Decoding location-specific and location-invariant stages of numerosity processing in subitizing

Short title: Location-specific and -invariant number decoding

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Abstract

Extracting the number of objects in perceived scenes is a fundamental cognitive ability. Number processing is proposed to rely on two consecutive stages: an early object location map that captures individuated objects in a location-specific way and a subsequent location-invariant representation that captures numerosity at an abstract level. However, it is unclear whether this framework applies to small numerosities that can be individuated at once ("subitized"). Here we used EEG-based multivariate pattern decoding to test for location-specific and location-invariant stages of numerosity processing in the subitizing range. In two experiments, 1-3 targets were presented in the left or right hemifield, which allowed for decoding target numerosity within each hemifield separately (location-specific) or across hemifields (location-invariant). Experiment 1 indicated the presence of a location-specific stage (180-200 ms post-stimulus), followed by a location-invariant stage (300 ms post-stimulus). Experiment 2 showed that both location-specific and invariant components are engaged only during tasks that explicitly require numerosity processing, ruling out automatic, passive recording of numerosity. Overall, the results suggest that numerosity coding in subitizing is strongly grounded on an attention-based, location-specific stage. This stage remains active in parallel with the subsequent activation of a location-invariant stage, where a full representation of numerosity is finalized.
Introduction

How the brain processes numerosity, for instance during object enumeration, has interested cognitive neuroscientists for decades. According to traditional models\(^1\)-\(^4\), numerosity coding is the result of a multi-stage process that transforms the initial non-symbolic sensory input into an abstract representation of the number of an object set (but see Ref.\(^5\)). These models rely on a core assumption about a (broad) distinction between location-specific and location-invariant stages of numerosity processing.

The location-specific stage (“object location map”) represents the position of the relevant items in a “normalized” fashion (i.e. irrespective of other physical factors, such as size), so that their numerosity is reflected in the number of spatially distinct positions occupied by the elements. Psychophysical\(^6\) and computational\(^7\) studies have further supported the plausibility of a spatially selective processing stage of numerosity coding. This stage is not specifically tuned to numerosity, but provides a representation that is shared by many visuospatial functions, including numerosity coding\(^8\). In a subsequent location-invariant stage(s) of numerosity processing, the numerosity of the set of objects is represented in an abstract way, independently of the location in the visual field. The final output is a representation of the specific numerical value of the object set\(^3\).

Neuroimaging findings\(^9\)-\(^11\) have lent initial support to this distinction, and mainly for the existence of location-invariant numerosity representations in parietal areas\(^10\). However, studies on this issue are scant. Additionally, anatomical segregation alone could prove difficult to reach a firm conclusion about the existence of two independent stages of numerosity coding. For instance, whether the stages operate simultaneously or sequentially cannot easily be addressed on the basis of anatomical segregation. Thus, previous studies have not provided a definitive answer about the existence of a sequential two-stage processing mode of numerosity. In this respect, the higher time resolution provided by EEG measures may offer more stringent evidence for a temporal dissociation between location-specific and –invariant stages of numerosity processing.

Some previous EEG findings could be compatible with the existence of either an object location map in early stages of processing (although with disagreement on the exact time window, i.e. from about 75 ms to 150 ms post-stimulus; see Ref.\(^12\) and \(^13\), respectively), or a more abstract representation of numerosities (occurring at approximately 250-300 ms; see \(^14\)). However, there has been no systematic attempt to directly test in a single study the time course of location-specific versus -invariant components of numerosity coding. The only recent exception in this direction\(^15\) found an inversion of the early EEG responses in posterior areas (100 ms post-display onset) for the numerosities in the approximate number system range (i.e. 8-32) for upper versus lower stimulus presentations, and interpreted it as evidence of location-specific numerosity coding. This effect was followed by a second response occurring at later time (200 ms post-stimulus onset), which was sensitive to the numerosities in a location-invariant fashion. However, this is so far the only electrophysiological support to the existence of a dual-mode coding of numerosity, which may become problematic for the credibility of models of numerosity coding. Moreover, the study focused on a specific numerosity range, the typical one used in estimation tasks. Therefore, whether the dual-mode coding of numerosity applies to all numerosities, and to small object sets in particular, has remained elusive.

Small object sets have a special status in enumeration tasks, leading to the so-called subitizing effect\(^16\),\(^17\). Subitizing is the effortless processing of a small set of items (up to 3-4 elements), and it
seems to be a universal trait of humans (including infants) and several animal species for a review see \(^ {18}\). According to some influential models (e.g. \(^ {18,19,20}\)), the effect is considered a main feature of exact enumeration (as opposed to approximate enumeration that applies to larger numerosities), wherein the visual system is capable of individuating each element of the relevant set to ensure that it is enumerated once and only once\(^ {21}\). As such, subitizing seems to rely on a different mechanism with respect to enumeration or estimation of larger quantities. Does subitizing still reflect the outcome of a dual-mode coding of numerosity? In other words, is there a two-stage process in subitizing, as in the case of larger numerosities?

An electrophysiological distinction between subitizing and the processing of larger numerosities has been recently provided\(^ {13,15}\), with small numerosities activating stages in the mid-latency range (i.e., around 150-180 ms post-stimulus onset). The distinction was taken as further support to the suggestion that the neural circuitry dedicated to small numerosity coding is different from the mechanism for estimating larger numerical quantities. However, this distinction was not directly grounded on the test for a location-specific versus –invariant component. Therefore, whether the activation of the mid-latency stages (i.e. approximately 180 ms post-stimulus onset) found in these previous studies for subitizing still rely on a location map has remained elusive.

Overall, since no direct test for temporal segregation of a location-specific versus –invariant component in subitizing has been conducted so far, it has remained unclear the extent to which the dual-mode coding of numerosity applies to subitizing. Here, we provide direct evidence for a temporal (and spatial) segregation of the stages involved in subitizing. Specifically, the present EEG study used multivariate pattern analysis (MVPA) to test for a dissociation between location-specific and location-invariant neural processing of small numerosities (1-3 elements, subitizing effect) in terms of time course and temporal order. Following the literature on the subitizing effect in human adults, where the relevant items have to be enumerated (e.g. \(^ {17,22}\)), Experiment 1 used an explicit enumeration task requiring to report the number (or to detect a specific numerosity) of targets presented among distracters. The use of distracter elements ensures that the overall area occupied by the items remains constant despite the variation in target numerosity. This (at least, partially) allowed us to exclude an explanation of the effects in terms of sensory-based coding, namely that any distinction across numerosities could be exclusively related to a passive encoding of the variation in continuous magnitudes, such as overall area, that typically covary with variation in numerosity. The inclusion of distracting objects should not modify the nature of the subitizing effect, as shown by previous studies\(^ {22,23}\).

Crucially, the objects to be enumerated were presented in either the left or right hemifield. By decoding target numerosity within each hemifield separately (location-specific) or across hemifields (location-invariant), we were able to disentangle the time courses of location-specific versus -invariant stages: To isolate the location-specific stage we trained a classifier to discriminate targets appearing in the left hemifield and tested the classifier using targets appearing in the same hemifield. The same was done for targets appearing in the right hemifield. Importantly, the location-specific stage is expected to be processed mainly contralaterally to the hemifield. We therefore tested for the lateralization of location-specific numerosity decoding effects, which served as the critical criterion for the location-specific stage: An interaction of decoding of left vs. right target numerosities in the right vs. left hemisphere can only be explained by location-specific numerosity representations. To isolate the location-invariant stage we trained a classifier to discriminate targets appearing in the left
hemifield and tested the classifier using targets appearing in the right hemifield (and vice versa). Thus, numerosity decoding across hemifields can only be explained by location-invariant numerosity representations. Taken together, this decoding approach provides the critical selectivity for segregating location-specific and -invariant stages. Finally, we ran a time-by-channel searchlight analysis for location-specific and -invariant numerosity decoding to thereby test for the spatial segregation of the dual-mode coding of numerosity.

Experiment 2 was conducted to test the extent to which the effects found in Experiment 1 were ascribed to “explicit” enumeration (the typical task used to study subitizing in human adults, e.g. 20), or to an automatic, passive encoding of target numerosities and their physical variation, as typically seen in studies with larger object sets (e.g. 24).

Results

Behavioral

The main findings from the behavioral analyses are summarized below and shown in Fig. 1B. For detailed descriptions see Mazza and Caramazza (2011). For Experiments 1 (a, b) and 2, proportion of correct responses and reaction times (RTs, calculated for correct responses between 200 and 1500 ms) were measured. As Experiment 1a and 1b yielded comparable results, the data were collapsed. All values were submitted to repeated-measures ANOVAs with numerosity (3 levels) as withinsubjects factor.

In Experiment 1, the ANOVA on RTs revealed a significant effect of Target numerosity (F(2, 46) = 40.002, p < .001, ηp² = .635). RTs were slower for 2 than 1 and 3 targets (ps < .001). Also for accuracy, Target numerosity was significant (F(2, 46) = 21.020, p < .001, ηp² = .478). In line with RTs, the proportion of correct responses was lower for 2 than 1 and 3 targets (ps < .001). In Experiment 2, the ANOVA on RTs only showed a trend towards significance for Target numerosity (F(3, 33) = 3.259, p = .053, ηp² = .229). RTs were faster when 2 and 3 targets were presented compared to 1-target condition (ps < .039). No effect was significant with accuracy data (p = .095).
Figure 1. Stimuli and behavioral results. (A) Temporal sequence of a trial. (B) Mean response times of Experiment 1 and 2. Vertical bars represent standard error of the mean.

EEG Results

Experiment 1

To investigate the time course of location-specific and -invariant numerosity representation, we first performed multivariate pattern decoding on target numerosity (1, 2, and 3) for each hemifield separately (within hemifield decoding) and across hemifields, respectively. For the location-specific decoding, we trained and tested the classifier on targets from the same hemifield. For the location-invariant decoding, we trained the classifier on left targets and tested it on right targets, and vice versa. All channels were used in this analysis. We found that location-specific numerosity representations were reliably present from 180 ms post-stimulus (peaking around 270-320 ms after stimulus onset). Location-invariant representations started at approximately 300 ms, peaking much later (around 550 ms after stimulus onset). Significant differences between location-specific and location-invariant decoding started at 184 ms after stimulus onset (Fig. 2A, upper row).
Next, we investigated the location-specific numerosity stage in more depth. To provide additional, compelling evidence for the location-specific decoding, we tested the prediction that location-specific decoding is stronger for contralateral as compared to ipsilateral channels with regard to the hemifield in which the targets appeared. We therefore repeated the location-specific numerosity decoding for left and right channels separately. As predicted, we found stronger decoding in contralateral vs. ipsilateral channels (Fig. 2B, upper row). A significant interaction between HEMIFIELD (left, right targets) and HEMISPHERE (left, right channels) were found after 224 ms, with a second peak at 508 ms after stimulus onset.

Experiment 2

Experiment 2 was identical to Experiment 1 except that participants just had to indicate the presence or absence of targets irrespective of their numerosity. Except for a subtle effect of location-specific numerosity decoding around 300 ms after stimulus onset, no effects were observed (Fig. 2, bottom row). This suggests that the numerosity representations decoded in Experiment 1 were not due to a
passive processing of object numerosity but depended on the explicit requirement to enumerate the relevant objects.

**Time-by-channel searchlight MVPA**

To corroborate the identified segregation between the location-specific and location-invariant stage and to provide a coarse idea about the location of these stages in channel space, we performed a time-by-channel searchlight analysis. The resulting topographical maps for the location-specific numerosity decoding in Experiment 1 revealed classification accuracies above chance that peaked around posterior channels of the contralateral hemisphere from around 200 to 300 ms (Fig. 3, top and middle row). Later decoding was more widespread and less lateralized, peaking around central channels. The location-invariant decoding started later (250 ms), with bilateral peaks around more anterior parietal channels (sparing the most posterior channels that revealed the strongest effects in the location-specific decoding; Fig. 3, bottom row), suggesting not only a temporal but also a spatial segregation of the two stages. Experiment 2 revealed no significant effects of location-specific and location-invariant decoding.

**Figure. 3.** Searchlight MVPA for location-specific and -invariant numerosity representation in Experiment 1. For visualization purposes, time-by-channel searchlight maps were averaged across time every 50 ms. Black dots indicate center EEG channels that revealed significant numerosity decoding accuracies above chance (corrected for multiple comparisons) in at least one time point (i.e. 4 ms) within each 50 ms step.

**Discussion**

The human brain is endowed with the ability to efficiently enumerate up to three-four objects, a phenomenon known as subitizing effect\(^\text{16}\). Despite being a pervasive phenomenon, some aspects of subitizing have remained unclear. By means of EEG decoding the present study addressed whether a crucial aspect of the neural architecture of numerosity representation, namely the presence of a dual-stage numerosity code, also applies to the special case of subitizing.

In line with some previous neuroimaging findings\(^\text{9,15,25}\), the present EEG results lent support to the existence of a distinction between location-specific and location-invariant numerosity coding of small object numerosities. Experiment 1 indicated that there are two subsequent stages of representation: a
location-specific stage that starts at approximately 180-200 ms post-stimulus, and a location-invariant stage with an onset latency of 300 ms post-stimulus. Crucially, the results of the additional analysis on the interaction between hemisphere and hemifield further disclosed the spatially-selective organization of the first stage of numerosity coding by pointing to a predominant contralateral processing of the target numerosities in this stage.

The nature and time course (approximately 180-200 ms post-stimulus) of the location-specific stage of numerosity coding resonate with previous ERP work on attention individuation of multiple targets in various contexts (e.g., enumeration, multiple object tracking, delayed match to sample tasks\cite{26-32}). In all these studies, a numerosity-related contralateral ERP response with a latency of approximately 200 ms (N2pc, \cite{33,34}) was found, suggesting that an attention-based mechanism of object individuation is a core component of the visual system involved in processing multiple targets (up to the 3-4 objects) in a variety of tasks, including enumeration. In general, the current results are in accordance with the idea that a spatially-selective, attention-based mechanism may have a first important role for numerosity coding\cite{3,7,8,35}. For instance, according to some influential proposals (e.g. \cite{8}), the attention system could operate on numerosities as it does for other physical dimensions, such as space or time. The idea that numerosity could be encoded independently and in the same fashion as other primary attributes (e.g. shape, color) has been successfully demonstrated in some recent studies (for a recent review see \cite{36}; but see \cite{5}).

Despite there has not been any previous EEG attempt to directly test for the dissociation between location-specific versus location-invariant stages of small numerosity representation, the present results are in line with some previous ERP studies that separately disclosed stages with similar latencies (approximately 200 ms and 250 ms, respectively) as the ones seen here. The first stage has been associated with the existence of an object file system that spatially tags multiple locations at once\cite{13}, while the latter has been interpreted as evidence of abstract coding for number\cite{14}. However, none of these studies have tried to investigate whether these stages were location-specific. Interestingly, recent investigations\cite{12,15} have also shown an early effect (75 ms ca) related to the specific activation of occipital areas, and interpreted this as evidence of the location-map stage where object locations are represented regardless of other physical dimensions (e.g. size). This early stage would only be activated by large numerosities\cite{15}, whereas a later stage (approximately 180-200 ms) would instead be associated with a summation layer where the results of the location-map stage are added and an abstract representation of quantity is formed, irrespective of the numerical range used. However, since no direct test for location-sensitive versus location-invariant stages was addressed for small numerosities, a direct comparison between these previous findings and the present results becomes difficult.

Finally, we found that the early location-specific and later location-invariant stage were associated with different topographical distributions, peaking around posterior occipital channels and more anterior parietal channels, respectively. This might suggest that the two stages are processed by different neural substrates. While the EEG topography of the numerosity decoding effects does not allow for a precise anatomical localization, it appears plausible (based on related fMRI findings) that location-specific effects originate from the occipitotemporal or occipitoparietal cortex and location-invariant effects originate from the inferior parietal cortex, specifically the intraparietal sulcus\cite{9,11,37}.

Overall, Experiment 1 provided a compelling piece of evidence that small numerosities are processed via an attention-based stage that initially takes into account the location of the to-be-enumerated
elements, followed by a stage that is invariant to the elements’ location and (likely) represents numerosities in a more abstract way. Once activated, both stages seem to remain active throughout the trial duration.

Experiment 2 further specified the nature of the numerosity coding stages involved in the task used in the present study. The results showed that there was no numerosity-related modulation when numerosity was irrelevant for the task. This finding perfectly matches the typical context in which subitizing emerges, namely enumeration tasks where the observers have to explicitly report the numerosity of the relevant elements (e.g. 22). Therefore, the findings suggest that the location-specific and invariant components seen in Experiment 1 were not merely triggered by an automatic, passive recording of numerosities and their variation (as well as other, continuous magnitudes related to this variation).

Likewise, these results further rule out alternative explanations for the numerosity effect observed in Experiment 1, such as those related to passive recording of changes in continuous dimensions (e.g. density, local area etc.) that typically correlate with variations in numerosity. The existence of a mechanism for coding numerosity independently of other continuous magnitudes (e.g., size, area) is still debated (for a recent review see 38). However, the results of Experiment 2 indicated that (passive) recording of continuous magnitudes is insufficient to explain the effects found in Experiment 1.

Altogether, the results of Experiment 1 and Experiment 2 point out that the decoding of numerosity addressed in the present study only pertains to contexts where numerosity are task-relevant, rather than to passive viewing of numerosities.

In conclusion, by means of EEG decoding we successfully disentangled location-specific and location-invariant stages of small numerosity representation in (explicit) enumeration. The results suggest that numerosity coding in subitizing is strongly grounded on an attention-based stage that operates according to coordinates of a location map. This stage remains active in parallel with the subsequent activation of a location-invariant stage, where a complete abstract representation of numerosity is finalized by the brain. The approach taken in the present study could successfully be extended to larger numerosities and for different task requirements in order to fully disclose the neural architecture of number coding.
Methods

Data were taken from Mazza and Caramazza (2011) and analyzed here with a different approach. Data of Experiment 1 were originally collected in two separate experiments (Experiment 1 and Experiment 3, see Mazza & Caramazza, 2011, hereafter Experiment 1a and Experiment 1b), but were collapsed here to increase power for the EEG decoding procedure, and given that virtually identical results were obtained.

Participants

Twenty-four volunteers participated in Experiment 1 (20 females) and 12 in Experiment 2 (8 females). They all provided their written informed consent. The experimental procedures were conducted in accordance with the declaration of Helsinki guidelines and approved by the Ethics Committee for research involving human participants at the University of Trento, Italy.

Stimuli and procedure

In both Experiment 1 (Experiment 1a, Experiment 1b) and Experiment 2, on each trial red and green diamond shapes were presented. The display contained 16 diamonds, 8 in each hemifield, and appeared for 150 ms. Participants had up to 1500 ms to respond and the inter-trial interval lasted 1500 ms (Fig. 1A). In each trial, in one hemifield 1, 2 or 3 diamonds had a unique color (either red or green), serving as targets. Experiment 1a and Experiment 2 included also zero-target trials. In Experiment 1a, participants had to report the exact number (0/1/2/3) of targets presented. In Experiment 1b, in each block participants decided (Yes/No) whether a specific target numerosity (designated at the beginning of each block) was presented. In Experiment 2, the task was to decide (Yes/No) whether at least one target was shown on display. For further specific details, see Mazza and Caramazza (2011).

EEG recording and data pre-processing

The EEG signal was recorded from 25 electrodes (including PO7 and PO8) with a 1000 Hz sampling rate (bandpass filter: 0.01-200 Hz). A right earlobe channel was used as online reference and horizontal eye movements were recorded through two channels positioned on the outer canthi of both eyes. The signal was then offline down-sampled to 250 Hz, low-pass filtered (40 Hz) and then re-referenced to the average of both earlobe channels. Trials yielding correct responses were segmented from -100 to 600 ms with respect to stimulus onset and baseline corrected over the 100 ms preceding the stimulus. Finally, those trials containing artifacts were removed (when HEOG exceeded ± 30 μV and/or any other channel exceeded ± 80 μV; on average, 8.8% of trials were excluded).

Multivariate Pattern Classification

To decode numerosity from EEG signals, the CoSMoMVPA Toolbox (2011) was used. The procedure for Experiment 1 and 2 was identical: For each participant, channel, and condition, we generated pseudotrials that were used for training and testing a linear discriminant analysis (LDA) classifier:
First, we randomly divided the data into 8 chunks. For each chunk, we then generated an equal number of pseudotrials consisting of the average of 2 trials each. We resampled each trial with a maximum number of 3 times, i.e., each trial was averaged with another, randomly selected trial maximally 3 times. As a result, the number of trials for each chunk and numerosity was identical. Since resampling was done for each chunk separately, data for training and testing classification were guaranteed to be independent.

A temporal searchlight MVPA was performed using a temporal radius of 2 time bins, i.e., for each time point, EEG data from 2 preceding to 2 following time points was used for classification.

Location-specific numerosity representations should be lateralized to the contralateral hemisphere, i.e., numerosity of left targets should be represented in the right hemisphere (and thus be decoded better from right electrodes) and vice versa for right targets. Since within-hemifield decoding could in principle be driven by both location-specific and location-invariant numerosity representations, the interaction of hemifield- and hemisphere-specific decoding thus provides a compelling proxy for location-specific coding of numerosity.

Numerosity decoding was performed using either all EEG channels or for left and right EEG channels separately (excluding channels along the midline), using the following multiclass decoding schemes: (1) For the location-specific decoding, we used all channels to decode targets for each hemifield separately, i.e., we trained and tested the classifier on targets appearing on the left side only and, in a separate classification, we did the same for targets appearing on the right side. Classification performance was assessed using leave-one-chunk-out cross validation: The classifier was trained to decode numerosity using data of 7 out of the 8 chunks and tested on its ability to decode numerosity using data of the held out chunk. This was iterated 8 times, leaving out each chunk once. Resulting decoding accuracies were then averaged across the iterations and across hemifield. (2) For the location-invariant decoding, we trained the classifier, using all channels, to discriminate the numerosity of left targets and tested the classifier on its ability to decode numerosity of right targets. The same was done vice versa, and resulting decoding accuracies were averaged. (3) For the location-specific/hemisphere-specific decoding, we repeated the location-specific decoding for left and right channels separately, i.e., for targets appearing on the left side we used either right (contralateral) or left (ipsilateral) channels, and vice versa for targets appearing on the right side. Resulting decoding accuracies were averaged only across the iterations, but not across hemifield or hemisphere.

For each decoding scheme, resulting accuracy time courses were entered into one-tailed one-sample t tests across participants against chance (= 33.3%). For the location-specific/hemisphere-specific decoding, we also performed repeated measures ANOVA with the factors HEMIFIELD and HEMISPHERE. To correct for multiple comparisons, we used cluster-based a Monte Carlo simulation algorithm as implemented in the CoSMoMVPA Toolbox. We used a threshold of $p = 0.05$ (one-tailed) at the cluster level, an initial threshold of $p = 0.001$ per time bin, and 10000 iterations of Monte Carlo simulations.

For illustration purposes, plotted time series were smoothed using a 5-point moving average.

*Time-by-channel searchlight MVPA*
To provide further evidence for a segregation between the location-specific and location-invariant stage and to investigate the topographical distribution of these stages on the scalp, we performed a searchlight analysis across time and EEG channels. This was realized by crossing the feature neighborhoods of the temporal dimension (radius = 2 time bins around each center time bin) and the spatial dimension (radius = 2 EEG channels around each center channel), resulting in time-by-channel neighborhoods. For each time-by-channel neighborhood, we performed the location-specific and location-invariant numerosity decoding using the same parameters and procedures as described above, except that for the location-specific decoding, resulting accuracy maps were not averaged across hemifields. Resulting time-by-channel maps were corrected for multiple comparisons using cluster-based Monte Carlo simulations as described above, with the specification that clusters do not have to be connected by neighboring time points, which increases the threshold to reach significance but allows more accurate inferences about time points of significant effects. The time-by-channel accuracy maps were converted into FieldTrip structures to generate topographical plots for visualization.

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Author Contributions
M.F.W. and C.F.T. analyzed the data and wrote the manuscript, V.M. designed the experiments, ran the study, and wrote the manuscript.

Competing Interests:
The authors declare no competing interests.