

Disentangling feedforward versus feedback processing in numerosity representation

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ABSTRACT

Numerosity is a fundamental aspect of the external environment, needed to guide our behavior in an effective manner. Previous studies show that numerosity processing involves at least two temporal stages (~100 and ~150 ms after stimulus onset) in early visual cortex, possibly reflecting the initial feedforward processing followed by feedback signals from higher-order cortical areas that underlie the segmentation of visual inputs into the perceptual units that define numerosity. Alternatively, multiple stages of feedforward processing might progressively refine the input leading to the segmented representation. Here, we distinguish these two hypotheses by exploiting the connectedness illusion (i.e., the systematic underestimation of pairwise-connected dots), backward masking (to suppress feedback signals), and serial dependence (i.e., perceptual bias making a stimulus appear to be more similar to its preceding one). Our results show that a connected dot array biases the numerosity representation of the subsequent dot array based on its illusory perception, irrespective of whether it is visible or suppressed by masking. These findings demonstrate that feedback processing is not strictly necessary for the perceptual segmentation that gives rise to perceived numerosity, and instead suggest that different stages of feedforward activity presumably carrying low and high spatial frequency information are sufficient to create a numerosity representation in early visual areas.

Keywords. Numerosity perception; serial dependence; connectedness; masking; visual processing.

1. INTRODUCTION

Approximate numerical magnitude – or simply numerosity – represents a fundamental attribute of a visual scene (e.g., Anobile, Cicchini, & Burr, 2016). Humans, as well as many other animal species, are thought to possess a natural sense of number that allows them to rapidly estimate the approximate number of objects in a visual scene (Agrillo, Dadda, Serena, & Bisazza, 2008; Dehaene, 2011; Gallistel & Gelman, 1992; Pepperberg, 2006; Piantadosi & Cantlon, 2017; Rugani, Vallortigara, Priftis, & Regolin, 2015). This sense of number appears to be phylogenetically ancient, and ontologically innate, as human newborns are able to discriminate the numerosity of different sets shortly after birth (Izard, Sann, Spelke, & Streri, 2009; Xu, 2003; Xu & Spelke, 2000). Similarly to many other visual features like orientation, color, or motion, numerosity has been shown to be subject to adaptation (e.g., Burr & Ross, 2008), suggesting that it is a primary visual attribute fundamental to construct an accurate representation of a visual scene (e.g., Anobile, Cicchini, et al., 2016; Cicchini, Anobile, & Burr, 2016). Several studies suggest that numerosity processing may exploit dedicated brain mechanisms independent from other continuous magnitudes like density (Anobile, Cicchini, & Burr, 2016; Park, Dewind, Woldorff, &

Brannon, 2016; Van Rinsveld et al., 2020) creating an abstract representation shared across multiple sensory modalities (Arrighi, Togoli, & Burr, 2014), and across the perceptual and motor systems (Anobile, Arrighi, Togoli, & Burr, 2016; Anobile, Domenici, Togoli, Burr, & Arrighi, 2019; Togoli, Crollen, Arrighi, & Collignon, 2020) at their highest level, while other authors have suggested that numerosity is perceived via the representation of continuous magnitudes, such as density (Dakin, Tibber, Greenwood, Kingdom, & Morgan, 2011; Durgin, 1995, 2008; Leibovich, Katzin, Harel, & Henik, 2017).

One important question regarding the mechanisms underlying numerosity perception concerns the specific visual pathway leading to numerosity representation. The brain region most often associated with numerosity perception is the parietal cortex and, more specifically, the intraparietal sulcus (IPS; Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004), or the superior parietal lobule (SPL; Harvey, Klein, Petridou, & Dumoulin, 2013). The parietal cortex has been shown to contain topographic maps of numerosity (Harvey et al., 2013) and since it represents different numerical formats (i.e., symbolic and non-symbolic; Piazza, Pinel, Le Bihan, & Dehaene, 2007), it may be the locus where an abstract representation of quantity is formed (Anobile, Arrighi, et al., 2016; Arrighi et al., 2014; but see Cavdaroglu & Knops, 2018 for evidence against a format-independent representation). Several recent studies, however, started to report numerosity-related activity in early sensory cortices in both the visual (Castaldi, Piazza, Dehaene, Vignaud, & Eger, 2019; Cavdaroglu & Knops, 2018; DeWind, Park, Woldorff, & Brannon, 2019; Fornaciai & Park, 2018a; Harvey & Dumoulin, 2017; Roggeman, Santens, Fias, & Verguts, 2011; Van Rinsveld et al., 2020) and auditory (Cavdaroglu, Katz, & Knops, 2015) modality. In the visual modality, there is evidence that numerosity representations are formed throughout multiple processing stages (Fornaciai & Park, 2018a; Park et al., 2016; Roggeman et al., 2011), as predicted by computational models of numerosity perception (Dehaene & Changeux, 1993; Stoianov & Zorzi, 2012; Verguts & Fias, 2004).

In particular, studies exploiting the high temporal resolution of electroencephalography (EEG) show different processing stages representing numerosity, starting at extremely short latencies after the onset of a stimulus. For instance, Park et al. (2016) first showed number-sensitive activity at around 75 ms after stimulus onset, followed by another stage around 180 ms. Subsequent studies found that the earliest activity likely arises from areas such as V2 and V3 (Fornaciai, Brannon, Woldorff, & Park, 2017), and that an early processing stage is present also for numerosities in different ranges (i.e., very low numerosities around or less than four items, known as the “subitizing” range, and very high numerosities whereby individual items can no longer be distinguished as in a texture pattern; see Anobile, Cicchini, et

al., 2016 for a review), although with weaker sensitivity to numerical information (Fornaciai & Park, 2017a).

Although these studies demonstrate the involvement of early visual activity in numerosity representation, the role of such a processing stage is less clear. In a recent work (Fornaciai & Park, 2018a), we asked whether early visual activity is sufficient to explain the representation of numerosity, or whether it merely reflects an initial stage where a proper representation is not yet formed. To do so, we employed the connectedness illusion – that is, a systematic bias whereby the numerosity of pairwise-connected dot arrays is consistently underestimated. The connectedness illusion is thought to reflect the segmentation processes needed to create the set of “perceptual units” at the basis of numerosity perception (Fornaciai, Cicchini, & Burr, 2016; Franconeri, Bemis, & Alvarez, 2009; He, Zhang, Zhou, & Chen, 2009; He, Zhou, Zhou, He, & Chen, 2015). For the purpose of our investigation, this illusion allowed us to test whether a neural signal is based on the veridical numerosity likely reflecting the initial sensory representation of the stimulus, or the perceived numerosity likely reflecting the final conceptual representation of the stimulus. The results from that study (Fornaciai & Park, 2018a), utilizing EEG and functional magnetic resonance imaging (fMRI), confirmed that an initial sensory representation is formed early on in visual processing (100 ms) and in visual areas V2 and V3. However, activity reflecting connected items, and thus likely reflecting the conceptual representation, arises only later in the visual stream (150 ms), specifically in area V3 (Fornaciai & Park, 2018a). As the timing of the two processing stages is consistent with the timing of feedforward and feedback visual activity (Boehler, Schoenfeld, Heinze, & Hopf, 2008; Fahrenfort, Scholte, & Lamme, 2007), we had interpreted the later activity as reflecting the contribution of re-entrant processing enabled by feedback signals from higher-order areas. This would play a role in segmenting the items into perceptual units.

However, results from this previous study could not conclusively pinpoint feedback signals as the underlying source of the later activity. An alternative explanation is that the delayed brain activity related to connectedness reflects slower high-spatial frequency signals reaching the visual cortex in a feedforward manner (Jones & Keck, 1978; Maunsell & Gibson, 1992; Mazer, Vinje, McDermott, Schiller, & Gallant, 2002). According to this view, an initial sensory representation would be quickly created as soon as fast low-spatial frequency (magnocellular) information reaches the cortex. At a later time, such a representation would be refined by means of high spatial frequency information, conveying information about the thin lines connecting the items and allowing a segmentation into perceptual units.

We attempt to disentangle these two hypotheses by exploiting the connectedness illusion, in combination with a perceptual bias created by the recent history of stimulation (serial dependence; Fischer & Whitney, 2014), and visual masking. Serial dependence refers to a perceptual bias, whereby a visual stimulus appears to be more similar to its previous stimulus. As several studies have shown that the perceived numerosity of a stimulus can be strongly biased by this recent history of stimulation (Cicchini, Anobile, & Burr, 2014; Fornaciai & Park, 2018b, 2018c, 2019a, 2019b, 2020a), manipulation of serial dependence provides an ideal way to investigate the functional mechanisms of numerosity perception. Masking, or more specifically *backward* masking (Enns & Di Lollo, 2000), refers to a procedure that makes a target stimulus invisible by presenting another high-contrast “mask” stimulus shortly after it. Re-entrant processing in early visual cortex has been shown to be suppressed (along with the awareness of the masked stimulus), while early feedforward processing is spared (Lamme & Roelfsema, 2000).

In the present study, we first assessed the connectedness illusion, asking participants to discriminate the numerosity of a variable probe dot array compared to a constant reference, which could include either 18 isolated dots, or 18 pairwise-connected dots. According to previous studies (Fornaciai et al., 2016; Franconeri et al., 2009; He et al., 2009), connecting pairs of dots in an array is expected to yield a strong underestimation of numerosity. In the second experiment, we assessed the serial dependence effect provided by an irrelevant stimulus (“inducer”), which could contain either isolated or pairwise-connected dots. Namely, participants were asked to discriminate the numerosity of a reference and a probe array, which were preceded by a task-irrelevant inducer stimulus inducing serial dependence. Previous studies, using a very similar procedure, showed that such an inducer could significantly affect the perceived numerosity of the subsequent reference stimulus (Fornaciai & Park, 2018c, 2019a). More specifically, a reference preceded by a less numerous inducer is systematically underestimated, while a reference preceded by a more numerous inducer is overestimated.

Given these manipulations, the first question we ask is whether serial dependence operates on the veridical or the perceived (i.e., perceptually reduced by connectedness) numerosity of the inducer. Then, we used visual backward masking to suppress re-entrant processing of the inducer and to make it invisible. Under backward masking conditions, we have shown that the perceptual bias effect is reversed, resulting in a repulsive bias akin to perceptual adaptation as opposed to attractive serial dependence (Fornaciai & Park, 2019a). If the segmentation into perceptual units requires feedback signals, then masking should abolish connectedness, and the stimulus should provide an effect on subsequent task-relevant stimuli based on the veridical numerosity. Alternatively, if feedforward processing is sufficient for connectedness segmentation, then even a masked connected-dot stimulus should provide an effect

based on the perceived reduced numerosity. Our results support the latter hypothesis, showing that even when masking is applied, the effect provided by the inducer stimulus reflects the set of connected items rather than the veridical number of dots. This in turn suggests that feedback signals and re-entrant processing are not strictly necessary for the perception of connectedness and for creating a refined (i.e., segmented) numerosity representation.

2. METHODS

In the Methods section, we report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

2.1 Participants

A total of 51 subjects participated in the study (39 females, mean age = 21 years, SD = 4 years), including the author M.F. Participants were given course credit or monetary compensation (\$10/hour) for their time. Before participating in the study, all the subjects signed a written informed consent. With the exception of the author, all participants were naïve to the aims of the experiment. All participants had normal or corrected-to-normal vision and reported no history of neurological, attentional or psychiatric disorders. Experimental procedures were approved by the Institutional Review Board of the University of Massachusetts Amherst and were in line with the declaration of Helsinki. Six participants were excluded from data analysis due to poor performance (see *Behavioral data analysis*), leaving a total of 45 subjects included in the final sample. Note that the sample size was based on a previous study from our group employing a similar technique (Fornaciai & Park, 2019a). Namely, based on the effect size measured in our previous study (Cohen's $d = 0.49$; average effect size in no mask condition of Exp. 1 and 2, and the masking condition of Exp. 1 in Fornaciai & Park, 2019a), a desired power of 95%, and a one-tailed distribution (based on the expected direction of the effect), we calculated a required sample size of 47 participants. None of the experimental or analytical procedures used in this study was pre-registered.

2.2 Apparatus and stimuli

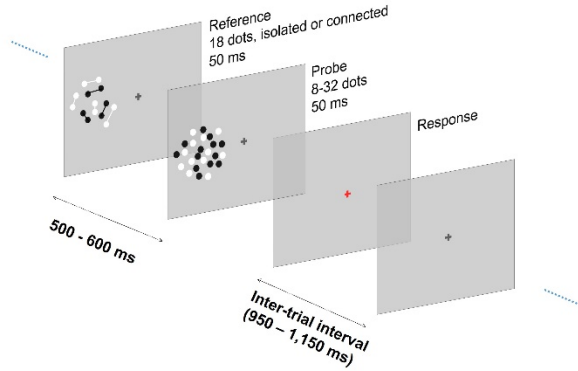
Visual stimuli across the two experiments were generated using the Psychophysics Toolbox (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997) for Matlab (version r2016b; The Mathworks, Inc.). Stimuli were presented on a 1920×1080 pixel monitor screen (144 Hz), encompassing approximately 35×20 degrees of visual angle from a viewing distance of about 80 cm.

Stimuli were visual arrays of black and white dots (50% and 50% in most of the cases; in case of odd numerosities the color of the exceeding dot was randomly selected) presented on a gray background. The parameters of the dot-array stimuli were chosen to range equally in three orthogonal dimensions, corresponding to numerosity (N), size (Sz), and spacing (Sp). Such a stimulus construction scheme was employed to ensure consistency with previous work from our group (e.g., Fornaciai & Park, 2018c, 2019a), and thus to ensure that the present results could be easily compared with previous findings. However, since the primary goal of the study concerns numerosity, the different levels of non-numerical dimensions were collapsed together during data analysis. For a more detailed description of the stimulus construction procedure and a characterization of the effect of non-numerical dimensions, see DeWind, Adams, Platt, & Brannon, 2015; Park et al., 2016. Specifically, the parameters of the stimuli were set as follows. The area of each individual dot ranged from 113 pixel² (0.038 deg²), equal to a diameter of 0.11 deg (6 pixels), to 452 pixel² (0.15 deg²), equal to a diameter of 0.22 deg (12 pixel). The field area of the stimuli (i.e., the circular area within which the dots were located) ranged from 70,686 pixel² (23.9 deg²), encompassing 5.5 degrees of visual angle in diameter (300 pixels), to 282,743 pixel² (95.7 deg²), encompassing 11 degrees in diameter (600 pixels). In all cases, the individual size of the dots was homogeneous within the stimulus, and we set a minimum distance between any two dots equal to at least the radius of the dots. Regarding numerosity, in the preliminary connectedness experiment the reference stimulus always contained 18 dots, while the probe stimulus contained a variable number of dots from trial to trial (8, 10, 13, 16, 20, 25, 32). In half of the trials, the dots in the reference stimulus were pairwise connected with lines (width = 2 pixels). Dot positions were calculated offline computing a set of coordinates compatible with pairwise connections in order to avoid crossing between lines or superimposition between lines and dots. The same offline procedure was applied for both the reference and probe stimuli in order to keep the low-level properties of the images (which are affected by the constraining presence of lines) similar. In the serial dependence experiment, the stimuli included a task-irrelevant inducer, including 18 dots, either isolated or connected, a reference including 16 isolated dots, and a variable probe containing 8-32 isolated dots. In all cases, dot positions were calculated offline in order to compute coordinates compatible with connecting lines, similarly to the connectedness experiment. For each numerosity, a set of 1,000 arrays was created and stimuli were randomly drawn from these sets during the experiment. Note that reference and probe numerosities were chosen to be in line with our previous work (e.g., Fornaciai & Park, 2018c, 2019a), which allows a direct comparison between the results across different studies when needed.

In addition, in some of the conditions a mask stimulus was briefly presented after the inducer stimulus (65 ms after inducer onset). The timing of the mask stimulus was chosen according to a previous study using

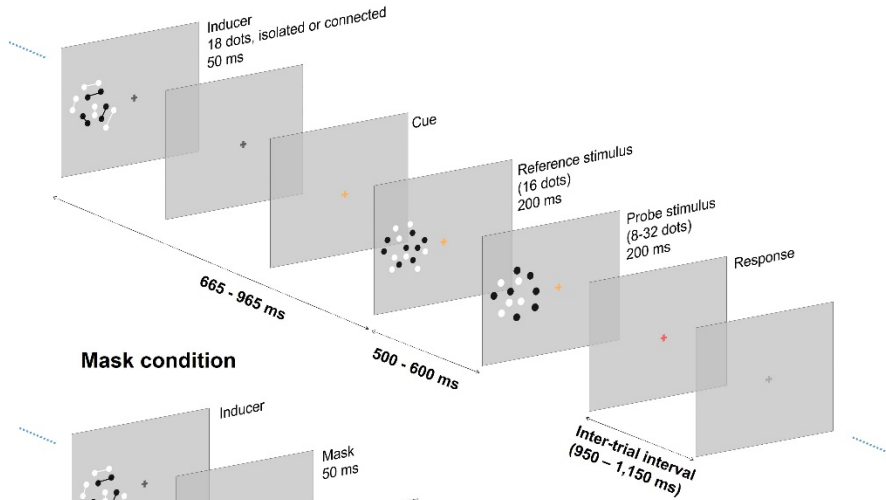
very similar stimuli (Fornaciai & Park, 2019a). The mask stimulus was a black/white square-pattern mask (side of each square = 22 pixel), presented through a circular aperture (radius = 5.7 deg) in the same position of the inducer stimulus.

A CONNECTEDNESS EXPERIMENT



B SERIAL DEPENDENCE EXPERIMENT

No mask condition



Mask condition

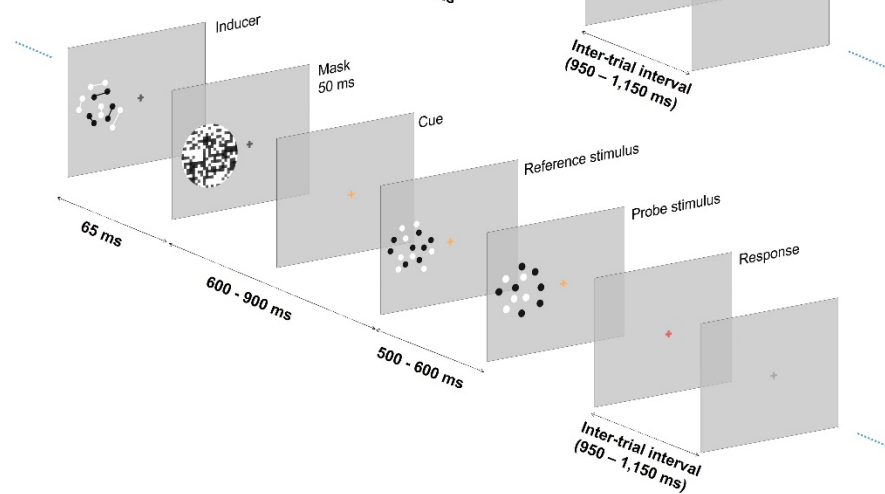


FIGURE 1. Experimental procedure. (A) Preliminary connectedness experiment. In this experiment, we measured the connectedness effect in numerosity perception. On each trial, participants saw a sequence

of two dot arrays presented in the same position on the screen (either left or right of the fixation point, randomized) for 50 ms. The reference array always contained 18 dots, and the probe array contained 8-32 dots. Participants were asked to indicate, at the end of each trial, which stimulus contained more dots. Crucially, in half of the trials the dots in the reference stimulus were pairwise connected by thin lines with the same color of the dots (i.e., forming all black or all white dot pairs). The presentation order of reference and probe was randomized from trial to trial. (B) In the serial dependence experiment, we tested to what extent isolated and connected dot-arrays affect the subsequent stimuli via serial dependence. To this aim, a series of three stimuli was presented on the screen: an inducer containing 18 isolated or connected dots, to induce serial dependence, followed by a reference (16 dots) and a probe (8-32 dots), in this order. In some trials (panel B, bottom figure), a pattern mask was presented shortly after the inducer stimulus (SOA = 65 ms) in order to make the stimulus invisible and suppress re-entrant processing. In both cases, to avoid confusion between reference/probe stimuli and the inducer, a cue (orange fixation cross) was presented before the onset of the reference and throughout the presentation of the stimuli. Stimuli are not depicted in scale.

2.3 General procedure

All experimental conditions were performed in a quiet and dimly lit room, with participants sitting in front of a monitor screen at a distance of about 80 cm. Each participant performed two experiments, (connectedness and serial dependence experiment) always in the same order. In the first connectedness experiment (Fig. 1A), we measured the connectedness effect using a previous procedure (Fornaciai & Park, 2018a). Namely, in each trial a sequence of a reference (18 dots, either isolated or connected) and a probe (8-32 isolated dots) stimulus was presented on the screen, either on the left or the right of a central fixation point (eccentricity = 9.2 deg; positions randomized across trials). The two stimuli were separated by a variable interstimulus interval (500-600 ms), and their order was randomized from trial to trial. At the end of the trial, participants were asked to report which stimulus contained more dots by pressing the appropriate key on a standard keyboard. After providing a response, the next trial started automatically after 950-1,150 ms. Additionally, participants were instructed to focus exclusively on the number of dots. In the second experiment (Fig. 1B), we measured serial dependence effects induced by isolated or connected dot arrays, either visible or made invisible by visual backward masking. In the “no-mask” condition, a sequence of three stimuli was presented in each trial, either on the right or on the left of a central fixation point (eccentricity = 9.2 deg; position randomized across trials). First, an inducer array containing 18 dots, either isolated or connected, followed by a reference stimulus (16 dots) after 600-900 ms, and finally a probe stimulus (8-32 dots) following the reference after 500-600 ms. All stimuli were

presented on the screen for approximately 50 ms, and always in the same order. In the “mask” condition, a pattern mask was presented for 50 ms shortly after the inducer (SOA = 65 ms) to induce masking. With the exception of the mask, the sequence and the other stimuli were identical to the no-mask condition, and both conditions were randomly intermixed within the same block. At the end of each trial, participants were instructed to report whether the reference or the probe stimulus contained more dots as fast as they could. Participants were told that although the inducer (and the mask) were irrelevant for the task, they should attend to the entire sequence of the stimuli. In the serial dependence experiment, to avoid confusion between reference/probe stimuli and the inducer, a cue (orange fixation cross) was presented before the onset of the reference and throughout the presentation of the stimuli. Subjects were told that the cue indicates when the task-relevant stimuli will be presented. The connectedness experiment comprised 4 blocks of 56 trials, while the serial dependence experiment comprised 7 blocks of 56 trials. Before starting the actual experiment, participants completed a brief training session (8-15 trials) to familiarize with the task and ensure that they understood the instructions. Participants were allowed to take breaks during the experiment, and an entire session took about 45 minutes. Note that while in the connectedness experiment, the order of stimuli was randomized from trial to trial to avoid time-order errors (i.e., under- or overestimation of the first stimulus in the sequence), the sequence of stimuli was fixed in the serial dependence experiment in order to always have the reference following the inducer. This is important as serial dependence is stronger on the immediately successive stimulus (Fornaciai & Park, 2020b). However, presenting both reference and probe stimuli in the same position as the inducer might cause serial dependence to affect also the probe, possibly reducing the magnitude of the bias. We nevertheless chose this stimulation procedure as it has proven to be effective in previous studies (Fornaciai & Park, 2018c, 2019a, 2019b, 2020a) and does not require to introduce attentional manipulations which are instead necessary when the stimuli are presented in different positions (Fornaciai & Park, 2018c). Additionally, we chose a peripheral stimulus presentation, as opposed to a central presentation, to increase the effectiveness of the masking procedure in the mask condition (Stewart & Purcell, 1970). To keep the stimulation procedure consistent across conditions, we used the same peripheral stimulus presentation in all the experimental conditions tested in the study.

2.4 Behavioral data analysis

Performance in the numerosity discrimination task was analyzed separately for each subject and condition, in order to characterize the connectedness effect and the serial dependence effect induced by isolated or connected stimuli. To achieve a measure of participants’ accuracy and precision in the task, the distribution of response probabilities as a function of probe numerosity was fitted with a Cumulative

Gaussian curve, according to the Maximum Likelihood method (Watson, 1979). The point of subjective equality (PSE; the probe numerosity perceptually matching the reference numerosity), reflecting the accuracy in the task (i.e., the reference perceived numerosity), was defined as the median of the best-fitting cumulative Gaussian curve. The just-noticeable difference (JND), the difference in numerosity between chance level (50%) responses and 75% “probe more numerous” responses, was taken as a measure of precision in the task. As an additional measure of precision, we computed the Weber’s fraction (JND/PSE), which was used to evaluate the participants’ performance in the task and to exclude subjects showing insufficient performance. During the fitting procedure, we also applied a finger error (or lapse) rate correction (2%; Wichmann & Hill, 2001), to account for random errors independent from the stimulus magnitude and lapses of attention. Such a correction involves the adoption of slightly narrower theoretical bounds of response probabilities during the psychometric fitting, which, with a 2% correction, will be from 0.02 to 0.98, instead of from 0 to 1. Doing so, we take into account random errors and lapses of attention which may prevent the cumulative Gaussian fit to converge to 0 and 1 at the extremes of the probe numerosity range. Finally, paired t-tests on PSEs were used to test the difference between pairs of conditions, in order to assess the connectedness and serial dependence effects. To exclude participants showing poor performance, we used the WF and computed a cut-off based on the interquartile range. Namely, we log-scaled WFs in each condition of the serial dependence experiment and computed the third quartile (Q3) and the interquartile range of the data (IQR). The cut-off was thus defined as $Q3 + 1.5 \times IQR$. Any participant showing WF higher than this cut-off in any of the serial dependence conditions was excluded. This criterion led to the exclusion of three participants. Additionally, participants were excluded also based on reaction times. Outlying participants were excluded based on the identical procedure used for WFs. This led to the exclusion of three more participants with very slow reaction times, leaving a total of 45 subjects in the final group. Note that the exclusion criteria were evaluated and applied only based on the data from the serial dependence experiment, as it represents the main experiment for the aims of the present study.

Besides the analysis based on PSE, we also computed a normalized serial dependence effect index according to the following formula:

$$\text{Serial dependence index} = ((\text{PSE}_{\text{iso}} - \text{PSE}_{\text{conn}}) / \text{PSE}_{\text{conn}}) \times 100;$$

Where PSE_{iso} indicates the PSE obtained with the isolated-dot inducer, and PSE_{conn} indicates the PSE obtained with the connected-dot inducer. We calculated such serial dependence index individually, and compared the indexes obtained in the no mask and mask condition with a paired t-test. In this context, a

positive index indicates an attractive effect whereby the presence of a connected-dot inducer leads to a relative underestimation of the reference stimulus, compared to when an isolated-dot inducer is presented. Conversely, a negative index indicates a repulsive effect whereby the presence of the connected-dot inducer leads to an overestimation compared to the isolated-dot inducer condition. A similar normalized effect was also calculated for the connectedness effect.

3. RESULTS

The study was divided into two different experiments (see Fig. 1). In the first experiment, we measured the connectedness effect (Franconeri et al., 2009; He et al., 2009) using a numerosity discrimination task. The purpose of this preliminary experiment was to assess how such pairwise-connected dot arrays are perceived in order to use them as inducers in the following serial dependence experiment. The results (Fig. 2A and 2D), in line with previous studies, confirmed a strong underestimation of perceived numerosity of pairwise-connected arrays. Looking at the average psychometric curves, there is a robust leftward shift of the curve relative to the connected-dot reference condition, indexing a strong underestimation of connected dots. PSEs across the group in the connected-dot condition were indeed significantly smaller than PSEs corresponding to the same amount of isolated dots (Fig. 2D; $t(44) = 10.15$, $p < 0.001$, Cohen's $d = 1.51$). Overall, the perceived numerosity of 18 connected-dot stimulus was reduced by about (average normalized effect \pm SD) $26\% \pm 17\%$ compared to isolated dots (average PSE \pm SD = 17.7 ± 1.9 and 12.9 ± 2.8 , respectively for the isolated and connected-dot condition). This reduction appears roughly in line with previous studies employing a similar procedure, although the magnitude of bias is stronger in the current study ($\sim 20\%$ reduction in Fornaciai et al., 2016; $\sim 19\%$ reduction in the 16-dots condition in Fornaciai & Park, 2018a). Although anecdotal, this is in line with the idea that the strength of the connectedness illusion is inversely related to the duration of the stimuli (He et al., 2009), which in the present study was much shorter (i.e., 50 ms in the current study versus 150 ms in previous studies from our group).

Regarding the participants' precision in the connectedness experiment (Weber's fraction, WF), we observed significantly higher WFs in the connected-dot condition, compared to the isolated-dot condition (average WF \pm SD = 0.52 ± 0.57 vs. 0.35 ± 0.19 ; paired t-test, $t(44) = 2.54$, $p = 0.015$, $d = 0.34$). This difference is however mostly due to the large difference in PSE, as JNDs appear very similar across the two conditions, as also suggested by the similar slope of the average psychometric curves in Fig. 2A (average JND \pm SD = 6.05 ± 3.18 and 5.87 ± 4.44 , respectively for the isolated and connected-dot condition; paired t-test, $t(44) = 0.44$, $p = 0.66$).

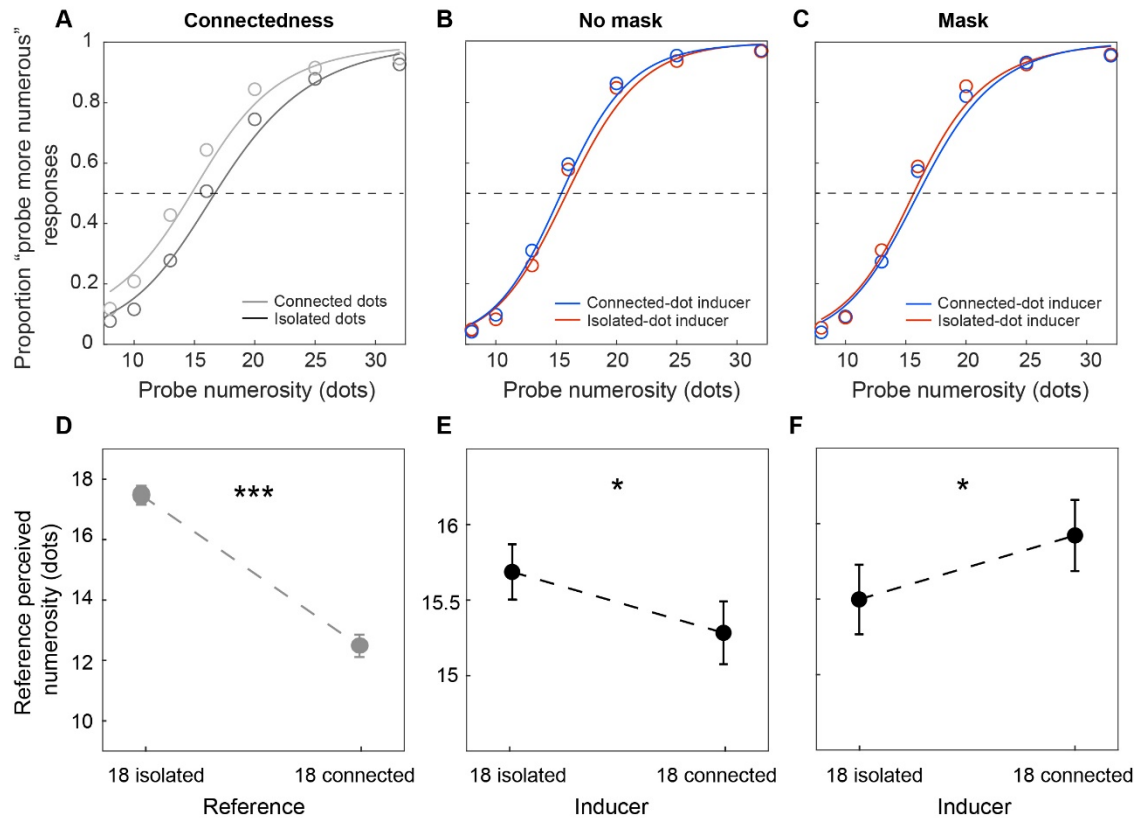


FIGURE 2. Results of the connectedness and serial dependence experiments. (A) Average psychometric curves in the connectedness experiment, describing the perceptual matching of the probe stimulus with either a connected-dot reference stimulus (light grey curve) or an isolated-dot reference stimulus (dark grey curve). (B) Average psychometric curves in the no mask condition of the serial dependence experiment, showing the average performance in the presence of a connected-dot inducer (blue curve) or an isolated-dot inducer (red curve). (C) Average psychometric curves in the mask condition of the serial dependence experiment. (D) Results of the connectedness experiment in terms of the average perceived numerosity (PSE) of the 18-isolated dot reference and the 18-connected dot reference. (E) Results of the no mask condition of the serial dependence experiment in terms of average PSE. (F) Results of the mask condition of the serial dependence experiment in terms of average PSE. Error bars are SEM. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

In the second experiment, the connected and isolated 18-dot arrays induced serial dependence, affecting a subsequent 16-dot reference stimulus. Similar to the previous connectedness experiment, participants performed a numerosity discrimination task, this time comparing a 16-dot reference (always containing isolated dots) with a variable probe. Crucially, the inducer was presented before the reference in the same spatial position. Considering the underestimation of connected dot arrays (Fig. 2D), if serial dependence

operates on veridical numerosity, then whether or not the inducer to a 16-dot reference contains 18 isolated dots or 18 connected dots should not affect the perception of the 16-dot reference. If serial dependence operates on perceived numerosity, then the perceived numerosity of the 16-dot reference would be influenced by whether or not the inducer contains 18 isolated dots or 18 connected dots.

In the no-mask condition, we observed a clear attractive serial dependence effect, as shown by the leftward shift in the average psychometric curve relative to the connected-dot inducer (Fig. 2B, blue curve), and by the difference in average PSE (Fig. 2E). Namely, the 18-connected-dots inducer caused a small but noticeable underestimation of the reference stimulus compared to the isolated-dot inducer (average PSE \pm SD = 15.7 ± 1.2 and 15.3 ± 1.4 , respectively for the isolated and connected-dot inducer). This effect was statistically significant (paired t-test, $t(44) = 2.17$, $p = 0.035$), though with a relatively small effect size ($d = 0.32$). Importantly, such an attractive effect operated according to the perceptually reduced numerosity of the connected inducer (i.e., due to connectedness), rather than its veridical numerosity.

Then, we used visual backward masking to suppress the re-entrant processing of the inducer making it invisible. The predictions of this condition are as follows: if connectedness, giving rise to the perceptual units of numerosity perception, relies on re-entrant processing enabled by feedback signals, masking should abolish the connectedness effect. In this scenario, we should expect no difference between the two inducer conditions, or even an underestimation in the connected-dot-inducer condition due to the additional presence of lines. Conversely, if connectedness does not rely on feedback signals, then the connected-dot-inducer should provide an effect based on a reduced numerosity. In this scenario, we should expect a repulsive aftereffect following our previous findings (Fornaciai & Park, 2019a): an isolated inducer (which is perceived to be relatively more numerous) would lead to an underestimation of the reference array while a connected inducer (which is perceived to be relatively less numerous) would lead to an overestimation of the reference array. The results (Fig. 2C) were consistent with the second hypothesis: the connected-dot inducer caused a systematic overestimation of the reference perceived numerosity, relative to the isolated-dot inducer (average PSE \pm SD = 15.5 ± 1.5 and 15.9 ± 1.6 , respectively for the isolated and connected-dot inducer). This pattern is consistent with a repulsive effect based on the “perceived” numerosity of the inducer reduced by connectedness. The difference between the two inducer conditions was statistically significant ($t(44) = -2.44$, $p = 0.018$), and with a similar effect size compared to the no mask condition ($d = 0.36$).

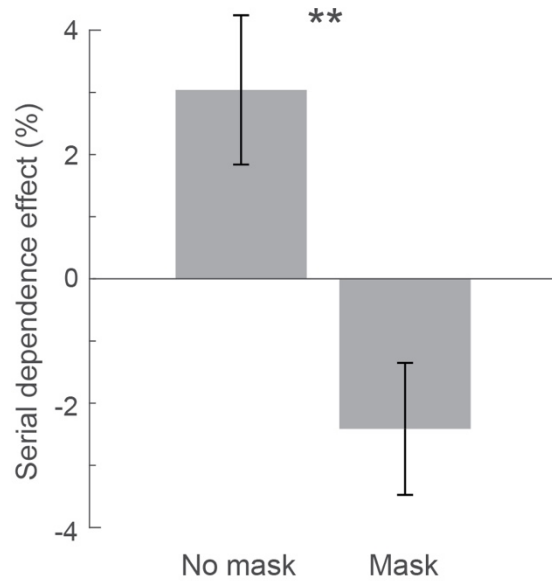


FIGURE 3. Average serial dependence effect indexes in the no mask and mask condition. Positive effect indexes, as observed in the no mask condition, represent an attractive effect whereby a connected-dot inducer leads to an underestimation of the reference stimulus numerosity compared to an isolated-dot inducer. Negative indexes, as observed in the mask condition, instead reflect a repulsive effect whereby a connected-dot inducer leads to a relative overestimation of the reference stimulus. Error bars are SEM. $**p < 0.01$.

Finally, we directly compared the effect of inducers in two different conditions (mask vs. no mask) using the normalized serial dependence effect index (see *Behavioral data analysis*), as it was the critical measure for our central hypothesis about whether or not masked inducers (or abolishing feedback signals) yield the same serial dependence outcomes as the unmasked inducers. The effect of serial dependence in the two conditions was significantly different ($t(44) = 3.04$, $p = 0.0039$, $d = 0.71$) and in opposite directions, reflecting the attractive and repulsive nature of the bias in each of the two conditions.

In addition, we assessed the pattern of participants' precision in the task (WF) by performing a two-way repeated measure ANOVA, with factor "inducer connectedness" (i.e., isolated vs. connected), and "experimental condition" (i.e., no mask vs mask). There was a main effect of experimental condition ($F(1,44) = 5.41$, $p = 0.025$) with no significant main effect of inducer connectedness ($F(1,44) = 0.087$, $p = 0.769$) nor the interaction ($F(1,44) = 0.009$, $p = 0.93$). The WFs were on average higher in the mask condition, although the difference in precision was very small (0.19 ± 0.07 vs. 0.17 ± 0.07).

4. DISCUSSION

Recent studies have highlighted several stages of numerosity processing along the visual hierarchy, starting from early occipital visual areas (V1-V3) to higher-order associative areas in parietal cortex (Castaldi et al., 2019; Cavdaroglu et al., 2015; Cavdaroglu & Knops, 2018; DeWind et al., 2019; M. Fornaciai & Park, 2018a; Harvey et al., 2013; Roggeman et al., 2011; Van Rinsveld et al., 2020). In one of our previous studies (Fornaciai & Park, 2018a), it was shown that a numerosity representation is formed across two processing stages in early visual areas (V2-V3): first, an early representation of the raw, unsegmented visual items (around 100 ms after stimulus onset), followed by a more refined representation reflecting segmented items forming the basis for numerosity perception (around 150 ms). The current study aimed to distinguish two hypotheses considering the mechanisms of these two stages: (1) they may reflect an initial feedforward stage followed by later feedback signals consistent with earlier studies concerning other forms of segmentation (Lamme, Zipser, & Spekreijse, 2002); or (2) they may reflect two subsequent stages of feedforward activity carrying different information – i.e., first low-spatial frequency signals (dots) carried by the faster magnocellular system, then high-spatial frequency signals (lines) carried by the slower parvocellular system (Jones & Keck, 1978; Maunsell & Gibson, 1992; Mazer et al., 2002). To this aim, we employed the connectedness illusion, in conjunction with the serial dependence effect and visual backward masking.

Results from the no-mask condition first showed that the serial dependence effect provides a bias to subsequent stimuli based on the perceived, rather than veridical, numerosity of the inducer. An 18 connected-dot inducer caused a stronger underestimation of a 16-dot reference, compared with the case of an 18-isolated-dot inducer (Fig. 2B and 2E). This result provides evidence that serial dependence is not based on initial sensory representations and operates on the basis of a more refined representation. In this case, serial dependence occurs only after the stimulus is segmented into a set of perceptual units closer to what the participant is likely experiencing. Interestingly, similar results have been previously observed in the case of numerosity adaptation, which has been shown to operate on perceived rather than physical numerosity (Fornaciai et al., 2016).

While we expected and indeed observed attractive serial dependence in the no-mask condition, our prediction concerned an opposite, repulsive, effect in the mask condition. In a previous study from our group (Fornaciai & Park, 2019a), we have shown that when the awareness of the inducer stimulus is suppressed by means of backward masking, its effect on the subsequent stimulus becomes repulsive. In other words, the perceived numerosity of the reference gets pulled away from that of the inducer (i.e., a

lower-numerosity inducer causes overestimation, while a higher-numerosity inducer causes underestimation) – an effect akin to perceptual adaptation (Kohn, 2007). This effect has been taken as evidence for the involvement of conscious high-level processing in establishing serial dependence. In other words, when conscious processing is suppressed by masking, lower-level cortices would be “released” from the attractive influence of serial dependence, allowing spontaneous and automatic perceptual adaptation effects to emerge. Thus, when masking is applied in the context of the present experiment to suppress feedback processing, the influence of the inducer is expected to become repulsive.

Results from the mask condition indeed showed a repulsive aftereffect which, importantly, is still based on a reduced numerosity due to connectedness (Fig. 2C and 2F). That is, an 18-connected-dot inducer compared with an 18-isolated-dot inducer led to a relative overestimation of the reference stimulus, consistent with a repulsive effect. First, this result confirms that the masking procedure used here, which is based on a preliminary test included in Fornaciai & Park (2019a), is highly effective. This is very important in this context, as the testing of our central hypothesis hinges upon the ability of the mask stimulus to suppress the awareness and feedback processing of the inducer. Second, this result shows that segmentation of “perceptual units” according to item connectedness occurs irrespective of masking. This suggests that feedback signals and re-entrant processing – which are suppressed by backward masking (Fahrenfort et al., 2007) – are not strictly necessary for connectedness. Additionally, the results show that even awareness of the stimulus is not required for this kind of segmentation, suggesting that it likely reflects a perceptual organization process occurring automatically and irrespective of other related perceptual or cognitive processes. Overall, the results are more consistent with a feedforward account of connectedness. In this account, an initial, rough numerosity representation is first formed based on the feedforward low-spatial frequency information carried by the faster magnocellular pathway (Jones & Keck, 1978; Maunsell & Gibson, 1992; Mazer et al., 2002). Later, such a representation is refined by high-spatial frequency information carried by the slower parvocellular system, allowing to resolve the thin lines connecting the dots and to correctly segment the set of perceptual units. Purely feedforward activity would thus be sufficient to create a proper numerosity representation in early visual areas, which is then fed to higher-order areas such as parietal cortex for further processing. Additionally, these results also imply that a numerosity representation is formed as soon as any visual information reaches the cortex, but then progressively refined when finer information becomes available.

While the present results are not consistent with the feedback hypothesis, we cannot exclude the role of feedback under normal stimulation conditions (i.e., without masking). Indeed, both feedback and feedforward processing could contribute to the segmentation process. For instance, when feedback signals

are available, they may be exploited for the purpose of segmenting composite objects like connected dots; otherwise, if feedback processing is disrupted, the image may be progressively refined using purely feedforward information, perhaps in a less efficient fashion. Our results thus do not point to feedforward processing as the sole responsibility for the perception of numerosity under the connectedness illusion, but suggest that under peculiar circumstances like masking, feedforward signals are sufficient to represent a set of segmented objects.

The observation that stimulus connectedness is processed despite the manipulation of backward masking has important implications for our understanding of numerosity perception. First, the present findings support the idea that numerosity starts to be represented very early in the visual processing stream (i.e., in occipital areas such as V1, V2, and V3; e.g., (DeWind et al., 2019; Fornaciai et al., 2017; Park et al., 2016; Van Rinsveld et al., 2020), and further show that the construction of such representation does not require feedback from higher-order areas and conscious processing. Second, our results could inform the development of computational models of numerosity processing. On the one hand, our results are consistent with models of numerosity processing such as the ones provided by Dehaene & Changeaux (1993) and Verguts & Fias (2004). In these models, numerosity is extracted and represented throughout a series of computational steps of increasing abstraction. Namely, the first step is an object-location map whereby items are represented by foci of activity in a topographically-organized map (consistent for instance with early visual areas), which is followed by a summation stage summing up the overall activity across the map, and finally a numerosity-selective stage whereby units are selectively activated by a specific numerosity. Our results are also in line with the model proposed by Stoianov & Zorzi (2012). This model, after an initial unsupervised learning phase, has been shown to be able to encode stimulus numerosity via relatively simple computations occurring across two hierarchically organized layers. However, models such as the one by Stoianov & Zorzi (2012), as well as other models (e.g., Morgan, Raphael, Tibber, & Dakin, 2014), are essentially based on spatial-frequency filters computing numerosity in terms of high-spatial frequency energy (Stoianov & Zorzi, 2017). Considering that the lines connecting pairs of items most likely increase the high-spatial frequency content of an array, additional computations are thus needed to correctly extract numerosities in more complex situations like in the presence of connectedness. On the other hand, and in a similar vein, our results are not consistent with frameworks of numerosity processing based on continuous magnitudes (e.g., Leibovich et al., 2017). Indeed, adding lines to a dot array effectively increases the density of the stimulus and the area covered by the items in the array, predicting an increase, rather than a decrease, in perceived numerosity. Differently from these models, our results suggest that even at the earliest levels of numerosity processing (Fornaciai & Park, 2018a) and during the initial feedforward activity, the representation is already based on “perceptual

units” defined by connectedness, rather than by other stimulus statistics like density or high-spatial frequency content, which represents an important factor that should be taken into account in the development of future models of numerosity perception.

From a computational point of view, however, what are the specific neural operations that may explain the present results? Considering the model proposed by Dehaene & Changeaux (1993), the effect of connectedness would most likely occur at the stage of the low-level object location map. Namely, while independent activation loci (as caused by isolated dots) would lead to a linear summation of their respective activity, the presence of a connection between them might drive an additional “normalization” process resulting in a sub-additive integration. In this scenario, the relation between different foci of activity across the object location map would thus modulate the overall activity across the map itself, leading to a biased read-out of numerosity at the subsequent stages. Although speculative, this interpretation is consistent with a previous study from our group (Fornaciai & Park, 2017b), in which we exploited motion to address the properties of low-level numerosity processing (see also Fornaciai et al., 2018). Namely, the results from this previous study (Fornaciai & Park, 2017b) show that while the numerosity of dots randomly changing position over time at a relatively fast frequency (2-8 Hz) is markedly overestimated, such an effect is significantly reduced if the dots move instead along a coherent linear motion trajectory. In other words, while the additional activity elicited by a dot displaced to a different position seems to be integrated into the final estimate of numerosity, the streak of activity elicited by a linearly moving dot is normalized to reduce this potential overestimation, like a sort of “connectedness” over time (rather than in space). The present results thus additionally suggest that while these normalization computations require more time compared to a less refined initial representation (Fornaciai & Park, 2018b), they are likely performed locally at the level of the putative object location map (i.e., for instance in early visual areas such as V1-V3), without the need for higher-level computations fed back from downstream processing stages.

Finally, a word of caution is in order when evaluating the effect size observed in the no mask and mask conditions of the serial dependence experiment. While some of the effect sizes seem relatively small, it has been expected given the parameters and the constraints in those parameters in our experimental design. Indeed, both the attractive serial dependence effect and the mask-induced repulsive effect have been shown to be relatively small even in experimental designs aimed to maximize them (Fornaciai & Park, 2019a). Here, the effect is further constrained by the choice of the inducer numerosity, which had to be balanced in order for connectedness to bring it (perceptually) below the reference numerosity. Additional variability to the effect is also introduced by the connectedness effect itself, which is expected

to vary from trial to trial. Furthermore, the masking procedure introduces further constraints in terms of timing and strength of the stimuli, which were optimized to effectively suppress the awareness of the inducer stimulus. Considering these factors, a relatively small effect size is the expected outcome of the present experimental design, and a stronger effect would be rather unrealistic. Finally, the crucial test of our central hypothesis concerns the difference between the effects yielded by the unmasked inducer and the masked inducer, which yielded a moderate effect size (Fig. 3). Considering the effect size of the difference between conditions ($d = 0.71$), we also performed a post-hoc power analysis to assess the power achieved with our experimental design. To this purpose, we considered an $\alpha = 0.05$, a two-tailed distribution, and our sample of 45 subjects. This analysis resulted in an estimated achieved power of 99%, further suggesting that our conclusions are founded on reliable evidence.

5. CONCLUSION

Overall, our results shed new light on the visual processing mechanisms involved in numerosity representation and the related serial dependence effect modulating perceived numerosity. Our findings show that, first, serial dependence operates on perceived rather than physical numerosity, suggesting that it occurs at a perceptual level involving a more refined, segmented, representation of sensory stimuli. Second, our results suggest that different stages of feedforward activity presumably carrying low and high spatial frequency information are sufficient to create a numerosity representation in early visual areas. These results thus provide a more comprehensive characterization of the role of early visual processing in numerosity representation.

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Data availability. The data generated during the experiments described in this manuscript and the related experimental materials are available on Open Science Framework at the following link <https://osf.io/fcwue/>.

Competing interests. We declare that none of the Authors has any competing interest.

Author contribution. M.F. and J.P. devised the experimental protocol and stimuli. M.F. collected and analyzed the data. M.F. and J.P. interpreted the results and wrote the manuscript.

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