long SOA, and mask conditions. First, we did not observe any main effect of experiment in the no-mask condition, $F(2, 80) = 0.225$, $p = 0.799$, showing that the attractive serial dependence effect does not show strong differences across different experiments. Similarly, we did not find any significant main effect of experiment in the long SOA condition, $F(2, 80) = 0.971$, $p = 0.383$. However, we instead observed a significant main effect of experiment in the masking condition, $F(2, 80) = 4.415$, $p = 0.015$. We further performed a series of post hoc tests in order to directly compare different masking conditions across the three experiments. On the one hand, the results show a significant difference between the effect of backward masking in Experiment 3 and the effect of forward masking in Experiment 2, $t(53) = 2.878$, $p = 0.015$, $d = 0.77$. On the other hand, we did not observe any significant difference between the two backward masking conditions (Experiments 1 and 3; $t[53] = 2.045$, $p = 0.086$, $d = 0.56$), and between forward masking (Experiment 2) and backward masking in Experiment 1, $t(55) = 0.891$, $p = 0.376$, $d = 0.24$. Such a difference in the magnitude of the effect (i.e., a significantly stronger effect in the masking condition of Experiment 3 compared with Experiment 2, but not in Experiment 1) may be due to the limitation of the sequential paradigm, which may have caused some residual effect to extend to the probe stimulus (see Discussion).

Discussion

Attractive serial dependence in visual perception has recently been interpreted as a consequence of an active process smoothing out noise and discontinuities in the service of visual stability (Fischer & Whitney, 2014). In the present study, we used visual masking to address the possibility that such a visual stability mechanism may operate via cortical feedback modulating early visual activity. Our results show that while attractive serial dependence consistently emerges in the no-mask conditions across the three experiments, backward masking strongly suppresses the attractive effect. In such a condition, a strong and systematic repulsive effect emerges instead, akin to perceptual adaptation.

These results obtained by exploiting visual masking thus shed new light on the mechanisms establishing this attractive bias, and on the consequences of inhibiting such mechanisms. One of the effects of visual backward masking is the suppression of recurrent processing in the visual cortex, effectively blocking high-level modulatory feedback to early visual areas (Fahrenfort et al., 2007). Thus, the finding that backward masking abolishes serial dependence provides evidence that it likely requires visual awareness, bolstering the idea that it arises from feedback signals from high-level brain areas (Fornaciai & Park, 2018b).

Even more striking, the backward masking resulted in a repulsive effect, indicating a rapid and spontaneous sensory recalibration in the absence of such high-level modulation. This finding has important implications for perceptual adaptation (Burr & Ross, 2008; Kohn, 2007), as the repulsive effect found by backward masking the inducer stimulus suggests that adaptation does not require long and sustained stimulation (see also Aagten-Murphy & Burr, 2016, for a similar interpretation). Indeed, such a repulsive aftereffect established by just 50 ms of stimulation is, to the best of our knowledge, one of the fastest adaptation aftereffects observed to date. Such a fast-scale adaptation was indeed previously reported in motion adaptation (after a 25-ms exposure) when participants were unaware of the adapting motion, which is consistent with the present results (Glasser, Tsui, Pack, & Tadin, 2011). Moreover, the strength of rapid motion adaptation diminished as the visibility of the adapting motion increased. The current study extends this previous report in two ways. First, rapid adaptation in numerosity suggests that such form of adaptation generalizes to different perceptual dimensions. Second, and more importantly, our findings provide a mechanistic explanation of what limits adaptation on very short timescales. Namely, a possibility is that at short timescales, when the inducer/adaptor stimulus is clearly visible, the mechanisms for serial dependence actively suppress the repulsive aftereffects resulting from sensory recalibration. In other words, the adaptation provided by brief stimuli is continuously suppressed by high-level modulatory processes establishing serial dependence. In our case, then, the repulsive effect is likely to be the consequence of the *absence* of stabilization, as visual masking suppresses the high-level and feedback processing needed for the attractive bias to occur. Similarly, results in the context of rapid motion adaptation (Glasser et al., 2011) may be explained in the same way, as the strongest repulsive effect was observed when the adapting motion was not perceptually discriminable. In that case, it likely lacked the higher level processing needed to trigger serial dependence. However, while the present results show that serial dependence is abolished in the absence of visual awareness of the stimulus, it is important to note that such an effect may be limited to the suppression of awareness provided by visual masking. Indeed, while several other techniques could be used to suppress, impair, or reduce awareness of a stimulus (e.g., attentional blink, crowding, continuous flash suppression, and other), they may not result in a similar pattern of effects. We specifically chose visual (backward) masking as it is thought to suppress feedback signals, which we deem essential for serial dependence, and hence the suppression of serial dependence and the emergence of a repulsive effect may not generalize to different disruptive techniques tapping onto different brain mechanisms.

Besides the strong attractive and repulsive effects observed in the no-mask and (backward) masking conditions, it is also interesting to consider the lack of effect in the long SOA conditions. Note that serial dependence is thought to represent the integration of perceptual representations over time. In fact, previous work has demonstrated that the influence of prior stimuli on the current one (provided that they are similar) decreases as a function of the number of preceding stimuli prior to the current one (Fischer & Whitney, 2014). Therefore, the presence of an intervening irrelevant stimulus (i.e., without a clear numerosity content as a dot array) in the long SOA condition of Experiment 1 could disrupt the attractive effect by interfering with the history of visual stimulation. In other words, attractive serial dependence would thus affect the reference stimulus also in the long SOA condition, but with the influence of the inducer numerosity weakened by the presence of the additional mask stimulus. This is also suggested by the stronger (although not significant) effect observed in the long SOA condition of Experiment 2 (where we used forward masking) as opposed to the long SOA condition in the other two backward-masking experiments. In this case, the attractive effect would still be more based on the inducer stimulus, with only a small interference from the mask stimulus presented further back in time before the inducer. While the effect is small with no statistical significance, there seems to be a slight tendency for an attractive effect in the long SOA condition of Experiment 2, in which the mask was presented prior to the reference, more so than in the long SOA condition of Experiment 1. This pattern is again consistent with the idea that the attractive bias effects are driven by the history of visual stimulation. That is, because the irrelevant mask stimulus was presented even prior to the inducer, the interference due to that mask would be weaker. In addition, the results from the long SOA condition help us rule out the possibility that the repulsive effect found in the masking conditions (i.e., in Experiments 1 and 3) merely reflects an interference provided by an intervening stimulus rather than resulting from masking.

Taken together, these results demonstrate the interplay between different perceptual processes: While at short timescales attractive modulation is imposed over spontaneous recalibration to facilitate the stability and continuity of the visual input, at longer stimulation timescales the repulsive recalibration overcomes high-level modulations. The suppression of the repulsive effect by forward masking further supports evidence for a local and spontaneous neurocomputational process, based on feedforward activation and independent from visual awareness and high-level processing. Importantly, these two processes resulting in attractive and repulsive effects would not be mutually exclusive, but occurring in parallel. In this scenario, different stimulation procedures and features of the stimuli—like, for instance, their uncertainty or their duration—would modulate the relative weight of the two effects, determining the result at the perceptual level. For instance, with short but visible stimuli, attractive serial dependence would overpower adaptation, while as the stimulus duration gets longer a repulsive effect will emerge (i.e., as in a classic numerosity adaptation paradigm; Burr & Ross, 2008). Conversely, when the stimulus is suppressed by masking, adaptation would be released from the overpowering attractive bias, and emerge even at very short durations. However, while we advance a very specific hypothesis concerning the possible neural underpinnings of attractive and repulsive effect, caution is in order in inferring the possible neural mechanisms responsible for the present results. Indeed, our psychophysical data alone do not allow us to take a strong position on this point, and further neural level investigations are needed to test our hypothesis.

Regarding the specific paradigm used, the sequential paradigm used in the first two experiments presents some limitations. First, it leaves open the possibility of an effect at the working memory level, as the probe stimulus is compared to a memory trace of the reference. This is indeed why we performed Experiment 3 with simultaneously presented stimuli, and the results allow us to rule out this possibility. Second, another possibility is that participants could just ignore the reference stimulus and judge only the variable probe. Indeed, in our paradigm the serial dependence effect was measured by matching a fixed stimulus (the reference) with a variable probe. Under such a circumstance, participants could have picked up (consciously or not) the regularity of the constant stimulus, and focused their attention to the variable stimulus, which would be sufficient to perform the task (i.e., for instance by comparing it with an internal representation of the reference or to the average numerosity of the probe itself). This is, however, less likely, as the serial dependence effect is indeed measured as a bias of the reference perceived numerosity. Thus, in such a case, we should expect little or no effect. Nevertheless, to avoid such a confound, future studies should address the same effect using variable reference stimuli, which would possibly also increase the effect due to increased uncertainty (i.e., as opposed to the regularity of a constant stimulus). Moreover, the sequential paradigm makes also the probe susceptible to attractive serial dependence (or the repulsive effect), as it is presented in the same position as the inducer (and reference). This in turn predicts an overall reduced effect (either attractive or repulsive) with sequential stimuli, and can indeed explain the difference in the magnitude of the effect between Experiments 1 and 2 and Experiment 3. Finally, there is still the possibility that the observed effect represents a trivial response bias, rather than a modulation of the reference perceived numerosity. However, this is unlikely as it should similarly apply in the long SOA condition, where instead we did not observe any significant effect.

Are the two opposite effects described here really a reflection of serial dependence and adaptation? Indeed, two alternative explanations can be proposed. First, as serial dependence depends on attention (Cicchini et al., 2017; Fischer & Whitney, 2014; Fornaciai & Park, 2018b), the lack of attractive effects in the masking condition in this study may be alternatively interpreted as the inability to pay attention to the masked stimulus. Two lines of evidence, however, refute that interpretation. First, previous studies show that spatial attention, rather than object- or feature-based attention, is more likely to be involved in serial dependence, at least in the paradigm used in the present study (Fornaciai & Park, 2018a, 2018b). Second, inability to properly pay attention to the inducer stimulus has been shown not only to reduce the effect of serial dependence but also to abolish any aftereffects (Fornaciai & Park, 2018a). In contrast, our data clearly indicate a repulsive aftereffect as a result of backward masking, the pattern that cannot be explained by this alternative account. Hence, an explanation based on impaired attention fails to fully account for the observed results.

Second, one may wonder if the attractive serial dependence reported in this and our previous studies is a form of priming (Wiggs & Martin, 1998). The paradigm used in the present study indeed differs from earlier other studies involving a time series of stimuli (Cicchini et al., 2014; Fischer & Whitney, 2014), as we measured the effect of an irrelevant stimulus on subsequent ones, which may seem similar to a priming paradigm. However, priming and the serial dependence effect described here and in previous studies (Fornaciai & Park, 2018a, 2018b) are largely different, both conceptually and functionally, as well as in terms of paradigm used and the neural mechanisms involved. "Perceptual priming" generally refers to a facilitation observed in various perceptual paradigms most often when task-relevant information (either sensory or conceptual) is repeated, in the form of better accuracy, lower thresholds, or faster responses (Tulving & Schacter, 1990). First, our paradigm does not involve stimulus repetition, as the inducer numerosity was always different from the numerosity of the subsequent reference stimulus. In addition, no difference in the perceptual precision (i.e., JND) was observed across different experimental manipulations, while widely different biases were observed. Second, while a priming effect may provide better accuracy in the task, the effect reported here concerns a bias in perceived numerosity, making accuracy actually worse. This behavioral outcome is in striking contrast with the outcome expected from perceptual priming, indicating that the effect found in this study has a different nature from perceptual priming. Third, priming has a long-lasting effect (Cave, 1997; Musen & Treisman, 1990; Tulving, Schacter, & Stark, 1982). In the context of the present experiment, where different stimuli were presented in a relatively short interval, a long-lasting time course would have caused the effect of different inducers to mix up, actually reducing or eliminating any net effect. Fourth, priming is relatively independent from attention (Kellogg, Newcombe, Kammer, & Schmitt, 1996; Szymanski & MacLeod, 1996), while serial dependence crucially depends on it (Fischer & Whitney, 2014; Fornaciai & Park, 2018b). Fifth, priming works similarly even when awareness of the stimulus is suppressed (Bar & Biederman, 1998), while we show that the serial dependence effect measured with our paradigm is reversed when the inducer stimulus is masked. Finally, the neural mechanisms underlying the two effects are largely different. While priming, at the neural level, involves a reduction of neural responses to the primed stimulus—i.e., due to the repetition of the same information (Badgaiyan & Posner, 1997; Rugg, Soardi, & Doyle, 1995)—we have previously shown that serial dependence causes an attractive shift of brain responses as a function of the inducer (Fornaciai & Park, 2018a). In sum, the attractive bias reported here and in previous studies from our group (Fornaciai & Park, 2018a, 2018b) cannot be explained by perceptual priming.

Instead, the present results are consistent with the idea of serial dependence operating at the level of perceptual representation (Fischer & Whitney, 2014; Cicchini et al., 2017). This is particularly clear by considering the data from Experiment 3, where we used a discrimination paradigm with simultaneously presented stimuli. While serial dependence has been alternatively interpreted as a working memory or decision bias (Fritsche et al., 2017), our results do not support such an interpretation for two reasons. First, the simultaneous presentation of task-relevant stimuli entails a perceptual judgment whereby the effect is very difficult to explain as a bias occurring during working memory retention, as in Fritche et al. (2017). Second, the spatially localized nature of serial dependence in Experiment 3 (i.e., the fact that the inducer affects only the stimulus in the corresponding position) speaks against the idea of a decision bias, which is not expected to show the spatial specificity predicted by a perceptual effect.

Conclusion

Overall, the current findings first demonstrate that attractive serial dependence requires recurrent feedback activity, which is thought to provide visual stabilization. More strikingly, the findings for the first time demonstrate that the *absence* of the visual stabilization mechanism achieved by abolishing the awareness of a preceding stimulus results in a systematic repulsive bias in the perception of a current stimulus, akin to perceptual adaptation. Such a result first suggests that adaptation is a spontaneous process occurring independently from awareness and during the initial feedforward sweep: Whenever a stimulus—even an extremely brief one—is processed by a sensory network, its processing causes an automatic shift in neural responses to subsequent stimuli causing the repulsive aftereffect. More interestingly, however, such a rapid and spontaneous recalibration occurs *only* in the absence of visual awareness, suggesting that this kind of neural computation is, in normal stimulation conditions, continuously suppressed by means of high-level modulatory feedback aimed to maintain stability and continuity of sensory signals. In sum, the current results highlight the interplay between two opposing perceptual bias effects at short timescales as a basis for our perceptual experience.

Keywords: serial dependence, *numerosity perception*, *visual stability*, *perceptual adaptation*, *visual masking*

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