Research Report

Brain dynamics of attention and working memory engagement in subitizing

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ABSTRACT

This study addressed the engagement of attention and working memory, as inferred from electrophysiological measurements, in the processing of small sets of objects. We recorded N2pc and CDA, two lateralized components of the EEG signal associated respectively with individuation and visual working memory, while participants enumerated a variable number (1–9) of uniquely colored targets among distractors. Behavioral results showed a clear subitizing effect, with lower error rates for smaller (1–3 targets) than larger sets. ERP results showed that both N2pc and CDA amplitudes increased as a function of target numerosity up to approximately three targets. However, individual differences in the enumeration efficiency were correlated only with the individual variation in the N2pc modulations. The results suggest that the constraints of the attentional individuation system play a significant role in the occurrence of the subitizing phenomenon.

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1. Introduction

Decades of behavioral research has indicated that humans are very accurate and fast when enumerating small set of objects, up to approximately three–four elements (Kaufman et al., 1949; Mandler and Shebo, 1982; Trick and Pylyshyn, 1994). This phenomenon is known as subitizing and it is signaled by the presence of an inflection point in the behavioral data function, corresponding to a sudden change in the enumeration slope. This inflection point is considered as the signature of the existence of two different ways of processing small and large numerosities (but see Whalen et al., 1999 for a different account). Neuroimaging experiments have provided support for this distinction by showing different brain activations associated with the enumeration of small versus large object quantities (Ansari et al., 2007; Vuokko et al., 2013). Additionally, studies on patients have reported dissociations in processing small and large quantities of objects (Dehaene and Cohen, 1994; Demeyere et al., 2012).

Despite the large number of studies on the subitizing phenomenon the nature of small-numerosity processing remains elusive. There are at least two contending accounts of the subitizing effect (e.g. Feigenson et al., 2004; Leslie et al., 1998; Trick and Pylyshyn, 1993; Whalen et al., 1999). On one account (Cavanagh and He, 2011; Trick and Pylyshyn, 1994), subitizing reflects a limitation in the simultaneous individuation of multiple objects. While early proposals (e.g. Trick and Pylyshyn, 1993) argued that individuation operates pre-attentively, there is growing consensus that it is one of the key functions of attention. Therefore, capacity limits of the

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attentional functions could play a key role in the subitizing phenomenon. In line with this explanation, recent studies have indicated that enumeration accuracy for small target numerosities varies with modulations of the attentional load (e.g. Egeth et al., 2008; Railo et al., 2008; Vetter et al., 2008). Support for this account has also come from neuroimaging studies (Ansari et al., 2007; Vetter et al., 2011), which have shown differential modulation of the temporo-parietal junction, a region previously linked to exogenous attention (e.g. Corbetta and Shulman, 2002), for small versus large target numerosities.

An alternative explanation of subitizing considers this effect as the result of late, capacity-limited processes related to visual working memory (Cowan, 2001; Feigenson et al., 2004; Feigenson, 2011). This account is based on the idea that working memory may be crucial for maintaining active the representations of individual items during the process of mapping the set of elements onto a specific numerical value. Since visual working memory is limited in capacity (Cowan, 2001) only a limited number of representations can be maintained active simultaneously, thus generating the subitizing effect. The working memory account of subitizing is inspired by previous research on multiple objects discrimination in infants and animals. In these studies participants choose between two groups of objects that were previously hidden behind a screen simultaneously (e.g., Rugani et al., 2009) or, in other paradigm (e.g., Feigenson and Carey, 2003, 2005) they search for objects that were sequentially hidden in a box. Results indicate that both infants and animals are able to retrieve correctly all the objects or to choose the larger amount of items only when their number does not exceed three or four, thus suggesting that they possess the ability to discriminate small numerosities. Support for the working memory account of subitizing is provided by a recent study on human adults that has found that individual differences in a working memory task are correlated with individual variations in the subitizing limit (Piazza et al., 2011; but see Tuholski et al., 2001). In that study participants had to count a variable number of items while maintaining two or four objects in visual working memory for a delayed match-to-sample judgment. The individual subitizing range varied as a function of the number of objects to be maintained in visual working memory, suggesting that this mechanism may have a significant role in the subitizing phenomenon.

In the present study, we used an electrophysiological approach to investigate the contributions of multiple object individuation and working-memory processes on subitizing. The high temporal resolution of EEG affords the opportunity to investigate temporally dissociable processes such as object individuation and visual working memory, which are assumed to operate in sequence and have therefore separate time courses. Using this approach, it is possible to address directly the involvement of these temporally separated mechanisms in enumeration of small quantities in a single task, without having to introduce a secondary task to probe the involvement of a specific process (attention versus VWM) on the subitizing effect. We focused on N2pc and CDA, two neural indexes that have been recently shown to track, respectively, individuation of multiple objects and their maintenance in visual working memory.

N2pc (N2 posterior contralateral) is a transient component of the ERPs that is recorded around 200 ms post-stimulus onset from the posterior electrodes contralateral to the side of presentation of lateralized targets (Eimer, 1996; Luck and Hillyard, 1994). The N2pc is considered to be the neural reflection of target selection (either through target enhancement or distracter suppression) and is elicited in a variety of tasks, ranging from present/absent judgments to visual discrimination and multiple object tracking (Drew and Vogel, 2008; Mazza et al., 2009a, 2009b). Recent studies on enumeration (Ester et al., 2012; Mazza and Caramazza, 2011; Mazza et al., 2013; Pagano and Mazza, 2012) have found that the N2pc amplitude changes as a function of target numerosity. For instance, Ester et al. (2012) found that the amplitude of N2pc was modulated by the number of targets to be enumerated, increasing up to three items and then reaching an asymptote for larger numerosities. This result suggests that subitizing depends on constraints operating at the individuation stage where only a limited number of objects can be individuated simultaneously (Pylyshyn, 1989; Trick and Pylyshyn, 1993).

CDA (Contralateral Delay Activity; also called SPCN, Sustained Posterior Contralateral Negativity) is a sustained negativity elicited at approximately 400 ms post-stimulus onset from posterior sites contralateral to the side of the target (Robitaille et al., 2009; Vogel and Machizawa, 2004). This component has been recorded mainly in delayed match-to-sample tasks during the maintenance phase (Ikkai et al., 2010; McCollough et al., 2007; Vogel and Machizawa, 2004) or in multiple object tracking tasks during the tracking period (Drew et al., 2012; Drew and Vogel, 2008). The CDA amplitude is also modulated by the number (up to 3–4) of objects that must be maintained in visual working memory, suggesting that this component reflects a capacity-limited mechanism that maintains active multiple visual representations (Vogel and Machizawa, 2004).

To assess the role of both individuation and visual working memory in subitizing here we asked participants to count an extended range of target numerosities (1, 2, 3, 4, 5, 6, 7, 8 and 9) while recording N2pc and CDA. We evaluated the involvement of N2pc and CDA in subitizing by concentrating on three key aspects of the electrophysiological activity.

First, we focused on the modulations of N2pc and CDA in response to changes in the number of targets to be enumerated. If both individuation and working memory are involved in simultaneously processing multiple targets during enumeration, both the N2pc and CDA should be modulated by the number of targets presented in the visual field. Second, given the limit in the number of objects that can be "subitized", we predicted that we should observe an inflection point in the neural mechanism(s) that underlies the subitizing phenomenon, a sort of "neural subitizing effect". For this reason, we assessed for the presence of an inflection point in the electrophysiological response (see also Ester et al., 2012). To anticipate, here we focused on a subset of target numerosities (1–5) instead of taking into account the whole range (1–9). This was done to make our results comparable to the extant ones (Ester et al., 2012). Third, we evaluated which of the mechanisms (individuation or working memory, or both) better reflects the subitizing phenomenon by focusing on the correspondence between individual differences in the behavioral subitizing and individual differences in the neural

components. Here we hypothesized that there should be a close relationship between individual differences in enumeration performance and individual differences in the efficiency of the neural component(s) that track the subitizing effect.

Previous studies (Ester et al., 2012; Mazza et al., 2013; Pagano and Mazza, 2012) have shown that the attentional mechanism indexed by N2pc plays a role in subitizing. However, the literature lacks a thorough assessment of the CDA pattern as a function of target numerosity during enumeration. To our knowledge, Pagano and Mazza (2012) is the only study that measured CDA during a task in which participants had to enumerate multiple targets presented among distractors. The study indicated that CDA was modulated by target quantity, suggesting that visual working memory may be involved in subitizing. However, the use of a sparse range of target numerosities in that study (i.e. 1, 3, 5 and 7 targets) may have induced the use of strategies (e.g., classification and/or estimation) that are not typically involved in exact enumeration of small target quantities. Moreover, the use of a limited range of numerosities may have shaped the enumeration function accordingly, inducing an "end effect" (Mandler and Shebo, 1982) for the largest numerosity in the set (i.e. 7), and thus reducing the possibility of a detailed assessment of the CDA modulations for object numerosities. By using a more extended and continuous set of numerosities in the present study we sought to overcome the limitations of the previous studies in assessing the functioning of individuation and visual working memory during subitizing. The use of the 1–9 numerosity range was motivated by previous research (e.g. Trick and Pylyshyn, 1993, 1994) showing that this range elicits a stable subitizing effect at approximately 3 targets. In addition, adding more data points to the enumeration function with several numerosities within and above the subitizing range allowed us to obtain a fine-grained assessment of the N2pc and CDA trends during enumeration.

2. Results

2.1. Behavioral results

Error rates increased as a function of target numerosity (see Fig. 1B), as confirmed by a significant main effect of target numerosity in the repeated measures ANOVA with numerosity (8 levels) as factor, $F(7,105)=181.2$, $p<.0001$. When testing separately the two numerosity ranges (small range: 1–4 targets; large range: 5–8 targets) there was a significant effect of target numerosity in both cases (small range: $F(3,45)=49.09$, $p<.001$; large range: $F(3,45)=12.45$, $p<.001$), indicating that error rates increased both in the small and in the large ranges. However, visual inspection of the error rate trend revealed that the steepness of the function was different in the two ranges, replicating the findings of previous studies on visual enumeration (e.g. Trick and Pylyshyn, 1993, 1994). A more thorough statistical assessment of the function steepness is reported in Section 2.5.

2.2. ERP results

The first ANOVA with component (N2pc and CDA) and numerosity (1–8) as factors showed significant effects of numerosity,

$F(7,105)=10.2$, $p<.001$, component $F(1,15)=15.08$, $p<.01$, and of the numerosity X component interaction, $F(7,105)=14.02$, $p<.001$. However, the follow-up ANOVAs conducted separately for the N2pc and CDA to explore the significant interaction indicated a significant effect of numerosity for both components (N2pc: $F(7,105)=p<.01$; CDA: $F(7,105)=13.04$, $p<.001$).

The ANOVA on the small numerosity range (1–4 targets) showed a significant effect of numerosity for both N2pc, $F(3,45)=7.74$, $p<.0001$, and CDA, $F(3.45)=27.4$, $p<.001$ The ANOVA on the large numerosity range (5–8 targets) revealed no significant effects (N2pc $p=.16$, CDA $p=.25$). These results suggest that the amplitude of both components increased as a function of target numerosity only in the small numerosity range (see Fig. 2A and B). The scalp topographies of both components confirmed this pattern by indicating that the amplitude modulations of both N2pc and CDA were present in the small numerosity range but not in the large range (see Fig. 2C and D).

2.3. Model fitting results

The results reported in the present section were computed for both behavioral and neural data using from 1 to 5 targets, as in the original study by Ester et al. (2012). The choice of this range additionally allowed us to avoid contaminations in the model fitting due to participants' performance (see Section 5 for a detailed explanation).

The results of the model fitting on the behavioral data showed that the exponential model (mean adjusted $R^2=.94$) and the bilinear model (mean adjusted $R^2=.98$) had a similar performance in fitting the error rate functions. However, the comparison between the two models indicated that the bilinear model explained better the results, $t(15)=13.2$, $p<.001$. We estimated the inflection point by averaging together the inflection points computed by the bilinear model for each participant, the mean estimated inflection point was 3.2 targets (see Fig. 3A). Overall, the model fitting confirmed the presence of a significant subitizing effect for up to approximately 3 targets.

The results of the model fitting on the N2pc showed the presence of a significant bilinear pattern in the data. As for the behavioral data, the bilinear model (mean adjusted $R^2=.65$) has a better performance in modeling the N2pc pattern than the logarithmic model (mean adjusted $R^2=-.22$), $t(15)=5.4$, $p<.001$. In line with the behavioral analysis, the mean estimated inflection point for N2pc was 3.02 targets (see Fig. 3B). A similar pattern of results was found for the CDA component. The model fitting showed that the bilinear model (mean adjusted $R^2=.77$) explained the data better with respect to the logarithmic model (mean adjusted $R^2=.25$), $t(15)=4.1$, $p<.001$. The average of the estimated inflection points for CDA was 3.01 (see Fig. 3C).[1]

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[1]To evaluate the robustness of the results we also run the model fitting procedure using the 1–6 target range on both the neural and behavioral data. Consistent with the results reported in the main text, these analyses showed that the bilinear model represented better the data with respect to the exponential/ logarithmic one.
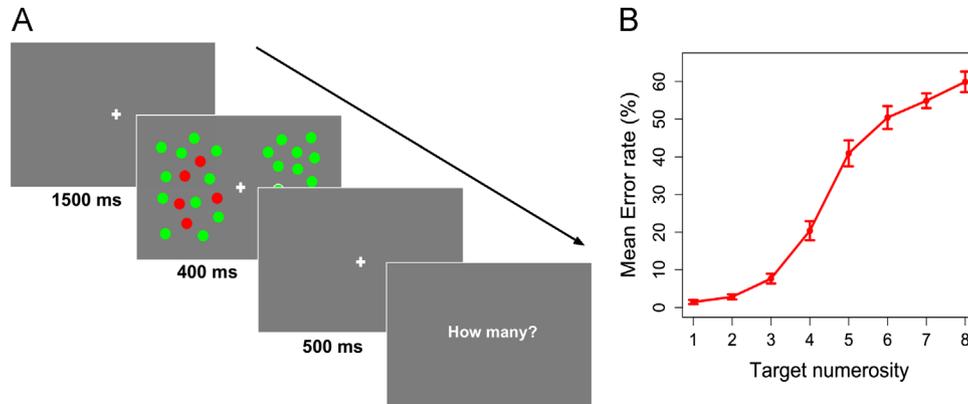
Fig. 1 – Procedure and behavioral results. (A) Example of a trial with five targets. (B) Error rates as a function of target numerosity. Error bars represent the standard error of the mean.

2.4. Correlational analyses

The results showed that the estimated slope of the N2pc between one and three targets was correlated with the individual inflection point in the behavioral data ($R = -0.64$, $p < .01$; Fig. 4). In particular, higher inflection points in error rates (i.e., higher enumeration efficiency) corresponded to a larger difference in the N2pc fitted values between one and three targets (see Fig. 4A and B). No significant effect emerged from the analysis on the CDA ($p = .18$).

2.5. Slope comparison

The results of the slope comparison on the range 1–8 for both behavioral and neural data showed the presence of a significant change in the slope of the pre- and post-inflection function. As expected, the slope for the error rate was steeper after the inflection point, $t(15) = -26.29$, $p < .001$ (pre-inflection slope = |7.62|%, post-inflection slope = |23.03|%).

The results of the comparison between the pre- and post-inflection slopes in the neural data converge with the behavioral results. The pre-inflection slope was considerably steeper than the post-inflection one for both components: N2pc $t(15) = -2.4$, $p < .01$ (pre-inflection slope = |0.63| μV, post-inflection slope = |0.50| μV) and CDA $t(15) = -3.5$, $p < .001$ (pre-inflection slope = |0.63| μV, post-inflection slope = |0.14| μV).

3. Discussion

The present study aimed at understanding the contribution of multiple object individuation and visual working memory to subitizing by comparing the electrophysiological markers of these two processes during enumeration. The results strengthen previous research and add new knowledge to the field of multiple object processing and visual enumeration.

First, in line with previous results (e.g., Ester et al., 2012; Pagano and Mazza, 2012), we found that the N2pc component was modulated by the number of targets to be enumerated and reached a plateau at around three targets. This result converges with a growing number of studies on N2pc (Ester et al., 2012; Mazza and Caramazza, 2011; Mazza et al., 2013; Pagano and Mazza, 2012) showing that this attentional component tracks the individuation stage of multiple object processing that is critical to enumeration of small object quantities.

Second, the modulations of the CDA during the enumeration task indicates that visual working memory is also involved in enumeration. Specifically, the results showed that CDA amplitude followed an asymptotic trend with a plateau at around three targets. This result is in line with previous behavioral (e.g. Cowan, 2001; Luck and Vogel, 1997) and neuroimaging (e.g. Todd and Marois, 2004) findings suggesting that visual working memory is a mechanism with a capacity limit at approximately three–four items. Similar findings on the CDA have been shown in tasks that require active and explicit maintenance of items and thus in which visual working memory plays a crucial role. For instance, numerosity-driven modulations of CDA have been found in delayed match-to-sample (Vogel and Machizawa, 2004) and multiple object tracking (Drew and Vogel, 2008) tasks in which participants are explicitly instructed to memorize the items either to recall them or to track them. Extending the results of Pagano and Mazza (2012), our findings indicate that numerosity-related modulations of CDA are also elicited during visual enumeration, confirming that visual working memory plays a role in the execution of visual tasks in which no active memory maintenance is required. More generally, this result suggests that visual working memory, as indexed by CDA, is sensitive to the quantity of information to be processed across different tasks.

The involvement of visual working memory in subitizing was also confirmed by the results of the model fitting. Here both the behavioral and neural data had a consistent bilinear pattern with an inflection point at around numerosity three. While this has already been demonstrated for error rates and N2pc (e.g., see Ester et al., 2012), the present results represent the first evidence that a similar pattern is present also for CDA during enumeration. Overall, this result resonates with previous studies showing a capacity limit in visual working memory (Cowan, 2001; Luck and Vogel, 1997), and adds the important information that visual working memory resources are recruited to some extent also when there is no explicit requirement to retain quantity information beyond the encoding phase.

Finally, the results of the correlational analysis provide important information regarding which of the two
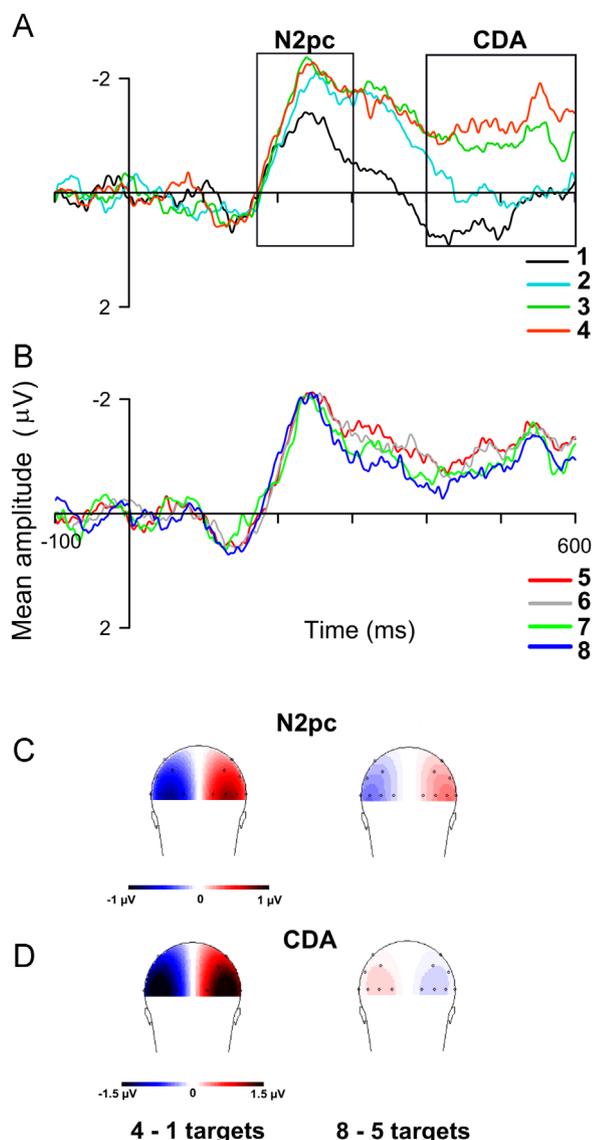
Fig. 2 – ERP results and scalp topographies. Top: N2pc and CDA difference waveforms as a function of target numerosity. Each line represents the contralateral minus ipsilateral difference in the activity at PO7/PO8 electrodes for numerosities 1–4 (A) and 5–8 (B). Bottom: topography of the numerosity effect in the small (left: 4−1 target difference) and in the large (right: 8−5 target difference) numerosity range for the N2pc (C) and the CDA (D). The maps (N2pc 180–300 ms and CDA 400–600 ms) were obtained from difference waveforms and mirrored across the midline.

mechanisms considered here played a significant role in subitizing. We found a correlation between the individual behavioral subitizing effect and the neural slopes between one and three items for the N2pc, but not for the CDA. This indicates that the strength of the N2pc modulation between one and three targets is associated with the individual subitizing range, with larger modulations of N2pc corresponding to higher enumeration performance. This result suggests that those individuals with an efficient individuation mechanism can apprehend more items simultaneously,

thus enlarging their subitizing range. In the light of the findings of Pagano and Mazza (2012) and Ester et al. (2012), this finding further extends the idea that individual limits in the individuation capacity shape the way multiple objects are enumerated.

In contrast with the N2pc pattern, the CDA component was not significantly correlated with the behavioral measures in our study suggesting that working memory capacity limits are not the proximal cause of the subitizing phenomenon and that the present CDA modulations may represent a byproduct of the functioning of the individuation mechanism. In other words, we can speculate that the limited capacity of individuation, as indexed by the N2pc pattern, limits the amount of information that enters visual working memory, thus inducing numerosity-driven modulation in the CDA component for up to three elements. This inference may seem to be in conflict with the results of previous studies on multiple object tracking and delayed match-to-sample judgments (Drew and Vogel, 2008; Vogel and Machizawa, 2004), which found significant correlations between behavioral capacity indexes and CDA modulations. However, it should be noted that visual working memory is particularly taxed in these tasks because they require maintaining information in memory for a relatively long period of time (i.e. some seconds). Therefore, it is likely that the capacity of visual working memory – which is supposed to maintain information over time – is more directly involved in the execution of these tasks, thus correlating better with behavioral performance.

4. Conclusions

The results of the present study add novel information on the dynamics of attention and visual working memory during enumeration of small object quantities. We found that both individuation, as indexed by N2pc, and visual working memory, as reflected by CDA, are involved during visual enumeration. Crucially, though, we showed that it is the individuation mechanism that plays the critical role in subitizing. These results suggest that constraints in the attentional stage of multiple object processing are directly linked to the emergence of the subitizing effect.

5. Experimental procedures

5.1. Participants

Sixteen healthy volunteers (males=2, mean age=23.3) were tested in two separate sessions after providing written informed consent. All participants had normal or corrected-to-normal vision. The study was approved by the local ethics committee.

5.2. Stimuli and procedure

A total number of 32 green (8 cd/m^2) and red (8 cd/m^2) dots, distributed equally on the right and on the left of a white fixation cross, were displayed on a dark gray background (6 cd/m^2). The dots appeared within an invisible 10 (rows) × 8
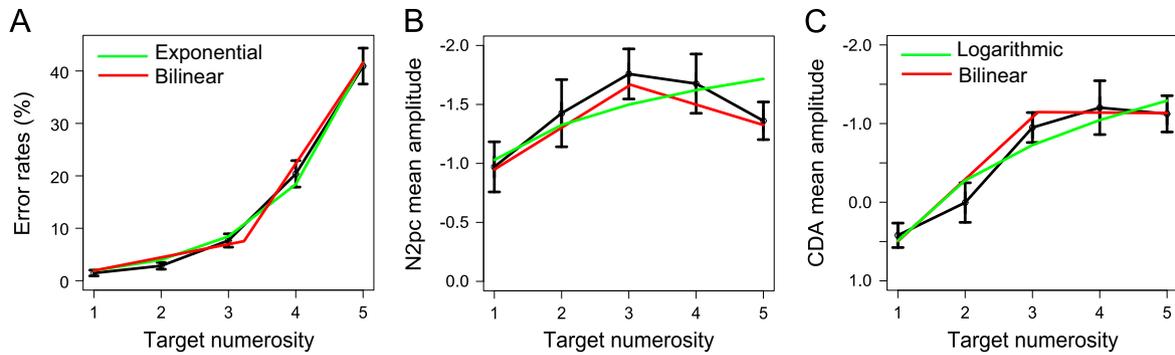
Fig. 3 – Model fitting results. Results of the bilinear (red line) and logarithmic/exponential (green line) model fitting superimposed on the behavioral (A), N2pc (B) and CDA (C) functions (black lines) in the 1–5 target range.

(columns) grid (10.7° × 5.4°). On each trial a varying number, ranging from 1 to 9, of uniquely colored targets (either green or red, counterbalanced across participants) was displayed either on the left or on the right side of the fixation cross in a random order. Targets could neither appear in the extreme columns or rows of the invisible grid, nor in the two columns adjacent to the fixation cross (see Fig. 1A). Participants' task was to report the number of targets by pressing one of the nine number keys in the upper row of the keyboard. The experimental procedure was the following. After an inter-stimulus interval of 1500 ms the stimulus was displayed for 400 ms. Subsequently, the fixation cross appeared for 500 ms (delay interval) followed by a prompt screen in which the question "How many?" was displayed. Participants were instructed to withhold from responding until the prompt display appeared. As soon as the prompt screen was displayed, participants had a maximum time of 2 s to press one of 9 keys on the keyboard. Only accuracy was recorded and analyzed. Participants completed a total of 1728 trials (192 trials for each target numerosity) divided in 24 blocks performed in two separate sessions. During the first session, an additional practice block was delivered before the experimental part.

During the experiment a remote eye-tracking device was used to control for horizontal ocular artifacts, providing an on-line feedback to the participants every five consecutive saccades. Ocular artifacts were defined as deviations of 1° either to the left or right of the fixation cross in the 0–600 ms post-stimulus interval.

5.3. EEG recordings and analyses

EEG was recorded from 25 channels (including PO7 and PO8) and from a left earlobe electrode. Data were referenced online to a right-earlobe electrode (bandpass filter: 0.01–200 Hz; A/D rate: 1000 Hz) and re-referenced offline to the average of the two earlobe sites. EEG was filtered using a 40 Hz low-pass filter with a 12 dB slope. The horizontal eye-movements (electro-hoculogram, HEOG) were recorded from two electrodes located at the external canthi of both eyes. Impedance was kept below 5 kΩ for all electrodes. Artifact rejection of horizontal eye-movements was carried out by rejecting trials with HEOG exceeding ±30 μV. Blinks, head movements and other muscular artifacts (any other channel exceeding

±80 μV) were also discarded. After artifact rejection, the average number of retained trials was 88.9%.

Averages for correct responses were computed separately for each target numerosity (from 1 to 8) and target side (left and right) using 700 ms long epochs starting 100 ms before stimulus onset. Trials with 9 targets were excluded a priori from the ERP and behavioral analyses in order to avoid contaminations due to the so called "end effect" (e.g., see Mandler and Shebo, 1982). The lateralized components were computed first by collapsing all electrodes across target side (i.e. left electrodes were labeled as ipsilateral and right electrodes as contralateral for left targets, and vice versa for right targets), and then by subtracting the ipsilateral activity from the contralateral one at posterior electrodes (PO7 and PO8) in two separate intervals: N2pc (180–300 ms) and CDA (400–600 ms).

5.4. Statistical analyses

5.4.1. General analyses
The first set of analyses was carried out on the entire range of numerosities (1–8) to evaluate the overall effect of target set size on the behavioral and neural data. For this reason, mean error rates, N2pc and CDA mean amplitudes were submitted to a repeated-measures ANOVA with numerosity (8 levels: 1–8 targets) and component (2 levels: N2pc and CDA; for the ERP data only) as factors.

In the second set of analyses we assessed more precisely the trends of the behavioral and neural data separately for the small and large numerosity range. To this purpose we split the eight levels of the factor numerosity in two sets and conducted two repeated measures ANOVAs, one for the small numerosity range (4 levels: 1, 2, 3, 4 targets) and one for the large numerosity range (4 levels: 5, 6, 7, 8 targets). This was done separately for error rates, N2pc and CDA amplitudes, for a total of six ANOVAs. When necessary, the results were corrected for the violation of the sphericity assumption using the Greenhouse–Geisser correction method. Only corrected p values are reported.

5.4.2. Model fitting and comparisons
In most of the previous studies (e.g. Trick and Pylyshyn, 1993, 1994) the subitizing effect is characterized by the presence of a "breaking point" in both error rates and/or reaction times.
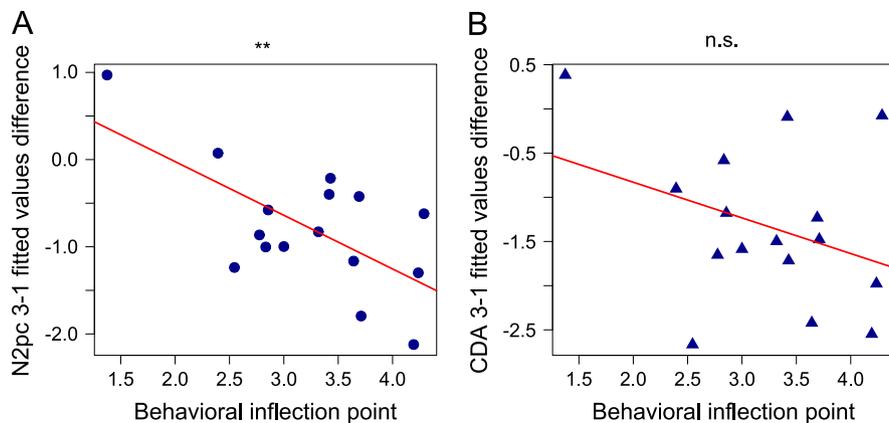
Fig. 4 – Correlations. Results of the correlation between the behavioral inflection point estimated by the model fitting on the error rates function (x axis) and the difference between 3 and 1 target in the fitted values calculated by the bilinear model for N2pc (A) and CDA (B).

This point corresponds to a sudden change in the slope of the enumeration function and should reflect a putative change in the underlying processing of object numerosities. The breaking point is usually observed at numerosity three or four and can be estimated by modeling the data according to a bilinear function (see Balakrishnanl and Ashby, 1991; Ester et al., 2012). Since the breaking point is considered the signature of the subitizing effect we reasoned that such inflection point should also be present in the neural component(s) involved in the generation of the subitizing phenomenon. Thus, following the same logic as in Ester et al. (2012), here we evaluated the presence of the inflection point by fitting the bilinear model on error rates, N2pc and CDA amplitudes for each participant. The modeling was performed using a piecewise linear model from the R library SiZer (Sonderegger, 2012). The goodness of fit of the bilinear model (adjusted R^2) was compared to the performance of a different model that does not predict the presence of a breaking point. This second function was different for the behavioral and the neural data since they have modulations in opposite directions (i.e. error rates are in the positive quadrant, N2pc and CDA are in the negative quadrant). Following Ester et al. (2012), we chose the exponential[2] function to model the error rates and the logarithmic[3] function to model the neural data. Differently from the bilinear model, the exponential and logarithmic functions do not predict any sudden change in the slope of the enumeration performance.

To compare the performance of the bilinear model with the exponential/logarithmic models we extracted for each participant and each measure (behavioral and neural) the adjusted R^2 of each model and compared them by means of a t-test. As in Ester et al. (2012), we restricted the modeling on both error rates and ERPs for the range between one and five targets in order to avoid contaminations in the model fitting due to participants' performance. This was necessary because for those participants who performed equally bad for the largest numerosities (i.e. seven and eight) the bilinear model considered the change in the steepness of this second part of the enumeration function (that actually did not represent the subitizing effect) to calculate the inflection point, thus overestimating the individual subitizing range. Differently from the Ester et al. (2012) study, which constrained the part of the curve post-inflection point to be parallel to the abscissa axis, we used a piecewise bilinear model that did not make any assumption on the slope of the function pre- and post-inflection point. This choice was driven by the fact that in the subitizing literature error rates between one and three–four items are rarely represented by a flat function but rather by a shallower function with respect to larger numerosities.

5.4.3. Correlations

To assess which of the two neural responses (N2pc and CDA) represents better the behavioral limit of subitizing, here we tested for individual differences in the behavioral subitizing effect and their correlation with the neural modulations. We reasoned that the individual inflection point of the error rates should correlate with the modulation of one or both neural responses, depending on whether individuation and/or visual working memory play a major role in the subitizing phenomenon. To this purpose, we correlated the individual behavioral inflection points estimated by the bilinear model with a slope index extracted separately for N2pc and CDA. This neural slope was calculated as the difference in amplitude between the smallest numerosity (one target) and the numerosity corresponding to the N2pc and CDA inflection points extracted by the model fitting procedure (i.e., three targets, see Section 5.4.2 for a description of the procedure and Section 2.3 for the results). The differences in amplitude as well as the inflection

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[2]The exponential function with two free parameters followed the same notation as in Ester et al. (2012): error$=\beta e^{\alpha n}$ where n is the set numerosity, e is the base of the natural logarithm and α and β are parameters to be estimated. The model fitting was performed using a customized R script based on the Nelder–Mead optimization algorithm (Nelder and Mead, 1965). This allowed to estimate the parameters and the adjusted R^2 of the model for each subject.

[3]The logarithmic function followed the same logic as in Ester et al. (2012): $y=\log_b X+\beta$ where b and β are respectively the base of the logarithm and a scalar value to be estimated. Also the logarithmic function was built using a customized code on R based on the Nelder–Mead optimization algorithm.

points were computed on the basis of the fitted values estimated by the bilinear model on each component. Our reasoning was that those individuals with higher enumeration efficiency (i.e., higher inflection points in error rates) may possess a better ability to individuate and/or maintain in working memory multiple targets simultaneously, and should therefore show a larger difference in the corresponding neural response between one and three targets (for a similar approach, see Ester et al., 2012). Thus, the difference of the fitted values between one and three targets should correlate with the individual inflection point in error rates (i.e. the individual capacity limit) for the neural component(s) underlying the subitizing effect.

5.4.4. Slope comparison

The model fitting procedure and the estimation of the inflection point on the neural and behavioral data capture a general difference in the slope pre- and post-inflection point without assessing which part of the function is steeper. This piece of information is important when testing for the presence of the subitizing effect. For instance, previous behavioral studies have demonstrated that the behavioral subitizing effect is associated with the shallower slope of the function (Trick and Pylyshyn, 1993, 1994). To assess the trends of the behavioral and neural functions, we compared the steepness of the slopes before and after the inflection point of each participant.

The pre- and post-inflection slopes were estimated individually using the whole range of numerosities from 1 to 8 and the inflection points estimated by the model fitting procedure. The pre-inflection slopes for the neural and behavioral data were calculated for each participant by subtracting the amplitude/error rate for 1 target (the smallest numerosity in the set) from the amplitude/error rate corresponding to the individual inflection point. The post-inflection slopes were computed by subtracting the amplitude/error rate of the first numerosity above the individual inflection point from the amplitude/error rate corresponding to 8 targets (the largest numerosity in the set). To compare the steepness of the pre- and post-inflection slopes we used a one tailed t-test. For the behavioral data, we tested the hypothesis that the pre-inflection slope would be smaller than the post-inflection slope. The opposite hypothesis (larger pre-inflection slopes relative to the post-inflection slopes) was tested for the neural data.

REFERENCES

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, http://dx.doi.org/10.1162/jocn.2007.19.11.1845.

Balakrishnanl, J.D., Ashby, F.G., 1992. Subitizing: Magical numbers or mere superstition?. Psychol. Res., 54 (2), 80–90.

Cavanagh, P., He, S., 2011. Attention mechanisms for counting in stabilized and in dynamic displays. In: Brannon, E., Dehaene, S. (Eds.), Space Time and Number, Attention & Performance XXIV. Oxford University Press.

Corbetta, M., Shulman, G.L., 2002. Control of goal-directed and stimulus-driven attentnion in the brain. Nat. Rev. Neurosci. 3, 201–215.

Cowan, N., 2001. The magical number 4 in short-term memory: a reconsideration of mental storage capacity. Behav. Brain Sci. 24 (1), 87–114, http://dx.doi.org/10.1017/S0140525 × 01003922.

Dehaene, S., Cohen, L., 1994. Dissociable mechanisms of subitizing and counting: neuropsychological evidence from simultanagnosic patients. J. Exp. Psychol.: Human Percept. Perform. 20 (5), 958–975, http://dx.doi.org/10.1037/0096-1523.20.5.958.

Demeyere, N., Rotshtein, P., Humphreys, G.W., 2012. The neuroanatomy of visual enumeration: differentiating necessary neural correlates for subitizing versus counting in a neuropsychological voxel-based morphometry study. J. Cogn. Neurosci. 24 (4), 948–964, http://dx.doi.org/10.1162/jocn_a_00188.

Drew, T., Horowitz, T.S., Wolfe, J.M., Vogel, E.K., 2012. Neural measures of dynamic changes in attentive tracking load. J. Cogn. Neurosci. 24 (2), 440–450, http://dx.doi.org/10.1162/jocn_a_00107.

Drew, T., Vogel, E.K., 2008. Neural measures of individual differences in selecting and tracking multiple moving objects. J. Neurosci. 28 (16), 4183–4191, http://dx.doi.org/10.1523/JNEUROSCI.0556-08.2008.

Egeth, H.E., Leonard, C.J., Palomares, M., 2008. The role of attention in subitizing: is the magical number 1?. Vis. Cogn., 16; 463–473, http://dx.doi.org/10.1080/13506280801937939.

Eimer, M., 1996. The N2pc component as an indicator of attentional selectivity. Electroencephalogr. Clin. Neurophysiol. 99 (3), 225–234, http://dx.doi.org/10.1016/0013-4694(96)95711-9.

Ester, E.F., Drew, T., Klee, D., Vogel, E.K., Awh, E., 2012. Neural measures reveal a fixed item limit in subitizing. J. Neurosci. 32 (21), 7169–7177, http://dx.doi.org/10.1523/JNEUROSCI.1218-12.2012.

Feigenson, L., 2011. Objects, Sets, and Ensembles. In: Brannon, E., Dehaene, S. (Eds.), Space Time and Number in the Brain: Searching for the Foundations of Mathematical Thought. Elsevier, London, pp. 13–22, http://dx.doi.org/10.1016/B978-0-12-385948-8.00002-5.

Feigenson, L., Carey, S., 2003. Tracking individuals via object-files: evidence from infants' manual search. Dev. Sci. 6 (5), 568–584, http://dx.doi.org/10.1111/1467-7687.00313.

Feigenson, L., Carey, S., 2005. On the limits of infants' quantification of small object arrays. Cognition 97 (3), 295–313, http://dx.doi.org/10.1016/j.cognition.2004.09.010.

Feigenson, L., Dehaene, S., Spelke, E., 2004. Core systems of number. Trends Cogn. Sci. 8 (7), 307–314, http://dx.doi.org/10.1016/j.tics.2004.05.002.

Ikkai, A., McCollough, A.W., Vogel, E.K., 2010. Contralateral delay activity provides a neural measure of the number of representations in visual working memory. J. Neurophysiol. 103 (4), 1963–1968, http://dx.doi.org/10.1152/jn.00978.2009.

Kaufman, E.L., Lord, M.W., Reese, T.W., Volkmann, J., 1949. The discrimination of visual number. Am. J. Psychol. 62 (4), 498, http://dx.doi.org/10.2307/1418556.

Leslie, A.M., Xu, F., Tremoulet, P.D., Scholl, B.J., 1998. Indexing and the object concept: developing 'what' and 'where' systems. Trends Cogn. Sci. 2 (1), 10–18, http://dx.doi.org/10.1016/S1364-6613(97)01113-3.

Luck, S.J., Hillyard, S.A., 1994. Electrophysiological correlates of feature analysis during visual search. Psychophysiology 31 (3), 291–308, http://dx.doi.org/10.1111/j.1469-8986.1994.tb02218.x.

Luck, S.J., Vogel, E.K., 1997. The capacity of visual working memory for features and conjunctions. Nature 390 (6657), 279–281, http://dx.doi.org/10.1038/36846.

Mandler, G., Shebo, B.J., 1982. Subitizing: an analysis of its component processes. J. Exp. Psychol.: Gen. 111 (1), 1–22, http://dx.doi.org/10.1037/0096-3445.111.1.1.

Mazza, V., Caramazza, A., 2011. Temporal brain dynamics of multiple object processing: the flexibility of individuation.

PloS one 6 (2), e17453, http://dx.doi.org/10.1371/journal.pone.0017453.

Mazza, V., Pagano, S., Caramazza, A., 2013. Multiple object individuation and exact enumeration. J. Cogn. Neurosci. 25 (5), 697–705, http://dx.doi.org/10.1162/jocn_a_00349.

Mazza, V., Turatto, M., Caramazza, A., 2009a. Attention selection, distractor suppression and N2pc. Cortex 45 (7), 879–890, http://dx.doi.org/10.1016/j.cortex.2008.10.009.

Mazza, V., Turatto, M., Caramazza, A., 2009b. An electrophysiological assessment of distractor suppression in visual search tasks. Psychophysiology 46 (4), 771–775, http://dx.doi.org/10.1111/j.1469-8986.2009.00814.x.

McCollough, A.W., Machizawa, M.G., Vogel, E.K., 2007. Electrophysiological measures of maintaining representations in visual working memory. Cortex 43 (1), 77–94, http://dx.doi.org/10.1016/S0010-9452(08)70447-7.

Nelder, J.A., Mead, R., 1965. A simplex method for function minimization. Comput. J. 7 (4), 308–313, http://dx.doi.org/10.1093/comjnl/7.4.308.

Pagano, S., Mazza, V., 2012. Individuation of multiple targets during visual enumeration: new insights from electro-physiology. Neuropsychologia 50 (5), 754–761, http://dx.doi.org/10.1016/j.neuropsychologia.2012.01.009.

Piazza, M., Fumarola, A., Chinello, A., Melcher, D., 2011. Subitizing reflects visuo-spatial object individuation capacity. Cognition 121 (1), 147–153, http://dx.doi.org/10.1016/j.cognition.2011.05.007.

Pylyshyn, Z.W., 1989. The role of location indexes in spatial perception: a sketch of the FINST spatial-index model. Cognition 32 (1), 65–97, http://dx.doi.org/10.1016/0010-0277(89)90014-0.

Railo, H., Koivisto, M., Revonsuo, A., Hannula, M.M., 2008. The role of attention in subitizing. Cognition 107 (1), 82–104, http://dx.doi.org/10.1016/j.cognition.2007.08.004.

Robitaille, N., Grimault, S., Jolicoeur, P., 2009. Bilateral parietal and contralateral responses during maintenance of unilaterally encoded objects in visual short-term memory: evidence from magnetoencephalography. Psychophysiology 46 (5), 1090–1099, http://dx.doi.org/10.1111/j.1469-8986.2009.00837.x.

Rugani, R., Fontanari, L., Simoni, E., Regolin, L., Vallortigara, G., 2009. Arithmetic in newborn chicks. Proc. Biol. Sci.: R. Soc. 276 (1666), 2451–2460, http://dx.doi.org/10.1098/rspb.2009.0044.

Sonderegger, D. , 2012. SiZer: SiZer: Significant Zero Crossings. R package version 0.1-4. http://CRAN.R-project.org/package=SiZer.

Todd, J.J., Marois, R., 2004. Capacity limit of visual short-term memory in human posterior parietal cortex. Nature 428 (6984), 751–754, http://dx.doi.org/10.1038/nature02466.

Trick, L.M., Pylyshyn, Z.W., 1993. What enumeration studies can show us about spatial attention: evidence for limited capacity preattentive processing. J. Exp. Psychol.: Hum. Percept. Perform. 19 (2), 331–351, http://dx.doi.org/10.1037/0096-1523.19.2.331.

Trick, L.M., Pylyshyn, Z.W., 1994. Why are small and large numbers enumerated differently? A limited-capacity preattentive stage in vision. Psychol. Rev. 101 (1), 80–102, http://dx.doi.org/10.1037/0033-295X.101.1.80.

Tuholski, S.W., Engle, R.W., Baylis, G.C., 2001. Individual differences in working memory capacity and enumeration. Mem. Cogn. 29 (3), 484–492, http://dx.doi.org/10.3758/BF03196399.

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, http://dx.doi.org/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, http://dx.doi.org/10.1162/jocn.2010.21472.

Vogel, E.K., Machizawa, M.G., 2004. Neural activity predicts individual differences in visual working memory capacity. Nature 428 (6984), 748–751, http://dx.doi.org/10.1038/nature02447.

Vuokko, E., Niemivirta, M., Helenius, P., 2013. Cortical activation patterns during subitizing and counting. Brain Res. 1497, 40–52, http://dx.doi.org/10.1016/j.brainres.2012.12.019.

Whalen, J., Gallistel, C.R.R., Gelman, R., 1999. Nonverbal counting in humans: the psychophysics of number representation. Psychol. Sci. 10 (2), 130–137, http://dx.doi.org/10.1111/1467-9280.00120.