Serial dependence in numerosity perception

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ABSTRACT

Our conscious experience of the external world is remarkably stable and seamless, despite the intrinsically discontinuous and noisy nature of sensory information. Serial dependencies in visual perception – reflecting attractive biases making a current stimulus to appear more similar to previous ones – have been recently hypothesized to be involved in perceptual continuity. However, while these effects have been observed across a variety of visual features and at the neural level, several aspects of serial dependence and how it generalizes across visual dimensions is still unknown. Here we explore the behavioral signature of serial dependence in numerosity perception, by assessing how the perceived numerosity of dot-array stimuli is biased by a task-irrelevant "inducer" stimulus presented before task-relevant stimuli. First, although prior work suggests that numerosity perception starts in subcortex, the current study rules out a possible involvement of subcortical processing in serial dependence, confirming that the effect likely starts in visual cortex. Second, we show that the effect is coarsely spatially localized to the position of the inducer stimulus. Third, we demonstrate that the effect is present even with a stimulus presentation procedure minimizing the involvement of post-perceptual processes, but only when participants actively pay attention to the inducer stimulus. Overall, these results provide a comprehensive characterization of serial dependencies in numerosity perception, demonstrating that attractive biases occur by means of spatially-localized attentional modulations of early sensory activity.

KEYWORDS
Serial dependence; numerosity perception; visual stability; perceptual continuity.

INTRODUCTION

One of the most basic feature of our conscious perceptual experience is its stability: we experience a coherent, stable, and seamless visual world. Such a remarkable stability is far from being trivial. Indeed, the noisy nature of neuronal information processing and the intrinsic instability of biological sensors like the eye make it difficult to explain the stability and continuity of our visual experience. Such features are indeed likely to arise from active stabilization processes involving complex neural machinery.

In recent years, novel findings concerning perceptual biases provided by the recent history of stimulation – or serial dependencies – have been interpreted as an active stabilization process, integrating stimulus features over space and time to smooth out noise in neural processing (Burr & Cicchini, 2014; Fischer & Whitney, 2014; Cicchini et al., 2017; but see Fritsche et al., 2017 for a different interpretation). In a seminal paper, Fischer & Whitney (2014) demonstrated that when participants have to adjust a bar to match the orientation of a visual stimulus, responses are systematically biased by the orientation of stimuli presented in previous trials, spanning several seconds in the past. In other words, current stimuli are perceived to be more similar to previous ones – an *attractive* effect in striking contrast to repulsive adaptation aftereffects (e.g. Kohn et al., 2007). Further studies also demonstrated that this attractive bias is not limited to orientation but extends to several visual domains like numerosity (Corbett et al., 2011; Cicchini et al., 2014), face identity (Liberman et al., 2014), face attractiveness (Xia et al., 2016), motion (Alais et al., 2017), position (Manassi et al., 2018), and even the summary statistics of a visual scene (Manassi et al., 2017). Computational analyses of such attractive effects suggest that incorporating the recent history of stimulation into current perceptual representation might be an effective way to stabilize perception (Burr & Cicchini, 2014).

Despite the growing amount of studies investigating the features of attractive serial dependence, much more work is needed to understand the generalization of this phenomenon across the many dimensions of visual perception. In the present study, we explore serial dependence in visual numerosity perception. Numerosity represents one of the fundamental attributes of the external

environment, and it has been shown to be underpinned by largely dedicated processing mechanisms (e.g. Anobile et al., 2016a; Cicchini et al., 2016; Burr et al., 2017), generalized across different sensory modalities (Arrighi et al., 2014) and between perceptual and motor systems (Anobile et al., 2016b). Recent studies further highlight the visual processing pathway subserving numerosity perception, showing that numerical information is represented at multiple levels in the visual hierarchy, starting from very early visual areas such as V2 or V3 (Roggeman et al., 2011; Park et al., 2016; Fornaciai et al., 2017; Harvey et al., 2017; Fornaciai & Park, In press), and likely interacting with multiple perceptual systems (Fornaciai & Park, 2017). In a previous work by our group (Fornaciai & Park, 2018), we reported a neural signature of attractive serial dependence emerging early in the visual stream, and even in an almost completely passive-viewing paradigm. However, the behavioral consequences and features of such attractive bias in numerosity perception require further investigation.

In Experiment 1, we first address the possibility that serial dependence in numerosity perception may arise from neuronal processing in subcortical regions, as suggested by a recent study showing numerosity encoding in subcortex (Collins et al., 2017). To do so, we either presented all the stimuli to the same eye or segregated inducer and reference stimuli to different eye, thus tapping onto either monocular subcortical visual pathways, or cortical binocular processing. In experiment 2, we tested for the spatial specificity of attractive biases, by presenting inducer and reference stimuli in either overlapping or non-overlapping positions. Moreover, while in the first two experiment stimuli were always presented as a sequence, in Experiment 3a, we presented reference and probe stimuli simultaneously, preceded by the inducer presented at the same location of the reference, in order to minimize the involvement or working memory in the observed effect (Fritsche et al., 2017). Finally, in Experiment 3b we expanded the results from Exp. 3a by including attentional modulations – i.e. participants were required to either actively attend the inducer stimulus to perform a secondary task, or actively ignore it to perform the secondary task at fixation.

Overall, our results demonstrate that attractive serial dependence biases start from cortical processing (i.e. rather than subcortical), and present several hallmarks of a perceptual effect, supporting the idea of serial dependence as a perceptual phenomenon linked to perceptual stability and continuity. Moreover, we also demonstrate that attractive effects in numerosity

perception require attention, suggesting that serial dependence is an active process concerning attended or relevant stimuli, which may be triggered by higher-level attentive processes modulating sensory activity in a spatially-specific fashion.

METHODS

Participants

A total of 110 subjects participated in the study (81 females, mean age (mean ± SD) = 22 ± 4 years old). Participants were rewarded with course credit and signed a written informed consent before participating in the study. All participants were naïve to the aims of the experiment, 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.

Apparatus and stimuli

Visual stimuli were created using the Psychophysics Toolbox (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997) on Matlab (version r2016b; The Mathworks, Inc.), and presented on a monitor screen running at 144 Hz, with a resolution of 1920 × 1080 pixel, and encompassing approximately 35×20 degrees of visual angle from a viewing distance of about 80 cm. Only in Experiment 1, we used shutter glasses (NVIDIA GeForce 3D Vision 2 Wireless Glasses) synchronized with the screen refresh rate in order to present the stimuli separately to different eyes, or only to the same eye (see *Experiment 1*).

Stimuli were arrays of black and white dots (50% and 50%; in case of odd probe numerosities, the color of the exceeding dot was randomly determined) presented on a gray background. 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). All the stimuli were systematically constructed to range equally in three orthogonal dimensions, corresponding to numerosity (*N*), size (*Sz*), and spacing (*Sp*) (see Park et al., 2016; DeWind et al., 2015). The two other dimensions orthogonal to the numerosity (Sz and Sp) are obtained by logarithmically scaling and combining the area of the individual items (IA), the total area occupied by all the items in an array (TA), the area of the circular field containing

the dots (FA), and sparsity of the items (Spar; the inverse of density of the array). In other words, size represents the dimension along which both TA and IA changes at the same rate, while N is kept constant; the dimension of size is defined as log(Sz) = log(TA) + log(IA). Spacing represents the dimension where both FA and Spar are concurrently modulated, while N is kept constant; Spacing is defined as log(Sp) = log(FA) + log(Spar). The inducer stimuli were constructed so that the dimension of Sz and Sp consisted of two levels each, while for probe and reference stimuli they consisted of seven levels each. Note that since the effect of serial dependence on numerosity comparisons was the primary goal of this study, we collapsed together the different non-numerical dimensions during data analysis. For details about this stimulus construction scheme, see Park et al. (2016) and DeWind et al. (2015).

Stimulus parameters were set as follows. Inducer dot-arrays comprised either 8 or 32 dots (Experiment 1 and Experiment 2), or 12, 16, or 24 dots (Experiment 3a and 3b). The reference stimulus always comprised 16 dots. Probe arrays comprised 8, 10, 13, 16, 20, 25, or 32 dots. The smaller IA was set to 113 pixel^2 (0.038 deg^2), corresponding to a diameter of 0.11 deg (6 pixels), while the maximum IA was 452 pixel^2 (0.15 deg^2), corresponding to a diameter of 0.22 deg (12 pixel). The minimum FA was 70,686 pixel^2 (23.9 deg^2), encompassing 5.5 degrees of visual angle in diameter (300 pixels), while the maximum FA was 282,743 pixel^2 (95.7 deg^2), encompassing 11 degrees in diameter (600 pixels). In all cases, individual dot size was homogeneous within an array, and the minimum distance between any two dots was no smaller than the radius of the dots.

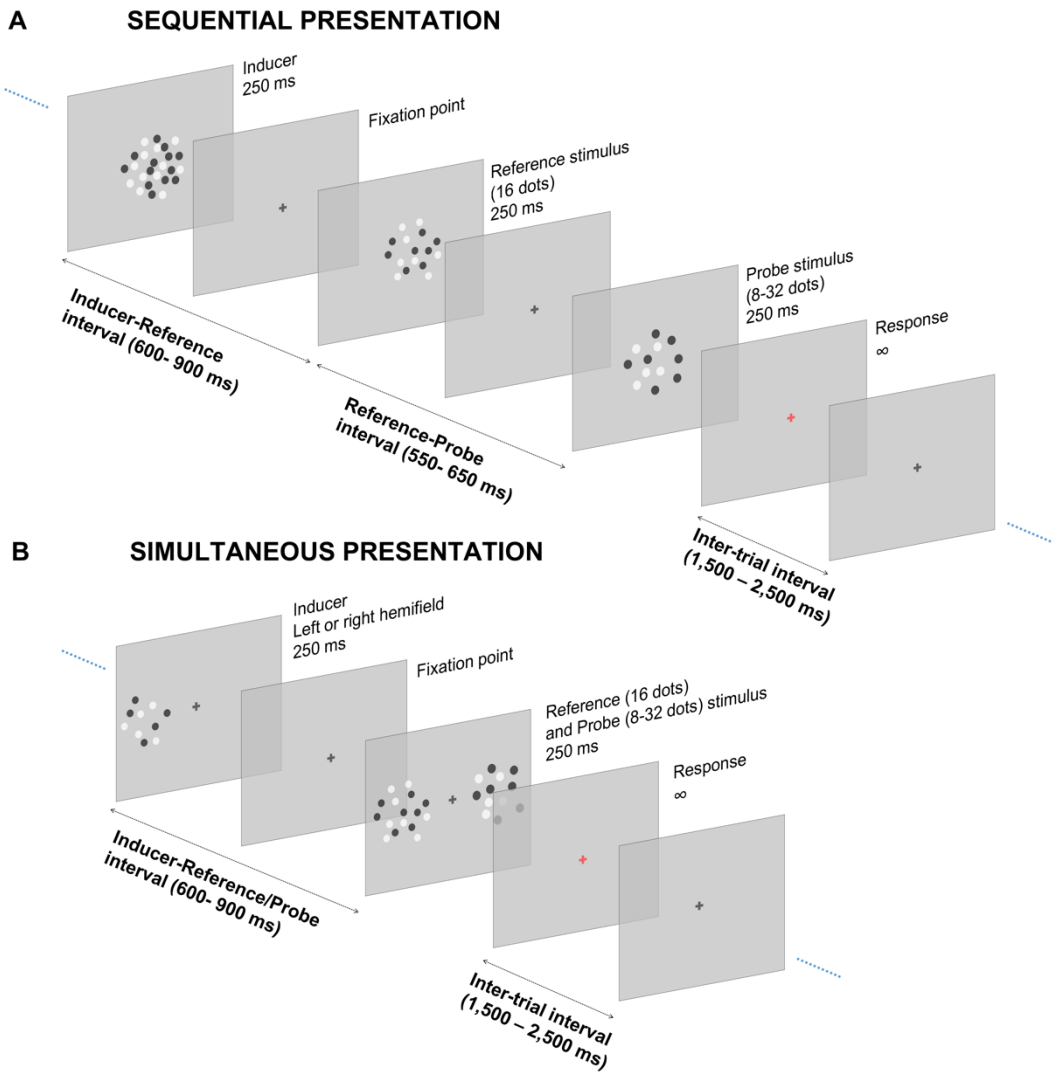

FIG. 1 – General experimental procedures. (A) Sequential presentation procedure employed in Experiment 1 and 2. While participants fixate on a central fixation cross, a series of three stimuli was presented on each trial. First, a task-irrelevant inducer stimulus (8 or 32 dots) was presented on the screen, followed by a reference stimulus (16 dots) after 600-900 ms, and then a probe stimulus (8-32 dots) after 550-650 ms from the reference. All the stimuli were presented for 250 ms each. Participants were instructed to discriminate whether the second (reference) or third (probe) stimulus in the sequence contained more dots. After providing a response, the next trial started automatically after 1500-2500 ms. Participants were also told that the first stimulus was not relevant for the task, but anyway to pay attention to the entire sequence of the stimuli. (B) Simultaneous presentation of reference and probe in Experiment 3a and 3b. In this case,

reference and probe were presented simultaneously on the screen (duration = 250 ms) to minimize the involvement of working memory, with their position (left or right of the fixation point) randomly determined on each trial. Before them, an inducer stimulus was presented on each trial, at the same position of the reference stimulus. Participants were instructed to judge whether the stimulus on the right or the one on the left contained more dots. Only in Experiment 3b, the inducer stimulus was relevant for a secondary task (see Experiment 3b in the Results section). Stimuli are not depicted in scale.

General procedure

The experiment took place 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, participants performed a numerosity discrimination task, determining whether a reference (16 dots) or a variable probe (8-32 dots) stimulus contained the larger number of dots. Serial dependence was induced by presenting a task-irrelevant "inducer" stimulus at the beginning of each trial. In Experiment 1 and 2, the presentation procedure was fully sequential (Fig. 1A), with inducer, reference, and probe (in this order) presented on the screen for 250 ms each. Stimuli were separated by a variable inter-stimulus interval (ISI) of 600-900 ms (inducer-reference) or 550-650 ms (reference-probe). In Experiment 1, all the stimuli were presented at the center of the screen, while in Experiment 2 the inducer stimulus could be presented either centrally, overlapping with the position of the subsequent stimuli (overlapping presentation condition; 50% of the trials), or in an adjacent, completely non-overlapping position (non-overlapping presentation condition), either on the left or on the right of the central fixation point (25% of the trials each), and with an eccentricity depending on the radius of the inducer and reference stimulus (see *Apparatus and stimuli*; center-to-center eccentricity from the fixation point ranging from 6.5 to 12 deg). Irrespective of the specific eccentricity depending on the radius of the inducer stimulus, the distance between inducer and reference position (in terms of separation between the edges of the convex hulls encompassing the dots in the two arrays) was always 1 deg. In Experiment 3a and 3b, reference and probe stimuli were presented simultaneously on the screen for 250 ms (Fig. 1B), with their position (left or right of the fixation point) randomly determined on each trial (center-to-center distance = 22 degrees of visual angle). With this simultaneous presentation procedure, the inducer stimulus was presented before the task-relevant stimuli (ISI = 600-900 ms) always at the same location as the reference stimulus, so with its

194 position (left or right of the fixation point) varying from trial to trial according to the position of
195 the reference. Participants were instructed to judge only the second (reference) and third (probe)
196 stimulus presented on the screen in Experiment 1 and 2, or to judge the two stimuli presented
197 simultaneously in Experiment 3a and 3b. In all cases (with the exception of Experiment 3b where
198 more specific instructions were provided), participants were told that the first stimulus presented
199 on each trial was not relevant for the task, but to pay attention anyway to the entire sequence of
200 the stimuli. In Experiment 3b, participants performed an additional secondary task designed to
201 modulate their attention. Besides the numerosity discrimination task, participants were asked to
202 perform a color oddball detection task concerning the inducer or the fixation cross (in two
203 separate conditions). Namely, on some trials (4 trials per block) either the inducer or the fixation
204 cross was presented in red (oddball stimulus duration = 250 ms in both cases), and in those cases
205 participants were asked to disregard the subsequent stimuli and press a different key. Average
206 (mean ± SEM) detection rate in the color oddball task was 0.95% ± 0.02%, and 0.91% ± 0.04%,
207 respectively for the "attention to fixation" and "attention to inducer" condition. Participants
208 performed 6 blocks of trials (56 trials per block) in Experiment 1, 5 blocks of trials (56 trials per
209 block) in Experiment 2, 6 blocks of trials (63 trials per block) in Experiment 3a, and 4 blocks of
210 trials (63 trials per block) in each condition of Experiment 3b. In all the experiments, participants
211 did not receive any feedback concerning their responses.
212
213 *Behavioral data analysis*
214 Numerosity discrimination performance was analyzed separately for each subject and condition
215 to obtain measures of participants' accuracy and precision in the task. The distribution of
216 response probabilities as function of probe numerosity was fitted with a Cumulative Gaussian
217 curve, according to the Maximum Likelihood method (Watson, 1979). The point of subjective
218 equality (PSE), reflecting the accuracy of subjects' numerosity discrimination performance, was
219 defined as the median of the best-fitting cumulative Gaussian curve to all the data of each
220 participant in each condition. To control performance levels across participants and exclude
221 subjects showing insufficient performance, we used the just-noticeable difference (JND), defined
222 as the difference in numerosity between chance level responses and 75% correct responses. As a
223 criterion for exclusion from data analysis, we considered JND > 9. Additionally, in Experiment
224 3b, we excluded participants showing detection rate of the oddball stimulus < 33%. A total of 9
225 subjects was excluded from data analysis based on these criteria, across all the experiments. A

finger error rate correction ($\lambda = 2\%$) was additionally applied to reduce the noisiness of the data due to response errors or lapses of attention (Wichmann & Hill, 2001). An analysis of variance (ANOVA) or a t-test was performed when comparing multiple conditions or a pair of conditions, respectively. To directly compare effects in pairs of conditions, a serial dependence effect index was defined as the difference in PSE between the large (i.e. 32 or 24 in different experiments) and small (8 or 12 dots) inducer condition.

RESULTS

EXPERIMENT 1

While the most commonly acknowledged neural correlate of numerosity perception resides in the parietal cortex (e.g. Piazza et al., 2004; Harvey et al., 2013; Castaldi et al., 2016), recent studies demonstrated that numerical processing starts much earlier than that (e.g. Roggeman et al., 2011; Cavdaroglu et al., 2015; Fornaciai et al., 2017; Collins et al., 2017; Park et al., 2016). In particular Collins and colleagues (2017) showed evidence for the involvement of subcortex in representing numerical information by exploiting the idea that the encoding of a visual image is facilitated when the same information is presented previously to the same eye compared to when the information was presented to the different eye. Here we reasoned that if numerical processing starts as early as in the subcortex, serial dependence for numerosity perception may be rooted in that structure. To address this possibility, we followed the procedure used by Collins and colleagues and presented the successive stimuli either monoptically or dichoptically (see Fig 2A), using shutter glasses synchronized to the monitor refresh rate. If serial dependence starts in subcortical structures, we should observe a weaker effect in the dichoptic condition, as in this case inducer and reference are kept separated in different monocular pathways before reaching the cortex. A total of 19 participants was included in Experiment 1.

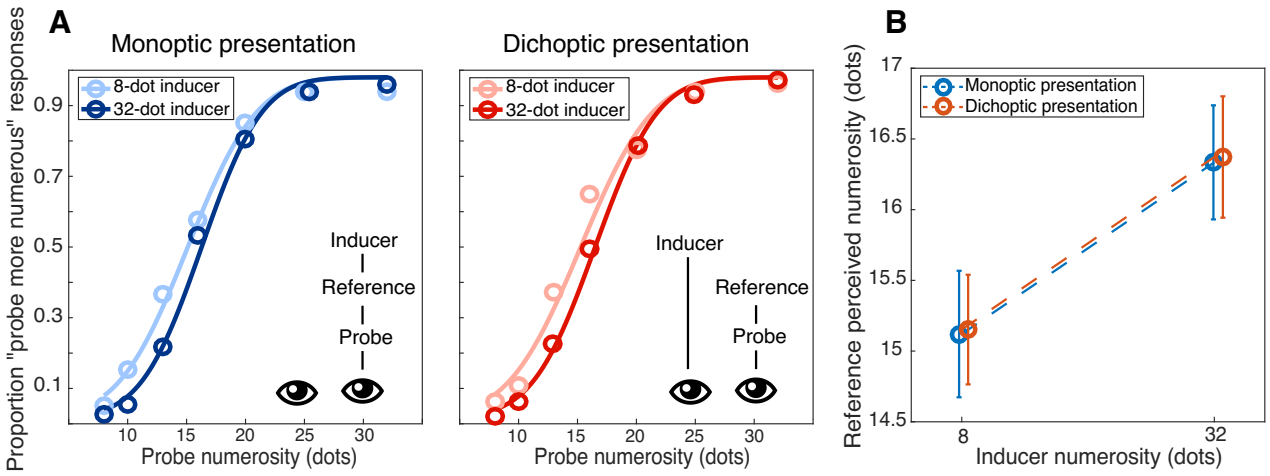

FIGURE 2 – Results of Experiment 1. (A) Average psychometric functions for the 8-dot and 32-dot inducers, in the monoptic (light and dark blue) and dichoptic (light and dark red) conditions. (B) Average PSEs corresponding to the different inducer numerosities, for the monoptic and dichoptic presentation conditions. As evident from data reported in both panels, serial dependence effects (i.e. separation of the two psychometric curves in panel A, or difference in data points corresponding to different inducer numerosities in panel B) were virtually identical in both the monoptic and dichoptic presentation condition, suggesting that attractive biases arise from a processing stage where monocular information is already combined. Error bars are SEM. Each of the two figures in panel A reports a depiction of the corresponding condition, although the eye to which the stimuli were displayed was randomly determined in each trial. The summary data points in panel B are jittered for the ease of visualization.

Figure 2 shows the results of Experiment 1. First, it is immediately clear that the inducer stimulus had a noticeable impact on numerosity discrimination performances, resulted in shifted psychometric curves (Fig. 2A). Such a shift in psychometric curves as a function of the numerical magnitude of the inducer stimulus appears to be attractive, with the smaller inducer (8 dots) resulting in systematically smaller numerical estimates of the reference stimulus, and vice versa. However, the difference in the effect provided by the inducer appears to be nearly identical in the monoptic and dichoptic conditions. Fig. 2B better illustrates that such biases are undistinguishable between the two conditions. A two-way repeated measures ANOVA with factors “inducer numerosity” (8 vs. 32 dots) and “presentation mode” (monoptic vs. dichoptic) confirmed a main effect of inducer numerosity on perceptual estimates ($F(1,18) = 26.04$, $p < 0.001$), while showed no effect of presentation mode ($F(1,18) = 0.019$, $p = 0.89$), and no

interaction between the two factors ($F(1,18) = 0.0001$, $p = 0.99$). This lack of difference between the monoptic and dichoptic conditions suggests that attractive serial dependence likely starts from cortical structures where signals from the two eyes are already combined.

EXPERIMENT 2

Earlier results on serial dependence in orientation perception (Fischer & Whitney, 2014) showed that attractive biases have a relatively broad spatial selectivity, working across large spatial distances provided that stimuli are attended. Here, we investigated the spatial selectivity of the serial dependence effect in a numerosity discrimination task. To do so, we employed a fully sequential presentation procedure similar to Experiment 1, except that the inducer could be presented either centrally, in a position corresponding to the position of the subsequent stimuli (overlapping presentation condition), or at a lateral position, completely non-overlapping with the position of the subsequent stimuli (non-overlapping presentation condition; 1 deg edge-to-edge separation between the areas of the stimuli; center-to-center distance spanning from 6.5 deg to 12 deg [average = 9.1 deg]). If serial dependence in numerosity perception presents the same broad spatial localization as the previous studies on orientation perception (Fischer & Whitney, 2014), we might expect similar effects across the two presentation conditions. Otherwise, if the attractive bias is spatially localized to the position of the inducer stimulus, presenting inducer and reference stimuli at different locations should abolish or reduce the effect. A total of 19 participants was included in Experiment 2.

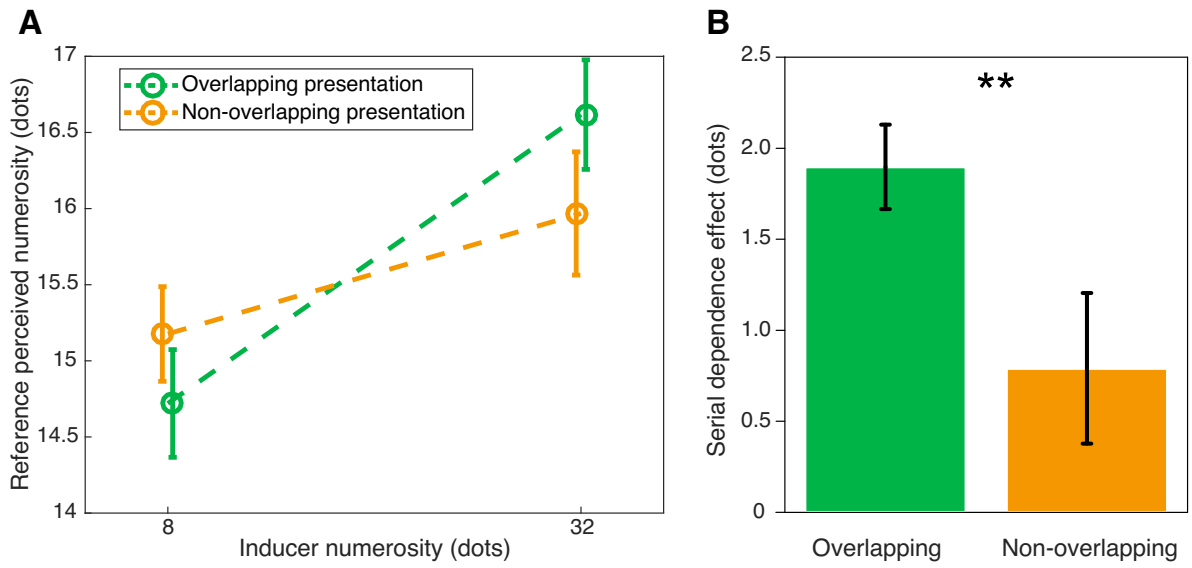

*FIGURE 3 – Results of Experiment 2. (A) Average PSEs for the two inducer numerosities, in the two inducer position conditions. (B) Average difference between PSEs in the two inducer conditions, for the overlapping and non-overlapping inducer position. Both panels clearly illustrate that the attractive serial dependence effect is much stronger when the stimuli are presented in the same position, compared to when the inducer position is presented in an adjacent, non-overlapping position. The summary data points in panel A are jittered for the ease of visualization. Error bars are SEM. ** $p < 0.01$.*

Figure 3 shows the results of Experiment 2. A two-way repeated measures ANOVA with factors "inducer numerosity" (8 vs. 32 dots) and "inducer position" (overlapping vs. non-overlapping), revealed a main effect of inducer numerosity ($F(1,18) = 23.90$, $p < 0.001$), reflecting numerical estimates shifted according to the numerical magnitude of the inducer stimulus (Fig. 3A), and no main effect of inducer position ($F(1,18) = 0.13$, $p = 0.72$). However, we found a significant interaction between the two factors, showing that the magnitude of the attractive effect actually depends on the position of the inducer ($F(1,18) = 7.11$, $p = 0.016$). Post-hoc tests further confirmed that the attractive effect is significantly stronger in the overlapping presentation condition (Fig. 3B; paired sample t-test on the difference in PSE between different inducer conditions [serial dependence effect]: $t(18) = 2.66$, $p = 0.008$, effect size = 0.61), suggesting that the effect is spatially localized to the position of the inducer.

EXPERIMENT 3

Results so far have shown that (1) attractive serial dependencies likely start in cortical rather than subcortical structures, and (2) the effect is spatially localized to the position of the inducer stimuli. However, both in our previous study and in the first two experiments of the current one, we employed a fully sequential paradigm. Presenting a sequence of stimuli could mean that the numerosity discrimination task is performed by comparing the probe stimulus (the last in the sequence), with the memory trace of the preceding reference stimulus. Although a discrimination paradigm is still less taxing in terms of cognitive and working memory processes compared to an adjustment task (e.g. Fritsche et al., 2017), this sequential presentation procedure thus leaves open the possibility of an involvement of working memory. Then, while results from Experiment 2 suggest a spatially-localized *perceptual* effect, we cannot exclude a contribution from working memory processes. Thus, in Experiments 3a and 3b, we employed a paradigm minimizing the involvement of working memory in which the reference and probe stimuli were presented simultaneously on the screen and were preceded by an inducer stimulus presented at the same location of the reference stimulus. In both experiments, we used three inducer numerosities: 12 and 24 dots to induce serial dependence, and 16 dots (i.e. same as the reference) to achieve a baseline measure of numerosity discrimination performance. The reason to use different inducer numerosities (closer to the reference) from Experiment 1 and 2 was to make the effect less prone to spurious repulsive adaptation effects, which are more easily induced when stimuli are very different from each other (Cicchini et al., 2017). In a preliminary experiment, we tested the effect of 12- and 24-dot inducers compared to 8- and 32-dot inducers with the sequential paradigm used in Exp. 1 and 2, and we found no statistically significant difference between the effect provided by the two pairs of inducers ($N = 20$; data not shown; paired sample t-test on the difference in PSE between 12 and 24, and 8 and 32: $t(19) = 0.07$, $p = 0.94$). Such a preliminary result ensured that using 12- and 24-dot arrays as inducers is equally effective to using 8- and 32-dot arrays. A total of 22 participants was included in Experiment 3a.

Experiment 3a

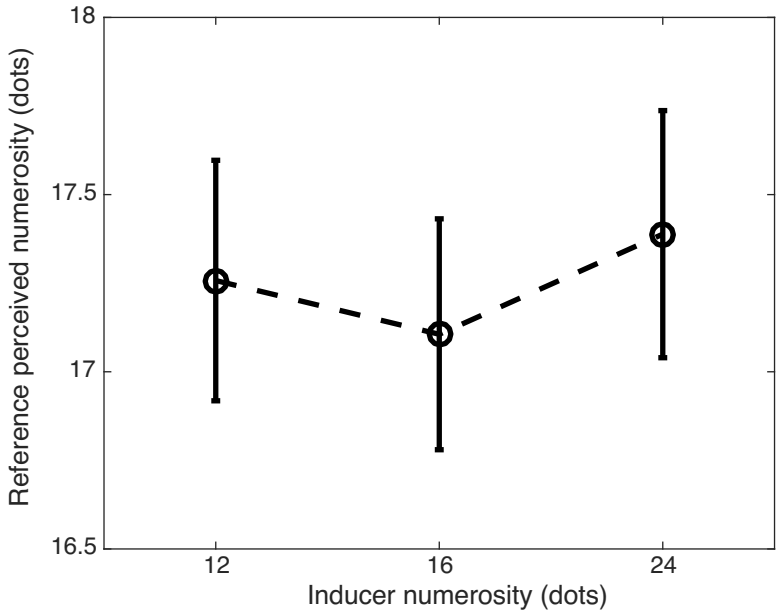

FIGURE 4 – Results of Experiment 3a. Effect of different inducer numerosities on perceptual estimates, obtained by simultaneously (rather than sequentially) presenting the reference and probe stimuli. No significant effect was observed with such presentation procedure. Error bars are SEM.

In Experiment 3a, we presented the reference and probe stimuli simultaneously aiming to reduce the involvement of working memory in numerosity comparisons. As shown in Fig. 4, the difference between different inducer conditions appears very small – nearly negligible compared to previous conditions in Experiment 1 and 2. By directly comparing perceptual estimates with the 12-dot vs. 24-dot inducer, we did not observe any significant effect (paired sample t-test: $t(21) = -0.28$, $p = 0.78$; note that the 16-dot inducer condition was not included in the analysis as the expected null effect in this condition might mask a significant difference between the two conditions expected to induce a bias). This lack of effect with simultaneous presentation compared to the strong and systematic effect found in the previous experiments (employing sequential presentation) suggests that working memory and/or post-perceptual decision processes might be actually involved in the serial dependence effect, by amplifying an otherwise small effect (as also suggested by the results of Fornaciai & Park, 2018).

Experiment 3b

In Experiment 3a, we did not observe any effect – neither attractive, nor repulsive. In Experiment 3b we further investigated the reasons underlying this lack of effect. One possibility, as suggested by previous studies (Fritsche et al., 2017) is that the effect actually concerns post-perceptual processes arising when participants have to keep a stimulus in memory to perform the task (i.e. like in our sequential paradigm in Exp. 1 and 2), while the effect would disappear in tasks more relying on the perceptual representation of the stimuli. An alternative hypothesis, however, is that this lack of effect might be due to participants not paying enough attention to the inducer stimulus. Indeed, previous results (Fischer & Whitney, 2014) suggested that the attractive serial dependence effect strongly relies on attention. In our simultaneous presentation procedure, however, the inducer could randomly appear on the left or on the right of the fixation point, with these two positions separated by a large distance (22 deg). In these circumstance, it is more likely that participants attended both task-relevant positions leaving less attentional resources for the inducer stimulus, which in turn may have caused the attractive effect to disappear. In other words, the simultaneous presentation of both task-relevant stimuli on the two sides of the screen may have forced participants to distribute attention to a large portion of the screen, thus leaving less attentional resources for the processing of the single inducer stimulus presented before the reference and probe stimuli. Here we addressed these possibilities by using a secondary task, making participants to actively attend the inducer stimulus, or to actively ignore it by performing the secondary task at fixation, in two separate conditions. Namely, participants had to perform a color-oddball detection task, concerning either the inducer ("detect the red dot-array"; attention to inducer condition) or the fixation cross ("detect the red fixation cross"; attention to fixation condition). Note that the simultaneous-presentation procedure used in these experiments may look similar to the one used by Fritsche et al. (2017) in which an orientation reproduction and a discrimination task on gratings were performed in succession on each trial. However, our experiments are different from the one in Fritsche et al. (2017) in that the appearance of the red image in the color-oddball task happened only occasionally and the dimension of numerosity was completely irrelevant to that task. Each participant performed both conditions in a counterbalanced fashion, but only the first condition was included in data analysis, thus dividing the participants into two independent groups. This procedure ensured to avoid spurious effect due to the carry-over of one task strategy to the second task performed in the session (Fornaciai et al., In press). In other words, a participant initially instructed to attend

the fixation point may be more prone (voluntarily or not) to continue paying attention to the fixation point also in the second part of the session, even if instructed otherwise. Including only the first task performed by participants thus ensures to obtain a cleaner index of the attentional modulation effect. A total of 22 and 19 participants was included in the experiment, respectively for the attention to fixation and attention to inducer condition.

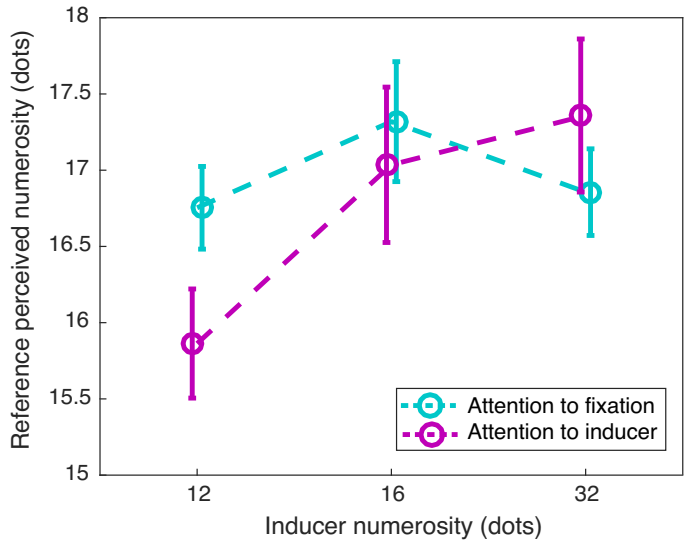

FIGURE 5 – Results of Experiment 3b. Average numerical estimates as a function of inducer numerosity, in the two condition of Experiment 3b. By manipulating subjects' attentional allocation with a secondary task, we observed two markedly different patterns of results. When participants actively paid attention to the fixation point (cyan data points), we observed no effect of inducer numerosity, similarly to Experiment 3a. Conversely, when participants actively attended the inducer stimulus (magenta data points), we observed robust attractive biases as a function of inducer numerosity. Error bars are SEM.

As shown in Fig. 5, by making participants actively attend either the inducer or the fixation cross, we found two markedly different patterns of results. When participants actively paid attention to the fixation cross, we observed a somewhat similar pattern compared to Experiment 3a, with a clear lack of influence of the inducer stimulus. This is confirmed by a paired sample t-test comparing perceptual estimates in the 12-dot inducer condition with the 24-dot inducer condition ($t(21) = -0.36$, $p = 0.72$). In stark contrast, when participants actively paid attention to the inducer stimulus, we found a pattern of effects more similar to Experiment 1 and 2. Namely,

we found a robust and significant attractive bias, with a reduction in perceived numerosity in the 12-dot inducer condition and an increase in perceived numerosity with the 24-dot inducer ($t(18) = -2.2$, $p = 0.042$, effect size = 0.52). This markedly different pattern of results induced by attentional modulations suggests that attractive serial dependence biases are modulated by attention, and likely selective for attended or task-relevant stimuli only.

DISCUSSION

Serial dependence has recently attracted much scholarly attention, producing much research springing from novel insight into the neural mechanisms underpinning such attractive biases. The nature of attractive serial dependence and how such bias generalizes across the many features and dimensions of visual perception, however, is still unclear. In the present study, we explore the behavioral signature of serial dependence in numerosity perception, aiming to characterize attractive biases in numerical magnitude processing. In our previous study (Fornaciai & Park, 2018), we demonstrated a strong neural signature of serial dependence in numerosity perception even without an explicit task. However, the behavioral consequences of serial dependence in numerosity perception still remain unclear, compared to other features such as orientation which has undergone more extensive investigation (Fischer & Whitney, 2014; Fritsche et al., 2017; Alais et al., 2017; Cicchini et al., 2017).

In Experiment 1, we first rule out a possible involvement of subcortical visual areas in the attractive effect. Numerosity perception has indeed been shown to start even before the early cortical stations of visual processing, along the monocular pathways conveying information from the retina to the cortex. Namely, Collins et al. (2017) showed that numerical judgment is facilitated when successive stimuli are presented to the same eye as opposed to separately to different eyes. Results from Experiment 1, however, show no difference in serial dependence effects between monoptic and dichoptic presentation conditions, suggesting that attractive biases arise at processing stages where monocular information is already combined (i.e. starting at least from the primary visual cortex).

Results from Experiment 2 show that the attractive effect occurs in a spatially-localized fashion, specific for the position of the inducer stimulus. Indeed, when the inducer stimulus was presented in an adjacent non-overlapping position, a much weaker effect emerges. Interestingly. spatial specificity is a hallmark of perceptual effects, and usually interpreted as reflecting the involvement of visual areas possessing a topographic map of the visual field. Conversely, such spatial specificity is more difficult to explain assuming solely a cognitive effect, which would more likely affect all the stimuli in the visual field irrespective of their position. While the strongest effect emerges when inducer and reference stimulus occupy the same position, some residual effect seems to leak out to neighboring locations, suggesting that the effect may be mediated by relatively large receptive fields, possibly corresponding to extrastriate visual areas. Nevertheless, such spatial localization suggests that serial dependence at least begins as a perceptual phenomenon emerging from sensory computations, in line with previous results (Burr & Cicchini, 2014; Cicchini et al., 2017; Fornaciai & Park, 2018; Manassi et al., 2018).

To further characterize attractive serial dependence biases in numerosity perception, in Experiment 3a and 3b we employed a different presentation procedure. Indeed, in both Experiment 1 and 2, as well as in our previous study (Fornaciai & Park, 2018), we employed a completely sequential procedure. This paradigm was used to keep the stimulus presentation procedure similar to the EEG procedure used in Fornaciai & Park (2018). Although the sequential paradigm provides practical advantages, it makes the interpretation of the effect more difficult due to the lack of a direct comparison between reference and probe stimuli. That is, participants could possibly be comparing the probe stimulus with the memory traces of the reference stimulus, introducing the possibility of working memory being involved in the effect. To overcome this confound, we thus followed a procedure previously employed in other studies (Fritsche et al., 2017; Cicchini et al., 2017), presenting reference and probe simultaneously, which minimizes the influence of working memory encoding. Strikingly, however, results from Experiment 3a employing this simultaneous presentation procedure show no attractive serial dependence effect (see Fig. 4). Does this lack of effect suggest a crucial role of working memory, or it may be due to other factors like attention? Indeed, in our paradigm, participants could be completely ignoring the inducer stimuli (or to be precise whenever there is only a single dot array presented on the screen) because the task was only performed when two dot arrays appeared simultaneously on the screen, or could be distributing attention to a large portion of the

screen which may reduce the attentional resources available for processing the inducer stimulus. In contrast, in the sequential presentation paradigm, only one stimulus was presented at each time, making it easier for the participants to pay attention to the inducer (although it was irrelevant for the task) without having to divide resources to attend both task-relevant locations.

When participants' attention to inducer was modulated with a secondary task in Experiment 3b, we indeed found two starkly different patterns of results: while no serial dependence effect was found when participants performed a secondary task that required them to pay attention to the fixation cross, we observed a robust attractive bias when participants actively attended the inducer (Fig. 5). This result demonstrates that serial dependence in numerosity perception is evident even when the involvement of memory is minimized, provided that the inducer stimulus receives sufficient attentional processing. Again, the effect appears to be spatially specific for the position of the inducer stimulus (i.e. it does not extend to the probe stimulus presented in the opposite hemifield, which would have canceled out any effect), thus supporting the results from Experiment 2. Such spatially-specific effect triggered by attention appears to be consistent with a spatially-specific attentional modulation (Somers et al., 1999; Grothe et al., 2018), whereby attention modulates specific regions of topographically-organized early visual cortex corresponding to specific positions in the visual field. Intriguingly, these results may also suggest that the spatial specificity of the effect is directly determined (and modulated) by attention. Indeed, when participants attended both spatial locations of reference and probe in Exp. 3a (in the absence of any specific instructions regarding the inducer), such a distributed allocation of attention may have made the inducer to affect both reference and probe, thus canceling out any net effect. Additionally, this may also explain the spatial selectivity observed in Exp. 2, which instead of being purely dependent on the spatial overlap between the stimuli may be determined by the attended spatial region.

Finally, these results also demonstrate that attention to a completely orthogonal dimension (i.e. color) is sufficient to induce a robust serial dependence effect on the numerosity dimension. This suggests that the attractive serial dependence effect is an automatic process occurring relatively independently from task goals, as also previously demonstrated in Fornaciai & Park (2018).

Taken together, these results suggest that attractive biases may arise from cortical sensory computations, involving spatially-specific attentional modulations triggered by previous (even task irrelevant) stimuli. This modulation would in turn affect the sensory processing of subsequent stimuli, starting from relatively early visual areas. Previous results concerning the numerosity processing pathway show that numerical information is strongly represented in relatively early areas such as V2 or V3 (Fornaciai et al., 2017), although with a more crucial involvement of area V3 (Fornaciai & Park, Under review). We could reason, then, that serial dependence in numerosity perception may start from this level of processing as well. More specifically, a possibility is that attentional processing of a stimulus (i.e. the inducer, in our paradigm) triggers a cascade of processes resulting in modulation of sensory responses in early numerosity-sensitive visual regions, likely by means of feedback signal from high-level processing stages (i.e. parietal areas) to low-level visual areas. Such modulation would thus affect the processing of subsequent stimuli – for instance by modulating the synaptic input to areas like V2 and V3 (Grothe et al., 2018) – which would in turn be represented as more similar to previous ones. Crucially, the modulation would be directly at the level of the perceptual representation, rather than concerning only a working memory representation at a post-perceptual processing stage, supporting the idea of serial dependence as a perceptual phenomenon (e.g. Fischer & Whitney, 2014; Cicchini et al., 2017; Fornaciai & Park, 2018), as opposed to a cognitive effect arising at the decision stage (Fritsche et al., 2017; Alais et al., 2017; Bliss et al., 2017). This mechanistic explanation further illustrates the active nature of attractive effects, which would be limited to attended or relevant stimuli, and cannot be explained as a by-product of sensory processing or an automatic recalibration of sensory activity like adaptation (e.g. see Kohn, 2007 for a review). In turn, this supports the idea that serial dependence reflects visual stability processes actively integrating information over time to reduce noise in neural signals (Burr & Cicchini, 2014) and facilitating a continuous and seamless experience of the visual world.

To conclude, by exploring the behavioral signature of serial dependence in numerosity perception, we provide a more comprehensive characterization of this effect, and novel evidence concerning the ongoing debate about the nature of attractive effects. Our results pinpoint a clear cortical effect, with dynamic attentional modulations biasing perceptual representations in early numerosity-sensitive visual areas. This mechanistic explanation, although based on behavioral

data, further suggests that attractive serial dependence is an active process integrating past and present information in the service of visual stability and continuity.

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DECLARATION OF INTEREST

The authors declare no competing interest.

AUTHOR CONTRIBUTIONS

M.F. and J.P. devised the experiments. M.F. collected and analyzed the data. M.F. and J.P. interpreted the results and wrote the manuscript.

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