Neural dynamics of serial dependence in numerosity perception

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ABSTRACT

Serial dependence – an attractive perceptual bias whereby a current stimulus is perceived to be similar to previously seen ones – is thought to represent the process that facilitates the stability and continuity of visual perception. Recent results demonstrate a neural signature of serial dependence in numerosity perception, emerging very early in the time course during perceptual processing. However, whether such a perceptual signature is retained after the initial processing remains unknown. Here, we address this question by investigating the neural dynamics of serial dependence using a recently developed technique that allowed a reactivation of hidden memory states. Participants performed a numerosity discrimination task during EEG recording, with task-relevant dot-array stimuli preceded by a task-irrelevant stimulus inducing serial dependence. Importantly, the neural network storing the representation of the numerosity stimulus was perturbed (or pinged) so that the hidden states of that representation can be explicitly quantified. The results first show that a neural signature of serial dependence emerges early in the brain signals, starting soon after stimulus onset. Critical to the central question, the pings at a later latency could successfully reactivate the biased representation of the initial stimulus carrying the signature of serial dependence. These results provide one of the first pieces of empirical evidence that the biased neural representation of a stimulus initially induced by serial dependence is preserved throughout a relatively long period.

Keywords

Serial dependence; numerosity perception; visual stability; event related potentials; neural decoding.

INTRODUCTION

In perception, the incoming sensory information is noisy, and biological sensors like the eye are highly unstable (i.e., due to frequent eye and head movements). Yet, the brain provides us with a stable and seamless conscious experience of the visual world, and how the brain achieves this stability remains an open question. Recent studies suggest that one way to stabilize perception is to integrate stimulus information over time, in order to smooth out noise from neural signals (Fischer & Whitney, 2014; Burr & Cicchini, 2014). This operation may indeed represent a successful strategy (Burr & Cicchini, 2014; Cicchini et al., 2018), due to the stability of our visual environment over short timescales. However, in the experimental context where visual stimuli can be arbitrarily modulated, such operation predicts systematic biases in perceptual tasks, with current stimuli appearing more similar to previous ones – a bias that is commonly referred to as *attractive serial dependence*.

A growing literature outlines several characteristics of serial dependencies in visual perception. First, such an attractive bias seems to generalize across many and very different visual features, starting from basic attributes such as orientation (Fischer & Whitney, 2014; Cicchini et al., 2017; Fritsche et al., 2017), position (Manassi et al., 2018), motion (Alais et al., 2017), or numerosity (Corbett et al., 2011; Cicchini et al., 2014; Fornaciai & Park, 2018a; Fornaciai & Park, 2018b; Fornaciai & Park, 2019a; Fornaciai & Park, 2019b), to more complex attributes such as the ensemble representation of a visual scene (Manassi et al., 2017), the perception of visual variance (Suárez-Pinilla et al., 2018), or face perception (Liberman et al., 2014; Taubert et al., 2016; Xia et al., 2016; Liberman et al., 2018). This suggests that serial dependence represents a global brain process affecting all aspects of perception. Second, serial dependencies are dependent on attention, mostly occurring when the object (Fischer & Whitney,

2014) or at least its spatial position (Fornaciai & Park, 2018a; Fornaciai & Park, 2018b) is attended by participants and/or relevant for a task. Finally, although the nature of serial dependence has been subject to debate (e.g., Fritsche et al., 2017; Alais et al., 2017; Bliss et al., 2017), evidence suggests that it is a bias arising during perceptual processing, and not at later working memory encoding or decision stages (Cicchini et al., 2017; Fornaciai & Park, 2018a; Fornaciai & Park, 2018b; Manassi et al., 2018; Pascucci et al., 2019). However, this does not exclude the possibility that the initial perceptual bias interacts with subsequent stages and potentially gets amplified (Fritsche et al., 2017; Cicchini et al., 2017; Fornaciai & Park, 2018a).

While the behavioral signature of serial dependence has been thoroughly investigated, much less is known about the neural mechanisms underlying the attractive bias. Results using functional magnetic resonance imaging (fMRI) have shown that, in the context of orientation perception, the bias arises in the primary visual cortex (St. John-Saaltink et al., 2017) – potentially implicating a very early sensory/perceptual mechanism, although due to the nature of the fMRI technique such an activity in early visual cortex may alternatively reflect re-entrant signals. Furthermore, in a previous study from our group using electroencephalography (EEG) (Fornaciai & Park, 2018a), we have demonstrated that a neural signature of serial dependence – in the context of numerosity perception – emerges very early (~50 ms) after stimulus onset, thus supporting the idea of a bias operating on the initial perceptual representation of the stimulus. Moreover, in that study, participants passively watched a sequence of dot arrays while paying no attention to their numerosity, only making a response to occasional oddball stimuli, which provides strong evidence that serial dependence occurs independently from a decision process. However, the rapid nature of such a paradigm did not allow us to track how the *biased* neural representation of numerosity evolves over time. Indeed, there is evidence that the behavioral effect of serial dependence seems to increase over time, if a forced pause is introduced between the stimulus and response (Fritsche et al., 2017; Bliss et al., 2017). Such results were interpreted as an increasingly distorted stimulus representation during working memory storage, although it is not clear what process may be involved in that effect.

Here, we aim to investigate how a visual representation affected by serial dependence evolves over time during an active perceptual decision-making task. More specifically, we tested whether or not the biasedness of a representation induced by the recent history of stimulation is retained throughout the time course of a trial. Participants performed a numerosity discrimination task during EEG recording, judging which stimulus contains more items between a “reference” and a “probe” dot-array. To induce serial dependence, a task-irrelevant “inducer” stimulus was presented before the task relevant ones, following the procedure used in previous studies (e.g., Fornaciai & Park, 2018a; Fornaciai & Park, 2018b). Additionally, we took advantage of the recent findings which demonstrated that activating a neuronal network by presenting brief, high-energy neutral stimuli evokes a brain signal carrying the signature of information stored in such a network (Wolff et al., 2015; Wolff et al., 2017). Following this technique, we presented two bright flashes between the reference and probe, serving as “pings,” to reactivate the working memory representation of the reference stimulus affected by serial dependence. We reasoned that activity evoked by pings should reflect a stimulus representation carrying the signature of serial dependence. In other words, the activity evoked by the pings should reflect the current content of visual working/short-term memory (Wolff et al., 2015; Wolff et al., 2017), including the stored perceptual representation of the reference stimulus biased by serial dependence. We complement this pinging approach with a multivariate neural decoding technique to assess how patterns of brain activity evolve over time.

Our design and approach entertained the following hypothesis. If memory traces of the visual representation biased by serial dependence are preserved after the initial perceptual processing stage, then the neural pattern associated with this initial visual representation should be detectable (or decodable) at a later time point, when this trace of representation is reactivated by the pings. To preview, our results first show that serial dependence starts very early after stimulus onset, in line with previous findings and suggesting that the effect starts at the early level of perceptual processing. Second, the results show that the neural representation associated with this initial perceptual processing, when pinged, is detectable at a later time point, providing evidence that the biased representation remains stored throughout a relatively long retention period.

METHODS

Participants

A total of 35 participants took part in the study. Participation in the study was rewarded with course credits or monetary compensation (10 USD/hour). All participants had normal or corrected-to-normal vision and were naïve to the purpose of the study. All participants signed an informed consent form before participation in the study. Experimental procedures were approved by the University of Massachusetts Internal Review Board, and are in line with the Declaration of Helsinki. A total of 8 subjects was excluded from data analysis (see below *Exclusion criteria* paragraph below), leaving 27 participants in the final group (20 females; mean age (± SD) = 22.5 ± 3.6 years).

Apparatus and Stimuli

Stimuli were generated using the Psychophysics Toolbox (Pelli, 1997; Kleiner et al., 2007), for Matlab (version r2013b; The Mathworks, Inc.), and were presented on an LCD screen located at approximately 90 cm from the participant. The screen encompassed approximately 34×19 degrees at the viewing distance of 90 cm, and was running at 144 Hz.

Stimuli were dot-arrays, including black and white dots (50/50% in most of the cases; in case of odd numerosities the color of the exceeding dot was randomly assigned) presented on a gray background. A mixture of black and white dots was employed in order to keep the global luminance across the array approximately similar to the luminance of the gray background. Three different dot-array stimuli were presented on each trial in the main conditions of the study (in this order): a task-irrelevant "inducer" comprising either 11 or 23 dots, a reference stimulus always comprising 16 dots, and a probe stimulus with a variable numerosity from trial to trial (8, 10, 13, 16, 20, 25, or 32 dots). The arrays were built in order to span similar ranges in three orthogonal dimensions: numerosity, size, and spacing, following the design previously used by DeWind et al. (2015) and Park et al. (2016). As the purpose of the study is to investigate serial dependence in numerosity perception, and since the effect of other non-numerical dimensions has been addressed elsewhere (Park et al., 2016; Fornaciai & Park, 2017; Fornaciai et al., 2017; Fornaciai et al., 2018), the different levels of non-numerical dimensions were collapsed together during data analysis. See DeWind et al. (2015) and Park et al. (2016) for more details about this stimulus construction procedure.

Regarding the stimulus parameters, the minimum individual area of the dots was set to 113 pixel^2, equal to a diameter of 0.21 deg (12 pixel); the maximum value was instead 452 pixel^2, corresponding to a diameter of 0.42 deg (24 pixel). Regarding the field area, which refers to the virtual circular area within which the dots were drawn, the minimum value was set to 70,685 pixel^2, corresponding to a diameter of 5.16 deg (300 pixel), while the maximum value was 223,960 pixel^2, equal to a diameter of 10.32 deg (600 pixel).

The “ping” stimulus (see *Procedure* below) that was flashed during the interval between the reference and probe stimulus was a white circle covering an area equal to the area of the preceding reference stimulus.

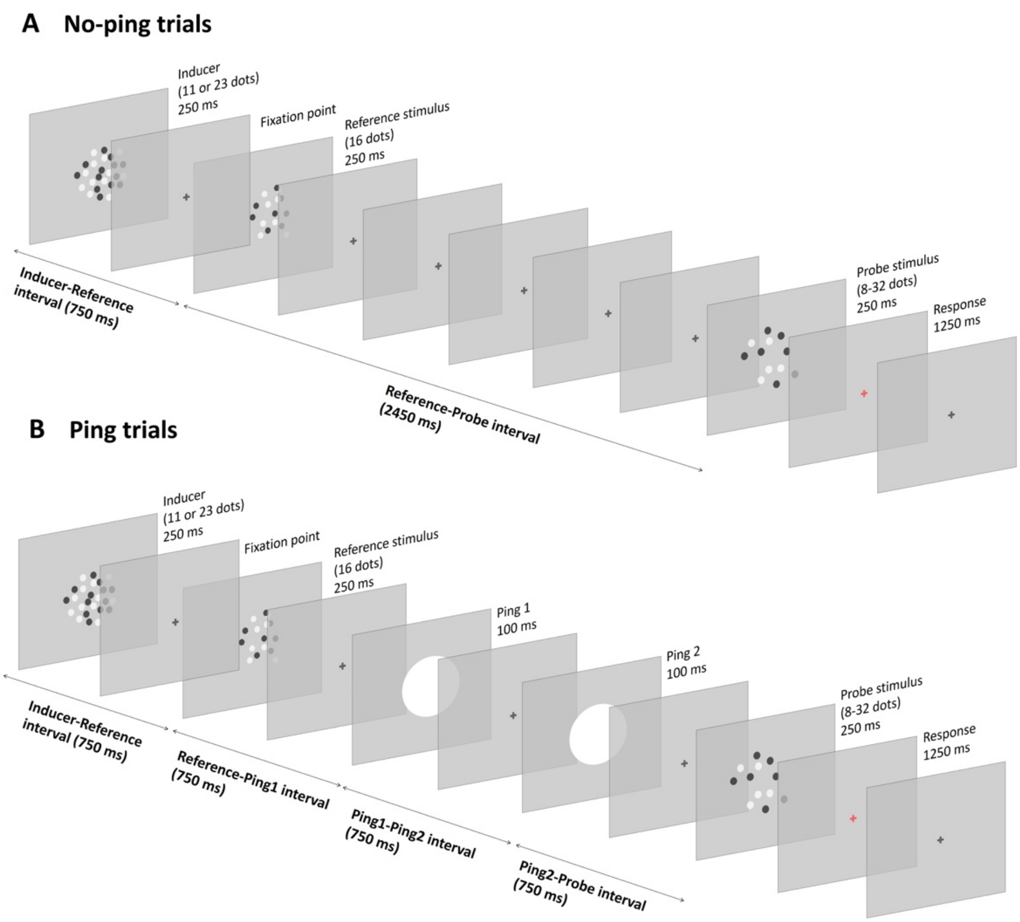

FIGURE 1 *– Experimental procedure. (A) Presentation procedure in the “no-ping trials.” While participants kept their gaze on a central fixation cross, a sequence of three dot arrays was*

presented at the center of the screen. First, a task-irrelevant inducer stimulus (11 or 23 dots) was presented, followed by the reference stimulus (16 dots) after 750 ms, and then a probe stimulus (8-32 dots) after 2,450 ms. All the stimuli were presented on the screen for 250 ms each. At the end of the trial, participants were instructed to report whether the second (reference) or third (probe) array in the sequence contained more dots, by pressing the appropriate key on a standard keyboard. The period during which a response was accepted was marked by the fixation cross turning red, and was limited to 1,250 ms after probe onset, and participants were told to respond as fast as they can. After the end of the response period, the fixation cross returned black, and the next trial started after 1,500 ms. Before starting the experiment, participants were told that the first stimulus was not relevant for the task but anyway to pay attention to the entire sequence of the stimuli. (B) Presentation procedure in the "ping trials." The sequence of inducer, reference, and probe dot arrays was identical to the no-ping trials, with the exception that two bright white circles were presented on the screen (duration = 100 ms) between the reference and probe. Finally, on some occasions only the inducer stimulus was presented on the screen ("catch" trials), and the fixation cross turned orange right after it (not shown in the figure). In those cases, participants were instructed to press the spacebar as fast as they can. Note that the stimuli depicted in the figure are not in scale. The timing measures reported in the figure refer to the inter-stimulus interval between different stimuli.

Procedure

The experiment took place in a quiet and dimly illuminated room. Throughout each block, three trial types were intermixed: "no-ping" trials, "ping" trials, and "catch" trials. The sequence of stimuli presented in the no-ping and ping trials is shown in Fig. 1. In all cases, participants fixated on a central fixation point, while the sequence of stimuli was presented at the center of the screen. In the no-ping trials (Fig. 1A), a sequence of three stimuli was presented on the screen. First, a task-irrelevant inducer stimulus (11 or 23 dots), followed by the reference stimulus (16 dots) after 750 ms, and then a probe stimulus (8-32 dots) after 2,450 ms. All the stimuli were presented on the screen for 250 ms each. At the end of the trial, participants were instructed to report whether the reference or the probe stimulus contained more dots. Response time was limited to 1,250 ms after probe onset and was marked by the fixation cross turning red. Participants were instructed to respond as fast as they could. After the end of the response period, the fixation cross returned black, and the next trial started after 1,500 ms.

In the ping trials, the sequence of inducer, reference, and probe stimuli was identical to the no-ping trials. However, two bright white circles were additionally presented on the screen (duration = 100 ms) between the reference and probe. In those cases, the sequence was as follows. First, the inducer was presented on the screen, followed by the reference stimulus after 750 ms. Then, the reference stimulus was followed by a sequence of two white circle (ping) stimuli, and finally the probe stimulus. The inter-stimulus interval between different stimuli was in all cases 750 ms (Fig. 1B). To avoid presenting always similar sequences of stimuli, we included some catch trials intermixed with the other types of trial.

In the catch trials, only the inducer stimulus was presented on the screen, and the fixation cross turned orange right after it. In those cases, participants were instructed to press a different button as fast as they could. Doing so, participants thus had to pay attention to the inducer in order to promptly provide a response in the case of a catch trial. Overall, the study comprised 10 blocks of trials. Each block included 24 no-ping trials, 24 ping trials, and 6 catch trials, randomly ordered. Participants were free to take breaks between different blocks, and the procedure took about one hour.

Electrophysiological recording and analysis

EEG recording. While participants performed the task described above, the EEG was continuously recorded for the entire duration of the experiment. To this aim, we used a 64-channel, extended coverage, triangulated equidistance cap (M10, EasyCap, GmbH), with a sampling rate of 1000 Hz (actiCHAmp, Brain Products, GmbH). During the experiment, the channels were referenced to the vertex (Cz). The electro-oculogram (EOG) was monitored by means of electrodes positioned below the left eye and lateral to the left and right canthi, in order to monitor artifacts due to blinks or eye movements, and exclude EEG epochs contaminated by artifactual activity. Across all the channels, impedance was usually kept below 15 kΩ, but on some occasions impedances up to 35 kΩ were tolerated.

Preprocessing and ERPs. EEG data were analyzed offline using Matlab (version R2015b, The Mathworks, Inc.), exploiting the functions provided by the EEGLAB package (Delorme & Makeig, 2004) and the ERPLAB toolbox (Lopez-Calderon & Luck, 2014). Continuous data were first visually inspected to remove noisy segments, before proceeding with preprocessing. During the preprocessing, the EEG signals were high-pass filtered (0.1 Hz) and were re-referenced to the average value of all the 64 channels. The continuous EEG data were then segmented into epochs from -300 ms before to 2700 ms after stimulus onset time-locked to the onset of the reference stimulus, with a baseline correction using the pre-stimulus interval. We then performed an independent component analysis (ICA), in order to remove eye-movement and other muscular artifacts. After ICA, we further excluded trials containing eye-blink artifacts or other large artifacts by applying the step-like artifact rejection tool provided by EEGLAB. Trials were rejected whenever activity from the eye-channel and a set of posterior channels of potential interest (i.e., based on previous studies; Iz, O9', O10' Oz, O1', O2', PO7' PO8'; Fornaciai & Park, 2017; Fornaciai & Park, 2018a) exceeded a threshold equal to 30 μV (in a time window spanning 400 ms, with 20 ms steps). This procedure led to an average (± SD) rejection rate of 8.55% ± 10.94%. To create event-related potentials (ERPs), the epochs were selectively averaged, and low-pass filtered (30 Hz). Finally, ERPs were smoothed with a 100-ms sliding window in order to remove alpha noise, prior to computing the grand average.

Time window of interest selection for the ERP analysis. Time windows of interest for the ERP analyses and statistical tests were chosen based on previous results. Previous ERP studies of numerosity perception have shown that the brain waves around 150-200 ms after stimulus onset are most sensitive to numerosity, and to modulations affecting perceived numerosity (Park et al., 2016; Fornaciai et al., 2017; Fornaciai & Park, 2018c). Furthermore, previous results also show that a signature of serial dependence in numerosity perception emerges from ERPs around 200 ms. Thus, when assessing the serial dependence effect on ERPs evoked by the reference stimulus, our statistical analysis focused on a broad 100-ms time window centered at 200 ms after reference onset. Unlike the ERPs evoked by the reference stimulus, we did not have specific predictions concerning precisely when the ERPs evoked by the neutral "ping" stimulus should carry information about the representation in working memory (Wolff et al., 2017). Thus, the time window of interest was chosen as a 100-ms window around the peak of the collapsed ERP evoked by the pings including the two inducer conditions, separately for the first and second ping. Single-subject ERPs were then averaged across these time windows, separately for the two inducer conditions, and tested with a paired t-test.

Multivariate pattern analysis in the time domain. To achieve a better description of the temporal dynamics of serial dependence during the numerosity discrimination task, we applied a multivariate pattern analysis in the time domain method (King & Dehaene, 2014), using the Neural Decoding Toolbox (Meyers, 2013). This method allows us to evaluate how neural activity patterns coming from multiple sensors across the scalp differ between different experimental conditions and combinations of stimuli, and how such patterns of activity generalize across time. In other words, we used this analysis to assess how serial dependence affects the pattern of brain activity evoked by the reference (or the ping) stimulus as a function of the preceding inducer stimulus, and whether and to what extent the serial dependence effect changes over time. This neural decoding analysis involved the training of a support vector machine (SVM) classifier on a subset of the data corresponding to specific conditions, and made predictions about which stimulus was presented in the remaining subset of data and across the entire time-course of activity. Conditions were based on the inducer stimulus presented on each trial, so that the activity to be decoded always corresponded to the reference, but with trials divided as a function of the inducer numerosity.

Using this neural decoding approach, we thus evaluated whether and to what extent the pattern of brain activity evoked by the reference stimulus differs as a function of the inducer numerosity, and whether the activity evoked by the ping stimulus carries the signature of the biased reference representation. Brain responses were evaluated across the full epoch spanning from -300 to 2700 ms. Different comparisons were tested individually for each participant, training the SVM classifier with the responses (i.e., activity recorded at all the channels with the exception of the EOG channels) to the two class of stimuli at hand (i.e., trials divided as a function of inducer numerosity) and testing it on another subset of trials not used in the training phase (using a leave-one-trial-out cross validation). To optimize the analysis, we followed a series of practices suggested by Grootswagers et al. (2017), to account for high noise in single trial EEG data and improve the decoding procedure. First, we created "pseudo trials" taking the average of randomly chosen groups of 12 trials, in order to improve signal to noise ratio. Second, to avoid overfitting, the number of features (i.e., channels) included in the analysis was limited to the five most significant ones, determined using a univariate ANOVA. Moreover, we averaged activity across large time windows to smooth out noise such as alpha oscillations (i.e., 100-ms time windows with 25 ms step). Finally, the decoding procedure was repeated 30 times for each participant using different subsets of data for training and testing (as well as different groups of trials to generate pseudo trials), and the average of the 30 runs was taken as the final estimate of the classification performance. The outcome of the decoding analysis was a temporal generalization plot showing the performance of the classifier at each time point, with classification accuracy (CA) reflecting how well the pattern classifier can discriminate two conditions (see Fig. 5A). Namely, activity along the diagonal of the temporal generalization matrix reflects the classification accuracy obtained by training and testing the classifier at the same time point, while off-diagonal decoding reflects the classification accuracy obtained by performing training at one time point and testing at all the different time points. This latter procedure allows to assess whether and to what extent a specific pattern of brain activity generalizes to activity at different time points (King & Dehaene, 2014).

Time window of interest selection for the multivariate pattern analysis. Classification accuracies obtained from the multivariate pattern analysis were tested across several time windows of interest in order to assess the effects of inducer numerosity on the reference and ping stimuli. The analysis in this context was divided in two parts. The first part concerns the patterns of activity along the diagonal of the temporal generalization matrix, where classification is performed by training and testing the classifier at the same time point; the second part concerns off-diagonal patterns of activity, revealing whether and to what extent a specific pattern generalizes over different times. This latter analysis, involving training and testing the classifier at different time points, allows to assess whether and to what extent the specific pattern of brain responses at one time point generalizes to different time points. This thus represents the crucial part of the analysis aimed to test our main hypothesis, concerning the stability over time of the reference representation biased by serial dependence. Time windows of interest corresponding to times around the reference onset were chosen according to our previous study (Fornaciai & Park, 2018a). Namely, two time windows were selected, spanning 0-250 ms and 250-500 ms after reference onset. Time windows along the diagonal corresponding to the ping onsets were chosen to span a similar extent compared to the reference time windows (250 ms), starting from the ping onset. Off-diagonal time windows were chosen to span a broad temporal extent in order to capture how the reference representation gets reactivated by the pings. To this aim, we chose 8 time windows (4 along the vertical dimension, and 4 along the horizontal dimension). Time windows chosen in this way spanned 0-250 and 250-500 ms corresponding to the reference time windows and from the onset to 500 ms after each of the two ping onsets. Corresponding time windows along the two off-diagonal directions were then collapsed together leaving a total of 4 windows of interest. A depiction of all the time windows used for assessing the classification performance is reported in Fig. 5A, with windows along the diagonal identified by letters (A-D), and off-diagonal windows identified by numbers (1-4). Classification accuracy across these time windows was averaged separately for each participant. For the two early time windows corresponding to the reference (time windows A and B in Fig. 5A), the effect of inducer was tested using one-sample t-tests against chance level performance (50%). In the later time windows, we used paired t-tests comparing the classification accuracy in the ping condition against the classification accuracy in the no-ping condition. Indeed, the effect of inducer at later time windows was expected only in the presence of pings, so that the no-ping condition served as a baseline for the ping condition.

Behavioral data analysis

Numerosity discrimination performance across ping and no-ping trials was analyzed separately for each subject, assessing the serial dependence effect by binning trials according to the inducer numerosity. In order to obtain a measure of accuracy and precision in the task, we fitted a Cumulative Gaussian curve to the distribution of response probabilities as function of probe numerosity, according to the Maximum Likelihood method (Watson, 1979). The point of subjective equality (PSE), which corresponds to the probe numerosity perceptually matching (i.e., indistinguishable from) the reference numerosity, was taken as a measure of accuracy in the task and of the reference perceived numerosity. The PSE was defined as the median of the best-fitting cumulative Gaussian curve to all the data of each participant in each condition. To assess the level of performance, in order to exclude subjects showing insufficient performance, we used the just-noticeable difference (JND), which was calculated as the difference in numerosity between chance level (50%) responses and 75% “probe more numerous” responses. A finger error rate correction (5%) was applied to account for lapses of attention or random response errors independent from the stimuli (Wichmann & Hill, 2001). To assess serial dependence effects at the behavioral level, a paired t-test was performed comparing the distribution of PSEs corresponding to different inducer numerosity conditions, separately for no-ping and ping trials in order to assess whether presenting the pings affected the effect. To compare the two conditions, we calculated a serial dependence effect index, which represent the difference in PSE between the 23-dot inducer condition and the 11-dot inducer condition. The distributions of serial dependence effect indexes across the two conditions was compared using a paired t-test.

Exclusion criteria

Due to the nature of the effect investigated in this work, we thoroughly checked both the behavioral and EEG data in order to exclude participants showing an insufficient level of performance and/or EEG data of insufficient quality. To this aim we excluded participants showing either very high JND in the behavioral task (JND > 10) or other indications that they may have not understood or complied with the task (i.e., opposite responses). Regarding the EEG data, participants were excluded during preprocessing based on either a too large number of rejected trials due to artifact (> 45%) or based on visual inspection of continuous data and/or ICA components (i.e., large portions of noisy data even after ICA correction, or too many large ICA components likely not related to brain signals). A total of 7 participants was excluded before data analysis based on behavioral (4) and/or EEG (3) data quality. One more participant was excluded after data analysis due to the failure of the decoding procedure, which showed systematically below-chance decoding accuracy in the majority of the tested time points.

RESULTS

Behavioral results

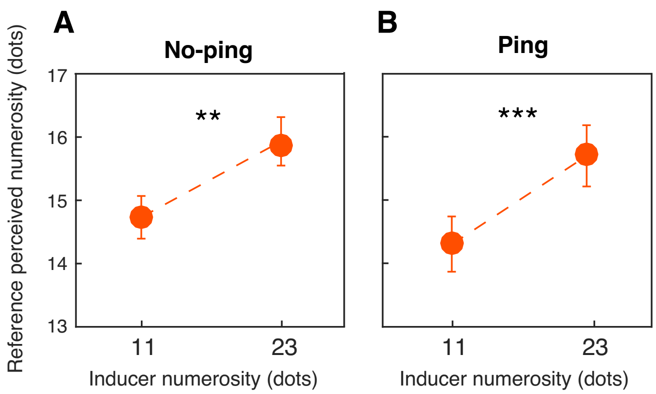

FIGURE 2 *– Behavioral results. (A) Average PSEs in the two inducer conditions in the no-ping trials. (B) Average PSEs in the ping trials. In both cases, strong and significant attractive serial dependence effects were observed. ** p < 0.01, *** p < 0.001. Error bars are SEM.*

First, we analyzed the behavioral results to confirm that our specific design successfully induced attractive serial dependence biases, separately for the no-ping and ping condition. The reason to separate the two conditions is to assess whether reactivating the reference representation affected by serial dependence could modulate behavior, increasing or decreasing the effect. The behavioral results are shown in Fig. 2. As shown in the figure, we found strong attractive serial dependence effects in both conditions. Namely, the perceived numerosity of a 16-dot reference appeared to be significantly underestimated when it was preceded by an 11-dot inducer, compared to when it was preceded by a 23-dot inducer ($t(26) = 3.3266$, $p = 0.0026$, $d = 0.64$; $t(26) = 4.1796$, $p < 0.001$, $d = 0.80$, respectively for the no-ping and ping condition). Even if the effect seems slightly stronger in the ping condition (Fig. 2B), comparing the serial dependence effect across the two conditions revealed no significant difference ($t(26) = 0.4076$, $p = 0.6869$). This shows that while our paradigm is generally very sensitive to the attractive bias provided by the inducer, the presence of the pings does not systematically modulate the effect – in line with a previous observation showing that reactivating a representation by means of pings does not affect behavior (Wolff et al., 2017).

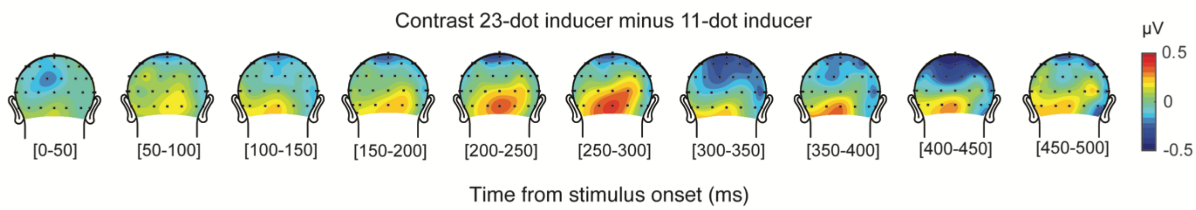

FIGURE 3 *– Topographic plots (posterior view) of event-related activity. Distribution of activity across posterior channels, corresponding to the contrast between the 23-dot inducer condition and the 11-dot inducer condition. Plotting such a distribution of activity reveals a relatively strong effect of inducer starting from early latencies and peaking at around 250-300 ms after stimulus onset. The most involved channels appear to be a group of posterior channels centered around Iz.*

ERP results

After confirming that our paradigm successfully induced serial dependence in numerosity perception, we analyzed the brain responses to the reference stimulus. First, we looked at the topographic distribution of brain activity in a relatively early time window consistent with previous studies (Fornaciai & Park, 2018a), collapsing no-ping and ping trials together. Fig. 3 shows the distribution of activity representing the contrast between the two inducer conditions, across posterior channels. As shown in the figure, there was a relatively large difference in the responses to the same 16-dot reference as a function of the inducer numerosity emerging at relatively early latencies over posterior-inferior scalp locations. Such a difference – reflecting higher positive amplitude in the more numerous inducer condition – peaked at around 250-300 ms after stimulus onset, with activity centered at channel Iz (peak = 261 ms, contrast amplitude = 0.484 μV).

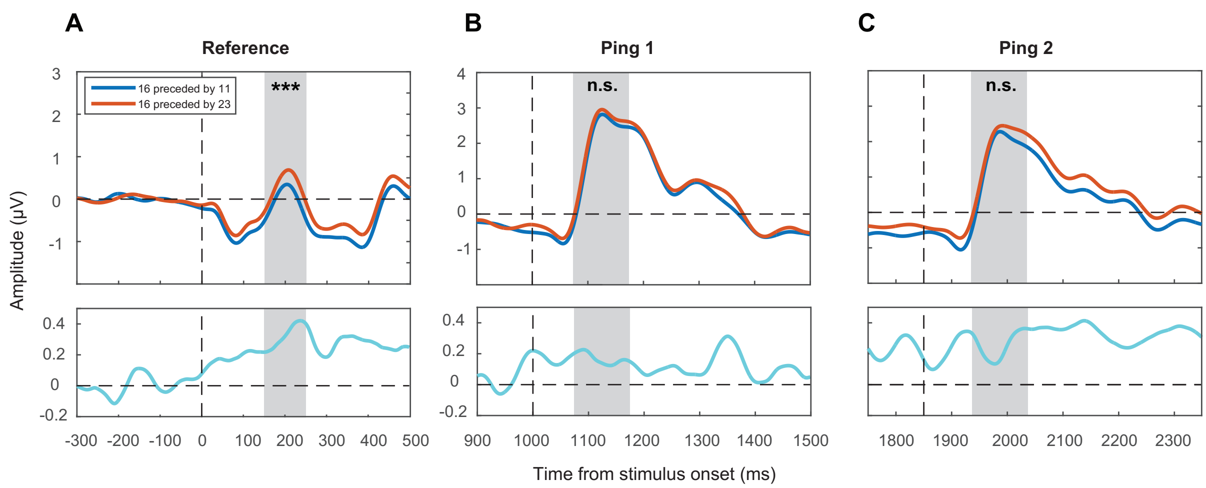

FIGURE 4 *– Event-related potentials at channel Iz. (A) ERPs time-locked to the onset of the reference stimulus (collapsing together ping and no-ping trials), sorted by the numerosity of the preceding inducer stimulus (upper panel) and the contrast between the two waveforms (lower panel). (B) ERPs time-locked to the onset of the first ping in the ping condition (upper panel) and their contrast (lower panel). (C) ERPs time-locked to the onset of the second ping in the ping condition (upper panel) and their contrast (lower panel). Shaded areas represent the time windows used for a statistical test. In the case of brainwaves corresponding to the reference stimulus (A), the time window of interest was defined based on previous studies (see Methods). In the case of the activity evoked by the pings (B & C), time windows were chosen according to the peak of the two brainwaves collapsed together. n.s. = not significant, *** p < 0.001.*

Then, in order to characterize the temporal effect of serial dependence on the ERPs, we plotted and analyzed the brainwaves at channel Iz, which appeared as the center of the occipital focus of activity. The brainwaves corresponding to different stimuli and latency windows are shown in Fig. 4. Note that for the purpose of ERP analysis at latencies around the reference onset, we collapsed together the ping and no-ping trials, as no difference is expected between the two conditions. Relatively early ERPs evoked by the reference stimulus (Fig. 4A) showed a clear attractive modulation, peaking at around 240 ms after stimulus onset. In other words, the amplitude of brain responses was modulated so that a larger inducer numerosity (23 dots) results in a more positive amplitude of the brainwaves evoked by the reference, compared to the less numerous inducer (11 dots) – which was consistent with what we observed at the behavioral level. The ERP effect of serial dependence was quantified in a 100-ms time window around 200 ms after reference onset (marked with a shaded area in Fig. 4A) based on our previous finding (Fornaciai & Park, 2018a), and was tested using a paired t-test (between the two inducer conditions across participants). The results showed a significant difference between ERPs corresponding to different inducer numerosities ($t(26) = 3.434$, $p < 0.001$).

Fig. 4B and 4C show the brainwaves corresponding to the two pings presented between the reference and the probe, in the ping condition. As illustrated, the bright flashes evoked a strong visual response starting early after stimulus onset. However, the difference between different inducer conditions appeared to be very small at the time of the first ping, while slightly stronger at the time of the second ping. A 100-ms time window around the peak of the activity of the inducer conditions collapsed together (peak = 125 ms and 137 ms after the onset of the first and second ping, respectively) did not show any significant difference between the two inducer conditions, neither after the first ping nor after the second ping (paired t-test, $t(26) = 0.9467$, $p = 0.1762$, and $t(26) = 1.1617$, $p = 0.1280$).

Multivariate neural decoding results

In order to assess whether the initial neural representation of the reference numerosity is retained in the memory traces (which are reactivated by the pings), we performed a multivariate pattern analysis in the time domain (e.g., see King & Dehaene, 2014 for a review). Although ERP analysis can show a signature of serial dependence, it is not sensitive enough to pick up subtle differences in the stimulus representation and does not provide a full characterization of the time course of the effect. A multivariate analysis, instead, has been shown to be much more sensitive to serial dependence biases, and allows a better characterization of the time-course of the effect (Fornaciai & Park, 2018a). Such a multivariate analysis involves training and testing a pattern classifier (i.e., support vector machine) in order to assess whether and to what extent it can predict the pattern of brain activity related to a particular condition. Moreover, assessing the temporal generalization of specific patterns of brain activity across different time windows allows us to assess how the—biased—representation of the reference stimulus evolves over time during a trial in the present study. More specifically, we compared the activity time-locked to the onset of the reference, dividing the trials according to the preceding inducer stimulus, resulting in two categories: 16 preceded by 11, and 16 preceded by 23. The analysis was performed separately for no-ping and ping trials, and the no-ping conditions was used as a comparison to assess the effect related to the pings.

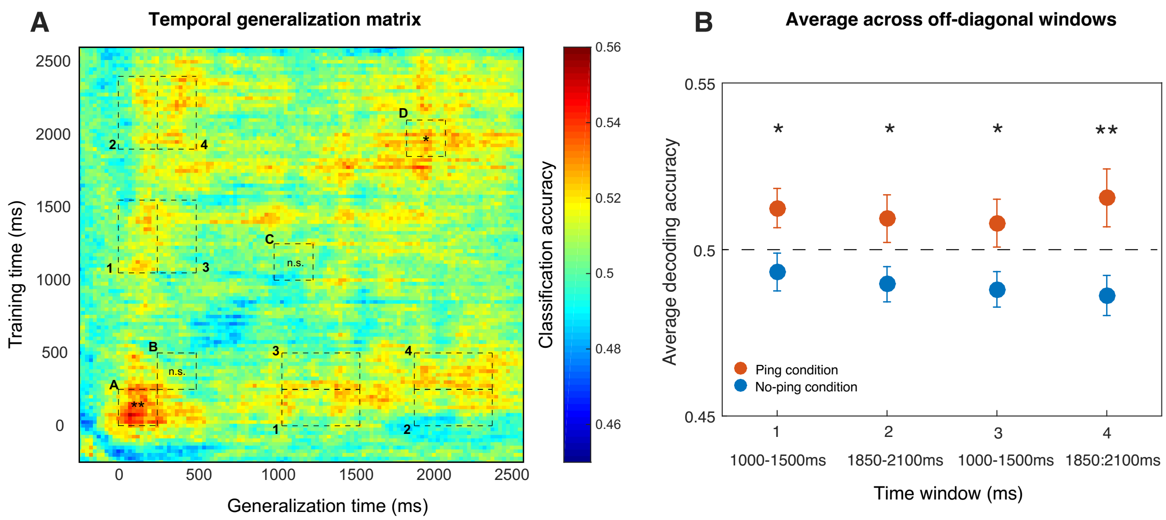

FIGURE 5 *– Decoding results. (A) Temporal generalization matrix, representing classification accuracies obtained by training the classifier at one time point and testing at all the time points. The temporal generalization shows how the specific pattern of brain activity at one time point generalizes at different time points, possibly showing the reactivation of the same representation and/or the same neural generator at different times. The dashed lines delimit the different temporal windows of interest used to perform statistical tests on the classification performance. Time windows of interest along the diagonal are marked with letters, while off-diagonal time windows are labeled with numbers. (B) Average classification accuracy across the off-diagonal windows, for the ping and no-ping condition. Error bars are SEM. Number labels on the x-axis refer to the numbering of time windows reported in panel A. n.s. = not significant, * $p < 0.05$, ** $p < 0.01$.*

Figure 5A illustrates the results of the neural decoding analysis in terms of a temporal generalization matrix, which characterizes the degree to which patterns of neural activity evoked by the identical reference numerosity (16 dots) and the two pings can be dissociated as a function of two inducer numerosities (11 or 23 dots) that was presented prior to the reference. The results are quantified in various time windows of interest. We first set two time windows corresponding to 0-250 (labeled as A in Fig. 5A) and 250-500 ms (labeled as B) after reference onset. Across these two time windows, we found significantly above chance decoding in the earlier time window (0-250 ms, average classification accuracy = 0.5291; one-sample t-test against chance level, $t(26) = 3.0669$, $p = 0.005$) but not in the later time window (250-500 ms, average classification accuracy = 0.5069, $t(26) = 0.5918$, $p = 0.5591$). However, while the decoding accuracy in the later window (B) was not significant, it was much stronger in the off-diagonal directions adjacent to such a later window (i.e., at time windows adjacent to window B, in the horizontal and vertical direction, similarly spanning 250 ms). We thus also tested the average decoding performance in these two windows. Doing so, we indeed found above chance classification accuracy ($t(26) = 2.26$, $p = 0.033$, and $t(26) = 2.44$, $p = 0.22$, respectively for the off-diagonal windows adjacent to the reference window in the vertical and horizontal direction), suggesting that activity from the earlier window generalizes to later time points corresponding to the late reference window. We then examined the time windows 1000-1250 ms and 1850-2100 ms which correspond to a 250-ms window after the first and the second ping, respectively. The decoding classification accuracy after the first ping (labeled as C in Fig. 5A) was negligible (average classification accuracy = 0.5036, paired t-test against the no-ping condition: $t(26) = 0.5027$, $p = 0.6194$); however, the classification accuracy after the second ping (labeled as D) was significantly higher than that in the absence of a ping stimulus (average classification accuracy = 0.5183, paired t-test against the no-ping condition: $t(26) = 2.6667$, $p = 0.013$).

More importantly, the extent to which the neural patterns are generalized across time at later time windows (e.g., from reference to pings) was evaluated by observing off-diagonal time windows in the temporal generalization matrix. Generalized patterns across the off-diagonal directions would indeed show whether the biased representation of the reference stimulus exists in the perceptual memory traces after the initial processing of it. To this aim, we focused on broad 500-ms time windows corresponding to the reference time windows, but shifted in time to the onset of the two pings (time windows labeled 1, 2, 3, and 4 in Fig. 5A) to capture the time windows in which the neural decoding classifier is trained with the neural activity pattern evoked by the reference numerosity and tested with the pattern evoked by the pings (and vice versa). In other word, these off-diagonal time windows allowed us to evaluate whether the pattern of serial dependence effects observed at the time of reference processing generalizes to activity evoked by the pings. As the temporal generalization matrix (Fig. 5A) is two-dimensional, there are two directions in which we could look for the generalization of patterns of brain activity: "horizontal" and "vertical." Corresponding time windows along the two directions were collapsed together for statistical analyses.

Comparisons concerning off-diagonal windows (ping versus no ping condition) are shown in Fig. 5B. As shown, average classification accuracies obtained in the ping condition were greater than those in the no-ping condition. The inducer-dependent pattern of neural activation evoked by the reference in the 0-250 ms time window was decodable by the neural activation pattern evoked by the first ping (paired t-test of ping vs. no-ping; $t(26) = 2.10$, one-sided $p = 0.0228$) and by the pattern evoked by the second ping ($t(26) = 2.24$, $p = 0.0171$) (see the time windows labeled 1 and 2 in Fig. 5). The inducer-dependent pattern of neural activation evoked by the reference in the 250-500 ms time window was decodable by the pattern evoked by the first ping ($t(26) = 2.16$, $p = 0.0202$) and by the pattern evoked by the second ping ($t(26) = 2.57$, $p = 0.0081$) (see the time windows labeled 3 and 4 in Fig. 5). In other words, the same differences between the neural activity patterns evoked by the reference under the two inducer conditions could be used to distinguish the activity patterns evoked by the pings under the two inducer conditions. These results provide evidence for the reactivation of a stored representation of the initial reference stimulus. While these results show a significant difference between ping and no-ping activities, the average classification accuracy in the no-ping condition appeared to be below the theoretical chance level of 50%. Although puzzling at first glance, below-chance classification results have been previously interpreted in terms of dependence from subsample means in the context of cross-validation procedures (Jamalabadi et al., 2016). Namely, in the presence of a small effect size and a relatively small number of observations (trials), pulling out the subset of data used for testing the classifier from the training set during cross-validation could shift the means of the remaining training set to the opposite direction, making the trained classifier to predict the test set to be the other class. This in turn results in a classification error, and hence in below-chance classification accuracy. The possibility of these spurious effect thus makes it very important to use the "baseline" classification accuracy obtained in the no-ping condition to assess the effect provided by the pings, instead of using a fixed 50% chance level. Nevertheless, we performed an additional series of one-sample t-tests against the theoretical chance level of 50%. The results were significant in window 1 ($t(26) = 2.12$, $p = 0.022$) and window 4 ($t(26) = 1.79$, $p = 0.043$).

DISCUSSION

In the present study, we investigated the neural signature and dynamics of serial dependence across the time course of perceptual decision making. Specifically, we questioned whether the biased representation of the visual stimulus (due to serial dependence) is transient or whether it is retained in visual memory traces. To do so, we exploited a recently developed technique aimed to reactivate hidden memory representations (Wolff et al., 2015; Wolff et al., 2017). Namely, the neural signal evoked by a brief, high-energy "ping" reflects the signature of underlying representations currently encoded in the neural network (i.e., for instance stored in working memory). Using a relatively long time-course in an active task, incorporating this pinging technique in combination with a neural decoding analysis, we characterized how serial dependence emerges and evolves throughout the time course of a trial.

Our results first show that the specific paradigm used in this study successfully induces strong and systematic attractive serial dependence, virtually identical to a previous study employing a similar paradigm but in a faster rate of stimulus presentation (Fornaciai & Park, 2018b). Specifically, we observed a relative under- or over-estimation of the reference stimulus as a function of the inducer numerosity, in line with the attractive effect observed in previous studies (Corbett et al., 2011; Cicchini et al., 2014; Fornaciai & Park, 2018a; Fornaciai & Park, 2018b; Fornaciai & Park, 2019a; Fornaciai & Park, 2019b).

As in the behavioral results, the ERPs evoked by the reference stimulus were modulated by the numerosity of the preceding stimulus, showing a signature of serial dependence consistent with our previous study (Fornaciai & Park, 2018a). Such a signature likely reflects a distorted encoding of stimulus numerosity according to the numerosity of the preceding inducer stimulus, with a clear attractive pattern – i.e., the amplitude of brain signals evoked by the reference is higher (more positive) following an inducer containing a larger numerosity, compared to an inducer containing fewer items. Such an effect peaks at around 200-250 ms, consistently with recent studies investigating the dynamics of numerosity processing (i.e., Hyde & Spelke, 2009; Park et al., 2016; Fornaciai et al., 2017; Fornaciai & Park, 2018c), and with the timing of serial dependence in our previous study (Fornaciai & Park, 2018a). ERPs evoked by the two pings, on the other hand, show little or no effect (i.e., did not reliably distinguish the two inducer conditions), despite the large visually evoked potentials induced by the bright flashes (Fig. 4B&C).

To test our central hypothesis concerning the temporal evolution of neural representation of these numerosity stimuli, we employed a multivariate neural decoding analysis, which has previously proven to be sensitive in distinguishing subtle experimental manipulations (Fornaciai & Park, 2018a; Fornaciai & Park, 2018c). Such an analysis allows to assess the pattern of brain activity corresponding to a specific stimulation condition, and how such a pattern can successfully predict the stimulus presented in another specific condition. Looking at a brief epoch around the onset of the reference stimulus (Fig. 5A, time window A and B), it is clear that a signature of serial dependence emerges very early after stimulus onset, consistent with previous results (Fornaciai & Park, 2018a). Comparing the present results with our previous study, however, the decoding accuracy remains high only at relatively early latencies after the reference onset (0-250 ms), while our previous data showed that the effect is amplified at later latencies. Instead, in the current data, there was an increase in decoding accuracy in the off-diagonal direction (see the area simultaneously adjacent to windows A and B in Fig. 5A), illustrating the generalization of the classification across time points close to the reference representation. This result suggests that the pattern of activity corresponding to the initial (0-250 ms) processing stage (and likely the same neural generator) remains sustained at subsequent latencies up until 500 ms after stimulus onset. In other words, while in our previous work (Fornaciai & Park, 2018a) we observed a series of two potentially distinct processing stages rapidly unfolding after stimulus presentation (0-200 and 200-450 ms), here we observed just one of them spanning the first 250 ms and then lingering up until 500 ms. Such a difference between the current and the previous results may be due to the large differences in the paradigms employed. Indeed, the two paradigms differed in terms of stimulus timing (much longer interstimulus interval in the present work), task (oddball detection vs. numerosity discrimination), and the attended feature (color of the stimuli in the oddball task vs. numerosity in the present task), which by themselves can modulate the brain responses recorded with EEG (e.g., Strüber & Polich, 2002; Nakata et al., 2005; Potts, 2004; Senkowski & Herrmann, 2002; Zani & Proverbio, 1995; Koivisto et al., 2009; Zhang & Luck, 2009). In particular, a longer intestimulus interval can significantly delay evoked responses linked to stimulus processing (Nakata et al., 2005), or even affect the pattern of responses evoked by a stimulus (Strüber & Polich, 2002). Although previous results on the effect of interstimulus interval concern very different stimuli and tasks, some of the differences may be driven by the much slower paradigm employed in the present study as opposed to the rapid stimulus presentation in Fornaciai & Park (2018a). In other words, the slower presentation rate in the current paradigm may have made activity at subsequent processing stages (for instance related to the reactivation of working memory traces in order to perform the task) to be delayed at later latencies closer to the presentation of the second stimulus. However, due to the large differences in both the stimulus dynamics and the task used, it is difficult to precisely pinpoint the reason for such different results.

Similarly to the ERP analysis, the first ping was ineffective in distinguishing the two inducer conditions (Fig. 5A, time window C). This lack of significant decoding along the diagonal shows that, at least for the first ping, the stimulation did not evoke any distinctive pattern of activity carrying the serial dependence effect. In contrast, the second ping did result in successful decoding (Fig. 5A, at time window D), suggesting that the pattern of activity evoked by this second ping carries information about the reference affected by the serial dependence effect. However, the pattern of effects seems to spread across a relatively broad area around the ping onset. The fact that we observe a signature of serial dependence only at the time of the second (not the first) ping and with activity spread around this presentation time can be interpreted in several ways. First, predictability and expectations concerning the timing of the second ping and the end of the trial may explain the spread of the effect to time points even prior to the ping presentation and a stronger effect of the second ping. Indeed, the timing of the pings was consistent across trials, which made it possible to predict the presentation of the second ping after seeing the first one; in turn, expectations may have caused a sharpening of the pattern of brain activity (e.g., see De Lange et al., 2018 for a review), making the underlying serial dependence effect more easily decodable. Second, the effect emerging exclusively at the second ping may reflect the increase of the serial dependence effect over time observed in previous studies (Fritsche et al., 2017; Bliss et al., 2018), although the magnitude of the effect in our behavioral results is comparable to previous results employing much shorter presentation times (Fornaciai & Park, 2018b). Additionally, increased attention towards the end of the trial may have played a role in amplifying the responses to the second ping (e.g., Müller et al., 2006), resulting in stronger signals related to the serial dependence effect. Finally, considering that the second ping is closer to the end of the trial, neural activity evoked by the second ping may reflect a decision-stage representation (i.e., the activity of perceptual decision circuits) in line with a recently proposed framework of serial dependence (Pascucci et al., 2019). According to this proposition, serial dependence would emerge because of "perceptual decision" or "read-out" templates persisting from the processing of past stimuli to the representation of current ones. Such decision templates are for instance represented by the set of read-out weights of low-level activity at a higher-order decision stage, with the lingering template from a previous stimulus biasing the representation of a current one. In the context of the present results, the activity found at the time of the second ping may thus reflect activity arising at such perceptual decision stage, related to the reactivated decision template. Following the previous points, the fact that we observe this effect only at the time of the second ping may be related to predictions and expectations about the timing of the incoming probe stimulus. Indeed, the predictability of the stimulus timing may have induced an anticipated activation of the perceptual decision circuits, in order to speed up and facilitate the representation of the incoming probe stimulus, in line with the idea that expectations can speed up perception (e.g., Pinto et al., 2015).

The crucial point for testing our main hypothesis, however, concerns the *reactivation* of the reference representation induced by the pings. Such a reactivation has to be searched in the off-diagonal direction in the temporal generalization matrix (Fig. 5A). Our results show that the pings successfully reactivate the reference representation, carrying the signature of serial dependence. Interestingly, significant effects emerge not only at off-diagonal times corresponding to the early window of the reference stimulus (off-diagonal windows 1 and 2, which are aligned with the early window A in Fig. 5A), but also at times corresponding to the later window (off-diagonal windows 3 and 4, which are aligned with the early window B in Fig. 5A), where there is actually little or no effect at the time of reference processing along the diagonal. Even if activity in the late window after reference onset provides a relatively poor classification of inducer conditions, the effect may be amplified at later latencies, especially when such a pattern gets reactivated by the pings.

In general, however, caution is in order when interpreting these results, as our main decoding analysis shows relatively low classification accuracies, especially at off-diagonal windows corresponding to activity reactivated by the pings. Considering the nature of the effect tested and the specific analysis used, such low classification accuracies are however not surprising. First we need to consider that serial dependence is a relatively subtle behavioral effect, causing in our specific case an under-/over-estimation of about 1 dot in a dot-array of 16 dots. It is reasonable to hypothesize that any difference at the neural level would be similarly if not more subtle. Moreover, we used large temporal windows to average classification accuracies at different time points, especially in the off-diagonal direction, which may have diluted the effect. Future studies with more specific predictions may achieve better results by using narrower windows. Nevertheless, at least in the context of the later windows corresponding to the pings, the no-ping condition provides a control by showing that in the absence of these stimuli the serial dependence effect is not decodable from neural signals at late latencies, thus suggesting that the effect evoked by the pings is genuine rather than an artifact.

In summary, the current findings suggest that there are multiple patterns of activity involved in the serial dependence effect. First, consistently with previous reports (Fornaciai & Park, 2018a), the effect of serial dependence develops during a relatively short interval immediately after the onset of the stimulus, suggesting that may arise directly at the earliest level of perception. Regarding this point, however, the fact that the decoding analysis does not provide information about the direction of the effect (i.e., attractive versus repulsive), leaves open the possibility that the very early activity may be driven by other sensory/perceptual processes, like adaptation. Adaptation resulting from very short visual stimulation has been indeed observed when serial dependence is suppressed by means of visual backward masking (Fornaciai & Park, 2019a). However, the fact that ERP results show an attractive effect within the early window of activity (around 200 ms after stimulus onset) suggests that the decoding results within this same window may similarly reflect an attractive effect.

After the relatively early processing, then, the effect is evident in possibly two distinct processes. On the one hand, the off-diagonal pattern of activity indicates that—borrowing the interpretation of King & Dehaene (2014)—the same neural generators yield the pattern of activation for the initial biased representation and the pattern of activation evoked by the pings. One parsimonious interpretation is that the exact same trace of the initial biased representation gets stored throughout a trial (and is reactivated by the pings later). On the other hand, the diagonal pattern of activity especially around and after the second ping indicates—again according to King & Dehaene (2014)—a distinct set of neural generators decoding the two inducer conditions. The functional role of this second mechanism remains to be studied, as we can only speculate as discussed above. Nevertheless, both diagonal and off-diagonal patterns found in the neural decoding analyses lend support for at least two distinct processing stages involved in the representation of serial dependence in the time course of a trial, which serves as an important starting point for future research.

CONCLUSION

The present results advance our knowledge of the neural underpinnings of the serial dependence effect, by showing the dynamics of its neural signature over a relatively long temporal interval. We show that serial dependence starts very early after stimulus onset, similarly to what has been demonstrated before with a passive-viewing paradigm. We further show that the representation of a stimulus affected by serial dependence can be reactivated by task-irrelevant pings. The effect of pinging memory has two results: on the one hand, it reactivates a memory representation that remains similar to the stimulus representation generated immediately after its onset. This suggests that once the bias is induced during perceptual processing, a trace of the biased stimulus representation is stored throughout a relatively long epoch. Second, it highlights a different, later processing stage, which likely reflects the involvement of possibly a different neural generator yielding a distinctive pattern of activity, but still carrying the signature of serial dependence. The present results thus show that serial dependence directly alters the perceptual representation of a stimulus, and propagates throughout subsequent processing stages.

Author contributions

M.F. and J.P. designed the study. M.F. collected the data. M.F. and J.P. analyzed the data, interpreted the results, wrote the manuscript and revised it.

Conflict of interest

The authors declare no conflict of interest.

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