Three-systems for visual numerosity: A single case study

G. Anobile, F. Tomaiuolo, S. Campana, G.M. Cicchini

PII: S0028-3932(19)30301-X

DOI: https://doi.org/10.1016/j.neuropsychologia.2019.107259

Reference: NSY 107259

To appear in: Neuropsychologia

Received Date: 5 July 2019

Revised Date: 18 September 2019

Accepted Date: 8 November 2019

Please cite this article as: Anobile, G., Tomaiuolo, F., Campana, S., Cicchini, G.M., Three-systems for visual numerosity: A single case study, *Neuropsychologia* (2019), doi: https://doi.org/10.1016/j.neuropsychologia.2019.107259.

This is a PDF file of an article that has undergone enhancements after acceptance, such as the addition of a cover page and metadata, and formatting for readability, but it is not yet the definitive version of record. This version will undergo additional copyediting, typesetting and review before it is published in its final form, but we are providing this version to give early visibility of the article. Please note that, during the production process, errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

© 2019 Published by Elsevier Ltd.



## **CRediT** author statement

**Giovanni Anobile:** Conceptualization, Methodology, Data curation, Software, Writing-Original draft preparation, Visualization, Investigation, Formal Analysis. **Francesco Tomaiuolo:** Investigation, Supervision, Conceptualization, Writing-Original draft preparation, Data curation, Formal Analysis. **Serena Campana**: Supervision, Methodology, Investigation, Data curation. **Guido Marco Cicchini:** Conceptualization, Methodology, Data curation, Software, Writing-Original draft preparation, Writing-Reviewing and Editing, Supervision, Visualization, Formal Analysis, Investigation, Validation.

Sonution

### Three-systems for visual numerosity: a single case study. 1 2 Anobile G.<sup>1</sup>, Tomaiuolo F.<sup>2</sup>, Campana S.<sup>3</sup> & Cicchini G. M.\*<sup>4</sup> 3 4 5 1. Department of Developmental Neuroscience, IRCCS Stella Maris Foundation, Pisa, 6 7 Italv 8 2. Department of Clinical and Experimental Medicine, University of Messina, Messina, 9 Italy 10 3. Unità Gravi Cerebrolesioni Acquisite, Auxilium Vitae Volterra, Pisa, Italy 4. Institute of Neuroscience, National Research Council, Pisa, Italy. 11 12 subitizing; density perception; numerosity perception; approximate number 13 Keywords: system; numerical cognition; simultanagnosia. 14 15 16 \* Corresponding author Dr. Cicchini G. M. 17 18 Email: cicchini@in.cnr.it Address: Institute of Neuroscience - CNR 19 Via Moruzzi, 1 – 56124 – Pisa (ITALY) 20 21 22

- 23 Abstract
- 24

Humans possess the remarkable capacity to assess the numerosity of a set of items over a 25 26 wide range of conditions, from a handful of items to hundreds of them. Recent evidence is starting to show that judgments over such a large range is possible because of the presence of 27 three mechanisms, each tailored to specific stimulation conditions. Previous evidence in 28 29 favour of this theory comes from the fact that discrimination thresholds and estimation reaction times are not constants across numerosity levels. Likewise, attention is capable of 30 dissociating the three mechanisms: when healthy adult observers are asked to perform 31 32 concurrently a taxing task, the judgments of low numerosities (<4 dots) or of high numerosities is affected greatly, not so however for intermediate numerosities. Here we bring 33 34 evidence from a neuropsychological perspective. To this end we measured perceptual performance in PA, a 41 year-old patient who suffers simultanagnosia after an hypoxic brain 35 36 injury. PA showed a profound deficit in attentively tracking objects over space and time 37 (multiple object tracking), even in very simple conditions where controls made no errors. PA also showed a massive deficit on sensory thresholds when comparing dot-arrays containing 38 39 extremely low (3 dots) or extremely high (64, 128 dots) numerosities as well as in comparing dot-distances. Surprisingly, PA discrimination thresholds were relatively spared for 40 intermediate numerosity (12 and 16 dots). Overall his deficit on the numerosity task results in 41 a U-shape function across numerosity which, combined with the attentional deficit and the 42 inability to judge dot-distances, confirms previously suggested three-systems for numerosity 43 44 judgments.

## 45 46

48

## 47 1. Introduction

49 Humans can estimate a wide range of numerosities, from few items to several hundreds. 50 Whether a single mechanism or several mechanisms are engaged in numerosity perception 51 across different numerical ranges, is an open question. While the existence of a single mechanism may look parsimonious, evidence is starting to mount in favour of three separate 52 systems (Anobile, Cicchini, & Burr, 2016; Burr, Anobile, & Arrighi, 2017). Here we address 53 54 this issue from a neuropsychological perspective by looking at performance obtained with a single brain-damaged patient suffering simultanagnosia. In brief, data showed, for the first 55 56 time, a simple dissociation between numerosity thresholds measured for very low, 57 intermediate and very high numerosities.

58

59

A first classical distinction in the mechanisms for numerosity has been made for very low and 60 61 intermediate numbers. Jevons (1871) discovered that judgements of low numerosities, 62 usually up to 4 items, are very fast (with constant reaction times) and virtually errorless. The 63 ability to enumerate quickly and effortlessly numbers up to four has been coined "subitizing" (Kaufman & Lord, 1949). Past this numerical range a new mechanism takes over, where 64 65 errors and reaction times covary with numerosity (Atkinson, Campbell, & Francis, 1976; Jevons, 1871; Kaufman & Lord, 1949; Mandler & Shebo, 1982). This system has been called 66 67 "estimation" (or Approximate Number System), to underline its approximate and inexact nature (Feigenson, Dehaene, & Spelke, 2004). The performance discontinuity between very 68 low and higher numbers resulted in the initial proposal of two separate systems for 69 70 "subitizing" and "estimation".

71

72 Recent works examined several psychophysical variables across a broader range of stimuli and highlighted another possible break-in performance, suggesting the existence of a third 73 74 system. In their initial observation Anobile et al (2014) measured discrimination thresholds for numerosity judgments, finding that, until a critical numerosity, Weber's Law held (a 75 signature of the Approximate Number System, henceforth ANS) but, past this numerosity, 76 77 the Weber Fraction decreased with numerosity following another psychophysical rule (square root law). The data were consistent with the idea that intermediate numerosities are perceived 78 79 by the ANS but only up to a certain point, indicating the kick in of a third system which 80 operates on higher numerosities (Anobile et al., 2014; Anobile, Cicchini, et al., 2016; 81 Cicchini, Anobile, & Burr, 2016, 2019). This latter system operates on highly 82 numerous/dense stimuli, when the items cannot be segregated and merge together in what can be defined as a "texture". For such stimuli, even when numerosity judgements are requested, 83 84 visual perception is dominated by object density (e.g. inter object distances) rather than numerosity (Anobile, Cicchini, Pomè, & Burr, 2017; Cicchini et al., 2016). Within this 85 numerical range, the limiting factors appears to be the relative center-to-center objects 86 87 distance (sparsity) and viewing eccentricity, not so much the absolute number (Anobile, Turi,

88 Cicchini, & Burr, 2015). This system has been named "*texture-density system*" (Anobile,
89 Cicchini, et al., 2016).

There is evidence to suggest that subitizing, estimation and texture-density systems lie on, at 90 least partially, distinct mechanisms. As briefly mentioned above, while discrimination 91 thresholds in the subitizing range are constantly near to zero, thresholds in the estimation 92 93 range obey Weber Law (Revkin, Piazza, Izard, Cohen, & Dehaene, 2008). Within this range, the Just Notable Difference increases linearly with numerosity, making the Weber Fraction 94 (JND normalised by perceived numerosity) almost flat. For highly dense stimuli (texture-95 density regime) thresholds decrease as a function of square-root of numerosity. Importantly, 96 97 discrimination thresholds for texture-density (not numerosity) judgments follow a square-root law as well, suggesting that density is the feature driving numerical decisions for dense 98 99 stimuli. Decoupling numerosity from density, by scattering dots in different areas, made numerosity threshold for highly dense stimuli, again, follow Weber's Law (Anobile et al., 100 101 2014).

102

Strong evidence comes also from two other recent psychophysical works testing which visual 103 104 feature spontaneously dominates perceptual decisions when observing dot-arrays (Cicchini et al., 2016, 2019). These studies employed stimuli that varied unpredictably in numerosity, 105 density or area and participants were asked to identify the odd-one-stimulus among three or 106 107 to reproduce a single dot-image (adjustment method). Importantly, participants were not instructed on which stimulus features defined the odd-one (number, density or area) nor 108 which features they had to reproduce. Results clearly show that, for numerosities in the 109 110 estimation range, performance was dominated by the number of items. On the other hand, for high density stimuli, performance follows that of a mechanism sensitive to patch area and 111 112 texture density.

113

114 Several studies have shown that the three systems work on largely independently neural structures with different neural signatures. Employing an adaptation paradigm, Zimmermann 115 has been able to demonstrate that sparse and dense stimuli impinge on visual channels with 116 different receptive field size (Zimmermann, 2018). Likewise, in a series of studies, Park 117 group has demonstrated that when passively viewing arrays of dots from the three ranges. 118 a specific early occipital neural signature that covaries with numerosity appeared only for 119 stimuli in the estimation range (Fornaciai & Park, 2017; Park, DeWind, Woldorff, & 120 Brannon, 2016). Not least, out of the three systems only that for numerosity estimation 121 122 predicts mathematical acquisition (Anobile et al., 2018; Anobile, Stievano, & Burr, 2013; 123 Burr et al., 2017), whilst those for subitizing (Anobile, Arrighi, & Burr, 2019) and texture 124 density (Anobile, Castaldi, Turi, Tinelli, & Burr, 2016) do not.

125

Interestingly, the three systems pose different attention requirements. Employing a magnitude estimation task, it has been demonstrated that thresholds in the subitizing range suffer attentional deprivations much more than those in the estimation range (Anobile, Cicchini, & Burr, 2012; Burr, Turi, & Anobile, 2010) suggesting a heavy reliance on attentional resources in order to attain near perfect performance which characterises subitizing. These results fit

131 well with an fMRI study showing that the right temporal-parietal junction (rTPJ), an area

thought to be involved in stimulus-driven attention (Corbetta & Shulman, 2002), is activated during a numerosity comparison task, but only for numbers in the subitizing range, not for the estimation range (Ansari, Lyons, van Eimeren, & Xu, 2007). Moreover, Vetter and colleagues (2011) showed that this area responds to small numbers only in conditions of low attentional load.

137

More recently Pomè and colleagues (2019) measured discrimination thresholds for a wide numerosity range, from very few items to high density stimuli, and measured the cost of introducing a concurrent dual task. The results replicated a high cost in the subitizing range, and an almost complete immunity in the estimation range but also revealed that, when numerosity increases, attentional cost was raised again. In line with this, and using a very similar paradigm, Tibber, Greenwood, and Dakin (2012) found strong visual attentional costs on numerosity and density thresholds, for high numerosities (128 dots).

145

Overall these studies suggest that numerosity can be processed by 1) an attentional subitizing
system; 2) a relatively attentional free estimation system, linked to the abstract numerical
value of the stimuli; 3) an attentional dependent texture-density system, encoding texturedensity rather than numerosity and not related to mathematical abilities.

150

In the current study, we tested the three-system hypothesis from a neuropsychological standpoint, taking our lead from the differential attentional demands observed in the three regimes. We will describe a single case of a 41 years-old men (PA) who, following a heart attack, developed clinical signs of simultanagnosia. Psychophysical testing, performed 6 months later, revealed a profound spatial attention deficit, massively impairing his ability to attentively track moving objects (Multiple Object Tracking task).

157

158 According to the results described above, the three-system model provides a clear prediction 159 on PA numerosity performance: the patient should demonstrate stronger thresholds deficits for those numerical ranges that are more attention dependent. More precisely, the three-160 system hypothesis predicts massive deficit in the subitizing range, relatively spared 161 thresholds in the estimation range and again, impaired thresholds in the texture-density 162 regime. In other terms, PA performance measured in single-task condition should 163 qualitatively mirror those obtained previously (Burr et al., 2010; Pomè et al., 2019) in dual-164 task condition with control subjects. 165

- 166
- 167
- 168 2. Methods
- 169

171

**170 2.1.** *Participants.* 

Eight subjects participated in this study, one clinical (PA) and seven neurologically healthy
volunteers. One of the neurotypical participants (Control 1 in the figures) was one of the
authors (GMC, 41 years). The other controls (average 34.5 years) has some experience in
psychophysical studies but was totally unaware of the purpose of the study.

The study was approved by the regional ethics committee at the *Azienda Ospedaliero- Universitaria Meyer* (protocol code: GR-2013-02358262). Participants signed the appropriate
informed consent forms.

180

181

## 182 2.2. Patient description

183

PA is a 40-year old right-handed male who suffered from hypoxic insult due to a heart attack. 184 He was transferred to the rehabilitation centre "Auxilium Vitae" in Volterra from the 185 intensive care unit and was finally discharged after 120 days from the hypoxic insult. He had 186 difficulty in recognising simple everyday objects, perceiving more than a single object at the 187 time (simultagnosia), controlling voluntary and purposeful eye movement (oculomotor 188 189 apraxia) and moving the hand to a specific position driven by vision (optic ataxia). He also showed ideomotor apraxia, reduction of digit span capacity, slight anterograde memory 190 deficit and mild impairment of the executive functions. He was autonomous in walking, 191 192 feeding, and daily personal care. One year after the heart attack he went back to work. The MRI of the brain collected 15 days after the hypoxic insult revealed absence of any specific 193 lesion and a very subtle variation of the signal into the basal ganglia. These findings were 194 much less evident at the brain MRI scan collected at 90 days from the event (Figure 1). 195 However, in this latter scan, there was evidence of an overall brain atrophy, in particular in 196 the occipitotemporal inferior regions and in the frontal and parietal paracentral regions and in 197 198 the hippocampal areas.

199

Neuropsychological measures were taken at 6 months from injury (Table 1). He had clear 200 201 clinical signs of simultanagnosia, and a less severe oculomotor and optic ataxia. The Verbal 202 Comprehension Index (VCI) and the Working Memory Index (WMI) of the Wechsler Adult Intelligence Scale (WAIS-IV) were assessed. The VCI is a score derived from the 203 administration of WAIS-IV sub-tests: information, similarities and vocabulary. It provides a 204 measure of verbally acquired knowledge and verbal reasoning. The WMI was obtained from 205 WAIS-IV sub-tests: digit span and arithmetic. It measures the ability to absorb information 206 presented verbally, to manipulate that information in short-term immediate memory, and then 207 to formulate a response. PA scored in the normal range for the VCI, and he scored below the 208 normal range for the WMI; thus PA did not have verbal knowledge and verbal reasoning 209 210 difficulties but he had reduced attention and memory. PA have 15 years of formal schooling 211 and before the critical event was employed in a local museum.

- 212
- 213

176

### 214

Table 1. Neuropsychological measures.			
WAIS-IV	Raw scores	Standardised scores (M=10, STD= 3)	Percentile rank
Similarities	25	11	
Vocabulary	51	13	
Information	19	12	
Digit span	15 *	3	
Arithmetic	8 *	4	
Verbal			79
Comprehension			
Index		6	
Working			1*
Memory Index			

215 216

Table 1. Neuropsychological measures. VMI (Verbal Comprehension Index) and WCI 217 (Verbal Comprehension Index) indexes were obtained at 6 months from injury. The VCI is a 218 219 score derived from the WAIS-IV sub-tests: information, similarities and vocabulary and provides a measure of verbally acquired knowledge and verbal reasoning. The WMI score is 220 obtained from the WAIS-IV sub-tests: digit span and arithmetic. It measures the ability to 221 222 absorb information presented verbally, to manipulate that information in short-term 223 immediate memory, and then to formulate a response. Performance below normal range is 224 indicated with a \* symbol.

225

226

228

## 227 2.3. Apparatus for psychophysical testing

Stimuli were generated by Matlab 9.3 using PsychToolbox routines. Experiments were run on a Mac-book Pro governing a 15-inch Macintosh monitor with 1680 x 1050 resolution at a refresh rate of 60 Hz and mean luminance of 60  $cd/m^2$ . Subjects viewed the stimuli binocularly at a distance of 57 cm from the screen.

233

235

- 234 2.4. *Stimuli and procedure*
- 236 2.5. Visual attention
- 237

We measured attentional abilities with a multiple-object tracking task (Arrighi, Lunardi, & Burr, 2011; Pylyshyn & Storm, 1988), sketched in Figure 2A. Stimuli were coloured disks, each with a 0.9° diameter and moving randomly at 2°/s. Some disks, coloured in green, were to be followed, while the red disks were distractors. The target number was kept constant at two while the number of distractors was varied in separate sessions and were: 3, 4, 6, 8, 10, 18 for controls; 3, 4, 6, 8, 10 for the patient. On each trial, two green disks (targets) and a certain number of red disks moved randomly across a grey full screen background for a

245 period of 3 s, and participants had to hold their attention on the targets. After 3s, the green 246 targets were turned red (like the distracters), and subjects were to continue tracking them for a further 3 s. Afterwards, the disks were stopped and the subjects were asked to identify (and 247 point towards) which one of four possible items (highlighted in orange) had previously been 248 green a target (4AFC). The subjects were not asked to respond quickly, but were given all the 249 250 time they needed to decide. Each experimental session comprised around ten trials. Participants performed one session for each distractor number condition. PA performed 52 251 trials (10, 16, 10, 10, 6 for each distractors level), Control 1 performed 60 trials (10 for each 252 level) and Control 2 performed 70 trials (10, 10, 20, 10, 20). No feedback was provided. 253 254 Performance was measured as a proportion of correct responses.

255 256

257

## 2.6. Numerosity discrimination

Numerosity thresholds were measured with a two-interval comparison task (2 IFC), sketched 258 259 in Figure 2B. The stimuli were two clouds of non-overlapping dots (0.5° diameter each), half black half white (in order to balance luminance). The position of each single dot was chosen 260 261 at random within a circular virtual region ( $10^{\circ}$  diameter), respecting the condition that two dots (center-to-center) should not be separated by less than 0.5°. Dot arrays were sequentially 262 presented for 500 ms each with a fixed blank inter-stimulus interval of 1 s. Dot clouds were 263 centered at  $\pm 10^{\circ}$  from a central fixation point. The side of the probe and test stimuli relative 264 to the central fixation point was kept constant in order to reduce the spatial uncertainty that 265 266 could add noise non-related to numerosity perception, especially for the patient. Participants were asked to indicate (by appropriate keyboard pressing), which stimulus contained more 267 dots. As in the attention task, subjects were not asked to respond quickly. In a particular 268 session, the left-side stimulus maintained the same numerosity across trials (test), while the 269 270 other (probe) varied around this numerosity. For each block the number of dots in the probe patch was varied according to the QUEST adaptive algorithm (Watson & Pelli, 1983), 271 perturbed with a Gaussian noise with a standard deviation 0.15 log-units. The QUEST 272 273 algorithm is an adaptive procedure for efficient threshold estimation. The algorithm decided 274 trial-by-trial, according to the subject performance, the best stimulus intensity for the next 275 trial, calculated as the maximum likelihood estimate of threshold. In separate blocks, 5 different test numerosities were tested: 3, 12, 16, 32, 64, 128. PA performed a total of 315 276 trials (95, 70, 40, 40, 40, 30 trials for each numerosity levels respectively), the first control 277 278 subject (Control 1) performed 660 trials (60, 120, 120, 120, 120, 120), the second control 279 subject (Control 2) performed 490 trials (90, 80, 80, 80, 80, 80, 80) all the others (Controls 2-7) 280 performed 80 trials for each numerosity level. For each participant, the proportion of trials where the probe appeared more numerous than the test was plotted against the number of test 281 dots in log-scale, and fitted with a cumulative Gaussian error function (lapse rate 5%). The 282 283 numerosity corresponding to 50% of correct response (chance) corresponds to the point of subjective equality (PSE). The difference in numerosity required to pass from 50% to 75% 284 correct responses defines the just-noticeable difference (JND), a measure of precision at each 285 286 test numerosity level. Precision (JND) divided by the PSE numerosity, yields the Weber 287 Fraction (WF), a dimensionless quantity that allows comparison of performance across 288 numerosities.

## 2.7. Serial counting

## 289 290

Counting ability was tested with a time-unlimited naming task. The stimuli were clouds of 291 non-overlapping white dots ( $0.5^{\circ}$  diameter each). The position of each single dot was chosen 292 at random within a circular virtual region ( $10^{\circ}$  diameter), respecting the condition that two 293 294 dots (center-to-center) should not be separated by less than 0.5°. On each trial, a single dot array containing from 2 to 10 dots, was presented in the center of the screen and remained on 295 until participants gave a verbal estimation. Participants were instructed to enumerate as fast 296 as they could the dot array, no feedback was provided. As soon as participants provided a 297 response, the experimenter (blind to the stimuli), pressed the space bar in order to save 298 299 response time. Finally, the experimenter entered the participant numerical response by the 300 keyboard. P.A. performed a total of 51 trials (7,7,7,5,5,5,5,5,5,5 for N 2,3,4,5,6,7,8,9,10), control subjects performed 45 trials (5 for each numerosity level). For each numerosity level 301 302 we computed mean response time (secs) and average response.

- 303
- 304
- 305 306

## 2.8. Object distance perception.

Peripheral distance judgements were assessed via a custom paradigm which displayed two rings made out of <u>twenty</u> small dots (5 pixels diameter), akin to beads making up a necklace (Figure 2C). The centre of the stimuli was positioned at 8° eccentricity from a central fixation point and dot positions were specified in polar coordinates. More specifically, the distance from the centre of the dots (r) was determined as a sum of two sinusoids, one repeating twice and the other repeating 5 times in a full circle ( $2\pi$  radiants) following the formula:

313

314

# $r = r_0 + A_5 \sin(5\vartheta + \varphi_5) + A_2 \sin(2\vartheta + \varphi_2)$

Where  $\vartheta$  is the polar angle,  $r_0$  is the average radius (chosen randomly between 3° and 4.5° 315 degrees for each stimulus), A<sub>5</sub> and A<sub>2</sub> are the amplitudes of the two sinusoids (random 316 between  $0.33^{\circ}$  and  $0.67^{\circ}$  the former and fixed at  $1.7^{\circ}$  the latter) and  $\varphi_5$  and  $\varphi_2$  are the two 317 phases (random between 0 and  $2\pi$ ). As in the numerosity task, stimuli were sequentially 318 presented for 500 ms each with a fixed blank inter-stimulus interval of 1 s and the side of the 319 320 probe and test stimuli relative to the central fixation point was kept constant. Participants were asked to indicate (by appropriate keyboard pressing), which stimulus contained less 321 interdot spacing. The left-side stimulus maintained the same interdot distance across trials 322 323 (test, 0.7 degrees), while the other (probe) varied between 0.1 and 1.5 degrees. Proportion of judgments in which the test was judged as "sparser" than the test was plotted as function of 324 test inter-bead distance and fitted with a standard psychometric function (see Figure 4). The 325 difference between the spacing that yield 50% and 75% "more sparse judgments" defines the 326 just-noticeable difference (JND) which, divided by the PSE, yields the Weber Fraction (WF). 327 PA performed a total of 53 trials, Control 1 performed 160 trials, all the others performed 110 328 329 trials. Standard Errors are calculated via bootstrap (Efron & Tibshirani, 1986). 330

### 332 2.9. Data analyses

333

331

Statistical differences between accuracy rates and chance level in the Multiple Object 334 335 Tracking were computed by binomial tests. Statistical differences on accuracy levels between 336 PA and controls were calculated by Chi-square tests.

337

The subjects' statistical differences on numerosity thresholds (WF) were calculated by a 338 bootstrap technique (Efron & Tibshirani, 1986). For each participant, and separately for each 339 340 numerosity level, raw data were randomly resampled (selecting a data set as large as the data set taken, sampled with replacement), a psychometric function was fitted and a WF 341 342 calculated. On each iteration, the WFs obtained by controls were averaged and compared to that obtained by PA. This procedure was repeated 1000 times. The proportion of time that 343 344 PA's WFs were lower than the controls' averages was the p-value. To compare deficit magnitude across numerical regimes, for each iteration we separately averaged PA's and the 345 controls' WFs on numerosity 12 and 16 (estimation range) as well as those for numerosity 64 346 347 and 128 (texture density) or N3 (subitizing). Then we computed the ratio between WFs in the subitizing, estimation and texture-density ranges obtained by PA and the controls (deficit 348 index) and counted the time the deficit in one range was higher than that in the other (p-349 value). Numerosity 32 was eliminated from this analysis because for one control participant 350 351 the WF already started to decrease at this numerosity level making it difficult to categorise it 352 as belonging to the estimation or texture-density regime.

353

We checked the presence of subitizing advantage in serial counting by looking at response 354 355 time (RT) variation as a function of item number. For each subjects and separately for each 356 numerosity, raw response time were randomly resampled (1000 iterations, selecting a data set 357 as large as the data set taken, sampled with replacement), the average RT computed, plotted against physical numerosity and fitted wither with a linear or a two limb linear function 358 starting with a constant segment and then rising as function of numerosity. On each iteration, 359 we calculated the goodness of fit of the linear and the two limb function by means of 360 361 Akaike information criterion (AIC). The p-value represents the fraction of times that a given AIC is lower than that of the competing model. 362

- 363
- 364

Object distance perception. The subjects' statistical differences on dot-distance thresholds 365 were calculated by a similar bootstrap technique: for each participant, raw data were 366 367 resampled and a WF calculated. On each iteration, the WFs obtained by the controls were averaged and compared to that obtained by PA. This procedure was repeated 1000 times. The 368 369 proportion of time that PA's WFs were lower than the controls' average was the p-value.

- 370
- 371
- 372
- 373



374 375

376 Figure 1. MRI 90 days from the insult. T2w FLAIR images were acquired using a SIEMENS Symphony 1.5T scanner and a spin-echo inverse recovery sequence (acquisition 377 378 parameters are: TR/TE/TI: 9400/124/2500ms, FA: 150, acquisition matrix: 320 x 260, voxel 379 size: 0.688x0.688x4.8mm, 30 axial slices; for TR/TE/TI: 10000/120/2500ms, FA: 150, acquisition matrix: 512 x 376, voxel size: 0.508x0.508x4.4mm, 28 axial slices; acquisition 380 parameters). In order to correct for inter-individual differences in brain size and brain volume 381 382 orientation, the MRI brain volume of PA was transformed into the standardized MNI space 383 using the software REGISTER (http://www.bic.mni.mcgill.ca/ServicesSoftwareVisualization/Register). This program uses 384 more than 5 neuroanatomical landmarks to match individual patient brain volumes to the 385 386 Colin-MNI brain. The selection of the PA brain MRI axial slices (z values) registered in MNI space was obtained using DISPLAY (J.D. McDonald, Brain Imaging Center, Montreal 387 Neurological Institute www.bic.mni.mcgill.ca/software/Display/Display.html), an interactive 388 389 program that allows for the simultaneous visualisation of the movement of the cursor on the 390 screen within the sagittal, horizontal and coronal planes of the brain MRI together with visualization of x, y, z coordinate. Brain sulci of PA a 40 years old man, were overall 391 392 increased as a result of the diffuse brain atrophy. No specific lesion and a very subtle variation of the signal into the basal ganglia are visible (z = +7). Axial slice at z=-13 shows a 393 brain atrophy in the occipitotemporal inferior regions and into the hippocampi; the axial slice 394 395 at z = +39 shows a frontal and parietal paracentral regions atrophy. To better recognize the brain areas, sulci or Gyri have been indicate: Calc =Calcarine Fissure, STg= Superior 396 Temporal gyrus, Sv= Vertical Ramus of the Sylvian fissure, SFs=Superior Frontal sulcus, 397 398 Cs= Central sulcus, IPs= Intraparietal sulcus. 399

400







Figure 2. Schematic illustration of tasks. Stimuli were not draw in scale in these images, 402 for stimuli details see the methods. A) Multiple object tracking. In the target selection 403 404 phase, participants attentively track green targets moving among red distracters (4 in the example), for a period of 3 s. At the end of this phase, the green targets turn red (like the 405 distracters) and subjects track them for 3 s. In the response phase, disks stop and participants 406 are asked to identified which of four possible items (highlighted in orange) was green in the 407 target selection phase. B) Numerosity comparison. A patch of dots with variable numerosity 408 (4 in the example) is briefly (500 ms) presented to the right side of a central fixation point. 409 410 After 1 second of blank screen, a second patch is presented on the left side, containing a fixed number of dots. Subjects are asked to indicate the side of the screen with more dots. C) Dot-411 *distance comparison.* A dotted-shape with inter-dots distance varying trial by trial is briefly 412 (500 ms) presented to the right side of a central fixation point. After 1 second of blank screen, 413 a second dotted-shape is presented on the left side, containing a fixed interdots distance. 414 Subjects are asked to indicate the stimulus with longer interdots distance. 415

- 416
- 417 418
- 419 **3. Results**
- 420
- 421 3.1. Visual Attention.
- 422

Visual-spatial attentional capacities were psychophysically measured by a Multiple Object
Tracking task (Figure 2A). The number of to-be-tracked targets was fixed at two and the
attentional load was manipulated, in separate sessions, by increasing the number of
distractors from 3 to 18 (3-10 for PA).

427 Figure 3 shows a proportion of correct responses as a function of the number of distractors.

428 For both control participants (greys lines and symbols), performance was almost perfect with

429 accuracy slightly decreasing at the most difficult condition (18 distractors) for one participant

430 (Control 1, in the figure).

PA was able to perform the task, with accuracy above the chance level (0.25 accuracy) in theless attention demanding conditions, namely when the number of distractors was three and

four (p<0.001 for both relative to chance). In these two distractors levels, PA's proportion of correct responses was around 0.8 and not statistically different from that obtained by both control subjects (all p=0.136). However, in cases of six, eight and ten distractors, while the controls' accuracy remained at the ceiling level, PA performance sharply dropped, becoming no different from the chance level (p>0.05) and statistically different from controls (all p< 0.01).

440



441

442 Figure 3. Visual attention. Accuracy in the multiple object tracking task as a function of
443 number of distractors in the control participants (greys) and for the patient PA (black).
444 Chance and perfect performance levels are highlighted by dashed lines.

- 445
- 446
- 447
- 448 3.2. *Numerosity discrimination*.
- 449

Having established the attentional deficit, we moved to the numerosity discrimination
thresholds measurement. According to the three-system hypothesis and previous studies on
attentional deprivation (Anobile, Cicchini, et al., 2012; Burr et al., 2010; Pomè et al., 2019),
PA should demonstrate stronger deficits for those stimuli requiring more attentional
resources, namely numerosities in the subitizing range and for highly dense arrays (highest
numerosities).

456

457 Numerosity discrimination thresholds were measured by a two alternative forced choices 458 method. On each trial, a dot-array (test, fixed numerosity) was briefly (500 ms) presented to 459 the right side of the screen followed by a blank pause and by a second patch to the left side 460 (probe, varying numerosity trial-by-trial). Subjects indicated the side of the screen with more

dots. Data were fitted by psychometric functions, and sensory thresholds (WF) werecalculated for each test numerosity level (see methods for details).

463

Figure 4A shows single subjects' psychometric functions for the different test numerosities (3, 12, 16, 32, 64 and 128 dots) with associated Weber Fraction estimates (inbox texts). On inspection it is clear that PA was able to perform the comparison task, producing many ordered functions. However, it is also evident that the PA fits for very small (test N=3 dots) and very high (test N=128 dots) numerosities had higher slopes, compared to the controls. The slopes of psychometric functions are indexes of sensory thresholds, with higher values indicating lower precision.

471

472 Figure 4B summarises better the results showing discrimination thresholds (WF) as a function of numerosity levels for the patient PA (black) as well as those obtained by the 473 474 controls (averaged across the two subjects, greys). Results from control participants replicated previous findings: thresholds were very low in the subitizing range ( $\cong 0.1$ ) then 475 rose ( $\cong 0.2$ ) and remained constant for higher numerosities (from 12 to  $\cong 64$ ); finally, WFs 476 477 decreased for the densest stimuli (WF<0.1 around N128). As described in the introduction, this three-phase discontinuity is the one that initially led to the hypothesis of the existence of 478 479 three systems.

480

The PA result were quite different. PA threshold level in the subitizing range (i.e. N3) was very high, with a WF near to 0.6, five times higher compared to the controls (p<0.001). Despite this huge deficit in the subitizing range, PA thresholds for intermediate numerosities (N12, 16 and 32) were similar and not statistically different than those obtained by the controls (p=0.075, p=0.11, p=0.075 for N12, 16 and 32). Finally, PA thresholds, at odds with controls performance, did not decreased for the densest stimuli, revealing a very strong deficit for dense stimuli (p=0.017 and p=0.023 for N=64 and N=128 dots).

488

Because PA generally completed fewer trials than the controls, possibly affecting thresholds measurements, we ran a more conservative bootstrap analysis (see methods) by selecting, on each iteration and for each participant, a number of trials equal to the minimum number of trials performed by all the three participants (60, 70, 40, 40, 40, 30 for numerosities 3, 12, 16, 64, 128 respectively). This analysis confirmed the pattern of results (p=0.001, p=0.087, p=0.065, p=0.056, p=0.01, p=0.02 for N3, 12, 16, 32, 64 and 128).

495

496 To better visualize the PA sensory thresholds deficit across numerosity levels, we computed a 497 "deficit index" as the ratio between PA's and the controls' average WF levels. Figure 4C 498 shows the deficit index as a function of test numerosity making evident that PA's deficit was not constant across numerosity, but drew a U-shape function. The average deficit for 499 numerosities in the estimation range (12 and 16) was 2.0 while that for numerosities in the 500 501 texture-density regime (64 and 128) was 8.2 (p=0.03). For the subitizing range (N3) the 502 average deficit was 7.1, higher than the estimation range (p=0.009) but not compared to the 503 texture-density regime (p=0.53).



504 505

**Figure 4. Numerosity discrimination.** A) Psychometric functions from two representative controls (light and dark grey) and the patient (PA) for various level of numerosity, spanning the three regimes. B) Discrimination thresholds (WF) for the patient PA (black), controls (thin coloured lines) and averaged across controls (greys) as a function of numerosity. C) Deficit factor calculated as the ratio between WF returned from PA's fits and the average performance of controls. Values higher than one mean higher thresholds in PA compared to controls.

513 \* p<0.05, \*\* p<0.01

- 514
- 515 516

517

## 3.3. No evidence of subitizing in counting task

518 In order to confirm that the deficit in the subitizing was not task dependent we measured PA 519 performance in a classical dot-counting task in the range 2-10. In this task control subjects 520 exhibit a classical signature of subitizing advantage: performance is fast and constant up to 521 ~4 items and then it is slower and depends on numerosity from 5 items on (Grey dots in Fig 522 5A).

523

PA behaviour dramatically differed from this classic pattern. His response times grew 524 steadily as function of numerosity even with the least numerous items and, for instance 525 526 counting 3 dots required more time than counting 2 items (Black dots, Fig 5A). This indicates the absence of the capacity of capture at a gist 2, 3 or 4 items, i.e. a lack of the subitizing 527 process. To confirm this quantitatively we fit the two datasets (PA and controls) with two 528 529 functions, either a linear function or a two-limb linear function and compared the two models 530 by means of Akaike Information Criterion. In case of controls the two limbed function was the better model, outperforming a simple linear fit near always (bootstrap of AIC p=0.008). 531

532 Conversely, for PA's data it was the linear function to provide a better model for the data 533 (p=0.04).

534

Figure 5B shows average responses of PA in the counting task. These data indicating that he 535 was well compliant with the task with responses that grew monotonically with stimulus 536 537 numerosity albeit with a slight overestimation (slope=1.14±0.06, p<0.001; 538 intercept=0.82±0.24, p=0.01). An overall overestimation has been reported previously in some simultagnosic patients and is generally due to the fact that these subjects, while 539 scanning the display, lose track of the items which they have already analysed and may count 540 541 twice the same dot (Dehaene & Cohen, 1994). Again, no signature of a specific process for 542 very low numerosities is evident from this data.

543



544

Figure 5. Dot-counting task. A) Response time (secs) as a function on numerosity for the
patient PA (left ordinate, black squares) and control subjects (right ordinate, thin lines report
single subjects data; grey squares represent average). B) Average response as a function on
numerosity for the patient PA and controls (conventions as panel A).

- 549
- 550 551
- 552 *3.4. Object distance perception.*
- 553

PA's numerosity thresholds at high numerosities was much worse than controls. Previous studies have shown that for very dense stimuli, perception is dominated by the dot-density. The distance between the elements is a stimulus parameter that has been proved to be a good quantitative descriptor of stimulus density (Anobile et al., 2014). For this reason, we also investigated PA's precision in discriminating distance between objects. If numerosity of dense stimuli is judged, even partially, through computing this visual feature, we expect higher discrimination thresholds compared to controls.

561

Figure 5 shows psychometric functions for PA (black) and controls (greys), with associated
Weber Fraction estimates (inbox texts). Both controls found the task particularly easy and

both produced very steep psychometric functions (WFs:  $0.05\pm0.01$ ). On the other hand, PA had severe difficulties in performing the task with ten times higher thresholds ( $0.56\pm0.29$ ) than controls average (p<0.001). The same result was obtained running a more conservative bootstrap analysis selecting, on each iteration and for each participant, the number of trials performed by PA.

569

570



571 572

Figure 6. Dot-distance discrimination. A) Psychometric functions from the controls (light coloured curves) and the patient (PA, black function and data points) obtained in the dot-distance discrimination task. B) Discrimination thresholds for PA and controls. Isolated data points show single subject data. Error bars represent S.E.M.

577 578

## 579 **4. Discussion**

580

Recent evidence suggests that numerosity perception can draw upon three distinct mechanisms: 1) an attentional dependent *subitizing* system encoding numbers up to around four; 2) a relatively "attentional-free" *estimation* mechanism for intermediate numbers and 3) an attentional demanding *texture-density* mechanism operating for high dense/numerous stimuli.

586

Here we tested this idea from a neuropsychological approach. We measured numerosity thresholds for a wide range of numerosities, spanning the three systems in a single patient (PA) displaying strong attentional deficits and signs of simultanagnosia (emerged after a hypoxic insult). PA also demonstrated impaired numerosity thresholds for numbers in the subitizing range (3 dots) as well as for highly numerous/dense patterns (64 and 128 dots). Interestingly, PA demonstrated relatively preserved numerosity thresholds for intermediate numerosity levels (12 and 16 dots).

# This is the first clinical case reported in the literature showing a (single) dissociation between perception of intermediate (estimation range) and high (texture-density range) numerosity. Moreover, the pattern of numerosity deficits showed by PA is difficult to explain with a single mechanism spanning all numbers but, instead, fit swell with the three-system model. Results on this simultanagnosic patient also extend nicely the evidence provided by previous studies which measured the role of attention on numerosity in controls under conditions of dual task (Anobile, Turi, Cicchini, & Burr, 2012; Burr et al., 2010; Pomè et al., 2019).

602

603 We would like to stress that the aim of the current study was not to describe visual perception 604 in simultanagnosia nor the link between math skills and numerosity perception in these 605 patients, both of which issues require certainly much more detailed testing. In the same vein we note that MRI evidence on our patient revealed a rather diffuse atrophy which hinders the 606 607 possibility to restrict the functional deficit to a circumscribed damage. In any event, our 608 patient, PA, developed a massive attentional deficit, a distinctive feature characterises simultanagnosia and has been suggested to have a key role in dissociating the three-number 609 610 mechanisms (Anobile, Cicchini, et al., 2016; Anobile, Turi, et al., 2012; Pomè et al., 2019).

611

The idea of studying numerosity perception in simultanagnosic patients is not entirely new, 612 and was similarly motivated by the fact that these patients fail to allocate attention to multiple 613 objects (Rizzo & Vecera, 2002; Robertson, 2014), one of the functions that support 614 numerosity encoding (Mazza, 2017). The few available studies, however, have focused 615 616 mostly on counting, namely the process involved in serial and slow exact enumeration, with only few measuring approximate estimation of briefly displayed stimuli, where counting is 617 prevented (Dehaene & Cohen, 1994; Demeyere & Humphreys, 2007). Moreover, a direct 618 619 measure of discrimination thresholds over a broad numerical range is lacking.

620

621 Despite no directly comparable studies being available, some evidence provides useful cues to frame better the current results. Dehaene and Cohen (1994) measured visual attentional 622 capacities by visual search tasks and numerosity performance by a verbal magnitude 623 estimation task with five simultanagnosic patients. Dot stimuli were either presented fast (200 624 ms) or displayed onscreen until response. Results showed that some but not all patients had 625 attentional deficits. In the numerical tasks, patients produced more errors than controls for 626 numerosities above three but had relatively preserved accuracy in quantification of one, two 627 628 and sometimes three items, demonstrating the subitizing effect. Demeyere, Lestou, and 629 Humphreys (2010) also found unimpaired exact counting for numbers up to four items but 630 impaired enumeration for higher numbers in a brain lesioned patient. Demeyere and Humphreys (2007) measured numerosity performance on GK, a patient with severe 631 632 simultanagnosic symptoms and clearly impaired attentional capacities. At odds with Dehaene 633 & Cohen patients, GK showed no sign of subitizing advantage, with error rates linearly 634 increasing with numerosity. Our data on serial counting mirrors those of patient GK, with no 635 evidence of subitizing advantage with response time linearly increasing with numerosity. 636 Interestingly, the authors found that when asked to compare the relative numerosity of two 637 fast consecutive displays, GK's performance (error rates) was significantly above chance for

594

many test numerosity levels (2, 4, 6, 8, or 10 dots), suggesting that he had a residual capacity to compare numerosities. The authors suggested that the capacity to distribute attention over space of GK was unimpaired and that distributed attention is the key attentional prerequisite when encoding global stimulus statistics, like numerosity. Following this idea, the same research group also demonstrated the remarkably good ability of GK to encode visual ensemble statistics of objects colour and size (Demeyere, Rzeskiewicz, Humphreys, & Humphreys, 2008).

645

On the basis of these few clinical studies and those demonstrating that subitizing requires 646 647 attentional resources (Anobile, Cicchini, et al., 2012; Burr, Anobile, & Turi, 2011; Burr et al., 648 2010; Egeth, Leonard, & Palomares, 2008; Juan, Walsh, & McLeod, 2000; Olivers & 649 Watson, 2008; Railo, Koivisto, Revonsuo, & Hannula, 2008; Vetter, Butterworth, & Bahrami, 2008; Xu & Liu, 2008), we speculate that PA's subitizing deficit is, at least 650 651 partially, linked to his poor visual attentional skills. Indeed, much previous literature has 652 suggested that subitizing is not a pure numerical ability but reflects a domain general capacity 653 to tag and monitor items of interest in the visual scene. These are attentional demanding 654 processes which, besides supporting target selection, may also provide intrinsically a precise numerosity estimation, at least for sets of very low numerosity (Burr et al., 2010; Piazza, 655 656 Fumarola, Chinello, & Melcher, 2011). Thus, a loss of the capacity to deploy attention upon 657 objects in space may well result in a loss of near perfect performance in the subitizing range.

658 659

660 The impairment at very high numerosities, whilst consistent with previous evidence of an impairment in dual task conditions (Pomè et al., 2019; Tibber et al., 2012), is also striking as 661 662 estimation of highly packed displays is often thought to rely on simple feature detectors 663 which are present in the earliest stages of analysis of a visual scene (Dakin, Tibber, 664 Greenwood, Kingdom, & Morgan, 2011; Morgan, Raphael, Tibber, & Dakin, 2014). So, how could an attentional deficit interfere with numerosity of dense patterns? In previous work we 665 have suggested that the pattern of square-root relationship governing thresholds in this 666 regime (Anobile et al., 2014; Anobile et al., 2015) may result from a mechanism that 667 computes interdot distance and assigns the label of more dense (or more numerous) to the one 668 that possesses the smallest average distance (Anobile et al., 2014). Consistently with this, PA 669 670 displayed a strong impairment in dots distance estimation. All this leads to the speculation that discrimination of highly packed arrays relies heavily on an attention-dependent local 671 672 feature extraction such as object distance. It is also interesting to note that PA, 673 notwithstanding the deficit in distance estimation, performs relatively well at intermediate 674 numerosities. This strongly suggests that perception of intermediate numerosities is governed 675 by a specific mechanism which depends little on low level features (Anobile et al., 2014; Anobile, Cicchini, et al., 2016; Cicchini et al., 2016, 2019). 676

677

678

The robustness of numerosity perception even in a patient with such severe attentional
deficits is consistent with the idea that numerosity of visual arrays is produced by a dedicated
primary mechanism which partially escapes cognitive control (Anobile, Cicchini, et al., 2016;

Cicchini et al., 2016, 2019). Finally, our data strengthen the parallel between numerosity
perception of sparse arrays and ensemble perception (Demeyere & Humphreys, 2007; Ross &
Burr, 2012). Both functions are resistant to attentional deprivation (Anobile, Cicchini, et al.,
2012; Burr et al., 2010; Whitney & Yamanashi, 2018), both are relatively spared in
simultanagnosic patients (Demeyere & Humphreys, 2007; Demeyere et al., 2008), and both
are candidates for primary visual feature (Anobile, Cicchini, et al., 2016; Whitney &
Yamanashi, 2018).

689 690

# 691 **5.** Conclusions

692

For the first time, we measured numerosity discrimination thresholds (Weber Fraction) in a patient with strong attentional deficits and simultanagnosic symptoms. Moreover, for the first time we investigated a large numerical range spanning from few items (3) to more than a hundred (128). Our data showed that thresholds for low (3 dots) and very high numbers strongly deviate from typical values while thresholds for intermediate numerosities were much less affected. These data can hardly fit with a single mechanism for numerosity and speak in favour of a recent model based on three-mechanisms for numerosity perception.

700 701

## 702 Acknowledgments

703

704 This research was funded by the Italian Ministry of Health and by Tuscany Region under the project 'Ricerca Finalizzata', Grant number GR-2013-02358262 to G.A.; from the European 705 Research Council FP7-IDEAS-ERC (Grant number 338866—'Early Sensory Cortex 706 707 Plasticity and Adaptability in Human Adults – ECSPLAIN); from European Research Council (ERC) under the European Union's Horizon 2020 research and innovation 708 709 programmes PUPILTRAITS (Grant number 801715); from European Union (EU) and Horizon 2020 - ERC Advanced "Spatio-temporal mechanisms of generative perception", 710 711 Grant number 832813 – GenPercept; from Italian Ministry of Education, University, and Research under the PRIN2017 programme (Grant number 2017XBJN4F—'EnvironMag' and 712 713 Grant number 2017SBCPZY-'Temporal context in perception: serial dependence and 714 rhythmic oscillations').

- 715
- 716
- 717

718

## 719 **References**

- 720
- Anobile, G., Arrighi, R., & Burr, D. C. (2019). Simultaneous and sequential subitizing are
  separate systems, and neither predicts math abilities. *J Exp Child Psychol*, *178*, 86103. doi:10.1016/j.jecp.2018.09.017
- Anobile, G., Arrighi, R., Castaldi, E., Grassi, E., Pedonese, L., Moscoso, P. A. M., & Burr, D. C.
  (2018). Spatial but not temporal numerosity thresholds correlate with formal math
  skills in children. *Dev Psychol*, *54*(3), 458-473. doi:10.1037/dev0000448

- Anobile, G., Castaldi, E., Turi, M., Tinelli, F., & Burr, D. C. (2016). Numerosity but not texture density discrimination correlates with math ability in children. *Dev Psychol, 52*(8),
   1206-1216. doi:10.1037/dev0000155
- Anobile, G., Cicchini, G. M., & Burr, D. C. (2012). Linear mapping of numbers onto space
   requires attention. *Cognition*, *122*(3), 454-459. doi:10.1016/j.cognition.2011.11.006
- 732
   Anobile, G., Cicchini, G. M., & Burr, D. C. (2014). Separate mechanisms for perception of

   733
   numerosity and density. *Psychol Sci, 25*(1), 265-270.

   734
   doi:10.1177/0956797613501520
- Anobile, G., Cicchini, G. M., & Burr, D. C. (2016). Number As a Primary Perceptual Attribute:
   A Review. *Perception*, 45(1-2), 5-31. doi:10.1177/0301006615602599
- Anobile, G., Cicchini, G. M., Pomè, A., & Burr, D. (2017). Connecting visual objects reduces
   perceived numerosity and density for sparse but not dense patterns. *Journal of numerical cognition*, 3(2). doi:10.5964/jnc.v3i2.38
- Anobile, G., Stievano, P., & Burr, D. C. (2013). Visual sustained attention and numerosity
  sensitivity correlate with math achievement in children. *J Exp Child Psychol*, *116*(2),
  380-391. doi:10.1016/j.jecp.2013.06.006
- Anobile, G., Turi, M., Cicchini, G. M., & Burr, D. C. (2012). The effects of cross-sensory
  attentional demand on subitizing and on mapping number onto space. *Vision Res*,
  745 74, 102-109. doi:10.1016/j.visres.2012.06.005
- Anobile, G., Turi, M., Cicchini, G. M., & Burr, D. C. (2015). Mechanisms for perception of
  numerosity or texture-density are governed by crowding-like effects. *J Vis*, 15(5), 4.
  doi:10.1167/15.5.4
- Ansari, D., Lyons, I. M., van Eimeren, L., & Xu, F. (2007). Linking visual attention and number
  processing in the brain: the role of the temporo-parietal junction in small and large
  symbolic and nonsymbolic number comparison. *J Cogn Neurosci, 19*(11), 1845-1853.
  doi:10.1162/jocn.2007.19.11.1845
- Arrighi, R., Lunardi, R., & Burr, D. (2011). Vision and audition do not share attentional
   resources in sustained tasks. *Front Psychol*, *2*, 56. doi:10.3389/fpsyg.2011.00056
- Atkinson, J., Campbell, F. W., & Francis, M. R. (1976). The magic number 4 +/- 0: a new look
  at visual numerosity judgements. *Perception*, 5(3), 327-334. doi:10.1068/p050327
- Burr, D. C., Anobile, G., & Arrighi, R. (2017). Psychophysical evidence for the number sense.
   *Philos Trans R Soc Lond B Biol Sci, 373*(1740). doi:10.1098/rstb.2017.0045
- Burr, D. C., Anobile, G., & Turi, M. (2011). Adaptation affects both high and low (subitized)
  numbers under conditions of high attentional load. *Seeing Perceiving*, 24(2), 141150. doi:10.1163/187847511X570097
- Burr, D. C., Turi, M., & Anobile, G. (2010). Subitizing but not estimation of numerosity
   requires attentional resources. *J Vis*, *10*(6), 20. doi:10.1167/10.6.20
- Cicchini, G. M., Anobile, G., & Burr, D. C. (2016). Spontaneous perception of numerosity in
   humans. *Nat Commun*, 7, 12536. doi:10.1038/ncomms12536
- Cicchini, G. M., Anobile, G., & Burr, D. C. (2019). Spontaneous representation of numerosity
  in typical and dyscalculic development. *Cortex*, *114*, 151-163.
  doi:10.1016/j.cortex.2018.11.019
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven
  attention in the brain. *Nature Reviews Neuroscience*, 3(3), 201-215.
  doi:10.1038/nrn755
- Dakin, S. C., Tibber, M. S., Greenwood, J. A., Kingdom, F. A. A., & Morgan, M. J. (2011). A
   common visual metric for approximate number and density. *Proceedings of the*

- 774 National Academy of Sciences of the United States of America, 108(49), 19552 775 19557. doi:10.1073/pnas.1113195108
- Dehaene, S., & Cohen, L. (1994). Dissociable mechanisms of subitizing and counting:
   neuropsychological evidence from simultanagnosic patients. J Exp Psychol Hum
   Percept Perform, 20(5), 958-975.
- Demeyere, N., & Humphreys, G. W. (2007). Distributed and focused attention:
   Neuropsychological evidence for separate attentional mechanisms when counting
   and estimating. *Journal of Experimental Psychology-Human Perception and Performance, 33*(5), 1076-1088. doi:10.1037/0096-1523.33.5.1076
- Demeyere, N., Lestou, V., & Humphreys, G. W. (2010). Neuropsychological evidence for a
  dissociation in counting and subitizing. *Neurocase*, 16(3), 219-237.
  doi:10.1080/13554790903405719
- Demeyere, N., Rzeskiewicz, A., Humphreys, K. A., & Humphreys, G. W. (2008). Automatic
   statistical processing of visual properties in simultanagnosia. *Neuropsychologia*,
   46(11), 2861-2864. doi:10.1016/j.neuropsychologia.2008.05.014
- Efron, B., & Tibshirani, R. (1986). Bootstrap Methods for Standard Errors, Confidence
   Intervals, and Other Measures of Statistical Accuracy. *Statistical Science*, 1(1), 23.
- 791
   Egeth, H. E., Leonard, C. J., & Palomares, M. (2008). The role of attention in subitizing: Is the

   792
   magical number
   1?
   Visual
   Cognition,
   16(4),
   463-473.

   793
   doi:10.1080/13506280801937939
   Cognition,
   16(4),
   463-473.
- Feigenson, L., Dehaene, S., & Spelke, E. (2004). Core systems of number. *Trends Cogn Sci*,
   8(7), 307-314. doi:10.1016/j.tics.2004.05.002
- Fornaciai, M., & Park, J. (2017). Distinct Neural Signatures for Very Small and Very Large
   Numerosities. *Frontiers in Human Neuroscience*, 11. doi:ARTN 21
- 798 10.3389/fnhum.2017.00021
- Jevons, W. S. (1871). The Power of Numerical Discrimination. *Nature*, *3*(67), 281-282.
   doi:10.1038/003281a0
- Juan, C. H., Walsh, V., & McLeod, P. (2000). Preattentive vision and enumeration.
   *Investigative Ophthalmology & Visual Science, 41*(4), S39-S39.
- Kaufman, E. L., & Lord, M. W. (1949). The discrimination of visual number. *Am J Psychol*,
   62(4), 498-525.
- Mandler, G., & Shebo, B. J. (1982). Subitizing an Analysis of Its Component Processes. *Journal of Experimental Psychology-General*, 111(1), 1-22. doi:Doi 10.1037/0096-3445.111.1.1
- 808 Mazza, V. (2017). Simultanagnosia and object individuation. *Cognitive Neuropsychology*,
   809 34(7-8), 430-439. doi:10.1080/02643294.2017.1331212
- Morgan, M. J., Raphael, S., Tibber, M. S., & Dakin, S. C. (2014). A texture-processing model
  of the 'visual sense of number'. *Proc Biol Sci, 281*(1790). doi:10.1098/rspb.2014.1137
- 812 Olivers, C. N. L., & Watson, D. G. (2008). Subitizing requires attention. *Visual Cognition*,
   813 16(4), 439-462. doi:10.1080/13506280701825861
- Park, J., DeWind, N. K., Woldorff, M. G., & Brannon, E. M. (2016). Rapid and Direct Encoding
  of Numerosity in the Visual Stream. *Cerebral Cortex, 26*(2), 748-763.
  doi:10.1093/cercor/bhv017
- Piazza, M., Fumarola, A., Chinello, A., & Melcher, D. (2011). Subitizing reflects visuo-spatial
  object individuation capacity. *Cognition*, 121(1), 147-153.
  doi:10.1016/j.cognition.2011.05.007

- Pomè, A., Anobile, G., Cicchini, G. M., Scabia, A., & Burr, D. C. (2019). Higher attentional
  costs for numerosity estimation at high densities. *Attention, Perception, & Psychophysics*. doi:10.3758/s13414-019-01831-3
- Pylyshyn, Z. W., & Storm, R. W. (1988). Tracking multiple independent targets: evidence for a parallel tracking mechanism. *Spat Vis, 3*(3), 179-197.
- Railo, H., Koivisto, M., Revonsuo, A., & Hannula, M. M. (2008). The role of attention in subitizing. *Cognition*, *107*(1), 82-104. doi:10.1016/j.cognition.2007.08.004
- Revkin, S. K., Piazza, M., Izard, V., Cohen, L., & Dehaene, S. (2008). Does subitizing reflect
   numerical estimation? *Psychol Sci, 19*(6), 607-614. doi:10.1111/j.1467 9280.2008.02130.x
- Rizzo, M., & Vecera, S. P. (2002). Psychoanatomical substrates of Balint's syndrome. J Neurol
   Neurosurg Psychiatry, 72(2), 162-178. doi:10.1136/jnnp.72.2.162
- Robertson, L. C. (2014). *Balint's syndrome and the study of attention*.: Oxford: Oxford
  University Press.
- Ross, J., & Burr, D. (2012). Number, texture and crowding. *Trends Cogn Sci*, *16*(4), 196-197.
   doi:10.1016/j.tics.2012.01.010
- Tibber, M. S., Greenwood, J. A., & Dakin, S. C. (2012). Number and density discrimination
  rely on a common metric: Similar psychophysical effects of size, contrast, and
  divided attention. *Journal of Vision*, *12*(6). doi:Artn 8
- 839 10.1167/12.6.8
- Vetter, P., Butterworth, B., & Bahrami, B. (2008). Modulating attentional load affects
   numerosity estimation: evidence against a pre-attentive subitizing mechanism. *PLoS One, 3*(9), e3269. doi:10.1371/journal.pone.0003269
- Vetter, P., Butterworth, B., & Bahrami, B. (2011). A candidate for the attentional bottleneck:
  set-size specific modulation of the right TPJ during attentive enumeration. *J Cogn Neurosci, 23*(3), 728-736. doi:10.1162/jocn.2010.21472
- Whitney, D., & Yamanashi, L. A. (2018). Ensemble Perception. *Annu Rev Psychol, 69*, 105 129. doi:10.1146/annurev-psych-010416-044232
- Xu, X. D., & Liu, C. (2008). Can subitizing survive the attentional blink? An ERP study.
   *Neuroscience Letters, 440*(2), 140-144. doi:10.1016/j.neulet.2008.05.063
- Zimmermann, E. (2018). Small numbers are sensed directly, high numbers constructed from
   size and density. *Cognition*, *173*, 1-7. doi:10.1016/j.cognition.2017.12.003
- 852
- 853
- 854
- 855
- 856
- 857

We tested precision in numerosity judgments in a rare simultanagnosic patient

Judgments of arrays of very few dots were strongly impaired

So they were judgments of very highly dense arrays

Nevertheless performance at intermediate numerosities was relatively spared

Numerosity judgments across numerosities impinge at least on three mechanisms

.at