

1 **Looking for more food or more people? Task context influences basic numerosity**
2 **perception**

3
4

5 Michele Fornaciai^{1,*}, Abigail Farrell¹, Joonkoo Park^{1,2}

6

7 ¹ Department of Psychological and Brain Sciences, University of Massachusetts, Amherst, MA,
8 USA.

9 ² Commonwealth Honors College, University of Massachusetts, Amherst, MA, USA.

10

11 * Corresponding author.

12 Michele Fornaciai

13 (mfornaciai@umass.edu)

14 University of Massachusetts

15 Department of Psychological and Brain Sciences

16 135 Hicks Way, Amherst, 01003

17 USA

18

19

20

21

22 **ABSTRACT**

23

24 Approximate numerical magnitude (or numerosity) is thought to represent one of the
25 fundamental sensory properties driving perceptual choices. Recent studies indicate that
26 numerosity judgment on a dot array is primarily driven by its numerical magnitude, largely
27 independent from its other non-numerical visual dimensions. Nevertheless, these findings do not
28 preclude the possibility that non-numerical cues such as size or spacing of a dot array influence
29 numerosity judgment. Here, we test the hypothesis that numerosity judgment is influenced by
30 non-numerical dimensions of a dot array depending on the context to which those non-numerical
31 cues could be useful. Participants were asked to choose the more numerous of two dot arrays in

32 two different contexts that differed only in one aspect. In one condition, the task was framed as
33 choosing a set with more fruits to consume. In the other condition, the task was framed as
34 choosing a group with more people to join. The results demonstrate that the influence of non-
35 numerical cues – and particularly of the dimension of size – was significantly smaller when
36 participants made quantitative choices about people than when they made choices about food,
37 illustrating that the representation of discrete magnitude is more pronounced in the former case.
38 These findings suggest that the information pooled to reach a decision about numerosity is
39 flexibly determined according to the context and the goals of such judgment.

40

41 **KEYWORDS**

42 Numerosity perception; numerical cognition; number sense; non-numerical cues.

43

44

45 **INTRODUCTION**

46

47 From an evolutionary point of view, the ability to rapidly estimate the approximate number of
48 items in a set (a.k.a. numerosity) has an adaptive value. For instance, approximate numerical
49 abilities would be advantageous for several activities spanning from foraging to social decisions
50 and to fight-or-flight decisions determining survival. That said, modern theories of numerical
51 cognition posit that our approximate numerical abilities have deep ontogenetic and phylogenetic
52 roots (e.g. Gelman & Cordes, 2001; Dehaene, 2011). This idea is empirically supported by
53 studies demonstrating that this *number sense* is widespread across animal species (Agrillo et al.,
54 2008; Pepperberg, 2006; Piantadosi & Cantlon, 2017; Rugani et al., 2015) and present from birth
55 in human newborns (Izard et al., 2009; Xu, 2003; Xu & Spelke, 2000).

56

57 One crucial question, however, is whether numerosity is processed by a dedicated perceptual
58 system independently from other non-numerical magnitude dimensions, or whether and to what
59 extent other continuous visual cues are used to derive the representation of numerosity.

60 According to the aforementioned lay evolutionary story, there is no particular reason for the
61 perceptual system to be specifically sensitive to one unique magnitude dimension (e.g., number,
62 which is a discrete magnitude, as opposed to total mass, which is a continuous magnitude).

63 Along this line of reasoning, some authors raise the hypothesis that numerosity is processed via
64 other visual attributes, like texture-density (e.g. Durgin, 2008) or some unknown combination of
65 other continuous magnitude dimensions (e.g. Gebuis et al., 2016; Leibovich et al., 2017).

66
67 While this issue between the numerical versus non-numerical nature of the brain's magnitude
68 system has been a polarizing topic in the past years, there is a growing amount of evidence
69 supporting the idea that numerosity is a fundamental perceptual attribute, not reducible to
70 combinations of other non-numerical cues (Anobile et al., 2016; Cicchini et al., 2016; Fornaciai
71 et al., 2016; DeWind et al., 2015; Park et al., 2016; Park, 2017; Fornaciai & Park, 2017;
72 Fornaciai et al., 2017). One critical contribution came from DeWind and colleagues (2015), who
73 developed an innovative method to quantify the relative contributions of various magnitude
74 dimensions to one's performance in a numerosity judgment task. Most prior work on numerosity
75 judgment attempted to de-correlate numerical magnitude from other non-numerical magnitudes
76 of a dot array, which is physically impossible. In contrast, DeWind and colleagues identified
77 three orthogonal dimensions (*numerosity*, *size*, and *spacing*) that serve as a basis for most, if not
78 all, magnitude dimensions of a dot array, and used a generalized linear model to quantify how
79 each of these basic dimensions contribute to one's numerical judgment. They found that
80 numerosity is the primary source of information driving one's performance in a numerosity
81 discrimination task, with very little influence of size and spacing. More crucially, subsequent
82 studies have now repeatedly demonstrated that brain responses (arising from early visual cortex)
83 to dot-array stimuli even in passive viewing paradigms are strongly modulated by the numerical
84 magnitude of the stimuli, with little contributions from other dimensions (Park et al., 2016; Park,
85 2017; Fornaciai & Park, 2017; Fornaciai et al., 2017). These results bolster the idea that discrete
86 numerosity information gets extracted very early in the brain largely independent from non-
87 numerical information of a visual scene.

88
89 These recent findings, however, do not preclude the possibility that non-numerical cues such as
90 size or spacing of a dot array influence numerosity judgment. Moreover, it is easy to imagine a
91 real-life situation where judgment based on non-numerical cues would be more advantageous.
92 Consider the lay evolutionary story again. In the case of foraging for food, aggregate size of the
93 items is perhaps more important for survival than merely the number of items, although in the

94 case of making social decisions like joining a group of people, the number of people may be
95 more important for survival than the aggregate body size of the people. Such reasoning leads to
96 the hypothesis that numerosity perception is supported by a flexible mechanism exploiting
97 different numerical and non-numerical dimensions according to the context and goals of the
98 judgment.

99

100 To investigate how numerical and non-numerical information contributes to numerosity
101 perception as a function of task context, we examined approximate numerical abilities in human
102 observers by simulating more realistic tasks in order to contextualize numerical choices. We
103 devised two conditions using nearly identical stimuli, but framed in different ways. In one
104 condition, participants were instructed to perform a numerosity discrimination task choosing a
105 set with more food items (i.e. more apples), while in the other condition participants had to
106 choose a group with more people. In both cases, the stimuli were systematically constructed to
107 span identical ranges of numerosity and non-numerical dimensions.

108

109

110 **METHODS**

111

112 *Participants*

113 Two hundred twenty-one subjects took part in the study (154 females, mean age = 20.2 ± 1.5
114 years). All participants had normal or corrected-to-normal vision, provided written informed
115 consent prior to participating in the study, and were compensated for their time with course
116 credit. Experimental procedures were approved by the University of Massachusetts Institutional
117 Review Board, and were in line with the declaration of Helsinki.

118

119 *Apparatus and stimuli*

120 The study was conducted in a large computer lab, with groups of 1 to 8 participants (most
121 typically around 3 or 4 participants) tested in parallel during each session, although each
122 participant completed the study individually. Stimuli were dot arrays constructed using the
123 Psychophysics Toolbox (Brainard, 1997; Pelli, 1997; Kleiner et al., 2007) for Matlab (R2013b,

124 The Mathworks, Inc.), and presented on a monitor screen encompassing 37 x 30 degrees of
125 visual angle from a distance of about 57 cm (resolution = 1280 x 1024, frame rate = 60 Hz).

126
127 Dot arrays comprised orange dots enclosed in a black outline, with two small lines (length scaled
128 as function of dot size, 10-14 pixel) added to characterize the dots according to the specific task
129 context (see Fig. 1B). Namely, in one case (“food” condition) the lines were arranged to
130 resemble the stem of an apple, while in the other condition (“people” condition) the two lines
131 were arranged to resemble two eyes. Such simple features used to differentiate the stimuli in the
132 two conditions were chosen to keep low level information (contrast, edges) as similar as
133 possible.

134
135 Stimuli were constructed, following the design previously used by DeWind et al. (2015), to span
136 similar ranges across three orthogonal dimensions: *numerosity*, *size*, and *spacing*. Numerosity
137 comprised 5 levels, evenly spaced in a \log_2 scale: 12, 14, 17, 20, 24 dots. The non-numerical
138 dimension of size is derived by combining the log-scaled values of the area of the individual
139 items and the overall area occupied by the items. The non-numerical dimension of spacing is
140 derived by combining the log-scaled values of the area of the invisible circular field in which the
141 items are drawn (field area) and the sparsity of the items (the inverse of item density). More
142 specifically, the dimension of size (Sz) refers to the dimension along which both the total area of
143 the items (TA) and their individual area (IA) change at the same rate, while numerosity (N) is
144 kept constant: $\log(Sz) = \log(TA) + \log(IA)$. The dimension of spacing (Sp) refers to the
145 dimension along which both field area of the stimuli (FA) and the sparsity ($Spar$) of the items
146 change concurrently, while numerosity is held constant: $\log(Sp) = \log(FA) + \log(Spar)$.

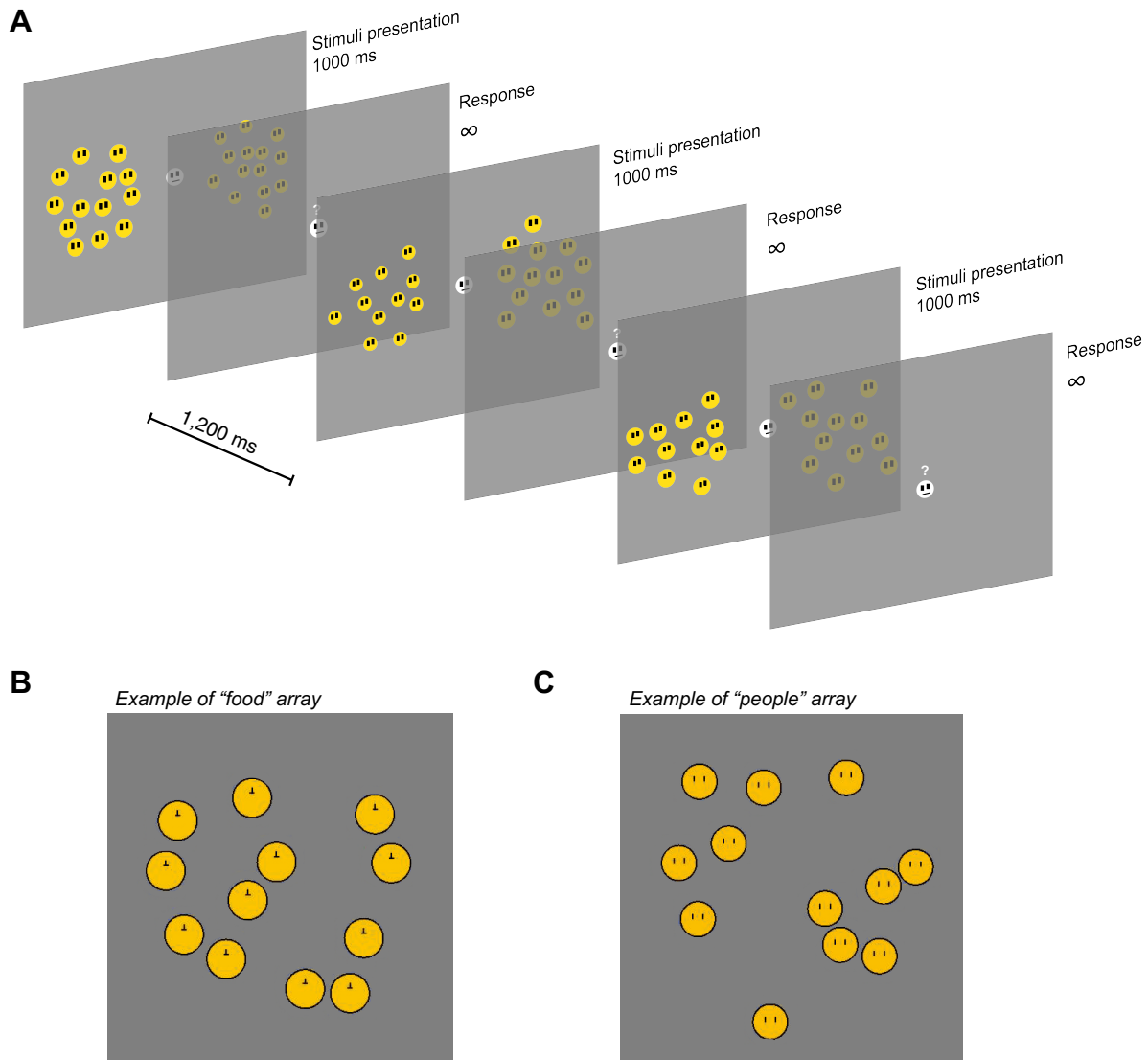
147
148 Furthermore, based on the dimensions of size and spacing, two additional attributes can be
149 defined: apparent closeness (AC) and coverage (Cov). Apparent closeness (AC) represents the
150 overall scaling of the dots independently from numerosity – i.e., an increase in apparent
151 closeness is equivalent to increasing both size and spacing at the same rate, and is defined as
152 $\log(AC) = \frac{1}{2}\log(Sz) + \frac{1}{2}\log(Sp)$. Coverage (Cov) represents the total area of the items (TA)
153 divided by the field area of the stimuli (FA), and is defined as $\log(Cov) = \frac{1}{2}\log(Sz) - \frac{1}{2}\log(Sp)$.

154

155 One important characteristic of this peculiar design is that all the non-numerical dimensions of
156 such stimuli (i.e., *IA*, *TA*, *FA*, *Spar*, *AC*, *Cov*) can be defined as a linear combination of the three
157 orthogonal dimensions of numerosity, size, and spacing. For more details about this design, see
158 also DeWind et al. (2015) and Park et al. (2016). Across the experiment, different numerosities
159 were tested an equal amount of times, while the levels of the other dimensions were randomly
160 chosen (independently for each of the stimuli) in each trial.

161
162 Regarding the specific values of the different attributes, the smallest individual area of the dots
163 (*IA*) was set to $\sim 1018 \text{ pixel}^2$, corresponding to a diameter of 1.04 deg (36 pixel), while the largest
164 individual area was $\sim 2290 \text{ pixel}^2$, corresponding to a diameter of 1.55 deg (54 pixel). On the
165 other hand, the smallest field area (*FA*) was set to 101,787 pixel^2 , encompassing a diameter of
166 10.4 deg (360 pixel), while the largest *FA* was 152,053 pixel^2 , corresponding to a diameter of
167 12.7 deg (440 pixel).

168



169

170 *FIGURE 1. Procedure and stimuli. (A) Example of the experimental procedure. Participants*
 171 *completed two conditions, where different contexts were provided. With the exception of the*
 172 *context and small details of the stimuli displayed (see panel B), the basic task was identical for*
 173 *both conditions. On each trial, two arrays, one on each side of the screen, were presented for*
 174 *1000 ms, and participants were asked to choose the more numerous stimulus. After providing a*
 175 *response, the next trial started after 1200 ms. Note that the stimuli are not depicted in scale (B)*
 176 *An exemplary array of “apples” in the “food” condition. (C) An exemplary array of “people” in*
 177 *the “people” condition. Note that the parameters (numerosity, size, and spacing) of the two*
 178 *sample stimuli were randomly drawn from the set of parameters used in the actual experiment,*

179 *and in this case the numerosity happened to be identical between the images in panels B and C*
180 *but not the size and spacing of the arrays.*

181

182 ***Procedure***

183 Each participant completed two different conditions, each comprising 5 blocks of 70 trials. At
184 the beginning of the experiment, a fictional character (“Jack”) was introduced and shown on the
185 screen as a smiley face throughout all the instruction screens and during the experiment.

186 Participants were told that the experiment will involve helping the character to solve some
187 problems. In both conditions, participants performed a two-alternative forced-choice numerosity
188 discrimination task, where the subject had to choose one of two stimuli presented on the right
189 and the left part of the screen (horizontal eccentricity = 8.25 deg). To avoid confusion about the
190 boundary of the two stimuli, the character was depicted at the center of the screen throughout the
191 task. Each pair of stimuli was presented for 1000 ms, and participants were free to look at the
192 stimuli during the presentation. Afterwards, a question mark appeared above the character, and
193 participants were instructed to choose one of the two stimuli according to the specific task, by
194 pressing the appropriate key on a standard keyboard.

195

196 In the “food” condition, the task was framed as a foraging expedition, and participants had to
197 help the character choose the set with more apples. Specifically, the instructions were as follows:
198 “Jack is very hungry and must go foraging for food in the forest. Jack finds two patches of apples
199 on either side of his path. However, Jack will only be able to collect the apples from one of the
200 two patches. In this condition, your task is to help Jack chose the patch with more apples.” In the
201 “people” condition, the task required participants to help the character choose the group with
202 more people. This task was framed as if the character had to escape a predator, and needed to
203 join the larger group to be safer. Specifically, the instructions were as follows: “Jack is being
204 pursued by a predator and must join another group of his kind for protection. Jack finds two
205 groups of which he could join either. However, the two groups are not traveling together and
206 Jack can only join one. In this condition, your task is to help Jack choose the group with more
207 members.” Besides these instructions, provided at the beginning of each task, the stimuli were
208 differentiated only by two lines, arranged to resemble two eyes or the stem of an apple (Fig. 1B).
209 Once a response was provided, the next trial started after 1200 ms.

210

211 Within each participant, the two conditions were performed in a random order. Each block took
212 approximately 5 minutes and participants were instructed to rest their eyes between blocks if
213 they wished. The entire procedure took approximately 50 minutes to complete (see Fig. 1A for a
214 depiction of the experimental procedure).

215

216 *Data analysis*

217 In order to assess participants' overall performance in the tasks, we first computed participants'
218 accuracy and precision in the numerosity discrimination task, separately for each of the two
219 conditions (food or people). To achieve these measures, subjects' responses as a function of the
220 difference in numerosity between the two stimuli presented in each trial were fitted with a
221 cumulative Gaussian function, following the maximum-likelihood method (Watson, 1979). The
222 point of subjective equality (PSE), representing the difference in numerosity between the two
223 stimuli yielding chance-level responses, was defined as the median of the best-fitting Gaussian
224 curve to all the data of a given subject in a given condition. The just noticeable difference (JND),
225 representing the minimum difference in the stimuli detectable by a subject, was defined as the
226 standard deviation of the Gaussian function. Participants with insufficient levels of performance
227 (i.e. $JND > 6$) were excluded from further analysis. This criterion led to the exclusion of 21
228 participants, leaving a total of 200 participants. Note that this relatively high number of excluded
229 participants may be due to little close supervision from the experimenters, as we ran the
230 experiment on relatively large groups of participants. Such lack of close supervision is likely to
231 have been occasionally resulted in poorly motivated participants not performing the task as
232 instructed (i.e. pressing keys at random).

233

234 In order to assess the contribution of numerical and non-numerical magnitude dimensions on
235 behavioral responses, the data were analyzed by modeling responses as a function of different
236 visual attributes of the stimuli presented on each trial (DeWind et al., 2015). This model was
237 indeed specifically designed to take into account the role of other non-numerical continuous
238 attributes, in order to include their influence on numerical judgments when modeling
239 participants' performances (eq. 1; adapted from DeWind et al., 2015). A generalized linear

240 model was fitted to the data, which included regressors for the dimensions of *numerosity*, *size*,
 241 and *spacing* (see *Apparatus and stimuli* for details about the construction of such dimensions).
 242

$$243 \quad p(\text{ChooseRight}) = (1 - \gamma) \left(\frac{1}{2} \left(1 + \operatorname{erf} \left(\frac{\log_2(r_{\text{num}}) - (-\beta_{\text{side}} - \beta_{\text{size}} \log_2(r_{\text{size}}) - \beta_{\text{spacing}} \log_2(r_{\text{spacing}}))}{\sqrt{2} \frac{1}{\beta_{\text{num}}}} \right) \right) - \frac{1}{2} \right) + \frac{1}{2}$$

244 (1)

245

246 More specifically, the parameters of the model included the log ratios of *numerosity*, *size*, and
 247 *spacing* (i.e. the ratio of the values of the different dimensions of the two stimuli presented on
 248 each trial, r_{num} , r_{size} , r_{spacing}). The model then fitted the behavioral responses (expressed as
 249 $p(\text{ChooseRight})$, representing the probability of choosing the stimulus on the right as more
 250 numerous) to estimate the regressors (β_{num} , β_{size} , β_{spacing}) of the log-ratio parameters. Additionally,
 251 the parameter γ represents the guessing rate – i.e. the proportion of trials where participants may
 252 have provided random responses due to a lapse of attention. However, as our task was relatively
 253 slowly-paced, we set the guessing term to zero. For more details about the model and a
 254 comparison with other models, see DeWind et al. (2015).

255

256 Finally, we tested whether each of the three beta estimates (i.e., the contribution of number, size,
 257 and spacing on judgment) differed in the two conditions. Importantly, because the order of the
 258 two conditions were given randomly across participants, we reasoned that the beta estimates
 259 could be modulated by that order (e.g., whether one performs the “food” condition first or the
 260 “people” condition first). As such, we used a repeated measure ANOVA with task condition
 261 (food vs. people) as a within-subject variable and condition order (food was given first vs. people
 262 was given first) as a between-subject covariate, allowing a full factorial design. Inspired by this
 263 model, we also analyzed individual participant’s PSE and JND as a function of both task
 264 condition and condition order, with which we begin the Results section.

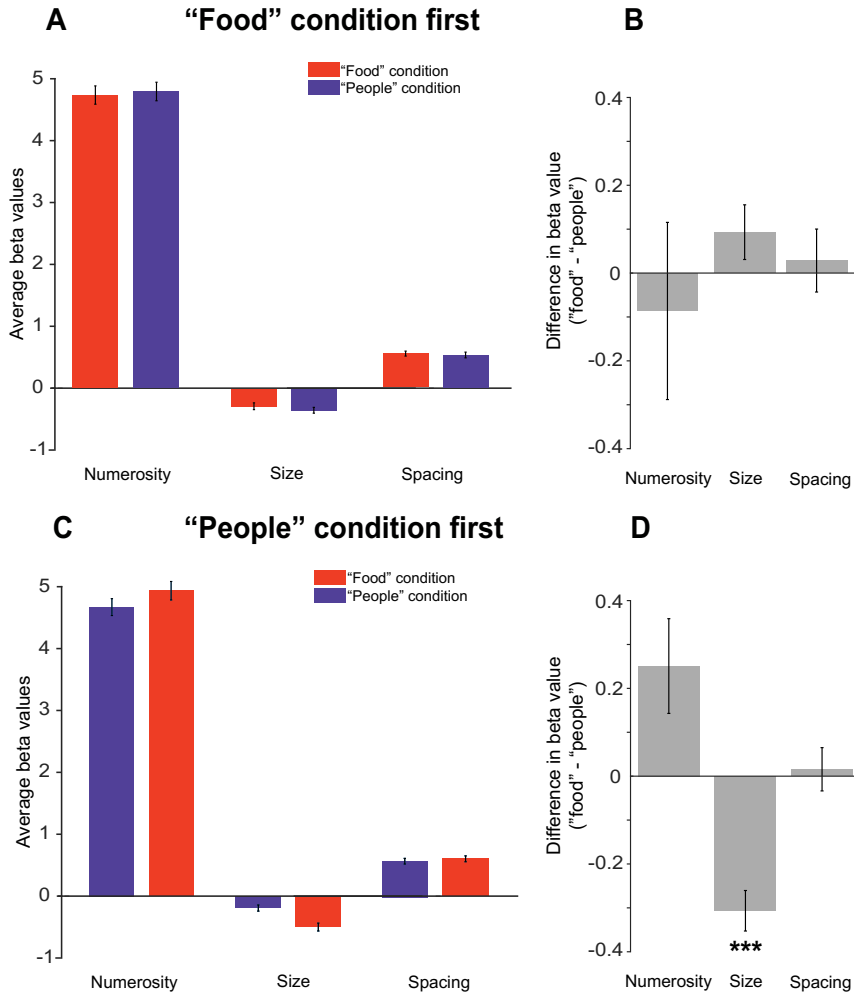
266 **RESULT**

267

268 We first assessed participants’ overall performance in terms of accuracy (PSE) and precision
 269 (JND). A repeated-measures ANOVA with task condition as a within-subject factor and

270 condition order as a between-subject factor was run separately on PSE and JND. There were no
271 significant effects of condition ($F(1,198) = 1.144, p = 0.286$), order ($F(1,198) = 0.56, p = 0.813$),
272 and the interaction ($F(1,198) = 1.144, p = 0.286$) on PSE. Similarly, there were no significant
273 effects of condition ($F(1,198) = 1.016, p = 0.315$), order ($F(1,198) = 1.466, p = 0.227$), and the
274 interaction ($F(1,198) = 1.016, p = 0.315$) on JND. These results indicate that there was a
275 negligible systematic difference in the general measures of performance across the two tasks.

276
277 The central goal of this study was to assess the extent to which numerical and non-numerical
278 visual attributes contribute to perceptual performance in different task contexts. To answer this
279 question, we quantified the contribution of numerosity, size, and spacing of a dot array to
280 participant's perceptual judgments following DeWind et al. (2015) and compared those estimates
281 of contribution between the two task contexts. Specifically, a repeated-measures ANOVA with
282 task condition as a within-subject factor and condition order as a between-subject factor was run
283 on each of the three beta estimates. Regarding the dimension of numerosity, we observed
284 negligible effect of condition ($F(1,198) = 1.145, p = 0.286$), negligible effect of order ($F(1,198) =$
285 $0.011, p = 0.917$), and only a weak effect of the interaction between condition and order
286 ($F(1,198) = 3.31, p = 0.070$). Similarly, the dimension of spacing did not show any effect of
287 condition ($F(1,198) = 0.238, p = 0.626$), order ($F(1,198) = 0.853, p = 0.357$), or interaction
288 ($F(1,198) < 0.01, p = 0.993$). More strikingly, however, the dimension of size revealed a
289 statistically significant effect of condition ($F(1,198) = 17.84, p < 0.001$) and interaction ($F(1,198)$
290 $= 34.88, p < 0.001$), although with no main effect of order ($F(1,198) = 0.011, p = 0.917$). The
291 strong effect of interaction warrants posthoc comparisons. As shown in Figure 2, the effect of
292 interaction was captured by a slight but nonsignificant difference in the beta estimates for size
293 between the "food" and the "people" condition in participants who performed the "food"
294 condition first (Fig. 2A-B; posthoc paired t-test, $t(101) = 1.27, p = 0.20$) and at the same time a
295 more negative beta estimate for size in the "food" condition in participants who performed the
296 "people" condition first (Fig. 2C-D; posthoc paired t-test, $t(97) = -6.71, p < 0.001$). One possible
297 explanation for this pattern is that participants exhibit a carry-over effect where their implicit
298 strategy in the second half of the experiment is influenced by the implicit strategy that they have
299 developed throughout the first half of the experiment, but that this carry-over effect is
300 asymmetric in the two conditions. We return to this point in the discussion.



302

303 *FIGURE 2. Comparison of the contributions of numerosity, size, spacing to the behavioral*
 304 *judgment across task conditions and order. (A) Beta estimates for the dimensions of numerosity,*
 305 *size, and spacing obtained with the generalized linear model, across the two conditions, in the*
 306 *cases where the “food” condition was performed first. (B) Differences in beta values between*
 307 *the two conditions, for each of the three orthogonal dimensions, for the “food” condition first*
 308 *case. (C) Beta estimates for numerosity, size, and spacing across the two conditions, in the cases*
 309 *where the “people” condition was performed first. (D) Differences in beta values between the*
 310 *two conditions when the “people” condition was performed first. Bars corresponding to different*
 311 *conditions in panels A and C are reported in the order in which they were performed. The*
 312 *difference in beta values reported in panels C and D represent beta values in the “food”*

313 *condition minus beta values in the “people” condition. Error bars represent SEM. *** p <*
314 *0.001.*

315
316 As a potential carry-over effect makes it difficult to interpret the influence of the task context in
317 the within-subject analysis, we assessed the between-subject effects of task context by
318 considering exclusively the first task performed by the participants. Doing so, we found larger
319 beta estimates (in the negative direction) in the food condition (-0.29 ± 0.05) than in the people
320 condition (-0.17 ± 0.05) ($t(198) = -1.74$, two-tailed $p = 0.083$; Cohen’s $d = 0.20$; see Fig. 2A and
321 2C), indicating a smaller bias from the dimension of size in those who looked for more people
322 compared to those who looked for more food.

323 324 **DISCUSSION**

325 Humans, as well as many other animal species, are endowed with an intuitive sense of number
326 that allows for a rapid and approximate estimation of numerical magnitude of a set of objects in a
327 visual scene. A growing amount of evidence suggests that such number sense could be
328 considered a basic perceptual ability, underpinned by a dedicated brain system (e.g. Burr & Ross,
329 2008; Park et al., 2016; Anobile et al., 2016; Nieder, 2016). Indeed, several recent studies have
330 demonstrated that using multi-dimensional stimuli modulated along numerical and non-
331 numerical dimensions, numerosity represents the most relevant information driving behavioral
332 responses in explicit numerical tasks (DeWind et al., 2015) and even driving brain responses in
333 passive-viewing paradigms (Park et al., 2016; Fornaciai & Park, 2017; Fornaciai et al., 2017).
334 However, most studies investigating approximate, non-symbolic numerical abilities are usually
335 performed in a laboratory setting (but see Piantadosi & Cantlon, 2017, for a work examining
336 quantitative abilities in wild baboons), employing generic stimuli and tasks with little or no
337 personal meaning. If our number sense has evolved as an adaptive strategy, a better
338 understanding of the mechanism underlying numerosity perception would be achieved by
339 considering a situation more relevant to a judgment in real life. We therefore aimed in this study
340 to test how context (e.g., foraging or joining social group) may influence numerosity judgment.
341
342 In the present study, we achieved this aim by employing a basic numerical task (two-alternative
343 forced-choice numerosity discrimination), but framed in two different ways. Participants were

344 asked to help a fictional character solve some specific problems. In one case, the character had to
345 find food, while in the other case the character had to choose a group of people to join. In both
346 cases, however, the key task instructions were identical, as participants were instructed to choose
347 the side with “more” items (either apples or people). This paradigm provides two advantages.
348 First, despite the fact that it is still a laboratory experiment, the different task contexts more
349 closely represent relevant tasks that have to be accomplished in the real environment. Second,
350 employing the exact same task instructions but only varying the context in which the task is
351 framed allows us to assess whether and to what extent the context itself affects numerosity
352 discrimination performance.

353

354 Our results show that this is indeed the case: the specific context systematically affects the extent
355 to which different magnitude dimensions are exploited to guide behavior, although an interaction
356 between condition and the order in which the conditions are performed suggests asymmetries
357 between the effect of different task contexts. More specifically, while on the one hand our results
358 show that numerosity is the primary source of information driving numerosity discrimination
359 judgments – in line with previous studies (e.g. DeWind et al., 2015) – the dimension of size
360 contributes differently between the two task contexts. Furthermore, such differences are
361 modulated by the task order. Namely, when participants perform the “food” condition first, there
362 is little difference between the average beta estimates for the dimension of size in the two
363 conditions. Conversely, when participants perform the “people” condition first, there is a sharp
364 difference between the two conditions: the contribution of size is much closer to zero in the
365 “people” condition, while it is much stronger in the “food” condition.

366

367 These different patterns of the effect of size could be explained by simultaneously considering
368 (1) an asymmetric effect of task context, with one condition (i.e., the “food” condition) providing
369 a stronger modulation compared to the other, and (2) a carry-over effect from the first condition
370 performed in a session to the second one. Evidence for the first idea above comes from the
371 between-subject analysis in which the “food” condition elicited a stronger bias in size than the
372 “people” condition. Such differences in the strength of modulation then could result in
373 asymmetric carry-over effect. That is, when those who performed the “people” condition first
374 were then given the “food” condition, their numerical judgment was drastically biased by the

375 size dimension. Conversely, when those who performed the “food” condition first were then
376 given the “people” condition, the bias of the size dimension may have been already strong in the
377 first part of the experiment and was carried over to the second part of the experiment. To
378 understand the asymmetric carry-over effect in the effect of size, it is first worth asking whether
379 it is the food condition that results in the implicit use of the size cue (in the more negative
380 direction) or whether it is the people condition that results in the implicit use of the size cue (in
381 the less negative direction). Previous studies employing the same modeling approach to basic
382 numerical judgments (DeWind et al., 2015; Starr et al., 2017) give the clue to this question.
383 Those previous studies demonstrated that the effect of size in numerosity judgment is very close
384 to zero, more similar to the current results of the people condition (when performed first). That
385 said, it is likely that the substantially more negative effect of size in the food condition is driven
386 by an implicit use of the size cue, and that the less negative (closer to zero) effect of size in the
387 people condition represents a more default, neutral use of the size cue. In addition to the effect of
388 size, the effects of spacing across the present and previous studies were very similar. The effect
389 of numerosity was much larger in the present result; however, that difference may easily be
390 explained by the differences in the difficulty of the task where the present study was much easier
391 with a substantially longer viewing time (i.e., 1000 ms vs. 250 ms in previous studies). This
392 asymmetric carry-over effect can then be explained by considering the use of a specific implicit
393 strategy in one context (i.e. food), as opposed to the use of a default, neutral, strategy in the other
394 case (i.e. people). if a non-numerical cue (i.e. size) was implicitly used to aid judgments in the
395 first condition (food), such an implicit strategy may remain in effect in the second condition. In
396 contrast, a decision free from such an implicit strategy at the beginning of the session (i.e. the
397 people task in the people first condition) could be altered with a different task that puts demand
398 on developing such a strategy. In other words, an implicit strategy once employed, and only
399 when it is employed, may continue to be exploited throughout the session.

400

401 These results overall indicate that the specific contributions drawn from non-numerical
402 dimensions depend on the specific task at hand. Interestingly, judging the number of members in
403 a group as in the “people” condition shows relatively smaller bias from non-numerical
404 dimensions (specifically by the size dimension), suggesting that such kind of perceptual choice is
405 more heavily driven by numerical as opposed to non-numerical information. Conversely, when

406 judging the amount of food, perceptual choices are more easily biased by non-numerical
407 information, and particularly by the size of the individual items. In a somehow counterintuitive
408 way, the bias provided by the dimension of size in the “food” condition is in the negative
409 direction, suggesting that smaller size is more often selected when choosing the patch with more
410 food items. Nevertheless, this pattern is plausible considering the nature of the task. The task
411 required participants to choose the patch with more apples to collect. In this context, a negative
412 weight for the size dimension might reflect the fact that it is easier to collect a more numerous set
413 of smaller items than larger items. More specifically, one way to interpret this pattern of results
414 is by considering the possibility of the fictional character to grasp and collect the food items.
415 Previous work in the literature concerning grasping movement reports that attempting to grasp a
416 large object (reaching the limits of graspable size), poses severe limitations to the grasping
417 movement (Bootsma et al., 1994). If participants project such kind of limitations of grasp
418 movements to the fictitious character involved in the task, this may explain the negative
419 contribution of size to numerical judgments. Indeed, the fictitious character was similar in size to
420 the dots, which makes sense in the people condition but is less realistic in the food condition.
421 Thus, the preference for smaller items might be driven by the need of avoiding food items
422 potentially very difficult to grasp or carry (i.e. items almost as big as the character itself), due to
423 the physical limitations of grasp movements. According to this interpretation, participants would
424 thus be more prone to choose items that appear to be more likely graspable by the character.
425 Interestingly, if this is correct, it may be possible to reverse the effect of size by modulating
426 relative size of the character and the food items – an interesting possibility that should be
427 addressed by future studies.

428

429 Alternatively, a second interpretation could be advanced in light of previous results showing a
430 peculiar negative relation between object size and perceived numerosity – i.e. whereby smaller
431 items tend to be slightly overestimated. For instance, in an early study by Ginsburg & Nicholls
432 (1988) where item size was modulated along with numerosity, participants systematically tended
433 to overestimate smaller items and underestimate larger items. A relative overestimation of
434 smaller-sized items has more recently been reported by other studies (Tokita & Ishiguchi, 2010,
435 2013) making it possible that this peculiar effect may represent a baseline feature of numerosity
436 perception. Although this negative relation between size and perceived numerosity seems in

437 contrast with reports by DeWind et al. (2015) and Starr et al. (2017), it should be noted that
438 unlike DeWind et al. (2015) and Starr et al. (2017) studies that found a negative relation between
439 size and perceived numerosity utilized a much longer presentation duration (Ginsburg &
440 Nicholls, 1988; Tokita & Ishiguchi, 2013) allowing a much more deliberate choice, as in our
441 current design. If that negative relation between object size and perceived numerosity is a
442 peculiar feature of numerosity perception, an implicit strategy in the use of the size cue could
443 have been employed in the people condition rather than in the food condition. In this scenario,
444 the effect of size in the food condition would represent a baseline tendency to overestimate sets
445 with smaller items, while the lack of effect of size in the people condition would represent a
446 suppression of such bias to achieve a better estimate of the number of individuals in a group. In
447 reality, of course, the inconsistencies between different studies makes it difficult to strongly
448 support one interpretation over the other, and it is plausible that the results of our study reflect a
449 combination of two implicit strategies: a more pronounced negative effect of size for food, and a
450 suppression of the effect of size for people. While the main goal of our work was to demonstrate
451 that different task contexts give rise to different behavioral patterns in a simple numerosity
452 perception task, clarifying which context provides the stronger contribution and how different
453 strategies are carried over to different contexts represents an interesting open question for future
454 studies.

455
456 Besides the general effect of the two task framings, one additional interesting question is whether
457 the contributions of non-numerical cues could be further modulated by other internal variables.
458 For instance, when estimating amounts of food, it naturally follows that estimation may be
459 modulated by a participant's hunger level. How internal state in combination with task context
460 may influence a seemingly simple perceptual task is an interesting question that should be
461 addressed in future studies.

462
463 Another important question following from these findings is: what are the neural bases of such
464 flexible use of numerical and non-numerical information for perceptual decision making? Does it
465 represent flexibility of the sensory mechanisms extracting magnitude information from a visual
466 scene, possibly enabled by top-down influences determining which information to be extracted
467 in early visual areas? Or, does it represent flexibility at the decision stage, where different

468 information might be exploited to guide behavior? Previous studies focusing on the neural
469 correlates of numerosity perception highlight a complex stream of processing stages, showing
470 both a cascade (i.e. a series of processing stages emerging over time; Park et al., 2016; Fornaciai
471 et al., 2017) and feedback dynamics (i.e. as suggested by potential interactions across multiple
472 perceptual systems in numerosity processing; Fornaciai & Park, 2017; Fornaciai & Park, under
473 review). More specifically, previous work has demonstrated evidence for numerosity processing
474 in subcortex (Collins et al., 2017), as early as V2/V3 in cortex (Fornaciai et al., 2017; Fornaciai
475 & Park, under review), and higher-level regions such as the intraparietal sulcus (Piazza et al.,
476 2004; Harvey et al., 2016) and in prefrontal areas (Viswanathan & Nieder, 2013; Nieder, 2016).
477

478 The first possibility is that the most relevant information for the task at hand is directly encoded
479 starting from the earliest level of numerosity processing (e.g. V2/V3 as found in Fornaciai et al.,
480 2017). Indeed, according to Lennie (1998), the primary visual cortex (V1) might contain a multi-
481 dimensional representation of the visual scene, encoding several visual attributes that are relayed
482 to specific areas and used to serve different aspects of visual sensory processing. In this view,
483 while V1 might contain a representation of all the magnitude dimensions of a dot array stimulus,
484 later areas such as V3 might exploit the most relevant information according to the specific task.
485 Then, how does the information get selected at such an early stage? One plausible explanation is
486 that feedback from higher-level areas (either on a trial-by-trial basis, or developed over the
487 course of the experiment) determines what kind of information is preferentially processed
488 starting from the earliest level of numerosity processing. Indeed, there is evidence showing that
489 the information represented in early visual areas could be determined by higher-level influences
490 (e.g. Lee et al., 2002; Gilbert & Li, 2013). Interestingly, according to a recent theoretical
491 framework proposed by Roelfsema & de Lange (2016), early visual cortex might represent a
492 cognitive blackboard used by high-level regions for read and write operations. The flexibility
493 provided by such a mechanism indeed fits well with the idea that information is selected on the
494 basis of current goals. According to the contextual information provided by the task context,
495 decision-related high-level areas (i.e. possibly the dorsolateral prefrontal cortex, related to
496 decision control; Rahnev et al., 2011; Rahnev 2017) might directly determine which information
497 is selectively used across all the processing stream.

498

499 The second possibility is that different sources of information are exploited at the decision level
500 in order to guide behavior according to the current goals, but without any change in the
501 information encoded at earlier levels. However, in this context, such explanation appears less
502 likely, as it would require different sensory information to be preserved throughout multiple
503 processing stages. Indeed, according to Lennie (1998), only very early visual areas such as V1
504 contains an exhaustive multidimensional representation of the visual scene, while downstream in
505 the processing hierarchy only the results of computations carried out at each specific level is
506 passed on to the next level. Also, neurophysiological evidence demonstrates that even at the
507 earliest level of numerosity processing (feed-forward processing in early visual cortex, at or
508 before 100 ms after stimulus onset; Fornaciai et al., 2017), brain responses are already driven by
509 specific contributions from different magnitude dimensions (and mostly by numerosity). Even if
510 these studies exploited very different tasks, this evidence seems to support the idea that only the
511 relevant information is passed on throughout the visual processing stream. According to this
512 reasoning, the most likely explanation is that the information extracted and processed starting
513 from early visual stages is determined by higher-level influences modulating sensory activity
514 according to the specific context.

515

516 By considering this latter interpretation, these results provide important implications for the idea
517 of a visual sense of number. Indeed, while current frameworks of numerosity perception regard it
518 as a very basic perceptual function (i.e. Anobile et al., 2016; Cicchini et al., 2016), our results
519 show that the information used to process and represent approximate numerosities is not
520 hardwired in sensory processing, but flexibly determined according to the goals of the task at
521 hand. This finding thus expands previous reports concerning the contributions of numerical and
522 non-numerical dimensions to numerical judgments in more general experimental contexts (i.e.
523 estimating number of dots; DeWind et al., 2015). Moreover, by considering the neural correlates
524 of numerosity processing pinpointed in early visual areas (i.e. V2 and V3; Fornaciai et al., 2017),
525 these results also add novel evidence to the literature documenting the remarkable plasticity of
526 early visual sensory processing. In particular, these results appear consistent with earlier reports
527 showing modulation of neuronal responses in V1 as a function of the task at hand (e.g. Li et al.,
528 2004): even if the same stimuli are presented, the same neurons in primary visual cortex show
529 different response profiles and tuning curves according to the specific task performed. Following

530 Li et al.'s (2004) interpretation, the present results then support the idea that early visual areas
531 are adaptable processing units analyzing relevant stimulus information according to the task
532 context.

533
534 Overall, our results show that numerosity perception is not a fixed mechanism. Rather, it has a
535 remarkable flexibility even with simulated task contexts provided in a laboratory environment.
536 Namely, the relevant information driving a quantitative decision is flexibly determined as a
537 function of contextual information, likely by means of feedback from higher-level areas to earlier
538 sensory cortices. This flexibility of numerical cognition well reflects the adaptive nature of
539 approximate numerical abilities.

540

541 ACKNOWLEDGEMENTS

542 We thank Brynn Boutin for assistance in data collection, and Dr. Matthew Davidson for providing
543 lab space and materials for testing. This study was supported by the National Science Foundation
544 CAREER Award BCS1654089 to J. P.

545

546 Declarations of interest: none.

547

548 REFERENCES

549

550 Agrillo, C., Dadda, M., Serena, G., & Bisazza, A. (2008). Do fish count? Spontaneous
551 discrimination of quantity in female mosquitofish. *Animal Cognition*, *11*(3), 495–503.
552 <https://doi.org/10.1007/s10071-008-0140-9>

553 Anobile, G., Cicchini, G. M., & Burr, D. C. (2016). Number As a Primary Perceptual Attribute:
554 A Review. *Perception*, *45*(1–2), 5–31. <https://doi.org/10.1177/0301006615602599>

555 Bootsma, R. J., Marteniuk, R. G., MacKenzie, C. L., & Zaal, F. T. J. M. (1994). The speed-
556 accuracy trade-off in manual prehension: effects of movement amplitude, object size and
557 object width on kinematic characteristics. *Experimental Brain Research*, *98*(3), 535–541.
558 <https://doi.org/10.1007/BF00233990>

559 Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–436.
560 <https://doi.org/10.1163/156856897X00357>

- 561 Burr, D., & Ross, J. (2008). A Visual Sense of Number. *Current Biology*, *18*(6), 425–428.
562 <https://doi.org/10.1016/j.cub.2008.02.052>
- 563 Cicchini, G. M., Anobile, G., & Burr, D. C. (2016). Spontaneous perception of numerosity in
564 humans. *Nature Communications*, *7*, 12536. <https://doi.org/10.1038/ncomms12536>
- 565 Dehaene, S. (2011). *The number sense: How the mind creates mathematics*. New York: Oxford
566 University Press.
- 567 DeWind, N. K., Adams, G. K., Platt, M. L., & Brannon, E. M. (2015). Modeling the approximate
568 number system to quantify the contribution of visual stimulus features. *Cognition*, *142*,
569 247–65. <https://doi.org/10.1016/j.cognition.2015.05.016>
- 570 Durgin, F. H. (2008). Texture density adaptation and visual number revisited. *Current Biology*,
571 *18*(18), R855–R856. <https://doi.org/10.1016/j.cub.2008.07.053>
- 572 Fornaciai, M., Cicchini, G. M., & Burr, D. C. (2016). Adaptation to number operates on
573 perceived rather than physical numerosity. *Cognition*, *151*, 63–67.
574 <https://doi.org/10.1016/j.cognition.2016.03.006>
- 575 Fornaciai, M., Brannon, E. M., Woldorff, M. G., & Park, J. (2017). Numerosity processing in
576 early visual cortex. *NeuroImage*, *157*, 429–438.
577 <https://doi.org/10.1016/j.neuroimage.2017.05.069>
- 578 Fornaciai, M., & Park, J. (Under review). Dynamics of numerosity representation in early visual
579 cortex.
- 580 Fornaciai, M., & Park, J. (2017). Distinct Neural Signatures for Very Small and Very Large
581 Numerosities. *Frontiers in Human Neuroscience*, *11*(January), 1–14.
582 <https://doi.org/10.3389/fnhum.2017.00021>
- 583 Gebuis, T., Cohen Kadosh, R., & Gevers, W. (2016). Sensory-integration system rather than
584 approximate number system underlies numerosity processing: A critical review. *Acta*
585 *Psychologica*, *171*, 17–35. <https://doi.org/10.1016/j.actpsy.2016.09.003>
- 586 Gelman, R., & Cordes, S. (2001). Counting in Animals and Humans. *Language, Brain, and*
587 *Cognitive Development: Essays in Honor of Jacques Mehler.*, *XXXIII*(2), 279–301.
588 <https://doi.org/10.1007/s13398-014-0173-7.2>
- 589 Gilbert, C. D., & Li, W. (2013). Top-down influences on visual processing. *Nature Reviews*
590 *Neuroscience*. <https://doi.org/10.1038/nrn3476>
- 591 Ginsburg, N., & Nicholls, A. (1988). Perceived numerosity as a function of item size. *Perceptual*
592 *and Motor Skills*, *67*(2), 656–658. <https://doi.org/10.2466/pms.1988.67.2.656>
- 593

- 594 Harvey, B. M., Klein, B. P., Petridou, N., & Dumoulin, S. O. (2013). Topographic representation
595 of numerosity in the human parietal cortex. *Science*, *341*(September), 1123–1126.
596 <https://doi.org/10.1126/science.1239052>
- 597 Izard, V., Sann, C., Spelke, E. S., & Streri, A. (2009). Newborn infants perceive abstract
598 numbers. *Proceedings of the National Academy of Sciences of the United States of America*,
599 *106*(25), 10382–5. <https://doi.org/10.1073/pnas.0812142106>
- 600 Kleiner, M., Brainard, D., Pelli, D., Ingling, A., Murray, R., & Broussard, C. (2007). What’s new
601 in Psychtoolbox-3? *Perception ECVP 2007 Abstract Supplement*, 14.
602 <https://doi.org/10.1068/v070821>
- 603 Lee, T. S., Yang, C. F., Romero, R. D., & Mumford, D. (2002). Neural activity in early visual
604 cortex reflects behavioral experience and higher-order perceptual saliency. *Nature*
605 *Neuroscience*, *5*(6), 589–597. <https://doi.org/10.1038/nn860>
- 606 Leibovich, T., Katzin, N., Harel, M., & Henik, A. (2017). From “sense of number” to “sense of
607 magnitude”: The role of continuous magnitudes in numerical cognition. *Behavioral and*
608 *Brain Sciences*, *40*, e164. <https://doi.org/10.1017/S0140525X16000960>
- 609 Lennie, P. (1998). Single units and visual cortical organization. *Perception*, *27*(8), 889–935.
610 <https://doi.org/10.1068/p270889>
- 611 Nieder, A. (2016). The neuronal code for number. *Nature Reviews. Neuroscience*, *17*(6), 366–82.
612 <https://doi.org/10.1038/nrn.2016.40>
- 613 Park, J. (2017). A neural basis for the visual sense of number and its development: A steady-state
614 visual evoked potential study in children and adults. *Developmental Cognitive*
615 *Neuroscience*. <https://doi.org/10.1016/j.dcn.2017.02.011>
- 616 Park, J., Dewind, N. K., Woldorff, M. G., & Brannon, E. M. (2016). Rapid and Direct Encoding
617 of Numerosity in the Visual Stream. *Cerebral Cortex*, *26*(2), 748–763.
618 <https://doi.org/10.1093/cercor/bhv017>
- 619 Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: transforming numbers
620 into movies. *Spatial Vision*, *10*(4), 437–442. <https://doi.org/10.1163/156856897X00366>
- 621 Pepperberg, I. M. (2006). Cognitive and communicative abilities of Grey parrots. *Applied*
622 *Animal Behaviour Science*, *100*(1–2), 77–86.
623 <https://doi.org/10.1016/j.applanim.2006.04.005>
- 624 Piantadosi, S. T., & Cantlon, J. F. (2017). True Numerical Cognition in the Wild. *Psychological*
625 *Science*, *28*(4), 462–469. <https://doi.org/10.1177/0956797616686862>

- 626 Piazza, M., Izard, V., Pinel, P., Le Bihan, D., & Dehaene, S. (2004). Tuning curves for
627 approximate numerosity in the human intraparietal sulcus. *Neuron*, 44(3), 547–555.
628 <https://doi.org/10.1016/j.neuron.2004.10.014>
- 629 Rahnev, D. (2017). Top-Down Control of Perceptual Decision Making by the Prefrontal Cortex.
630 *Current Directions in Psychological Science*, 96372141770980.
631 <https://doi.org/10.1177/0963721417709807>
- 632 Rahnev, D., Maniscalco, B., Graves, T., Huang, E., De Lange, F. P., & Lau, H. (2011). Attention
633 induces conservative subjective biases in visual perception. *Nature Neuroscience*, 14(12),
634 1513–1515. <https://doi.org/10.1038/nn.2948>
- 635 Roelfsema, P. R., & de Lange, F. P. (2016). Early Visual Cortex as a Multiscale Cognitive
636 Blackboard. *Annual Review of Vision Science*, 2(1), 131–151.
637 <https://doi.org/10.1146/annurev-vision-111815-114443>
- 638 Rugani, R., Vallortigara, G., Priftis, K., & Regolin, L. (2015). Number-space mapping in the
639 newborn chick resembles humans’ mental number line. *Science*, 347(6221), 534–536.
640 <https://doi.org/10.1126/science.aaa1379>
- 641 Starr, A., DeWind, N. K., & Brannon, E. M. (2017). The contributions of numerical acuity and
642 non-numerical stimulus features to the development of the number sense and symbolic math
643 achievement. *Cognition*, 168, 222–233. <https://doi.org/10.1016/j.cognition.2017.07.004>
- 644 Tokita, M., & Ishiguchi, A. (2010). How might the discrepancy in the effects of perceptual
645 variables on numerosity judgment be reconciled? *Attention, Perception, and Psychophysics*,
646 72(7), 1839–1853. <https://doi.org/10.3758/APP.72.7.1839>
- 647 Tokita, M., & Ishiguchi, A. (2013). Effects of perceptual variables on numerosity comparison in
648 5-6-year-olds and adults. *Frontiers in Psychology*, 4(JUL).
649 <https://doi.org/10.3389/fpsyg.2013.00431>
- 650 Viswanathan, P., & Nieder, A. (2013). Neuronal correlates of a visual “sense of number” in
651 primate parietal and prefrontal cortices. *Proceedings of the National Academy of Sciences of
652 the United States of America*, 110(27), 11187–92. <https://doi.org/10.1073/pnas.1308141110>
- 653 Watson, A. B. (1979). Probability summation over time. *Vision Research*, 19(5), 515–522.
654 [https://doi.org/10.1016/0042-6989\(79\)90136-6](https://doi.org/10.1016/0042-6989(79)90136-6)
- 655 Xu, F. (2003). Numerosity discrimination in infants: Evidence for two systems of
656 representations. *Cognition*, 89(1), B15–B25. [https://doi.org/10.1016/S0010-0277\(03\)00050-](https://doi.org/10.1016/S0010-0277(03)00050-7)
657 7
- 658 Xu, F., & Spelke, E. S. (2000). Large number discrimination in 6-month-old infants. *Cognition*,
659 74(1), B1–B11. [https://doi.org/10.1016/S0010-0277\(99\)00066-9](https://doi.org/10.1016/S0010-0277(99)00066-9)