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Three-systems for visual numerosity: A single case study

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ABSTRACT

Humans possess the remarkable capacity to assess the numerosity of a set of items over a 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 three mechanisms, each tailored to specific stimulation conditions. Previous evidence in 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 dissociating the three mechanisms: when healthy adult observers are asked to perform 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 evidence from a neuropsychological perspective. To this end we measured perceptual performance in PA, a 41 year-old patient who suffers simultanagnosia after a hypoxic brain injury. PA showed a profound deficit in attentively tracking objects over space and time (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 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 intermediate numerosity (12 and 16 dots). Overall his deficit on the numerosity task results in a U-shape function across numerosity which, combined with the attentional deficit and the inability to judge dot-distances, confirms previously suggested three-systems for numerosity judgments.

1. Introduction

Humans can estimate a wide range of numerosities, from few items to several hundreds. Whether a single mechanism or several mechanisms are engaged in numerosity perception 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 systems (Anobile et al., 2016a, 2016b; Burr et al., 2017). Here we address 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 time, a simple dissociation between numerosity thresholds measured for very low, intermediate and very high numerosities.

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

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 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 signature of the Approximate Number System, henceforth ANS) but, past this numerosity, the Weber Fraction

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decreased with numerosity following another psychophysical rule (square root law). The data were consistent with the idea that intermediate numerosities are perceived by the ANS but only up to a certain point, indicating the kick in of a third system which operates on higher numerosities (Anobile et al., 2014; Anobile et al., 2016a, 2016b; Cicchini et al., 2016, 2019). This latter system operates on highly 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, visual perception is dominated by object density (e.g. inter object distances) rather than numerosity (Anobile et al., 2017; Cicchini et al., 2016). Within this numerical range, the limiting factors appears to be the relative center-to-center objects distance (sparsity) and viewing eccentricity, not so much the absolute number (Anobile et al., 2015). This system has been named “*texture-density system*” (Anobile et al., 2016a, 2016b).

There is evidence to suggest that subitizing, estimation and texture-density systems lie on, at least partially, distinct mechanisms. As briefly mentioned above, while discrimination thresholds in the subitizing range are constantly near to zero, thresholds in the estimation range obey Weber Law (Revkin et al., 2008). Within this range, the Just Notable Difference increases linearly with numerosity, making the Weber Fraction (JND normalised by perceived numerosity) almost flat. For highly dense stimuli (texture-density regime) thresholds decrease as a function of square-root of numerosity. Importantly, 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 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., 2014).

Strong evidence comes also from two other recent psychophysical works testing which visual feature spontaneously dominates perceptual decisions when observing dot-arrays (Cicchini et al., 2016, 2019). These studies employed stimuli that varied unpredictably in numerosity, density or area and participants were asked to identify the odd-one-stimulus among three or 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 which features they had to reproduce. Results clearly show that, for numerosities in the 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 texture density.

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

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 et al., 2012a, 2012b; Burr et al., 2010) suggesting a heavy reliance on attentional resources in order to attain near perfect performance which characterises subitizing. These results fit well with a fMRI study showing that the right temporal-parietal junction (rTPJ), an area thought to be involved in stimulus-driven attention (Corbetta and Shulman, 2002), is activated during a numerosity comparison task, but only for numbers in the subitizing range, not for the estimation range (Ansari et al., 2007). Moreover, Vetter et al. (2011) showed that this area responds to small numbers only in conditions of low attentional load.

More recently Pomè et al. (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 et al. (2012) found strong visual attentional costs on numerosity and density thresholds, for high numerosities (128 dots).

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 texture-density rather than numerosity and not related to mathematical abilities.

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).

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

2. Methods

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.

2.2. Patient description

PA is a 40-year old right-handed male who suffered from hypoxic insult due to a heart attack. He was transferred to the rehabilitation center “Auxilium Vitae” in Volterra from the intensive care unit and was finally discharged after 120 days from the hypoxic insult. He had difficulty in recognising simple everyday objects, perceiving more than a single object at the time (simultagnosia), controlling voluntary and purposeful eye movement (oculomotor 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 deficit and mild impairment of the executive functions. He was autonomous in walking, 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 lesion and a very subtle variation of the signal into the basal ganglia. These findings were much less evident at the brain MRI scan collected at 90 days from the event (Fig. 1). However, in this latter scan, there was evidence of an overall brain atrophy, in particular in the occipitotemporal inferior regions and in the frontal and parietal paracentral regions and in the hippocampal areas.

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

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 1680×1050 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.

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 Comprehension Index			79
Working Memory Index			1*

VMI (Verbal Comprehension Index) and WCI (Verbal Comprehension Index) indexes were obtained at 6 months from injury. The VCI is a 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 obtained from the WAIS-IV sub-tests: digit span and arithmetic. It measures the ability to absorb information presented verbally, to manipulate that information in short-term immediate memory, and then to formulate a response. Performance below normal range is indicated with a * symbol.

2.4. Stimuli and procedure

2.4.1. Visual attention

We measured attentional abilities with a multiple-object tracking task (Arrighi et al., 2011; Pylyshyn and Storm, 1988), sketched in Fig. 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

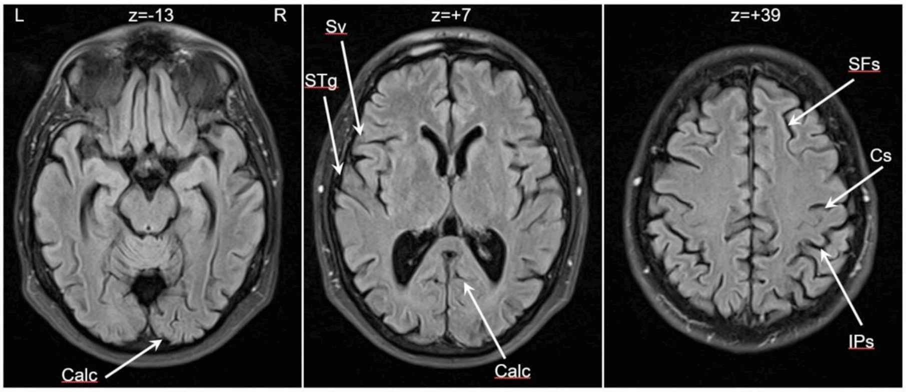

Fig. 1. MRI 90 days from the insult. T2w FLAIR images were acquired using a SIEMENS Symphony 1.5 T scanner and a spin-echo inverse recovery sequence (acquisition parameters are: TR/TE/TI: 9400/124/2500 ms, FA: 150, acquisition matrix: 320×260, voxel size: $0.688 \times 0.688 \times 4.8$ mm, 30 axial slices; for TR/TE/TI: 10000/120/2500 ms, FA: 150, acquisition matrix: 512×376, voxel size: $0.508 \times 0.508 \times 4.4$ mm, 28 axial slices; acquisition parameters). In order to correct for inter-individual differences in brain size and brain volume orientation, the MRI brain volume of PA was transformed into the standardised MNI space using the software REGISTER (http://www.bic.mni.mcgill.ca/ServicesSoftwareVisualization/Register). This program uses more than 5 neuroanatomical landmarks to match individual patient brain volumes to the 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 Neurological Institute www.bic.mni.mcgill.ca/software/Display/Display.html), an interactive program that allows for the simultaneous visualisation of the movement of the cursor on the screen within the sagittal, horizontal and coronal planes of the brain MRI together with visualisation of x, y, z coordinate. Brain sulci of PA a 40 years old man, were overall 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 brain atrophy in the occipitotemporal inferior regions and into the hippocampi; the axial slice 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 Temporal gyrus, Sv = Vertical Ramus of the Sylvian fissure, SFs = Superior Frontal sulcus, Cs= Central sulcus, IPs = Intraparietal sulcus.

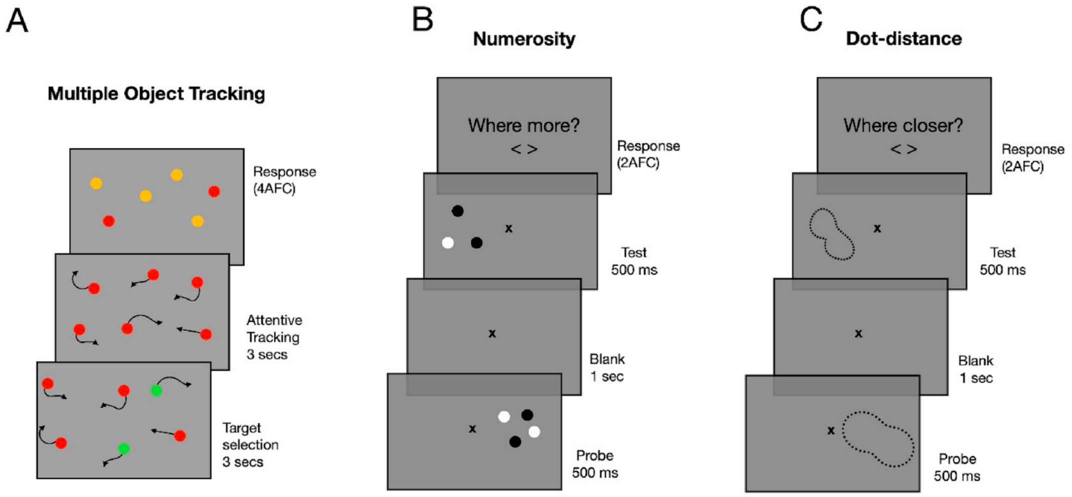

Fig. 2. Schematic illustration of tasks. Stimuli were not draw in scale in these images, for stimuli details see the methods. A) *Multiple object tracking.* In the target selection phase, participants attentively track green targets moving among red distracters (4 in the example), for a period of 3 s. At the end of this phase, the green targets turn red (like the distracters) and subjects track them for 3 s. In the response phase, disks stop and participants are asked to identified which of four possible items (highlighted in orange) was green in the target selection phase. B) *Numerosity comparison.* A patch of dots with variable numerosity (4 in the example) is briefly (500 ms) presented to the right side of a central fixation point. After 1 s 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-distance comparison.* A dotted-shape with inter-dots distance varying trial by trial is briefly (500 ms) presented to the right side of a central fixation point. After 1 s of blank screen, a second dotted-shape is presented on the left side, containing a fixed interdots distance. Subjects are asked to indicate the stimulus with longer interdots distance. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

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 period of 3 s, and participants had to hold their attention on the targets. After 3s, the green 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 point towards) which one of four possible items (highlighted in orange) had previously been green a target (4AFC). The subjects were not asked to respond quickly, but were given all the time they needed to decide. Each experimental session comprised around ten trials. Participants performed one session for each distractor number condition. PA performed 52 trials (10, 16, 10, 10, 6 for each distractors level), Control 1 performed 60 trials (10 for each level) and Control 2 performed 70 trials (10, 10, 20, 10, 20). No feedback was provided. Performance was measured as a proportion of correct responses.

2.4.2. *Numerosity discrimination*

Numerosity thresholds were measured with a two-interval comparison task (2 IFC), sketched in Fig. 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 at random within a circular virtual region (10° diameter), respecting the condition that two dots (center-to-center) should not be separated by less than 0.5°. Dot arrays were sequentially presented for 500 ms each with a fixed blank inter-stimulus interval of 1 s. Dot clouds were centered at ±10° from a central fixation point. The side of the probe and test stimuli relative to the central fixation point was kept constant in order to reduce the spatial uncertainty that 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 dots. As in the attention task, subjects were not asked to respond quickly. In a particular session, the left-side stimulus maintained the same numerosity across trials (test), while the 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 and Pelli, 1983), perturbed with a Gaussian noise with a standard deviation 0.15 log-units. The QUEST algorithm is an adaptive procedure for efficient threshold estimation. The algorithm decided trial-by-trial, according to the subject performance, the best stimulus intensity for the next 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 trials (95, 70, 40, 40, 40, 30 trials for each numerosity levels respectively), the first control subject (Control 1) performed 660 trials (60, 120, 120, 120, 120, 120), the second control subject (Control 2) performed 490 trials (90, 80, 80, 80, 80, 80) all the others (Controls 2–7) 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 dots in log-scale, and fitted with a cumulative Gaussian error function (lapse rate 5%). The 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% correct responses defines the just-noticeable difference (JND), a measure of precision at each test numerosity level. Precision (JND) divided by the PSE numerosity, yields the Weber Fraction (WF), a dimensionless quantity that allows comparison of performance across numerosities.

2.4.3. *Serial counting*

Counting ability was tested with a time-unlimited naming task. The stimuli were clouds of non-overlapping white dots (0.5° diameter each). The position of each single dot was chosen at random within a circular virtual region (10° diameter), respecting the condition that two 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 until participants gave a verbal estimation. Participants were instructed to enumerate as fast as they could the dot array, no feedback was provided. As soon as participants provided a response, the experimenter (blind to the stimuli), pressed the space bar in order to save response time. Finally, the experimenter entered the participant numerical response by the keyboard. P.A. performed a total of 51 trials (7,7,7,5,5,5,5,5,5 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 we computed mean response time (secs) and average response.

2.4.4. Object distance perception

Peripheral distance judgements were assessed via a custom paradigm which displayed two rings made out of twenty small dots (5 pixels diameter), akin to beads making up a necklace (Fig. 2C). The center 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 center 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 (2π radiants) following the formula:

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

where ϑ is the polar angle, r_0 is the average radius (chosen randomly between 3° and 4.5° degrees for each stimulus), A_5 and A_2 are the amplitudes of the two sinusoids (random between 0.33° and 0.67° the former and fixed at 1.7° the latter) and φ_5 and φ_2 are the two phases (random between 0 and 2π). As in the numerosity task, stimuli were sequentially presented for 500 ms each with a fixed blank inter-stimulus interval of 1 s and the side of the 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 interdot spacing. The left-side stimulus maintained the same inter-dot distance across trials (test, 0.7°), while the other (probe) varied between 0.1 and 1.5°. Proportion of judgments in which the test was judged as "sparser" than the test was plotted as function of test inter-bead distance and fitted with a standard psychometric function (see Fig. 4). The difference between the spacing that yield 50% and 75% "more sparse judgments" defines the just-noticeable difference (JND) which, divided by the PSE, yields the Weber Fraction (WF). PA performed a total of 53 trials, Control 1 performed 160 trials, all the others performed 110 trials. Standard Errors are calculated via bootstrap (Efron and Tibshirani, 1986).

2.5. Data analyses

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

The subjects' statistical differences on numerosity thresholds (WF) were calculated by a bootstrap technique (Efron and Tibshirani, 1986). For each participant, and separately for each 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 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 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 controls' WFs on numerosity 12 and 16 (estimation range) as well as those for numerosity 64 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 index) and counted the time the deficit in one range was higher than that in the other (p-value). Numerosity 32 was eliminated from this analysis because for one control participant the WF already started to decrease at this numerosity level making it difficult to categorise it as belonging to the estimation or texture-density regime.

We checked the presence of subitizing advantage in serial counting by looking at response time (RT) variation as a function of item number. For each subjects and separately for each numerosity, raw response time were randomly resampled (1000 iterations, selecting a data set 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 starting with a constant segment and then rising as function of numerosity. On each iteration, we calculated the goodness of fit of the linear and the two limb function by means of Akaike information criterion (AIC). The p-value represents the fraction of times that a given AIC is lower than that of the competing model.

Object distance perception. The subjects' statistical differences on dot-distance thresholds were calculated by a similar bootstrap technique: for each participant, raw data were 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 proportion of time that PA's WFs were lower than the controls' average was the p-value.

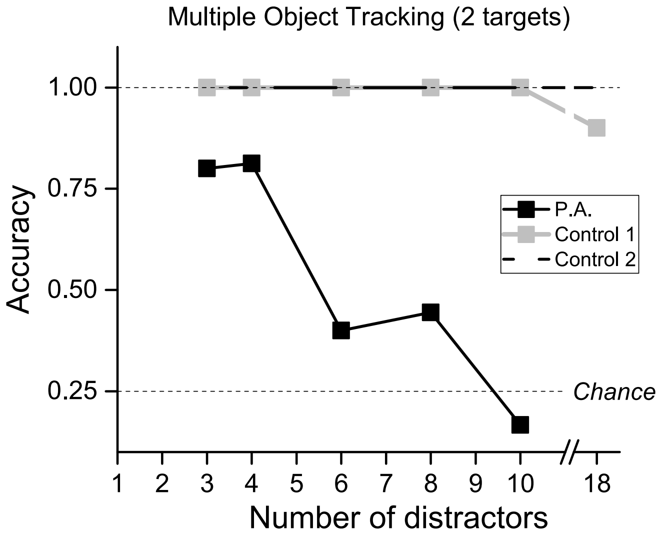

Fig. 3. Visual attention. Accuracy in the multiple object tracking task as a function of number of distractors in the control participants (greys) and for the patient PA (black). Chance and perfect performance levels are highlighted by dashed lines.

3. Results

3.1. Visual attention

Visual-spatial attentional capacities were psychophysically measured by a Multiple Object Tracking task (Fig. 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).

Fig. 3 shows a proportion of correct responses as a function of the number of distractors. For both control participants (greys lines and symbols), performance was almost perfect with accuracy slightly decreasing at the most difficult condition (18 distractors) for one participant (Control 1, in the figure).

PA was able to perform the task, with accuracy above the chance level (0.25 accuracy) in the less 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 $p < 0.01$).

3.2. Numerosity discrimination

Having established the attentional deficit, we moved to the numerosity discrimination thresholds measurement. According to the three-

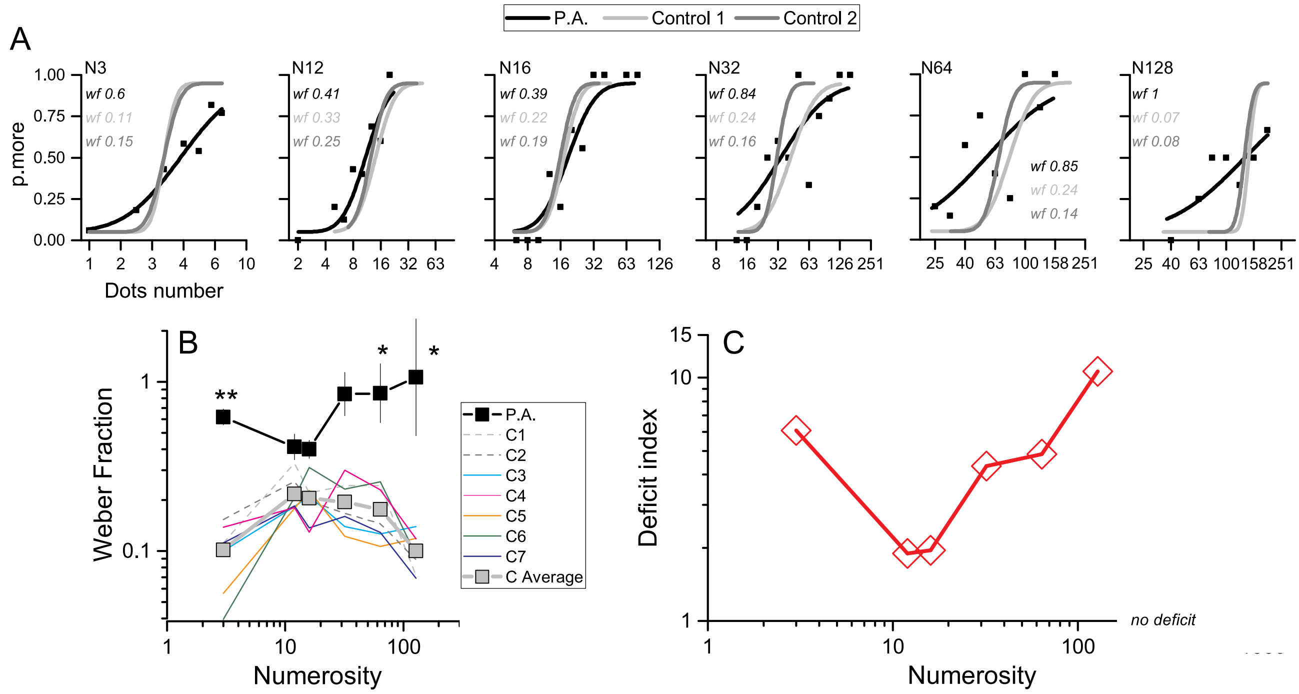

Fig. 4. Numerosity discrimination. A) Psychometric functions from two representative controls (light and dark grey) and the patient (PA) for various level of numerosity, spanning the three regimes. B) Discrimination thresholds (WF) for the patient PA (black), controls (thin coloured lines) and averaged 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. $^*p < 0.05$, $^{**}p < 0.01$.

system hypothesis and previous studies on attentional deprivation (Anobile et al., 2012a, 2012b; 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).

Numerosity discrimination thresholds were measured by a two alternative forced choices method. On each trial, a dot-array (test, fixed numerosity) was briefly (500 ms) presented to the right side of the screen followed by a blank pause and by a second patch to the left side (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) were calculated for each test numerosity level (see methods for details).

Fig. 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.

Fig. 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 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 rose ($\cong$ 0.2) and remained constant for higher numerosities (from 12 to $\cong$ 64); finally, WFs 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 three systems.

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).

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).

To better visualize the PA sensory thresholds deficit across numerosity levels, we computed a "deficit index" as the ratio between PA's and the controls' average WF levels. Fig. 4C 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 numerosities in the estimation range (12 and 16) was 2.0 while that for numerosities in the texture-density regime (64 and 128) was 8.2 ($p = 0.03$). For the subitizing range (N3) the average deficit was 7.1, higher than the estimation range ($p = 0.009$) but not compared to the texture-density regime ($p = 0.53$).

3.3. No evidence of subitizing in counting task

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

PA behaviour dramatically differed from this classic pattern. His response times grew steadily as function of numerosity even with the least numerous items and, for instance 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 process. To confirm this quantitatively we fit the two datasets (PA and controls) with two functions, either a linear function or a two-limb linear function and compared the two models 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 $p = 0.008$). Conversely, for PA's data it was the linear function to provide a better model for the data ($p = 0.04$).

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

3.4. Object distance perception

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.

Fig 6 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 ± 0.01). On the other hand, PA had severe difficulties in performing the task with ten times higher thresholds (0.56 ± 0.29) 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.

4. Discussion

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.

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 et al., 2012a, 2012b; Burr et al., 2010; Pomè et al., 2019).

We would like to stress that the aim of the current study was not to describe visual perception in simultanagnosia nor the link between math skills and numerosity perception in these 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 possibility to restrict the functional deficit to a circumscribed damage. In any event, our 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 mechanisms (Anobile et al., 2016a, 2016b; Anobile et al., 2012a, 2012b; Pomè et al., 2019).

The idea of studying numerosity perception in simultanagnosic patients is not entirely new, and was similarly motivated by the fact that these patients fail to allocate attention to multiple objects (Rizzo and Vecera, 2002; Robertson, 2014), one of the functions that support numerosity encoding (Mazza, 2017). The few available studies, however, have focused mostly on counting, namely the process involved in

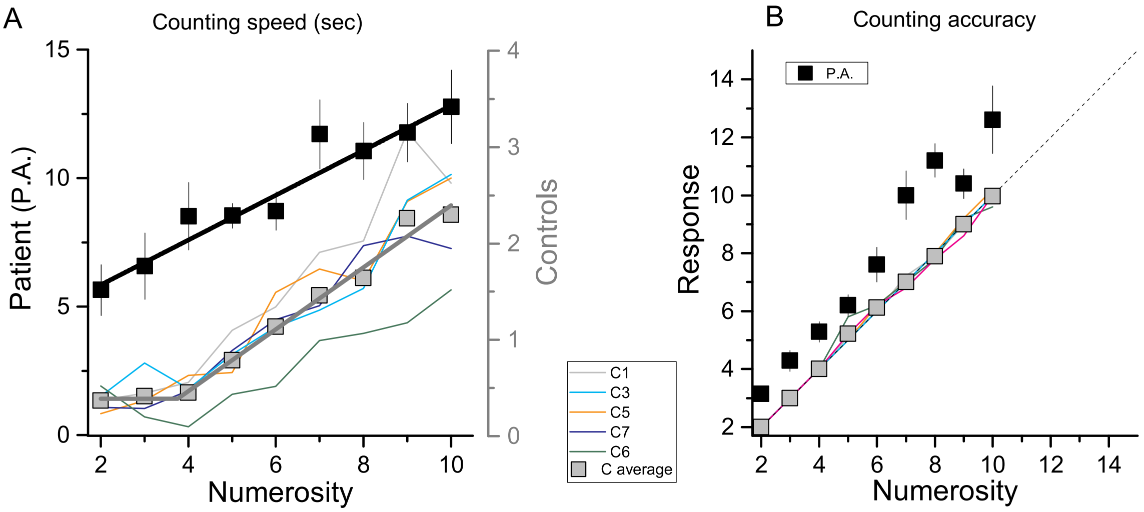

Fig. 5. Dot-counting task. A) Response time (secs) as a function on numerosity for the patient PA (left ordinate, black squares) and control subjects (right ordinate, thin lines report single subjects data; grey squares represent average). B) Average response as a function on numerosity for the patient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

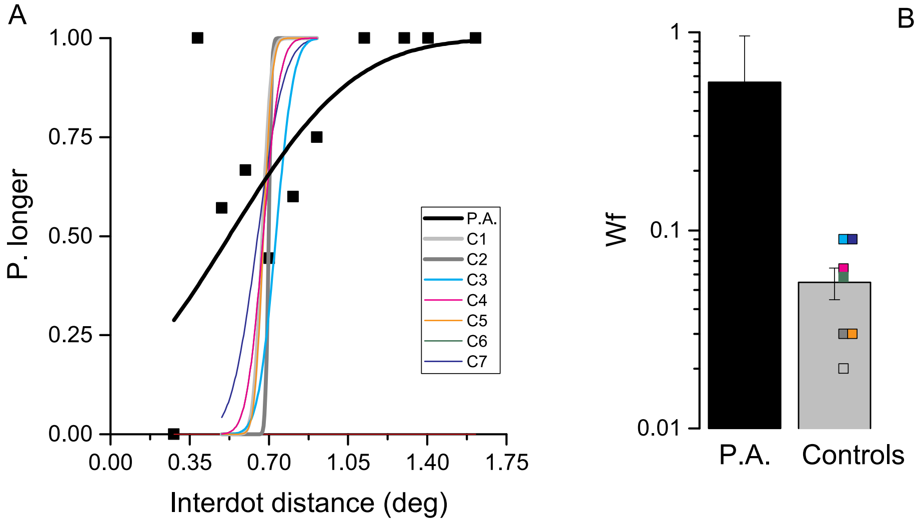

Fig. 6. Dot-distance discrimination. A) Psychometric functions from the controls (light coloured curves) and the patient (PA, black function and data points) obtained in the dot-distance discrimination task. B) Discrimination thresholds for PA and controls. Isolated data points show single subject data.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

serial and slow exact enumeration, with only few measuring approximate estimation of briefly displayed stimuli, where counting is prevented (Dehaene and Cohen, 1994; Demeyere and Humphreys, 2007). Moreover, a direct measure of discrimination thresholds over a broad numerical range is lacking.

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 capacities by visual search tasks and numerosity performance by a verbal magnitude estimation task with five simultanagnosic patients. Dot stimuli were either presented fast (200 ms) or displayed onscreen until response. Results showed that some but not all patients had attentional deficits. In the numerical tasks, patients produced more errors than controls for numerosities above three but had relatively preserved accuracy in quantification of one, two and sometimes three items, demonstrating the subitizing effect. Demeyere et al. (2010) also found unimpaired exact counting for numbers up to four items but impaired enumeration for higher numbers in a brain lesioned patient. Demeyere and Humphreys (2007) measured numerosity performance on GK, a patient with severe simultanagnosic symptoms and clearly impaired attentional capacities. At odds with Dehaene & Cohen patients, GK showed no sign of subitizing advantage, with error rates linearly increasing with numerosity. Our data on serial counting mirrors those of patient GK, with no evidence of subitizing advantage with response time linearly increasing with numerosity. Interestingly, the authors found that when asked to compare the relative numerosity of two fast consecutive displays, GK's performance (error rates) was significantly above chance for 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 et al., 2008).

On the basis of these few clinical studies and those demonstrating that subitizing requires attentional resources (Anobile et al., 2012a, 2012b; Burr et al., 2011; Burr et al., 2010; Egeth et al., 2008; Juan et al., 2000; Olivers and Watson, 2008; Railo et al., 2008; Vetter et al., 2008; Xu and Liu, 2008), we speculate that PA's subitizing deficit is, at least partially, linked to his poor visual attentional skills. Indeed, much previous literature has suggested that subitizing is not a pure numerical ability but reflects a domain general capacity to tag and monitor items of interest in the visual scene. These are attentional demanding 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 et al., 2011). Thus, a loss of the capacity to deploy attention upon objects in space may well result in a loss of near perfect performance in the subitizing range.

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 estimation of highly packed displays is often thought to rely on simple feature detectors which are present in the earliest stages of analysis of a visual scene (Dakin et al., 2011; Morgan et al., 2014). So, how could an attentional deficit interfere with numerosity of dense patterns? In previous work we have suggested that the pattern of square-root relationship governing thresholds in this regime (Anobile et al., 2014, 2015) may result from a mechanism that computes interdot distance and assigns the label of more dense (or more numerous) to the one that possesses the smallest average distance (Anobile et al., 2014). Consistently with this, PA 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 feature extraction such as object distance. It is also interesting to note that PA, notwithstanding the deficit in distance estimation, performs relatively well at intermediate numerosities. This strongly suggests that perception of intermediate numerosities is governed by a specific mechanism which depends little on low level features (Anobile et al., 2014; Anobile et al., 2016a, 2016b; Cicchini et al., 2016, 2019).

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

5. Conclusions

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.

CRediT authorship contribution statement

G. Anobile: Conceptualization, Methodology, Data curation, Software, Writing - original draft, Visualization, Investigation, Formal analysis. **F. Tomaiuolo:** Investigation, Supervision, Conceptualization, Writing - original draft, Data curation, Formal analysis. **S. Campana:** Supervision, Methodology, Investigation, Data curation. **G.M. Cicchini:** Conceptualization, Methodology, Data curation, Software, Writing - original draft, Writing - review & editing, Supervision, Visualization, Formal analysis, Investigation, Validation.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuropsychologia.2019.107259.

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