

1 **Disentangling feedforward versus feedback processing in numerosity representation**

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19 **ABSTRACT**

20 Numerosity is a fundamental aspect of the external environment, needed to guide our behavior in an
21 effective manner. Previous studies show that numerosity processing involves at least two temporal stages
22 (~100 and ~150 ms after stimulus onset) in early visual cortex, possibly reflecting the initial feedforward
23 processing followed by feedback signals from higher-order cortical areas that underlie the segmentation
24 of visual inputs into the perceptual units that define numerosity. Alternatively, multiple stages of
25 feedforward processing might progressively refine the input leading to the segmented representation.
26 Here, we distinguish these two hypotheses by exploiting the connectedness illusion (i.e., the systematic
27 underestimation of pairwise-connected dots), backward masking (to suppress feedback signals), and serial
28 dependence (i.e., perceptual bias making a stimulus appear to be more similar to its preceding one). Our
29 results show that a connected dot array biases the numerosity representation of the subsequent dot array
30 based on its illusory perception, irrespective of whether it is visible or suppressed by masking. These
31 findings demonstrate that feedback processing is not strictly necessary for the perceptual segmentation
32 that gives rise to perceived numerosity, and instead suggest that different stages of feedforward activity
33 presumably carrying low and high spatial frequency information are sufficient to create a numerosity
34 representation in early visual areas.

35
36 **Keywords.** Numerosity perception; serial dependence; connectedness; masking; visual processing.
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39 **1. INTRODUCTION**

40 Approximate numerical magnitude – or simply numerosity – represents a fundamental attribute of a visual
41 scene (e.g., Anobile, Cicchini, & Burr, 2016). Humans, as well as many other animal species, are thought
42 to possess a natural sense of number that allows them to rapidly estimate the approximate number of
43 objects in a visual scene (Agrillo, Dadda, Serena, & Bisazza, 2008; Dehaene, 2011; Gallistel & Gelman,
44 1992; Pepperberg, 2006; Piantadosi & Cantlon, 2017; Rugani, Vallortigara, Priftis, & Regolin, 2015).
45 This sense of number appears to be phylogenetically ancient, and ontologically innate, as human
46 newborns are able to discriminate the numerosity of different sets shortly after birth (Izard, Sann, Spelke,
47 & Streri, 2009; Xu, 2003; Xu & Spelke, 2000). Similarly to many other visual features like orientation,
48 color, or motion, numerosity has been shown to be subject to adaptation (e.g., Burr & Ross, 2008),
49 suggesting that it is a primary visual attribute fundamental to construct an accurate representation of a
50 visual scene (e.g., Anobile, Cicchini, et al., 2016; Cicchini, Anobile, & Burr, 2016). Several studies
51 suggest that numerosity processing may exploit dedicated brain mechanisms independent from other
52 continuous magnitudes like density (Anobile, Cicchini, & Burr, 2016; Park, Dewind, Woldorff, &

53 Brannon, 2016; Van Rinsveld et al., 2020) creating an abstract representation shared across multiple
54 sensory modalities (Arrighi, Togoli, & Burr, 2014), and across the perceptual and motor systems
55 (Anobile, Arrighi, Togoli, & Burr, 2016; Anobile, Domenici, Togoli, Burr, & Arrighi, 2019; Togoli,
56 Crollen, Arrighi, & Collignon, 2020) at their highest level, while other authors have suggested that
57 numerosity is perceived via the representation of continuous magnitudes, such as density (Dakin, Tibber,
58 Greenwood, Kingdom, & Morgan, 2011; Durgin, 1995, 2008; Leibovich, Katzin, Harel, & Henik, 2017).
59

60 One important question regarding the mechanisms underlying numerosity perception concerns the
61 specific visual pathway leading to numerosity representation. The brain region most often associated with
62 numerosity perception is the parietal cortex and, more specifically, the intraparietal sulcus (IPS; Piazza,
63 Izard, Pinel, Le Bihan, & Dehaene, 2004), or the superior parietal lobule (SPL; Harvey, Klein, Petridou,
64 & Dumoulin, 2013). The parietal cortex has been shown to contain topographic maps of numerosity
65 (Harvey et al., 2013) and since it represents different numerical formats (i.e., symbolic and non-symbolic;
66 Piazza, Pinel, Le Bihan, & Dehaene, 2007), it may be the locus where an abstract representation of
67 quantity is formed (Anobile, Arrighi, et al., 2016; Arrighi et al., 2014; but see Cavdaroglu & Knops, 2018
68 for evidence against a format-independent representation). Several recent studies, however, started to
69 report numerosity-related activity in early sensory cortices in both the visual (Castaldi, Piazza, Dehaene,
70 Vignaud, & Eger, 2019; Cavdaroglu & Knops, 2018; DeWind, Park, Woldorff, & Brannon, 2019;
71 Fornaciai & Park, 2018a; Harvey & Dumoulin, 2017; Roggeman, Santens, Fias, & Verguts, 2011; Van
72 Rinsveld et al., 2020) and auditory (Cavdaroglu, Katz, & Knops, 2015) modality. In the visual modality,
73 there is evidence that numerosity representations are formed throughout multiple processing stages
74 (Fornaciai & Park, 2018a; Park et al., 2016; Roggeman et al., 2011), as predicted by computational
75 models of numerosity perception (Dehaene & Changeux, 1993; Stoianov & Zorzi, 2012; Verguts & Fias,
76 2004).
77

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

86 al., 2016 for a review), although with weaker sensitivity to numerical information (Fornaciai & Park,
87 2017a).

88
89 Although these studies demonstrate the involvement of early visual activity in numerosity representation,
90 the role of such a processing stage is less clear. In a recent work (Fornaciai & Park, 2018a), we asked
91 whether early visual activity is sufficient to explain the representation of numerosity, or whether it merely
92 reflects an initial stage where a proper representation is not yet formed. To do so, we employed the
93 connectedness illusion – that is, a systematic bias whereby the numerosity of pairwise-connected dot
94 arrays is consistently underestimated. The connectedness illusion is thought to reflect the segmentation
95 processes needed to create the set of “perceptual units” at the basis of numerosity perception (Fornaciai,
96 Cicchini, & Burr, 2016; Franconeri, Bemis, & Alvarez, 2009; He, Zhang, Zhou, & Chen, 2009; He, Zhou,
97 Zhou, He, & Chen, 2015). For the purpose of our investigation, this illusion allowed us to test whether a
98 neural signal is based on the veridical numerosity likely reflecting the initial sensory representation of the
99 stimulus, or the perceived numerosity likely reflecting the final conceptual representation of the stimulus.
100 The results from that study (Fornaciai & Park, 2018a), utilizing EEG and functional magnetic resonance
101 imaging (fMRI), confirmed that an initial sensory representation is formed early on in visual processing
102 (100 ms) and in visual areas V2 and V3. However, activity reflecting connected items, and thus likely
103 reflecting the conceptual representation, arises only later in the visual stream (150 ms), specifically in
104 area V3 (Fornaciai & Park, 2018a). As the timing of the two processing stages is consistent with the
105 timing of feedforward and feedback visual activity (Boehler, Schoenfeld, Heinze, & Hopf, 2008;
106 Fahrenfort, Scholte, & Lamme, 2007), we had interpreted the later activity as reflecting the contribution
107 of re-entrant processing enabled by feedback signals from higher-order areas. This would play a role in
108 segmenting the items into perceptual units.

109
110 However, results from this previous study could not conclusively pinpoint feedback signals as the
111 underlying source of the later activity. An alternative explanation is that the delayed brain activity related
112 to connectedness reflects slower high-spatial frequency signals reaching the visual cortex in a
113 feedforward manner (Jones & Keck, 1978; Maunsell & Gibson, 1992; Mazer, Vinje, McDermott,
114 Schiller, & Gallant, 2002). According to this view, an initial sensory representation would be quickly
115 created as soon as fast low-spatial frequency (magnocellular) information reaches the cortex. At a later
116 time, such a representation would be refined by means of high spatial frequency information, conveying
117 information about the thin lines connecting the items and allowing a segmentation into perceptual units.

118

119 We attempt to disentangle these two hypotheses by exploiting the connectedness illusion, in combination
120 with a perceptual bias created by the recent history of stimulation (serial dependence; Fischer & Whitney,
121 2014), and visual masking. Serial dependence refers to a perceptual bias, whereby a visual stimulus
122 appears to be more similar to its previous stimulus. As several studies have shown that the perceived
123 numerosity of a stimulus can be strongly biased by this recent history of stimulation (Cicchini, Anobile,
124 & Burr, 2014; Fornaciai & Park, 2018b, 2018c, 2019a, 2019b, 2020a), manipulation of serial dependence
125 provides an ideal way to investigate the functional mechanisms of numerosity perception. Masking, or
126 more specifically *backward* masking (Enns & Di Lollo, 2000), refers to a procedure that makes a target
127 stimulus invisible by presenting another high-contrast “mask” stimulus shortly after it. Re-entrant
128 processing in early visual cortex has been shown to be suppressed (along with the awareness of the
129 masked stimulus), while early feedforward processing is spared (Lamme & Roelfsema, 2000).

130

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

143

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

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

158

159 **2. METHODS**

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

163

164 **2.1 Participants**

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

179

180 **2.2 Apparatus and stimuli**

181 Visual stimuli across the two experiments were generated using the Psychophysics Toolbox (Brainard,
182 1997; Kleiner et al., 2007; Pelli, 1997) for Matlab (version r2016b; The Mathworks, Inc.). Stimuli were
183 presented on a 1920×1080 pixel monitor screen (144 Hz), encompassing approximately 35×20 degrees of
184 visual angle from a viewing distance of about 80 cm.

185

186 Stimuli were visual arrays of black and white dots (50% and 50% in most of the cases; in case of odd
187 numerosities the color of the exceeding dot was randomly selected) presented on a gray background. The
188 parameters of the dot-array stimuli were chosen to range equally in three orthogonal dimensions,
189 corresponding to numerosity (N), size (Sz), and spacing (Sp). Such a stimulus construction scheme was
190 employed to ensure consistency with previous work from our group (e.g., Fornaciai & Park, 2018c,
191 2019a), and thus to ensure that the present results could be easily compared with previous findings.
192 However, since the primary goal of the study concerns numerosity, the different levels of non-numerical
193 dimensions were collapsed together during data analysis. For a more detailed description of the stimulus
194 construction procedure and a characterization of the effect of non-numerical dimensions, see DeWind,
195 Adams, Platt, & Brannon, 2015; Park et al., 2016. Specifically, the parameters of the stimuli were set as
196 follows. The area of each individual dot ranged from 113 pixel² (0.038 deg²), equal to a diameter of 0.11
197 deg (6 pixels), to 452 pixel² (0.15 deg²), equal to a diameter of 0.22 deg (12 pixel). The field area of the
198 stimuli (i.e., the circular area within which the dots were located) ranged from 70,686 pixel² (23.9 deg²),
199 encompassing 5.5 degrees of visual angle in diameter (300 pixels), to 282,743 pixel² (95.7 deg²),
200 encompassing 11 degrees in diameter (600 pixels). In all cases, the individual size of the dots was
201 homogeneous within the stimulus, and we set a minimum distance between any two dots equal to at least
202 the radius of the dots. Regarding numerosity, in the preliminary connectedness experiment the reference
203 stimulus always contained 18 dots, while the probe stimulus contained a variable number of dots from
204 trial to trial (8, 10, 13, 16, 20, 25, 32). In half of the trials, the dots in the reference stimulus were pairwise
205 connected with lines (width = 2 pixels). Dot positions were calculated offline computing a set of
206 coordinates compatible with pairwise connections in order to avoid crossing between lines or
207 superimposition between lines and dots. The same offline procedure was applied for both the reference
208 and probe stimuli in order to keep the low-level properties of the images (which are affected by the
209 constraining presence of lines) similar. In the serial dependence experiment, the stimuli included a task-
210 irrelevant inducer, including 18 dots, either isolated or connected, a reference including 16 isolated dots,
211 and a variable probe containing 8-32 isolated dots. In all cases, dot positions were calculated offline in
212 order to compute coordinates compatible with connecting lines, similarly to the connectedness
213 experiment. For each numerosity, a set of 1,000 arrays was created and stimuli were randomly drawn
214 from these sets during the experiment. Note that reference and probe numerosities were chosen to be in
215 line with our previous work (e.g., Fornaciai & Park, 2018c, 2019a), which allows a direct comparison
216 between the results across different studies when needed.

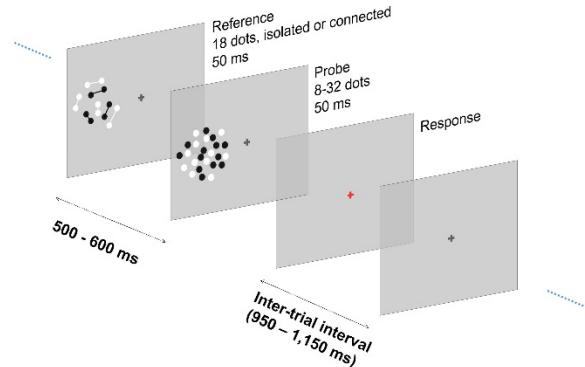
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218 In addition, in some of the conditions a mask stimulus was briefly presented after the inducer stimulus (65
219 ms after inducer onset). The timing of the mask stimulus was chosen according to a previous study using

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

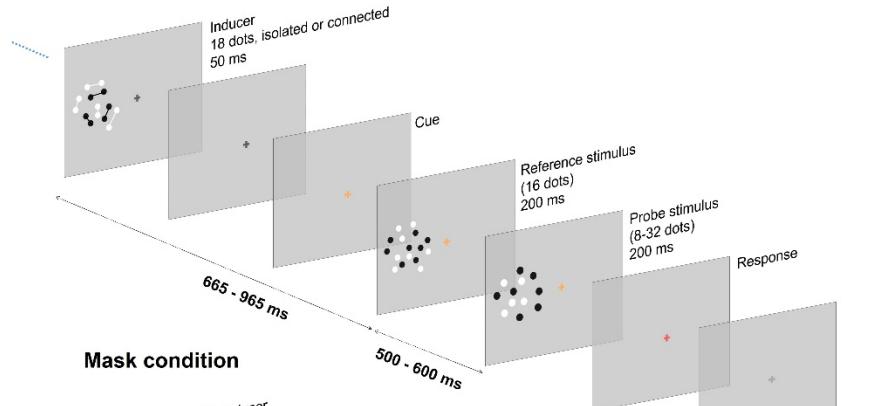
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A CONNECTEDNESS EXPERIMENT

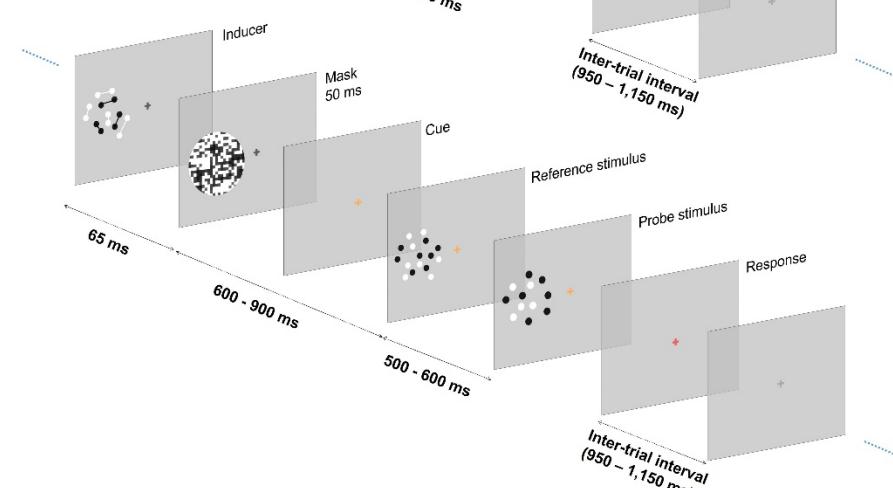


B SERIAL DEPENDENCE EXPERIMENT

No mask condition



Mask condition



224

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

227 of two dot arrays presented in the same position on the screen (either left or right of the fixation point,
228 randomized) for 50 ms. The reference array always contained 18 dots, and the probe array contained 8-
229 32 dots. Participants were asked to indicate, at the end of each trial, which stimulus contained more dots.
230 Crucially, in half of the trials the dots in the reference stimulus were pairwise connected by thin lines with
231 the same color of the dots (i.e., forming all black or all white dot pairs). The presentation order of
232 reference and probe was randomized from trial to trial. (B) In the serial dependence experiment, we
233 tested to what extent isolated and connected dot-arrays affect the subsequent stimuli via serial
234 dependence. To this aim, a series of three stimuli was presented on the screen: an inducer containing 18
235 isolated or connected dots, to induce serial dependence, followed by a reference (16 dots) and a probe (8-
236 32 dots), in this order. In some trials (panel B, bottom figure), a pattern mask was presented shortly after
237 the inducer stimulus (SOA = 65 ms) in order to make the stimulus invisible and suppress re-entrant
238 processing. In both cases, to avoid confusion between reference/probe stimuli and the inducer, a cue
239 (orange fixation cross) was presented before the onset of the reference and throughout the presentation of
240 the stimuli. Stimuli are not depicted in scale.

241

242

243 **2.3 General procedure**

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

261 presented on the screen for approximately 50 ms, and always in the same order. In the “mask” condition,
262 a pattern mask was presented for 50 ms shortly after the inducer (SOA = 65 ms) to induce masking. With
263 the exception of the mask, the sequence and the other stimuli were identical to the no-mask condition, and
264 both conditions were randomly intermixed within the same block. At the end of each trial, participants
265 were instructed to report whether the reference or the probe stimulus contained more dots as fast as they
266 could. Participants were told that although the inducer (and the mask) were irrelevant for the task, they
267 should attend to the entire sequence of the stimuli. In the serial dependence experiment, to avoid
268 confusion between reference/probe stimuli and the inducer, a cue (orange fixation cross) was presented
269 before the onset of the reference and throughout the presentation of the stimuli. Subjects were told that the
270 cue indicates when the task-relevant stimuli will be presented. The connectedness experiment comprised
271 4 blocks of 56 trials, while the serial dependence experiment comprised 7 blocks of 56 trials. Before
272 starting the actual experiment, participants completed a brief training session (8-15 trials) to familiarize
273 with the task and ensure that they understood the instructions. Participants were allowed to take breaks
274 during the experiment, and an entire session took about 45 minutes. Note that while in the connectedness
275 experiment, the order of stimuli was randomized from trial to trial to avoid time-order errors (i.e., under-
276 or overestimation of the first stimulus in the sequence), the sequence of stimuli was fixed in the serial
277 dependence experiment in order to always have the reference following the inducer. This is important as
278 serial dependence is stronger on the immediately successive stimulus (Fornaciai & Park, 2020b).
279 However, presenting both reference and probe stimuli in the same position as the inducer might cause
280 serial dependence to affect also the probe, possibly reducing the magnitude of the bias. We nevertheless
281 chose this stimulation procedure as it has proven to be effective in previous studies (Fornaciai & Park,
282 2018c, 2019a, 2019b, 2020a) and does not require to introduce attentional manipulations which are
283 instead necessary when the stimuli are presented in different positions (Fornaciai & Park, 2018c).
284 Additionally, we chose a peripheral stimulus presentation, as opposed to a central presentation, to
285 increase the effectiveness of the masking procedure in the mask condition (Stewart & Purcell, 1970). To
286 keep the stimulation procedure consistent across conditions, we used the same peripheral stimulus
287 presentation in all the experimental conditions tested in the study.

288

289

290 ***2.4 Behavioral data analysis***

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

295 Gaussian curve, according to the Maximum Likelihood method (Watson, 1979). The point of subjective
296 equality (PSE; the probe numerosity perceptually matching the reference numerosity), reflecting the
297 accuracy in the task (i.e., the reference perceived numerosity), was defined as the median of the best-
298 fitting cumulative Gaussian curve. The just-noticeable difference (JND), the difference in numerosity
299 between chance level (50%) responses and 75% “probe more numerous” responses, was taken as a
300 measure of precision in the task. As an additional measure of precision, we computed the Weber’s
301 fraction (JND/PSE), which was used to evaluate the participants’ performance in the task and to exclude
302 subjects showing insufficient performance. During the fitting procedure, we also applied a finger error (or
303 lapse) rate correction (2%; Wichmann & Hill, 2001), to account for random errors independent from the
304 stimulus magnitude and lapses of attention. Such a correction involves the adoption of slightly narrower
305 theoretical bounds of response probabilities during the psychometric fitting, which, with a 2% correction,
306 will be from 0.02 to 0.98, instead of from 0 to 1. Doing so, we take into account random errors and lapses
307 of attention which may prevent the cumulative Gaussian fit to converge to 0 and 1 at the extremes of the
308 probe numerosity range. Finally, paired t-tests on PSEs were used to test the difference between pairs of
309 conditions, in order to assess the connectedness and serial dependence effects. To exclude participants
310 showing poor performance, we used the WF and computed a cut-off based on the interquartile range.
311 Namely, we log-scaled WFs in each condition of the serial dependence experiment and computed the
312 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
313 was excluded. This criterion led to the exclusion of three participants. Additionally, participants were
314 excluded also based on reaction times. Outlying participants were excluded based on the identical
315 procedure used for WFs. This led to the exclusion of three more participants with very slow reaction
316 times, leaving a total of 45 subjects in the final group. Note that the exclusion criteria were evaluated and
317 applied only based on the data from the serial dependence experiment, as it represents the main
318 experiment for the aims of the present study.
319

320
321 Besides the analysis based on PSE, we also computed a normalized serial dependence effect index
322 according to the following formula:
323

324 $Serial\ dependence\ index = ((PSEiso - PSEconn) / PSEconn) \times 100;$
325

326 Where PSEiso indicates the PSE obtained with the isolated-dot inducer, and PSEconn indicates the PSE
327 obtained with the connected-dot inducer. We calculated such serial dependence index individually, and
328 compared the indexes obtained in the no mask and mask condition with a paired t-test. In this context, a

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

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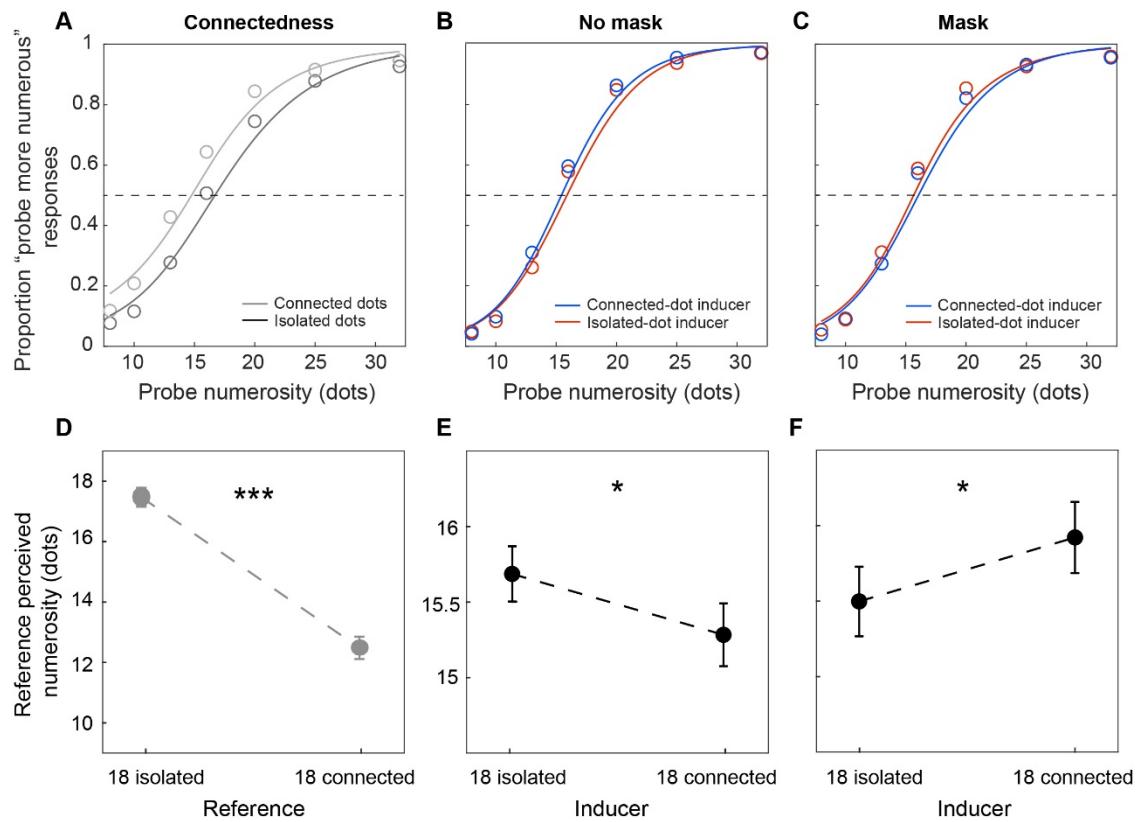
335 3. RESULTS

336

337 The study was divided into two different experiments (see Fig. 1). In the first experiment, we measured
338 the connectedness effect (Franconeri et al., 2009; He et al., 2009) using a numerosity discrimination task.
339 The purpose of this preliminary experiment was to assess how such pairwise-connected dot arrays are
340 perceived in order to use them as inducers in the following serial dependence experiment. The results
341 (Fig. 2A and 2D), in line with previous studies, confirmed a strong underestimation of perceived
342 numerosity of pairwise-connected arrays. Looking at the average psychometric curves, there is a robust
343 leftward shift of the curve relative to the connected-dot reference condition, indexing a strong
344 underestimation of connected dots. PSEs across the group in the connected-dot condition were indeed
345 significantly smaller than PSEs corresponding to the same amount of isolated dots (Fig. 2D; $t(44) =$
346 10.15, $p < 0.001$, Cohen's $d = 1.51$). Overall, the perceived numerosity of 18 connected-dot stimulus was
347 reduced by about (average normalized effect \pm SD) $26\% \pm 17\%$ compared to isolated dots (average PSE \pm
348 SD = 17.7 ± 1.9 and 12.9 ± 2.8 , respectively for the isolated and connected-dot condition). This reduction
349 appears roughly in line with previous studies employing a similar procedure, although the magnitude of
350 bias is stronger in the current study (~20% reduction in Fornaciai et al., 2016; ~19% reduction in the 16-
351 dots condition in Fornaciai & Park, 2018a). Although anecdotal, this is in line with the idea that the
352 strength of the connectedness illusion is inversely related to the duration of the stimuli (He et al., 2009),
353 which in the present study was much shorter (i.e., 50 ms in the current study versus 150 ms in previous
354 studies from our group).

355

356 Regarding the participants' precision in the connectedness experiment (Weber's fraction, WF), we
357 observed significantly higher WFs in the connected-dot condition, compared to the isolated-dot condition
358 (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
359 difference is however mostly due to the large difference in PSE, as JNDs appear very similar across the
360 two conditions, as also suggested by the similar slope of the average psychometric curves in Fig. 2A
361 (average JND \pm SD = 6.05 ± 3.18 and 5.87 ± 4.44 , respectively for the isolated and connected-dot
362 condition; paired t-test, $t(44) = 0.44$, $p = 0.66$).



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

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

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

386

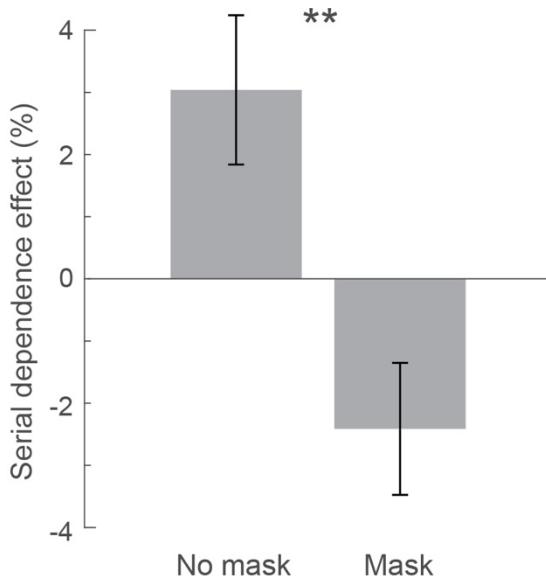
387 In the no-mask condition, we observed a clear attractive serial dependence effect, as shown by the
388 leftward shift in the average psychometric curve relative to the connected-dot inducer (Fig. 2B, blue
389 curve), and by the difference in average PSE (Fig. 2E). Namely, the 18-connected-dots inducer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

396

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

414

415



416

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

423

424

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

431

432 In addition, we assessed the pattern of participants' precision in the task (WF) by performing a two-way
 433 repeated measure ANOVA, with factor "inducer connectedness" (i.e., isolated vs. connected), and
 434 "experimental condition" (i.e., no mask vs mask). There was a main effect of experimental condition
 435 ($F(1,44) = 5.41$, $p = 0.025$) with no significant main effect of inducer connectedness ($F(1,44) = 0.087$, $p =$
 436 0.769) nor the interaction ($F(1,44) = 0.009$, $p = 0.93$). The WFs were on average higher in the mask
 437 condition, although the difference in precision was very small (0.19 ± 0.07 vs. 0.17 ± 0.07).

438

439

440 4. DISCUSSION

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

457

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

467

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

473 lower-numerosity inducer causes overestimation, while a higher-numerosity inducer causes
474 underestimation) – an effect akin to perceptual adaptation (Kohn, 2007). This effect has been taken as
475 evidence for the involvement of conscious high-level processing in establishing serial dependence. In
476 other words, when conscious processing is suppressed by masking, lower-level cortices would be
477 “released” from the attractive influence of serial dependence, allowing spontaneous and automatic
478 perceptual adaptation effects to emerge. Thus, when masking is applied in the context of the present
479 experiment to suppress feedback processing, the influence of the inducer is expected to become repulsive.
480

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

503

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

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

513

514 The observation that stimulus connectedness is processed despite the manipulation of backward masking
515 has important implications for our understanding of numerosity perception. First, the present findings
516 support the idea that numerosity starts to be represented very early in the visual processing stream (i.e., in
517 occipital areas such as V1, V2, and V3; e.g., (DeWind et al., 2019; Fornaciai et al., 2017; Park et al.,
518 2016; Van Rinsveld et al., 2020), and further show that the construction of such representation does not
519 require feedback from higher-order areas and conscious processing. Second, our results could inform the
520 development of computational models of numerosity processing. [On the one hand, our results are](#)
521 [consistent with models of numerosity processing such as the ones provided by Dehaene & Changeaux](#)
522 [\(1993\) and Verguts & Fias \(2004\).](#) In these models, numerosity is extracted and represented throughout a
523 series of computational steps of increasing abstraction. Namely, the first step is an object-location map
524 whereby items are represented by foci of activity in a topographically-organized map (consistent for
525 instance with early visual areas), which is followed by a summation stage summing up the overall activity
526 across the map, and finally a numerosity-selective stage whereby units are selectively activated by a
527 specific numerosity. Our results are also in line with the model proposed by Stoianov & Zorzi (2012).
528 This model, after an initial unsupervised learning phase, has been shown to be able to encode stimulus
529 numerosity via relatively simple computations occurring across two hierarchically organized layers.
530 However, models such as the one by Stoianov & Zorzi (2012), as well as other models (e.g., Morgan,
531 Raphael, Tibber, & Dakin, 2014), are essentially based on spatial-frequency filters computing numerosity
532 in terms of high-spatial frequency energy (Stoianov & Zorzi, 2017). Considering that the lines connecting
533 pairs of items most likely increase the high-spatial frequency content of an array, additional computations
534 are thus needed to correctly extract numerosities in more complex situations like in the presence of
535 connectedness. On the other hand, and in a similar vein, our results are not consistent with frameworks of
536 numerosity processing based on continuous magnitudes (e.g., Leibovich et al., 2017). Indeed, adding lines
537 to a dot array effectively increases the density of the stimulus and the area covered by the items in the
538 array, predicting an increase, rather than a decrease, in perceived numerosity. Differently from these
539 models, our results suggest that even at the earliest levels of numerosity processing (Fornaciai & Park,
540 2018a) and during the initial feedforward activity, the representation is already based on “perceptual

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

544

545 From a computational point of view, however, what are the specific neural operations that may explain
546 the present results? Considering the model proposed by Dehaene & Changeaux (1993), the effect of
547 connectedness would most likely occur at the stage of the low-level object location map. Namely, while
548 independent activation loci (as caused by isolated dots) would lead to a linear summation of their
549 respective activity, the presence of a connection between them might drive an additional “normalization”
550 process resulting in a sub-additive integration. In this scenario, the relation between different foci of
551 activity across the object location map would thus modulate the overall activity across the map itself,
552 leading to a biased read-out of numerosity at the subsequent stages. Although speculative, this
553 interpretation is consistent with a previous study from our group (Fornaciai & Park, 2017b), in which we
554 exploited motion to address the properties of low-level numerosity processing (see also Fornaciai et al.,
555 2018). Namely, the results from this previous study (Fornaciai & Park, 2017b) show that while the
556 numerosity of dots randomly changing position over time at a relatively fast frequency (2-8 Hz) is
557 markedly overestimated, such an effect is significantly reduced if the dots move instead along a coherent
558 linear motion trajectory. In other words, while the additional activity elicited by a dot displaced to a
559 different position seems to be integrated into the final estimate of numerosity, the streak of activity
560 elicited by a linearly moving dot is normalized to reduce this potential overestimation, like a sort of
561 “connectedness” over time (rather than in space). The present results thus additionally suggest that while
562 these normalization computations require more time compared to a less refined initial representation
563 (Fornaciai & Park, 2018b), they are likely performed locally at the level of the putative object location
564 map (i.e., for instance in early visual areas such as V1-V3), without the need for higher-level
565 computations fed back from downstream processing stages.

566

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

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

585

586 5. CONCLUSION

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

595

596

597 **Acknowledgements.** We thank Danielle Gruber for her assistance during data collection, and Rachael
598 McCollum for proofreading the manuscript.

599 **Funding.** This study was supported by the National Science Foundation CAREER Award BCS1654089 to
600 J. P.

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

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

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

607

608

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