Decoding of Electroencephalogram Signals Shows No Evidence of a Neural Signature for Subitizing in Sequential Numerosity

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Abstract

■ Numerosity perception is largely governed by two mechanisms. The first so-called subitizing system allows one to enumerate a small number of items (up to three or four) without error. The second system allows only an approximate estimation of larger numerosities. Here, we investigate the neural bases of the two systems using sequentially presented numerosity. Sequential numerosity (i.e., the number of events presented over time) starts as a subitizable set but may eventually transition into a larger numerosity in the approximate estimation range, thus offering a unique opportunity to investigate the neural signature of that transition point, or subitizing boundary. If sequential numerosity is encoded by two distinct perceptual mechanisms (i.e., for subitizing and approximate estimation), neural representations of the sequentially presented items crossing the subitizing boundary should be sharply distinguishable. In contrast, if sequential numerosity is encoded by a single perceptual mechanism for all numerosities and subitizing is achieved through an external postperceptual mechanism, no such differences in the neural representations should indicate the subitizing boundary. Using the high temporal resolution of the EEG technique incorporating a multivariate decoding analysis, we found results consistent with the latter hypothesis: No sharp representational distinctions were observed between items across the subitizing boundary, which is in contrast with the behavioral pattern of subitizing. The results support a single perceptual mechanism encoding sequential numerosities, whereas subitizing may be supported by a postperceptual attentional mechanism operating at a later processing stage. ■

INTRODUCTION

Humans and animals are endowed with an intuitive sense of number allowing them to rapidly grasp the numerosity of a set of items in space or in a sequence of events over time (Dehaene, 2011). Such a sense of number likely has evolutionarily ancient origins, being present in a large number of species spanning from spiders (Rodríguez, Briceño, Briceño-Aguilar, & Höbel, 2015; Nelson & Jackson, 2012) to birds (Wagener, Loconsole, Ditz, & Nieder, 2018; Pepperberg, 2006), fish (Agrillo, Piffer, & Bisazza, 2010; Agrillo, Dadda, Serena, & Bisazza, 2009), and monkeys (e.g., Nieder & Miller, 2004). In humans, numerosity perception seems to be present and operational shortly after birth (Izard, Sann, Spelke, & Streri, 2009), and psychophysical studies in adults show that numerosity can be regarded as a fundamental perceptual attribute independent from other continuous dimensions such as density (Park, 2018; Anobile, Cicchini, & Burr, 2016; Fornaciai, Cicchini, & Burr, 2016; Park, Dewind, Woldorff, & Brannon, 2016; DeWind, Adams, Platt, & Brannon, 2015). Moreover, there is also evidence that numerosity perception entails a generalized mechanism integrating information over space and time and across modalities to represent numerical magnitude in an abstract fashion (Anobile, Domenici, Togoli, Burr, & Arrighi, 2020; Anobile, Arrighi, Togoli, & Burr, 2016; Arrighi, Togoli, & Burr, 2014). Although at the top of the hierarchy numerosity is represented in an abstract and supramodal fashion, other studies show that it is nevertheless deeply rooted in the sensory processing stream and interacts with the processing of other basic perceptual attributes such as color and motion (Fornaciai, Togoli, & Arrighi, 2018; Fornaciai & Park, 2017b). Indeed, neuroimaging studies highlight a core system of numerical magnitude representation in parietal cortex (e.g., Harvey, Klein, Petridou, & Dumoulin, 2013; Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004), but also demonstrated the involvement of earlier visual occipital areas (Castaldi, Piazza, Dehaene, Vignaud, & Eger, 2019; DeWind, Park, Woldorff, & Brannon, 2019; Fornaciai & Park, 2018; Fornaciai, Brannon, Woldorff, & Park, 2017; Harvey & Dumoulin, 2017; Park et al., 2016; Cavdaroglu, Katz, & Knops, 2015; Roggeman, Santens, Fias, & Verguts, 2011).

An intriguing feature of numerosity perception is that it depends on the numerical range of items or events to be estimated. Whereas very few items or events are errorlessly perceived in an exact fashion (typically one to four items) via the process called "subitizing" (Kaufman, Lord, Reese, & Volkmann, 1949), larger numerosities in the

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so-called approximate number system (ANS) range are perceived in an intrinsically approximate fashion, easily prone to errors. For simplicity, we hereafter use the term *small* and *large* numerosities to refer to numerical ranges that are subitizable and ranges that are beyond subitizable.

The nature of the brain mechanism supporting the errorless subitizing performance has been subject to debate in the past decades. For instance, Gallistel and Gelman (1992) proposed that subitizing may be a form of very fast nonverbal counting. This idea, however, was challenged on the ground that items in small numerosities seem to be processed in parallel rather than sequentially in a counting-like fashion (Dehaene & Cohen, 1994). Another source of debate concerns whether subitizing is based on a unique mechanism independent of the ANS, or whether the exact perception of small numerosities simply depends on the low scalar variability of the ANS expected at such small numerosities (e.g., Cordes, Gelman, Gallistel, & Whalen, 2001). Indeed, according to the idea of scalar variability, the uncertainty of a given numerosity representation (and of the judgments based on it) is proportional to numerical magnitude: The higher the magnitude, the higher the uncertainty. This would for instance predict errorless performance at small numerosities such as 1, 2, and 3, as the variability is so low that it would be unlikely for an observer to misperceive any item in the set. However, this idea has been challenged, based on the evidence showing that making judgments on large numerosities with similarly distinct representations (10, 20, and 30 dots) results in a vastly different behavioral pattern (Revkin, Piazza, Izard, Cohen, & Dehaene, 2008). Further results also suggest that subitizing might be supported by a domain-general mechanism, shared with other functions like visual working memory (Piazza, Fumarola, Chinello, & Melcher, 2011). Finally, other results show that errorless subitizing estimation works only when attentional resources are available. Under conditions of attentional load, for instance, four or fewer items rely on approximate representations similar to larger numerosities (Burr, Turi, & Anobile, 2010; Olivers & Watson, 2008). Consistent with these behavioral findings, neural studies have shown that brain responses to small and large numerosities show markedly different dynamics when the numerical stimuli are attended to (e.g., Fornaciai & Park, 2017a; Libertus, Woldorff, & Brannon, 2007) but that those brain responses are similar when attention is disrupted (Hyde & Wood, 2011). These results suggest that subitizing is highly dependent on attention and is not a preattentive mechanism (Simon & Vaishnavi, 1996; Vuilleumier & Rafal, 2000).

Although most previous research on numerosity perception utilized simultaneously presented arrays of items, there is evidence that sequential numerosity (i.e., where numerosity is conveyed by a sequence of items presented over time) is subject to subitizing as well (e.g., Cheng et al., 2021; Anobile, Arrighi, & Burr, 2019; Repp, 2007). In this case, although variations exist from study to study likely because of how the threshold of subitizing is defined or how the stimuli are delivered (Anobile et al., 2019; Camos & Tillmann, 2008), subitizing seems mostly limited to one to four items, similarly to simultaneously presented numerosities (e.g., Cheng et al., 2021). However, the nature of the system supporting errorless subitizing remains unclear. Is subitizing achieved by a perceptual encoding system, constrained by the amount of information and attentional limits, independent from the perceptual mechanism for approximate estimation? Alternatively, is a single perceptual encoding system responsible for both small and large numerosities whereas errorless subitizing is achieved by a higher-order postperceptual mechanism? Sequential numerosities provide a unique way to test these hypotheses.

When perceiving sequential numerosity, the brain cannot know in advance whether a sequence of items will contain small or large numerosities. Indeed, unlike simultaneously presented numerosities where each stimulus presents all items at once, an individual stimulus in a sequence is not informative about the final numerosity in sequential numerosities. Thus, the progressive accumulation of sequentially presented stimuli introduces uncertainty about which perceptual system is going to be appropriate for representing the numerosity at the end of the sequence. This leads to two hypotheses concerning which perceptual mechanism (that happens early in the visual stream, usually within 200 msec after stimulus onset; Fornaciai & Park, 2017a, 2018; Fornaciai et al., 2017; Park et al., 2016; Hyde & Wood, 2011) gets activated during the accumulation of the stimuli. The first hypothesis is that two different perceptual mechanisms are each responsible for encoding small and large numerosities. In this scenario, at the beginning of a sequence when the numerosity still remains small (~3), only the first perceptual mechanism gets activated to encode the stimuli. If the sequence grows beyond the subitizing boundary, the second perceptual mechanism becomes activated to encode large numerosities, superseding the earlier perceptual system for small numerosities. The second hypothesis is that a single perceptual mechanism is responsible for encoding sequential numerosity regardless of its size from the beginning to the end of the sequence. In this scenario, errorless performance yielded by small numerosities would be achieved by a postperceptual mechanism engaged after stimulus encoding. This latter hypothesis would be consistent with previous findings on subitizing for simultaneous stimuli (Hyde & Wood, 2011; Burr et al., 2010). Nevertheless, it should be noted that subitizing performance for simultaneous stimuli does not correlate with performance for sequential stimuli across participants, suggesting that simultaneous and sequential numerosity perception is at least partially distinct (Anobile et al., 2019). Thus, this latter hypothesis need not be true solely based on what is known about subitizing for simultaneous stimuli.

To disentangle these two possibilities, we assessed and compared patterns of EEG activity evoked by individual

items presented sequentially over time. Participants performed a numerosity categorization task determining whether a sequence of visual items (2–12 singly presented items) was more or less numerous than a memorized reference (seven items). We then employed a multivariate decoding analysis to compare the pattern of brain activity evoked by items in different positions within a sequence. Specifically, a pattern classifier (i.e., support vector machine [SVM]) quantified the degree to which patterns of EEG activity, most critically, for two successive stimuli were distinguishable. We then tested if there is a sharp representational distinction between items around the subitizing boundary (e.g., the third vs. the fourth item in the sequence). Analytical methods based on a multivariate pattern analysis in the time domain (e.g., King & Dehaene, 2014) are increasingly used in EEG research and have been shown to be sensitive to subtle representational differences between different classes of stimuli or experimental conditions.

Our predictions were as follows. If two different perceptual mechanisms are separately responsible for encoding small versus large numerosities and the mechanism for small numerosities directly gives rise to subitizing, then we should observe a sharp representational distinction between the items crossing the subitizing boundary. Conversely, if a single perceptual mechanism is activated from the beginning to the end of a sequence irrespective of the position of the item in the sequence, then we should not observe any representational distinction between items across the subitizing boundary.

METHODS

Participants

Twenty participants took part in the main EEG experiment (12 women; mean $\pm$ *SD* age = 22.3 $\pm$ 1.1 years), and 10 additional participants were tested in the control numerosity estimation experiment (7 women, age = 29.7 $\pm$ 5.1 years; including the author M. F.). The sample size tested in the main experiment was decided a priori based on a previous study from our group, employing a similar analytical approach to investigate the representation of numerosity (Fornaciai & Park, 2018). All the participants were naïve to the purpose of the experiment (except the author M. F. in the control experiment), had normal or corrected-to-normal vision, and provided written informed consent prior to the participation in the experiment. All the experimental procedures were approved by the University of Massachusetts institutional review board and were in line with the Declaration of Helsinki. Two participants in the main experiment were excluded from data analysis because of excessively noisy EEG signal.

Apparatus and Stimuli

Stimuli were generated using the Psychophysics Toolbox (Kleiner, Brainard, & Pelli, 2007; Brainard, 1997; Pelli,

1997) in MATLAB (Version R2015b, The MathWorks, Inc.) and were displayed on a monitor screen running at 144 Hz with a resolution of 1920 × 1080 pixels. In the main EEG experiment, the sequences displayed in each trial contained a different number of items, spanning from 2 to 12, with the exception of 7, which was excluded from the range because it coincided with the judgment criterion (i.e., a sequence could comprise for instance 6 or 8 items, but never exactly 7; see Procedure section below). In the control numerosity estimation task, all the numerosities from 2 to 12 were tested. The items were defined as a random combination of shape (circle, square, up- or down-triangle, diamond) and color (red, green, blue, orange, cyan), for a total of 25 possible combinations (see Figure 1). Different combinations were randomly intermixed within the sequence, but the same combination was never included more than once in the same sequence. The different shapes were constructed in order to cover a similar area (36–38 deg^2). Such stimulus design involving many different stimuli was employed to avoid a reduction in brain responses because of repetition suppression, which has been shown to depend on stimulus similarity (Liu, Murray, & Jagadeesh, 2009). Furthermore, to avoid counting, we employed a fast stimulation sequence, with each individual item in the sequence presented for 16 msec, and with an ISI of 200 msec between any two successive items. Note that although the proportion of small numerosities (2 to 4) was smaller than the proportion of large numerosities (4 to 12), this should not limit the engagement of the subitizing system in our paradigm, as the presence of subitizing has been successfully demonstrated in previous studies using similar, or even larger, numerical ranges (e.g., Anobile et al., 2019; Pomè, Anobile, Cicchini, & Burr, 2019; Mandler & Shebo, 1982).

Procedure

The main EEG experiment took place in a quiet and dimly lit room. Participants sat in front of the screen at a distance of about 90 cm. As shown in Figure 1, each trial started with participants fixating on a small black cross at the center of the screen. Then, the fixation cross disappeared, and a rapid sequence of aforementioned items was presented at the center of the screen. Each item was presented on the screen for 16 msec, with an ISI of 200 msec between different stimuli. After the sequence presentation, the central fixation cross appeared again in red, signaling the end of the trial and to provide a response. Participants were asked to judge whether the sequence contained more or less than seven items, by pressing the appropriate key on a standard keyboard (up-arrow for more, down-arrow for less). After the keypress, the next trial started automatically after 1300–1450 msec. Before starting the experiment, participants were shown an example of the "reference" numerosity (i.e., seven items), and performed a brief training session of about 15 trials, in order to make sure that they understood the procedure. The reference numerosity (7)
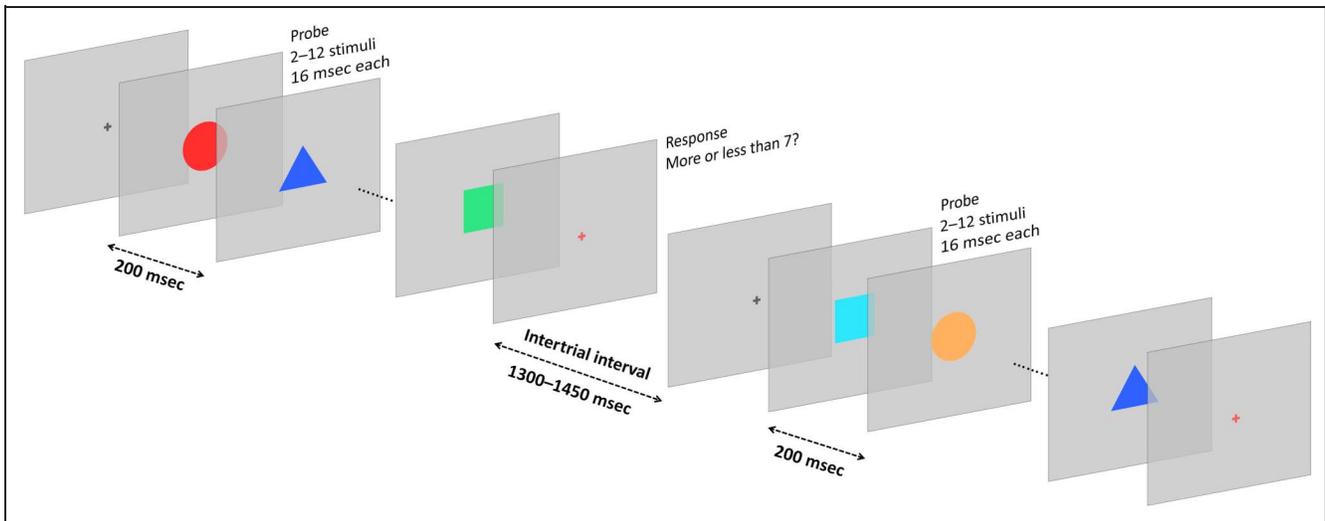
Figure 1. Experimental procedure. The experiment involved the presentation of a variable sequence of random items comprised between two and 12 items (with the exception of seven). Each item was presented for 16 msec, and they were separated by a 200-msec ISI. Items were composed of a random combination of shape (circle, square, up- or down triangle, diamond) and color (red, green, blue, orange, cyan), for a total of 25 unique possible combinations. At the end of each trial, participants judged whether the sequence contained more or less than seven items. After the response, the next trial started automatically after an intertrial interval of 1300–1450 msec. The procedure of the control numerosity estimation experiment was identical to the procedure of the main experiment, with the exception that, at the end of each trial, the participants were asked to estimate the numerosity of the sequence, by typing the exact number on the numerical pad of a standard keyboard.

was shown to the participants during the training session, before the start of the experiment, and once before the start of each block. Participants completed eight blocks of 80 trials and were encouraged to take frequent breaks between different blocks. An entire experimental session took approximately 2 hr. Participants were compensated for their time with $10/hr.

Note that the choice of setting the judgment criterion at 7 was motivated by avoiding a potential confound between the subitizing boundary and the decision criterion. In other words, numerosities both below and above the subitizing boundary (assumed to be around 3–4 at the time of design) were kept below the decision criterion (7) so that any differential effect we observe within the range of two to six dots cannot be attributed to a decision or response process. In addition, a constant presentation rate was chosen in order to keep the interval between different individual stimuli equal across numerosities. Indeed, although doing so introduces the potential confound with duration (i.e., the total duration of the sequence correlates with its numerosity; see Discussion section), keeping the duration equal across the sequences and varying their presentation rate would introduce a much more severe confound. Namely, a constant sequence duration would favor small numerosities and even make them countable, because a much larger ISI between individual items (i.e., as they would be presented in a much sparser fashion compared to large numerosities) may lead to a cleaner signal and sharper representations. This, in turn, would confound the hypothesis of a sharper numerical representation of smaller numerosities, making the interpretation of the EEG results difficult.

The classification task used in the main experiment was chosen in order to minimize the possibility of verbal encoding strategies and to maximize the number of trials enabled by such a fast-paced procedure. However, the classification task by itself does not allow us to confirm the presence of subitizing from behavioral responses and to estimate the subitizing boundary. We thus performed an additional control behavioral experiment to assess the presence of subitizing with the same stimuli used in the EEG experiment. The stimuli and procedure used in this control experiment were identical to the main experiment, with the exception that participants were asked to estimate the numerosity of each sequence of stimuli. The estimation response in each trial was provided by typing the response using the numerical pad of a standard keyboard and confirming it by pressing the enter key. Participants were not informed about the actual numerosity range in order to avoid edge effects, at least at the higher end of the range, but they were told that there were no more than 20 items. One hundred sixty-five trials were performed by each participant, corresponding to 15 repetitions of each level of numerosity. This control experiment took about 15 min.

Electrophysiological Recording and Preprocessing

While participants performed the sequential numerosity categorization task, the EEG was recorded throughout the experiment (actiCHAmp, Brain Products, GmbH), using a 64-channel, extended coverage, triangulated equidistance cap (M10, EasyCap, GmbH), with a sampling rate of 1000 Hz. During EEG recording, the vertex (Cz) was used as a reference for all the channels. The EOG was monitored by

means of electrodes positioned below the left eye and lateral to the left and right canthi, in order to monitor artifacts due to blinks or eye movements and remove them during preprocessing. Impedances across channels were usually kept below 15 kΩ, but, on some occasions, impedances up to 35 kΩ were tolerated.

EEG data analysis was performed off-line in MATLAB (Version R2013b), using the EEGLAB software package (Delorme & Makeig, 2004). EEG signals were first high-pass filtered (0.1 Hz) and were rereferenced to the average value of all the 64 channels. The continuous EEG data were then segmented into epochs from 0 to 200 msec time-locked to the onset of each item with no baseline correction, corresponding to each of the 11 stimulus positions (i.e., the second, third, fourth, fifth, sixth, seventh, eighth, ninth, tenth, eleventh, and twelfth stimulus in a sequence). Epoched data were cleaned first by visual inspection, removing epochs containing large artifacts or noise, and subsequently by means of an independent component analysis. After removing noise- and artifact-related components, we further used a step-like artifact rejection procedure (provided by EEGLAB) in order to remove any remaining large artifact (average number of rejected trials < 0.1%). To the purpose of epoching and binning data corresponding to different numerosities, we considered all the stimuli corresponding to a given position along the sequence. For instance, the second position referred to the second stimulus presented across all the given sequences; similarly, the third position referred to the third stimulus across all the sequences and so on. This led to having a different number of epochs corresponding to different stimulus positions, with earlier positions being represented more. However, in our main analysis, we controlled for these differences in the amount of data by including always the same number of trials for each numerosity (see below Multivariate Pattern Analysis in the Time Domain section).

ERPs Analysis

ERPs corresponding to each of the 11 stimulus positions (i.e., stimuli in the n-th position along the sequence) were analyzed in order to assess a potential signature of the increasing position within the sequence. First, as a channel of interest, we took Oz, as it has been consistently demonstrated to carry a strong signature of early numerosity processing in previous studies (Fornaciai & Park, 2017a, 2018; Fornaciai et al., 2017; Park et al., 2016). Then, we identified the peak activity in the data collapsed across all the stimulus positions, in two time windows of interest based on previous studies (i.e., an early time window at 100 msec after stimulus onset and a late window at around 150 msec; Fornaciai et al., 2017; Fornaciai & Park, 2017a; Park et al., 2016). Doing so, we identified a first negative peak of activity at 97 msec (amplitude = −2.42 μV), and a second positive peak at 147 msec after stimulus onset (amplitude = 4.74 μV). To analyze activity at these two peaks, we averaged brain waves in 20- and 50-msec time

windows around each peak (respectively for the first negative peak and the later positive peak), separately for each participant and stimulus position and used a one-way repeated-measures ANOVA to assess whether the amplitude of the ERPs are modulated by the position of the stimulus in a sequence.

Multivariate Pattern Analysis in the Time Domain

In order to compare and contrast the patterns of neural activity associated with each stimulus position (denoting the n-th position along the sequence), we performed a multivariate pattern analysis in the time domain (King & Dehaene, 2014), using Neural Decoding Toolbox (Meyers, 2013). This method quantifies to what extent patterns of brain activity from multiple electrodes elicited by different stimulus conditions can be discriminated. More specifically, the multivariate analysis involved the training of a pattern classifier (SVM) on a random subset of data corresponding to specific conditions (i.e., in this case, the presentation of stimuli corresponding to specific positions within each sequence) and testing how well the classifier could make predictions about which stimulus was presented in an independent subset of data.

For the purposes of the present work, we used the epoched EEG data corresponding to different stimulus positions and compared pairs of them (i.e., the responses elicited by the second stimulus vs. the responses elicited by the third stimulus) in order to assess whether and to what extent the two neural representations differ (Figure 2). Each comparison was tested independently, by training the SVM classifier with EEG responses from the two stimulus positions at hand using a leave-one-out cross validation. The analysis was repeated on EEG responses averaged across a series of 10-msec time windows (with a step size of 5 msec) throughout the 200-msec epoch time-locked to the onset of a given item. To optimize the analysis, we followed a practice suggested by Grootswagers, Wardle, and Carlson (2017). First, we created "pseudotrials" by averaging together randomly selected trials within each condition, which improves the signal-to-noise ratio of EEG data. Second, to avoid overfitting, the number of features (i.e., channels) used for decoding was limited to the five most significant ones assessed using a univariate ANOVA. Third, the decoding procedure was performed in 30 independent repetitions for each participant, time window, and condition, using different randomly generated pseudotrials. The average of the outcomes from these 30 repetitions was taken as the final result of the classification procedure. Finally, we took the average classification accuracy across a 100-msec window around the peak accuracy as the final estimate of decoding performance for each participant and comparison. Note that these procedures make it difficult to pinpoint the channels that contribute to the critical values that lead to the summarized classification accuracy for each participant, not to mention that distributed scalp
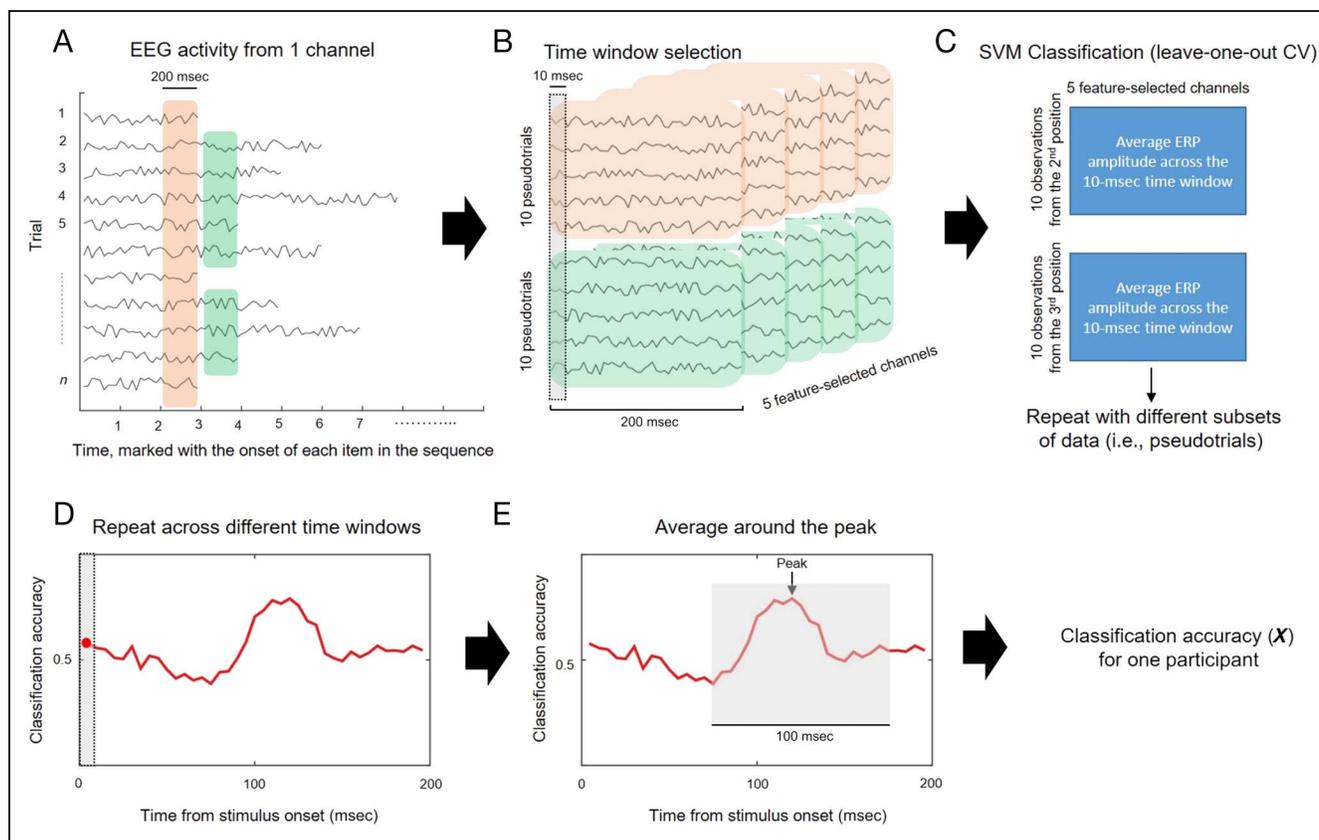
Figure 2. Multivariate pattern analysis in the time domain. Schematic depiction of the analysis procedure employed to characterize the pattern of brain activity in response to items in different positions along the sequence. (A) First, the EEG epochs (200 msec, time-locked to the onset of each item) corresponding to the given position along the sequence (henceforth called stimulus position) were selected according to the specific comparison to be performed (in this example, second vs. third). (B) The classification procedure was performed on activity averaged across 10-msec time windows. To increase the signal-to-noise ratio of the data, activity across groups of 10 trials was further averaged to form pseudotrials. (C) Ten pseudotrials were then chosen for each of the conditions being compared, and a leave-one-out classification procedure was performed. Namely, a classifier (SVM) was trained on a subset of pseudotrials from each condition and then tested on the remaining pseudotrial not used in the training procedure. In addition, to avoid overfitting, the classification procedure used data from only five EEG channels, selected according to a univariate ANOVA (i.e., feature selection procedure). This procedure was repeated 30 times using different subsets of trials to create pseudotrials and different subsets of pseudotrials for training and testing. Doing so, we obtained a measure of classification accuracy within the specific 10-msec time window of activity selected. (D) Furthermore, this classification procedure was repeated throughout the entire time course of an epoch (200 msec), with a step size of 5 msec. (E) Finally, we identified the peak of classification accuracy across the epoch and averaged classification accuracies measured within a 100-msec time window around the peak. This average classification accuracy was taken as the estimate of the decoding performance for one participant in a given comparison. The procedure was similarly repeated across all the participants, and the average of the group was taken as the final estimate of the decoding performance at the group level, indicating to what extent the brain activity patterns elicited by two given conditions are discriminable.

EEG channels for decoding analyses provide little, if any, information about the anatomical source of the signals.

In order to make classification performance measures comparable, we always used the same number of trials for each decoding iteration, comparison condition, and participant. Namely, we used a subset of 100 trials, divided into 10 cross-validation splits, with pseudotrials calculated as the average of 10 individual trials. The analysis was thus constrained by having a minimum number of available trials, limiting the number of comparisons to stimulus positions spanning from the second to ninth position in the sequence, as higher positioned stimuli were not tested a sufficient number of times. For example, the second item in a sequence was included in all the sequences across the experiment, whereas the twelfth item in a sequence was included only in the most numerous stimulus.

Overall, we thus performed comparisons of stimulus positions from the second to the sixth, against stimulus positions up to the ninth (i.e., second vs. third to ninth, third vs. fourth to ninth, and so on up until the sixth vs. seventh to ninth).

Statistical Analyses

Behavioral performance across different numerosities was assessed in terms of the proportion of wrong responses—or error rates—in the categorization task (i.e., responding to "more than 7" when the probe was lower than 7, and vice versa). We first tested the error rates across different numerosities with one-sample t tests against a theoretical minimum error rate of 2.5%. Such minimum error rate has been chosen with the rationale that achieving a perfect

performance of 0% error is usually unlikely, because of the presence of random errors independent from the magnitude of the stimuli, driven by button press errors or lapses of attention (e.g., Cheng et al., 2021; Wichmann & Hill, 2001; Sagi & Julesz, 1984). For instance, Wichmann and Hill (2001) empirically quantified the proportion of such errors to be between 1% and 5%. Accordingly, we chose 2.5% as a conservative estimate of the minimum error rate. This series of one-sample t tests was thus performed against a null hypothesis of 2.5% error rate, and with a one-sided alternative hypothesis of error rates > 2.5%. Then, to assess whether very small numerosities lead to better performance compared to large numerosities, we compared the average error rates at the lower end of the range (2–4) versus error rates at the higher end (10–12) of the range. The comparison between these numerosities was chosen to ensure the same numerical distance between them and the decision criterion (7).

Although the classification task was chosen in the EEG paradigm to minimize the involvement of linguistic processes (e.g., subvocal counting) likely involved in a verbal estimation paradigm, such a task did not allow us to unambiguously define the subitizing boundary. To better estimate the subitizing boundary in the current stimuli, we performed a control behavioral experiment involving a numerosity estimation task (see the Procedure section). Data from the control estimation experiment were analyzed in terms of error rates of numerical estimates. To assess the subitizing boundary, we used the same method as Anobile et al. (2019). Specifically, we fitted a sigmoid function to the error rate data across numerosities and assessed the inflection point of the curve (i.e., by computing the second derivative of the fitting function). In addition, to assess the precision of numerical estimates at different numerosities, we computed the Weber's fraction (WF) as the standard deviation of estimation responses divided by the average estimated numerosity. The pattern of WF was assessed with a one-way repeated-measures ANOVA with factor Numerosity.

Regarding the neural decoding analysis, we first focused on the comparisons central to our hypothesis. Namely, we evaluated classification accuracies for the comparison of successive stimulus positions (i.e., position difference of +1) and tested for any evidence of sharp representational distinction across the subitizing boundary. On the one hand, if the encoding of small and large numerosities is supported by two different early perceptual mechanisms, we should expect a representational distinction between the third versus the fourth position (see the Results section concerning the control behavioral experiment). On the other hand, if items across the entire sequence regardless of its numerosity are encoded by a single perceptual mechanism, we should expect no such representational distinction across the subitizing boundary. After this primary analysis on successive stimulus positions, we performed a more comprehensive series of tests incorporating position differences greater than +1 (up to +5).

Because our hypotheses include the observation of null effects (e.g., classification accuracy not significantly higher than chance level), frequentist statistics were supplemented by a Bayesian analysis. This analysis was performed by modeling the null hypothesis as a Cauchy prior centered on zero, with a scale of 0.707. The Bayes factor (BF) obtained with this analysis show how strongly the evidence supports the null or the alternative hypothesis (e.g., see Dienes, 2014). Namely, BFs from 0 to 0.33 provide support for the null hypothesis (i.e., no difference between two conditions), whereas BFs greater than 3 provide support for the alternative hypothesis (i.e., presence of a difference between two conditions).

RESULTS

Figure 3 shows the behavioral results obtained from the categorization task. Across numerosities both higher and lower than 7 (i.e., the categorization criterion), we observed a clear increase in error rates as the probe numerosity got closer to the criterion. This pattern is indeed what we expected from the task, as it becomes increasingly more difficult to discriminate numerosities around the decision criterion. To assess the pattern of behavioral performance across the different numerosities, we performed a series of t tests against a theoretical minimum error rate of 2.5% (Wichmann & Hill, 2001). With small numerosities (2–4; Cheng et al., 2021), error rates were not significantly higher than 2.5% (one-tailed one-sample t test, $t(17) = -0.74, p = .77$, Cohen's $d = 0.18$; $t(17) = -0.89, p = .65, d = 0.09$; $t(17) = 1.44, p = .08, d = 0.34$; respectively for numerosities 2, 3, and 4). At higher numerosities (i.e., 5+), however, error rates were significantly higher than the 2.5% threshold, $t(17) = 2.92, p = .005$,
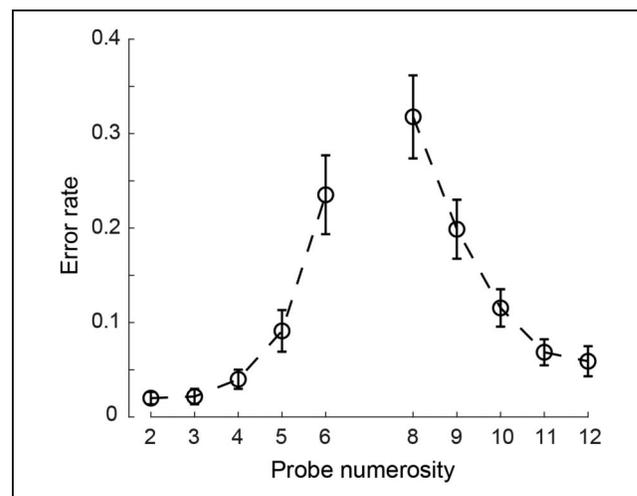
Figure 3. Behavioral results from the EEG categorization task. The proportion of wrong responses (error rate) showed a steep increase for numerosities closer to the task criterion (i.e., 7). Wrong responses were generally more frequent at the higher (i.e., 10–12) compared to the lower end (2–4) of the range. Error bars are *SEM*.

$d = 0.69; t(17) = 4.89, p < .001, d = 1.15; t(17) = 6.47,$ $p < .001, d = 1.53; t(17) = 5.39, p < .001, d = 1.26;$ $t(17) = 4.43, p < .001, d = 1.04; t(17) = 3.07, p = .003,$ $d = 0.71; t(17) = 2.09, p = .026, d = 0.49;$ respectively for probe numerosity 5, 6, 8, 9, 10, 11, 12. The very low error rates observed at numerosities 2–4 (on average 2.7% ± 0.7%) and the sharp increase in error rates between 4 and 5 (3.9% ± 1% vs. 9.1% ± 2.3%; paired t test, $t(17) = 2.99, p = .008, d = 0.70$) suggest a qualitative boundary around four items in our categorization paradigm, which would be in line with previous studies (e.g., Cheng et al., 2021). In addition, we further assessed whether very small numerosities are more precisely judged compared to larger numerosities with the same numerical distance from the judgment criterion. To do so, we compared the average error rates in numerosities 2, 3, and 4 (2.7% ± 0.7%) and the average error rates in numerosities 10, 11, and 12 (8.1% ± 1.6%). There was a statistically significant difference between those error rates in the lower and upper numerosity ranges (paired t test, $t(17) = 3.67, p = .004, d = 0.86$). It should be noted, however, that our classification paradigm is not positioned to define the subitizing boundary because low errors in the very low numerosity range could also be explained by the larger numerical distance and ratio between those numerosities and the decision criterion (seven items).

To test whether the stimuli used in the main EEG experiment successfully activated the subitizing system, we performed an independent (behavioral) control experiment employing a numerosity estimation task using the identical set of stimuli used in the EEG experiment. In this task, participants had to estimate the numerosity by typing the exact number on a keyboard. The results of this experiment, in terms of error rates, are shown in Figure 4A. The distribution of error rates as a function of numerosity showed a marked difference in performance between small and large numerosities. Namely, whereas numerosities such as 2 and 3 yielded quite low error rates (mean ± SD = 5.3% ± 5.2% and 15.3% ± 17.2%, respectively), the proportion of errors at the high end of the range was much bigger (77–90%, from 6 to 12). A one-way repeated-measures ANOVA with factor Numerosity first confirmed that the error rates of numerical estimates were significantly modulated by Numerosity, $F(10, 90) = 53.7, p < .001, \eta_p^2 = .86$. Following previous work on the subitizing system, we then estimated the subitizing boundary by fitting a sigmoid function to the error rate data (adjusted $R^2 = .98$) and defined the boundary as the inflection of the fitting curve. The resulting subitizing boundary was at 3.8. Although this method could potentially overestimate the subitizing boundary (Anobile et al., 2019), these results confirm that at least low numerosities such as 2 or 3 are indeed subitizable. For the following analyses, we have thus assumed a subitizing boundary at 3. Besides the error rates, we also computed the WF (Figure 4B) as a measure of precision in the task. Similarly to the error rates, a one-way repeated-measures ANOVA showed a significant main effect of Numerosity, $F(10, 90) = 3.11, p = .002, \eta_p^2 = .26$, suggesting that the level of precision in the task varied with the numerical magnitude of the stimuli. The pattern of WF showed in Figure 4B is consistent with subitizing occurring at numerosities 2 and 3, as shown by the relatively low WFs, and with approximate perception at higher numerosities (4–12).

We now turn to the analysis of EEG data obtained in our main experiment. Although our hypotheses are strictly related to the results of the neural decoding analysis described below, for completeness, we first report
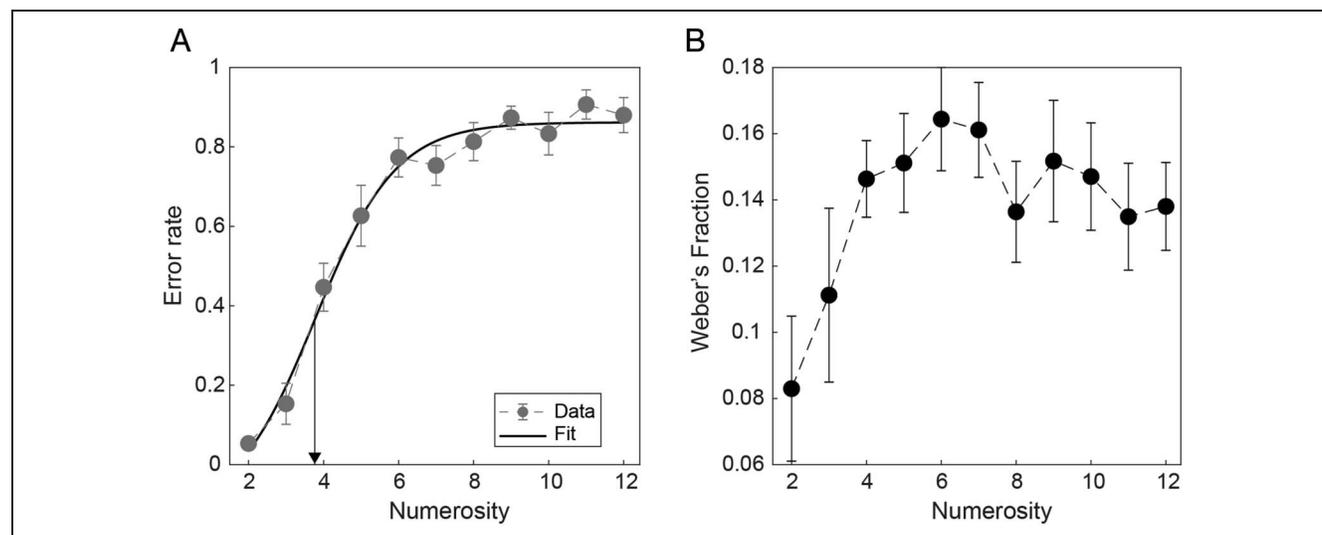

Figure 4. Results of the control estimation experiment. (A) Participants' performance measured in terms of the proportion of wrong responses (error rate) in the numerosity estimation task. The gray data points indicate the average error rates at each level of numerosity, whereas the continuous black line represents a sigmoid fit to the data. The arrow indicates the subitizing boundary, determined as the point of inflection of the fitting curve, which resulted to be 3.8. (B) Participants' precision in the task measured in terms of WF, computed as the standard deviation of numerical estimates divided by the mean estimated numerosity. Error bars are SEM.
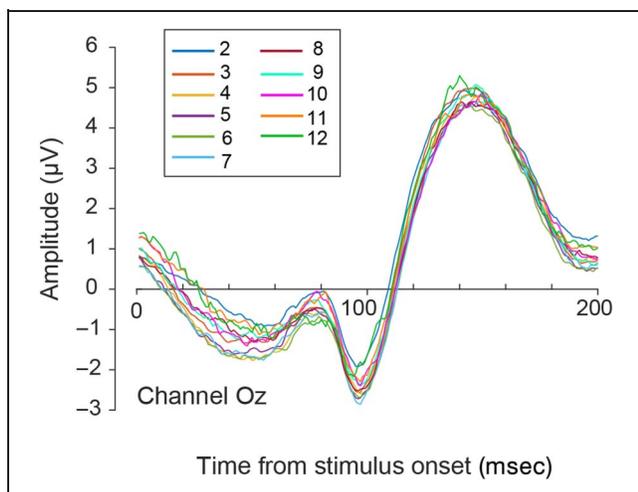
Figure 5. ERPs. ERPs evoked by stimuli in different positions along the sequence at channel Oz. In the ERP analysis, we focused on two main temporal windows of interest: the first concerning the negative deflection evident at around 100 msec after stimulus onset and the second concerning the later positive peak at around 150 msec after stimulus onset.

representative ERPs elicited by each stimulus in the sequence. Figure 5 shows the ERPs corresponding to different stimulus positions across the sequence, going from the second to the last one (twelfth), at channel Oz, which was chosen as a representative channel of interest based on previous studies (e.g., Fornaciai et al., 2017; Park et al., 2016). ERPs show two marked peaks at around 100 msec (negative deflecting) and 150 msec (positive deflecting). A one-way repeated-measures ANOVA with factor Stimulus position at a 50-msec time window around the first negative peak (97 msec) showed a main effect of Stimulus Position, $F(10, 170) = 2.94, p = .002, \eta_p^2 = .15$. However, activity at this time window did not show a relation to numerical magnitude as expected from a numerosity-sensitive brain response, but rather, it showed a U-shaped pattern, with the greatest amplitude at the sixth items (average amplitude $= -2.2$ μV) and with smaller amplitudes at the extremes of the range (-1.39 and -1.53 μV, respectively, at the second and twelfth items). On the other hand, activity around the later positive peak (147 msec) showed no main effect of Stimulus Position, $F(10, 170) = 1.50, p = .142, \eta_p^2 = .006$.

To assess the neural representation of items in different positions along the sequence, we employed a multivariate decoding analysis. Our central hypothesis was assessed first by examining measures of representational distinction between successive stimulus positions (Figure 6). A one-way ANOVA on the Classification Accuracy across comparisons showed no significant effect, $F(4, 68) = 0.66, p = .62$, and none of the individual comparisons showed a greater-than-chance classification accuracy, indicating that negligible signs of representational distinction across stimulus positions from the second to the seventh (max t value $= -0.82$, min p value $= .42$, BF, BF_{10} ranging from 0.24 to

0.32). In particular, we observed no reliable discrimination between patterns of activity from the third position and patterns of activity from the fourth position, $t(17) = 0.70$, $p = .49, BF_{10} = 0.30$, which marks the subitizing boundary according to our own behavioral results and to previous studies using sequential numerosity (e.g., Cheng et al., 2021).

One may wonder if the null results in our primary analysis (see Figure 6) indicate simply the lack of sensitivity in our design and analysis. We addressed this possibility by evaluating classification accuracies across a more comprehensive range of comparisons (Figure 7). The results show that classification accuracies in position differences greater than +1 are above chance (e.g., 2 vs. 4: $t(17) = 2.42, p = .027, d = 0.57$; 2 vs. 5: $t(17) = 3.77, p = .001, d = 0.89$; 2 vs. 6: $t(17) = 3.24, p = .004, d = 0.76$; 2 vs. 7: $t(17) = 6.98, p < .001, d = 1.64$), indicating that representational distinctions are indeed measurable using the current approach. However, consistent with our interim conclusions from the primary analysis on successive stimulus positions, representational distinctions across the broader range of comparisons did not show any signature across the subitizing boundary or any other positions within the sequence. Specifically, we tested whether the pattern of classification accuracy as a function of position difference changes at different positions within the sequence. A one-way ANOVA on the Classification Accuracy across the position difference of +2 (second vs. fourth, third vs. fifth, fourth vs. sixth, fifth vs. seventh, and sixth vs. eighth) showed no effect, $F(4, 68) = 0.21, p = .93, BF_{10} = 0.06$. The same analysis showed no effect across the position difference of +3 (second vs. fifth, third vs. sixth, fourth vs. seventh, fifth vs. eighth, and sixth vs. ninth; $F(4, 68) = 0.98, p = .42, BF_{10} = 0.17$), across the position difference of +4 (second vs. sixth, third vs. seventh, fourth vs. eighth, and fifth vs. ninth; $F(3, 51) = 1.91, p = .14, BF_{10} = 0.57$), and across the
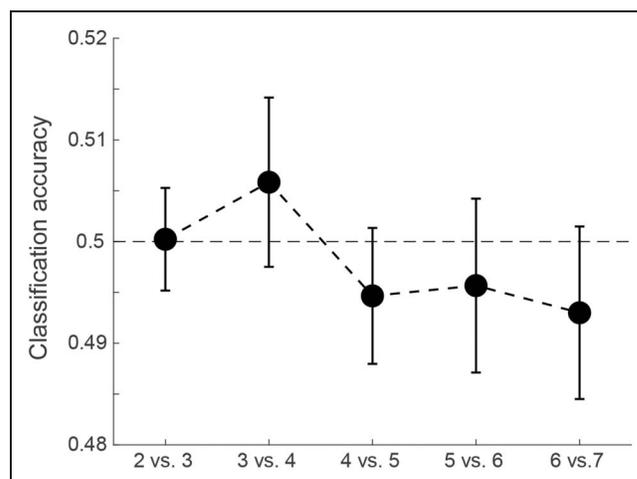

Figure 6. Decoding results. Average decoding results corresponding to comparisons of successive stimulus positions (i.e., position difference of +1). To address our central hypothesis, we evaluated evidence for a sharp representational distinction across the subitizing boundary (i.e., between third vs. fourth positions). Error bars are *SEM*.
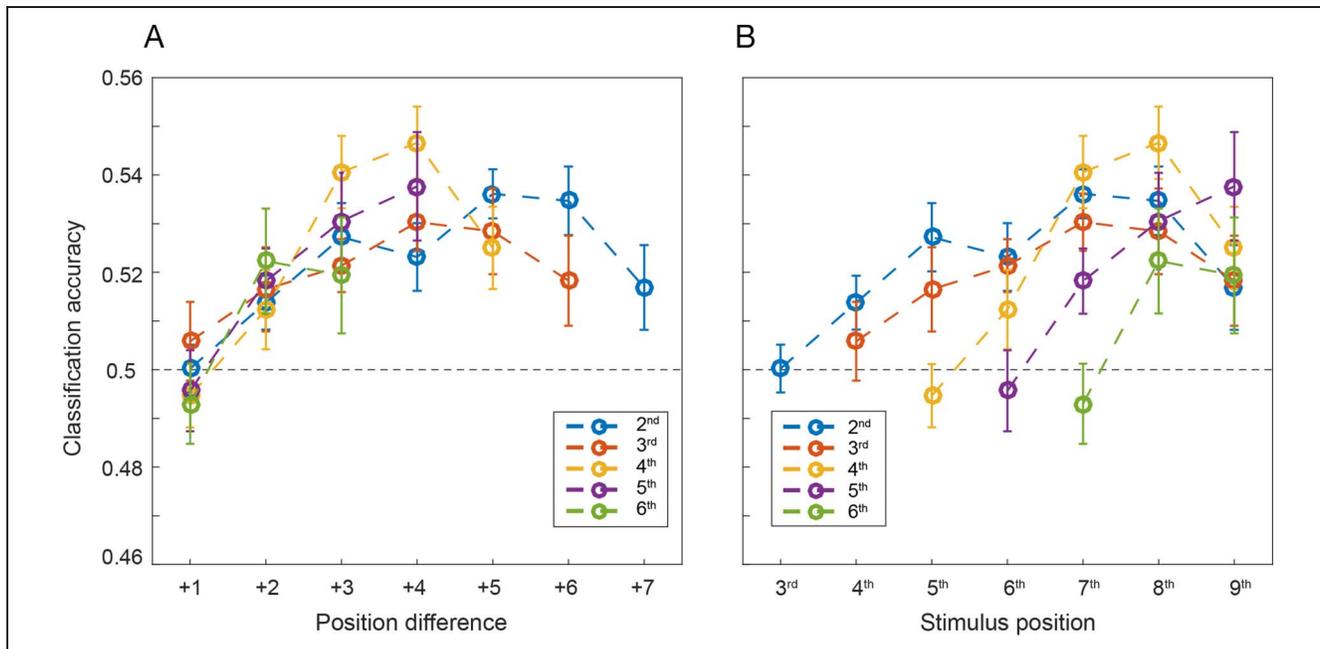
Figure 7. Results of the multivariate decoding analysis across the whole range of comparisons performed. (A) Decoding results sorted in terms of difference between stimulus positions. Each data point reflects classification accuracy (averaged across the group) obtained by comparing a given stimulus position, indicated in the legend, with other stimulus positions with increasing position difference as reported on the *x* axis. (B) The same data reported in A but sorted as a function of stimulus position. In this plot, each data point corresponds to a given stimulus position, as indicated in the legend, compared to successive stimulus positions as indicated on the *x* axis. For instance, the blue data points correspond to the second item in the sequence (second) compared to the third, fourth, and so on as indicated in the *x* axis. Error bars are *SEM*.

position difference of +5 (second vs. seventh, third vs. eighth, and fourth vs. ninth; $F(2, 34) = 0.65$, $p = .53$, $BF_{10} = 0.24$). These results illustrate that there is no evidence for any sharp representational distinction across the subitizing boundary or across any other stimulus positions within the sequence.

DISCUSSION

In the present work, we investigated the neural signature of sequential numerosity processing. An intriguing feature of numerosity perception is that it depends on the range. Although very few items up to 3 or 4 are estimated rapidly and virtually without error, higher numerosities are represented in an approximate fashion, leaving performance in this range easily prone to errors. However, the relation between these two numerosity perception systems and the nature of the errorless subitizing system remains unclear.

Most of the research on numerosity perception so far has focused on simultaneous or "spatial" numerosities. In this context, it has been shown that fast and errorless performance in the subitizing range strongly relies on attentional resources (Hyde & Wood, 2011; Burr et al., 2010). Indeed, results show that even a small numerosity that is otherwise subitizable can be perceived in an approximate fashion (i.e., it becomes prone to estimation errors) under conditions of attentional load (i.e., when participants have to perform a secondary task). In addition, with attentional load, small numerosities also

become susceptible to perceptual adaptation effects, which are normally observed only in large numerosities (Burr, Anobile, & Turi, 2011). These results collectively suggest that the representation of numerosity exploits a similar approximate mechanism irrespective of range, whereas, when attentional resources are available, an additional attentional mechanism takes its place allowing a superior representation virtually immune to errors.

At the neural level, evidence from several studies show that when attention is available, small and large numerosities are processed with markedly different dynamics (Fornaciai & Park, 2017a; Park et al., 2016; Cutini, Scatturin, Basso Moro, & Zorzi, 2014; Hyde & Spelke, 2009; Libertus et al., 2007). In particular, results from EEG studies show that while in the presence of just a few items (1–4), brain responses are modulated by numerical magnitude at the level of the N1 component, in the presence of larger numerosities, the modulation occurs at the level of the P2p component along with the earlier C1 component arising from the striate and early extrastriate areas (Fornaciai & Park, 2018; Fornaciai et al., 2017; Park et al., 2016). These results thus converge in supporting the idea that two distinct mechanisms are employed for small and large numerosities at the level of early perceptual encoding. However, when attentional resources are engaged by an additional task, the neural responses to small numerosities become similar to those to large numerosities, supporting the idea of a common approximate mechanism for numerosities in different ranges (Hyde & Wood, 2011). In contrast to

our understanding about simultaneous numerosity perception, much less work has been dedicated to sequential numerosities. There is evidence that small sequential numerosities can be judged in a fast and errorless fashion (e.g., Cheng et al., 2021; Anobile et al., 2019; Repp, 2007), with a boundary at about three to four items similar to the subitizing limit observed for simultaneous stimuli. Despite this similarity, results from the work of Anobile et al. (2019) show that there is no correlation between the subitizing properties measured with a sequence of flashes (i.e., sequential) and an array of dots (i.e., simultaneous), suggesting that subitizing with different types of stimuli may be supported by distinct underlying mechanisms. However, the nature of the mechanism involved in subitizing sequential numerosities is unclear.

Sequential numerosity represents a particularly interesting case, as the perceptual system does not "know" in advance the range of stimuli that will be presented—that is, whether it would be just a few stimuli in the subitizing range or would be more numerous. It is thus reasonable to assume that the brain must employ a flexible perceptual mechanism in order to process sequential numerosities. On the one hand, one possibility is that the brain employs two separate perceptual mechanisms, each responsible for encoding small and large numerosities. In this scenario, the first system is automatically engaged at the beginning of a sequence, which is then replaced by the second system at the subitizing boundary. On the other hand, another possibility is that a single perceptual system is engaged from the beginning to the end of a sequence regardless of the numerosity. In this scenario, the superior behavioral performance for estimating small numerosities would be supported by a separate, possibly, postperceptual system, either operating in parallel or engaged after stimulus offset. This additional postperceptual system would provide a better storage or access to the sensory information accumulated over time, provided that the information is limited to a few items. The former hypothesis predicts a sharp representational distinction between stimulus positions across the subitizing boundary. The latter hypothesis predicts instead no sharp representational distinctions between any successive items throughout the sequential numerosity, whereas the unique behavioral signature for subitizing may be achieved by how such perceptual information is accessed or stored.

Our results are in line with this latter hypothesis: There were no differences in the perceptual representation of successive items making up sequential numerosity. In other words, our decoding analysis showed difficulties in disentangling the pattern of brain activity related to items in successive positions across the subitizing boundary (third vs. fourth) or any other position within the sequence. This is in striking contrast with the typical behavioral signature of subitizing found in our behavioral experiment and reported in previous studies (e.g., Cheng et al., 2021; Anobile et al., 2019) in which small

numerosities are perceived nearly in an exact way, leading to virtually errorless performance. These results thus point to a common perceptual mechanism representing sequential numerosities irrespective of numerical range, whereas the superior performance with very low numbers would be enabled by a distinct mechanism dependent on attention—as it has been hypothesized in the case of simultaneous numerosities (Burr et al., 2010, 2011; Hyde & Wood, 2011).

What is the nature of the additional mechanism granting errorless performance when facing small numbers of items? For simultaneous numerosity, it has been hypothesized that when items are within the limits of attention (i.e., around four items), items can be processed and stored individually (e.g., Mazza & Caramazza, 2015; Piazza et al., 2011), preserving a much richer set of information and allowing errorless estimation of their number. Beyond the limits of attention, the entire set of items would be encoded as a "single" item, allowing only summary statistics to be extracted from the representation (e.g., Hyde, 2011). We conjecture that something similar may explain our results. Namely, although an early perceptual representation of sequential numerosity would operate in a similar fashion irrespective of range, an additional postperceptual mechanism would allow a better storage of and access to this information. This, in turn, would disentangle overlapping representations, provided that the amount of information is sufficiently limited. In other words, even if a small numerosity is processed by an approximate sensory system, the individual storage of very few items might allow the exact estimation of their number.

Overall, our results, showing no neural evidence of an early perceptual signature of the subitizing boundary, are in line with the idea that a single perceptual mechanism is engaged during the encoding of sequential numerosities from the very beginning of stimulus presentation. Our findings thus suggest a distinction between the mechanism engaged during early perceptual processing and what happens after the encoding of the items composing a sequence. Indeed, the fact that subitizing is measurable at the behavioral level but has no clear neural signature during perceptual processing suggests that it is implemented at a postperceptual processing stage. However, because absence of evidence does not indicate evidence of absence, there are limitations to our results. Different recording and analytic techniques more sensitive to the measures of interest may be able to identify some early perceptual signature of the subitizing boundary. Nevertheless, the fact that our more comprehensive analyses can identify representational distinctions between more distant stimulus positions lend support to the idea that early perceptual signature of subitizing boundary may be negligible or relatively trivial.

Although the use of sequential numerosities for investigating the mechanism of subitizing has many advantages as we noted, there are limitations as well. First, as we used

a constant rate of presentation, it is possible that participants either attempted to (subvocally) count the stimuli, or use other information correlated with numerosity, like duration. Regarding the possibility of counting, the fast rate of stimulus presentation and the categorization paradigm was intentionally used to minimize it. Empirically speaking, the large error rates observed when approaching the judgment criterion suggest that counting was in fact impossible with our stimuli. Regarding the possibility of using duration, it should be noted that the visual system is notoriously poor in the processing of temporal (i.e., duration) information (as opposed to spatial information, whereas the opposite is true, for instance, for the auditory modality; e.g., Alais & Burr, 2004; Vroomen & de Gelder, 2004; Kubovy, 1988; Welch & Warren, 1980). Using duration as a proxy for numerosity would thus represent a much less efficient strategy, making this explanation less likely. In addition, the results of our control experiment make this explanation less likely. Indeed, the pattern of precision observed in the task is consistent with subitizing occurring at two and three items and an approximate representation occurring at larger numerosities, as suggested by the relatively flat pattern of WF observed from 4 to 12, which would be unrealistic had participants relied on duration to make judgments. In this context, a typical approach to control for the confound between numerosity and duration would be to systematically vary the rate of presentation. However, had we kept the total duration of the sequence equal across numerosities to instead vary the rate of presentation, small numbers like two or three would have had much longer ISIs between items, which may potentially result in a cleaner signal and sharper neural representations only because of that. This would, in turn, make the data much more difficult to interpret. Second, another limitation of using the present paradigm is the generalizability of our results to different cases. Indeed, sequential subitizing and sequential numerosity perception, in general, seem mediated by different processing mechanisms compared to simultaneous numerosities and seem to differentially engage brain regions in the parietal and temporal cortex (e.g., Anobile et al., 2019; Cavdaroglu & Knops, 2019; Tokita & Ishiguchi, 2012). Thus, this difference leaves open the possibility that the activation of different numerosity processing mechanisms and their relation might be different as well with simultaneously presented stimuli. Finally, we also need to acknowledge the limitation in determining the exact subitizing boundary in our main EEG experiment. Indeed, the classification task is not suited to determine the presence and the limits of subitizing, as error rates are related to the distance (or ratio) of each numerosity compared to the judgment criterion—that is, error rates decline also at the higher end of the range. The results of our control experiment, however, show that, consistent with previous studies, numerosities as low as 2 and 3 are subject to subitizing even in our sequential paradigm.

Conclusion

To conclude, our results show that the neural representation of items that make up sequential numerosity do not show any signature of subitizing boundary, in contrast with the stark behavioral signature of subitizing. These results are consistent with the idea that sequentially presented numerosities rely on a single perceptual mechanism and possibly that a subsequent postperceptual mechanism provides a more detailed storage of and access to such perceptual information to achieve subitizing.

Author Contributions

Michele Fornaciai: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Project administration; Visualization; Writing—Original draft; Writing—Review & editing. Joonkoo Park: Conceptualization; Formal analysis; Funding acquisition; Methodology; Project administration; Writing—Original draft; Writing—Review & editing.

Funding Information

Diversity in Citation Practices

A retrospective analysis of the citations in every article published in this journal from 2010 to 2020 has revealed a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience* (*JoCN*) during this period were M(an)/M = .408, W(oman)/M = .335, M/W = .108, and W/W = .149, the comparable proportions for the articles that these authorship teams cited were M/M = .579, W/M = .243, M/W = .102, and W/W = .076 (Fulvio et al., *JoCN*, 33:1, pp. 3–7). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance.

REFERENCES

Agrillo, C., Dadda, M., Serena, G., & Bisazza, A. (2009). Use of number by fish. *PLoS One*, *4*, e4786. https://doi.org/10.1371/journal.pone.0004786, PubMed: 19274079

Agrillo, C., Piffer, L., & Bisazza, A. (2010). Large number discrimination by mosquitofish. *PLoS One*, *5*, e15232. https://doi.org/10.1371/journal.pone.0015232, PubMed: 21203508

Alais, D., & Burr, D. (2004). The ventriloquist effect results from near-optimal bimodal integration. *Current Biology*, *14*, 257–262. https://doi.org/10.1016/j.cub.2004.01.029, PubMed: 14761661

Anobile, G., Arrighi, R., & Burr, D. C. (2019). Simultaneous and sequential subitizing are separate systems, and neither predicts math abilities. *Journal of Experimental Child Psychology*, 178, 86–103. https://doi.org/10.1016/j.jecp.2018.09.017, PubMed: 30380457

Anobile, G., Arrighi, R., Togoli, I., & Burr, D. C. (2016). A shared numerical representation for action and perception. *eLife*, 5, e16161. https://doi.org/10.7554/eLife.16161, PubMed: 27504969

Anobile, G., Cicchini, G. M., & Burr, D. C. (2016). Number As a primary perceptual attribute: A review. *Perception*, 45, 5–31. https://doi.org/10.1177/0301006615602599, PubMed: 26562858

Anobile, G., Domenici, N., Togoli, I., Burr, D., & Arrighi, R. (2020). Distortions of visual time induced by motor adaptation. *Journal of Experimental Psychology: General*, 149, 1333–1343. https://doi.org/10.1037/xge0000709, PubMed: 31789572

Arrighi, R., Togoli, I., & Burr, D. C. (2014). A generalized sense of number. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 281, 20141791. https://doi.org/10.1098/rspb.2014.1791, PubMed: 25377454

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, 10, 433–436. https://doi.org/10.1163/156856897X00357, PubMed: 9176952

Burr, D. C., Anobile, G., & Turi, M. (2011). Adaptation affects both high and low (subitized) numbers under conditions of high attentional load. *Seeing and Perceiving*, 24, 141–150. https://doi.org/10.1163/187847511X570097, PubMed: 21864455

Burr, D. C., Turi, M., & Anobile, G. (2010). Subitizing but not estimation of numerosity requires attentional resources. *Journal of Vision*, 10, 20. https://doi.org/10.1167/10.6.20, PubMed: 20884569

Camos, V., & Tillmann, B. (2008). Discontinuity in the enumeration of sequentially presented auditory and visual stimuli. *Cognition*, 107, 1135–1143. https://doi.org/10.1016/j.cognition.2007.11.002, PubMed: 18068696

Castaldi, E., Piazza, M., Dehaene, S., Vignaud, A., & Eger, E. (2019). Attentional amplification of neural codes for number independent of other quantities along the dorsal visual stream. *eLife*, 8, 1–26. https://doi.org/10.7554/eLife.45160, PubMed: 31339490

Cavdaroglu, S., Katz, C., & Knops, A. (2015). Dissociating estimation from comparison and response eliminates parietal involvement in sequential numerosity perception. *Neuroimage*, 116, 135–148. https://doi.org/10.1016/j.neuroimage.2015.04.019, PubMed: 25887262

Cavdaroglu, S., & Knops, A. (2018). Evidence for a posterior parietal cortex contribution to spatial but not temporal numerosity perception. *Cerebral Cortex*, 29, 2965–2977. https://doi.org/10.1093/cercor/bhy163, PubMed: 30060143

Cheng, X., Lin, C., Lou, C., Zhang, W., Han, Y., Ding, X., et al. (2021). Small numerosity advantage for sequential enumeration on RSVP stimuli: An object individuation-based account. *Psychological Research*, 85, 734–763. https://doi.org/10.1007/s00426-019-01264-5, PubMed: 31696296

Cordes, S., Gelman, R., Gallistel, C. R., & Whalen, J. (2001). Variability signatures distinguish verbal from nonverbal counting for both large and small numbers. *Psychonomic Bulletin & Review*, 8, 698–707. https://doi.org/10.3758/BF03196206, PubMed: 11848588

Cutini, S., Scatturin, P., Basso Moro, S., & Zorzi, M. (2014). Are the neural correlates of subitizing and estimation dissociable? An fNIRS investigation. *Neuroimage*, 85, 391–399. https://doi.org/10.1016/j.neuroimage.2013.08.027, PubMed: 23973407

Dehaene, S. (2011). *The number sense: How the mind creates mathematics*. Oxford University Press.

Dehaene, S., & Cohen, L. (1994). Dissociable mechanisms of subitizing and counting: Neuropsychological evidence from simultanagnosic patients. *Journal of Experimental Psychology: Human Perception and Performance*, 20, 958–975. https://doi.org/10.1037/0096-1523.20.5.958, PubMed: 7964531

Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, 134, 9–21. https://doi.org/10.1016/j.jneumeth.2003.10.009, PubMed: 15102499

DeWind, N. K., Adams, G. K., Platt, M. L., & Brannon, E. M. (2015). Modeling the approximate number system to quantify the contribution of visual stimulus features. *Cognition*, 142, 247–265. https://doi.org/10.1016/j.cognition.2015.05.016, PubMed: 26056747

DeWind, N. K., Park, J., Woldorff, M. G., & Brannon, E. M. (2019). Numerical encoding in early visual cortex. *Cortex*, 114, 76–89. https://doi.org/10.1016/j.cortex.2018.03.027, PubMed: 29983159

Dienes, Z. (2014). Using Bayes to get the most out of non-significant results. *Frontiers in Psychology*, 5, 781. https://doi.org/10.3389/fpsyg.2014.00781, PubMed: 25120503

Fornaciai, M., Brannon, E. M., Woldorff, M. G., & Park, J. (2017). Numerosity processing in early visual cortex. *Neuroimage*, 157, 429–438. https://doi.org/10.1016/j.neuroimage.2017.05.069, PubMed: 28583882

Fornaciai, M., Cicchini, G. M., & Burr, D. C. (2016). Adaptation to number operates on perceived rather than physical numerosity. *Cognition*, 151, 63–67. https://doi.org/10.1016/j.cognition.2016.03.006, PubMed: 26986745

Fornaciai, M., & Park, J. (2017a). Distinct neural signatures for very small and very large numerosities. *Frontiers in Human Neuroscience*, 11, 1–14. https://doi.org/10.3389/fnhum.2017.00021, PubMed: 28583882

Fornaciai, M., & Park, J. (2017b). Spatiotemporal feature integration shapes approximate numerical processing. *Journal of Vision*, 17, 6. https://doi.org/10.1167/17.13.6, PubMed: 29114806

Fornaciai, M., & Park, J. (2018). Early numerosity encoding in visual cortex is not sufficient for the representation of numerical magnitude. *Journal of Cognitive Neuroscience*, 30, 1788–1802. https://doi.org/10.1162/jocn_a_01320, PubMed: 30063175

Fornaciai, M., Togoli, I., & Arrighi, R. (2018). Motion-induced compression of perceived numerosity. *Scientific Reports*, 8, 6966. https://doi.org/10.1038/s41598-018-25244-8, PubMed: 29725026

Gallistel, C. R., & Gelman, R. (1992). Preverbal and verbal counting and computation. *Cognition*, 44, 43–74. https://doi.org/10.1016/0010-0277(92)90050-R, PubMed: 1511586

Grootswagers, T., Wardle, S. G., & Carlson, T. A. (2017). Decoding dynamic brain patterns from evoked responses: A tutorial on multivariate pattern analysis applied to time series neuroimaging data. *Journal of Cognitive Neuroscience*, 29, 677–697. https://doi.org/10.1162/jocn_a_01068, PubMed: 27779910

Harvey, B. M., & Dumoulin, S. O. (2017). A network of topographic numerosity maps in human association cortex. *Nature Human Behaviour*, 1, 0036. https://doi.org/10.1038/s41562-016-0036

Harvey, B. M., Klein, B. P., Petridou, N., & Dumoulin, S. O. (2013). Topographic representation of numerosity in the human parietal cortex. *Science*, 341, 1123–1126. https://doi.org/10.1126/science.1239052, PubMed: 24009396

Hyde, D. C. (2011). Two systems of non-symbolic numerical cognition. *Frontiers in Human Neuroscience*, 5, 150. https://doi.org/10.3389/fnhum.2011.00150, PubMed: 22144955

Hyde, D. C., & Spelke, E. S. (2009). All numbers are not equal: An electrophysiological investigation of small and large number representations. *Journal of Cognitive Neuroscience*,

21, 1039–1053. https://doi.org/10.1162/jocn.2009.21090, PubMed: 18752403

Hyde, D. C., & Wood, J. N. (2011). Spatial attention determines the nature of nonverbal number representation. *Journal of Cognitive Neuroscience*, *23*, 2336–2351. https://doi.org/10.1162/jocn.2010.21581, PubMed: 20961170

Izard, V., Sann, C., Spelke, E. S., & Streri, A. (2009). Newborn infants perceive abstract numbers. *Proceedings of the National Academy of Sciences, U.S.A.*, *106*, 10382–10385. https://doi.org/10.1073/pnas.0812142106, PubMed: 19520833

Kaufman, E. L., Lord, M. W., Reese, T. W., & Volkmann, J. (1949). The discrimination of visual number. *American Journal of Psychology*, *62*, 498–525. https://doi.org/10.2307/1418556

King, J.-R., & Dehaene, S. (2014). Characterizing the dynamics of mental representations: The temporal generalization method. *Trends in Cognitive Sciences*, *18*, 203–210. https://doi.org/10.1016/j.tics.2014.01.002, PubMed: 24593982

Kleiner, M., Brainard, D., & Pelli, D. (2007). What's new in Psychtoolbox-3? *Perception*, *36*, 1–16.

Kubovy, M. (1988). Should we resist the seductiveness of the space:time::vision:audition analogy? *Journal of Experimental Psychology: Human Perception and Performance*, *14*, 318–320. https://doi.org/10.1037/0096-1523.14.2.318

Libertus, M. E., Woldorff, M. G., & Brannon, E. M. (2007). Electrophysiological evidence for notation independence in numerical processing. *Behavioral and Brain Function*, *3*, 1. https://doi.org/10.1186/1744-9081-3-1, PubMed: 17214890

Liu, Y., Murray, S. O., & Jagadeesh, B. (2009). Time course and stimulus dependence of repetition-induced response suppression in inferotemporal Cortex. *Journal of Neurophysiology*, *101*, 418–436. https://doi.org/10.1152/jn.90960.2008, PubMed: 18987118

Mandler, G., & Shebo, B. J. (1982). Subitizing: An analysis of its component processes. *Journal of Experimental Psychology: General*, *111*, 1–22. https://doi.org/10.1037/0096-3445.111.1.1, PubMed: 6460833

Mazza, V., & Caramazza, A. (2015). Multiple object individuation and subitizing in enumeration: a view from electrophysiology. *Frontiers in Human Neuroscience*, *9*, 162. https://doi.org/10.3389/fnhum.2015.00162, PubMed: 25883563

Meyers, E. M. (2013). The neural decoding toolbox. *Frontiers in Neuroinformatics*, *7*, 8. https://doi.org/10.3389/fninf.2013.00008, PubMed: 23734125

Nelson, X. J., & Jackson, R. R. (2012). The role of numerical competence in a specialized predatory strategy of an araneophagic spider. *Animal Cognition*, *15*, 699–710. https://doi.org/10.1007/s10071-012-0498-6, PubMed: 22526693

Nieder, A., & Miller, E. K. (2004). A parieto-frontal network for visual numerical information in the monkey. *Proceedings of the National Academy of Sciences, U.S.A.*, *101*, 7457–7462. https://doi.org/10.1073/pnas.0402239101, PubMed: 15123797

Olivers, C. N. L., & Watson, D. G. (2008). Subitizing requires attention. *Visual Cognition*, *16*, 439–462. https://doi.org/10.1080/13506280701825861

Park, J. (2018). A neural basis for the visual sense of number and its development: A steady-state visual evoked potential study in children and adults. *Developmental Cognitive Neuroscience*, *30*, 333–343. https://doi.org/10.1016/j.dcn.2017.02.011, PubMed: 28342780

Park, J., Dewind, N. K., Woldorff, M. G., & Brannon, E. M. (2016). Rapid and direct encoding of numerosity in the visual stream. *Cerebral Cortex*, *26*, 748–763. https://doi.org/10.1093/cercor/bhv017, PubMed: 28342780

Pelli, D. G. (1997). The videotoolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, *10*, 437–442. https://doi.org/10.1163/156856897X00366, PubMed: 9176953

Pepperberg, I. M. (2006). Cognitive and communicative abilities of Grey parrots. *Applied Animal Behaviour Science*, *100*, 77–86. https://doi.org/10.1016/j.applanim.2006.04.005

Piazza, M., Fumarola, A., Chinello, A., & Melcher, D. (2011). Subitizing reflects visuo-spatial object individuation capacity. *Cognition*, *121*, 147–153. https://doi.org/10.1016/j.cognition.2011.05.007, PubMed: 21679934

Piazza, M., Izard, V., Pinel, P., Le Bihan, D., & Dehaene, S. (2004). Tuning curves for approximate numerosity in the human intraparietal sulcus. *Neuron*, *44*, 547–555. https://doi.org/10.1016/j.neuron.2004.10.014, PubMed: 15504333

Pomè, A., Anobile, G., Cicchini, G. M., & Burr, D. C. (2019). Different reaction-times for subitizing, estimation, and texture. *Journal of Vision*, *19*, 14. https://doi.org/10.1167/19.6.14, PubMed: 31194220

Repp, B. H. (2007). Perceiving the numerosity of rapidly occurring auditory events in metrical and nonmetrical contexts. *Perception & Psychophysics*, *69*, 529–543. https://doi.org/10.3758/BF03193910, PubMed: 17727106

Revkin, S. K., Piazza, M., Izard, V., Cohen, L., & Dehaene, S. (2008). Does subitizing reflect numerical estimation? *Psychological Science*, *19*, 607–614. https://doi.org/10.1111/j.1467-9280.2008.02130.x, PubMed: 18578852

Rodríguez, R. L., Briceño, R. D., Briceño-Aguilar, E., & Höbel, G. (2015). Nephila clavipes spiders (Araneae: Nephilidae) keep track of captured prey counts: Testing for a sense of numerosity in an orb-weaver. *Animal Cognition*, *18*, 307–314. https://doi.org/10.1007/s10071-014-0801-9, PubMed: 25164624

Roggeman, C., Santens, S., Fias, W., & Verguts, T. (2011). Stages of nonsymbolic number processing in occipitoparietal cortex disentangled by fMRI adaptation. *Journal of Neuroscience*, *31*, 7168–7173. https://doi.org/10.1523/JNEUROSCI.4503-10.2011, PubMed: 21562280

Sagi, D., & Julesz, B. (1984). Detection versus discrimination of visual orientation. *Perception*, *13*, 619–628. https://doi.org/10.1068/p130619, PubMed: 6535985

Simon, T. J., & Vaishnavi, S. (1996). Subitizing and counting depend on different attentional mechanisms: Evidence from visual enumeration in afterimages. *Perception and Psychophysics*, *58*, 915–926. https://doi.org/10.3758/BF03205493, PubMed: 8768186

Tokita, M., & Ishiguchi, A. (2012). Behavioral evidence for format-dependent processes in approximate numerosity representation. *Psychonomic Bulletin & Review*, *19*, 285–293. https://doi.org/10.3758/s13423-011-0206-6, PubMed: 22231727

Vroomen, J., & de Gelder, B. (2004). Temporal ventriloquism: Sound modulates the flash-lag effect. *Journal of Experimental Psychology: Human Perception and Performance*, *30*, 513–518. https://doi.org/10.1037/0096-1523.30.3.513, PubMed: 15161383

Vuilleumier, P. O., & Rafal, R. D. (2000). A systematic study of visual extinction. *Brain*, *123*, 1263–1279. https://doi.org/10.1093/brain/123.6.1263, PubMed: 10825363

Wagener, L., Loconsole, M., Ditz, H. M., & Nieder, A. (2018). Neurons in the endbrain of numerically naive crows spontaneously encode visual numerosity. *Current Biology*, *28*, 1090–1094. https://doi.org/10.1016/j.cub.2018.02.023, PubMed: 29551415

Welch, R. B., & Warren, D. H. (1980). Immediate perceptual response to intersensory discrepancy. *Psychological Bulletin*, *88*, 638–667. https://doi.org/10.1037/0033-2909.88.3.638, PubMed: 7003641

Wichmann, F. A., & Hill, N. J. (2001). The psychometric function: I. Fitting, sampling, and goodness of fit. *Perception & Psychophysics*, *63*, 1293–1313. https://doi.org/10.3758/BF03194544, PubMed: 11800458