



Dissociating estimation from comparison and response eliminates parietal involvement in sequential numerosity perception



Seda Cavdaroglu ^{*}, Curren Katz, André Knops

Humboldt Universität zu Berlin, Faculty of Life Sciences, Department of Psychology, Rudower Chaussee 18, 12489 Berlin, Germany

ARTICLE INFO

Article history:

Received 23 December 2014

Accepted 7 April 2015

Available online 14 April 2015

Keywords:

Numerical cognition

fMRI

Multivariate pattern analysis

Number sense

Supramodal numerosity

ABSTRACT

It has been widely debated whether the parietal cortex stores an abstract representation of numerosity that is activated for Arabic digits as well as for non-symbolic stimuli in a sensory modality independent fashion. Some studies suggest that numerical information in time-invariant (simultaneous) symbolic and non-symbolic visual stimuli is represented in the parietal cortex. In humans, whether the same representation is activated for time-variant (sequential) stimuli and for stimuli coming from different modalities has not been determined. To investigate this idea, we measured the brain activation of healthy adults performing estimation and/or comparison of sequential visual (series of dots) and auditory (series of beeps) numerosities. Our experimental design allowed us to separate numerosity estimation from comparison and response related factors. The BOLD response in the parietal cortex increased only when participants were engaged in the comparison of two consecutive numerosities that required a response. Using multivariate pattern analysis we trained a classifier to decode numerosity in various regions of interest (ROI). We failed to find any parietal ROI where the classifier could decode numerosities during the estimation phase. Rather, when participants were not engaged in comparison we were able to decode numerosity in an auditory cortex ROI for auditory stimuli and in a visual cortex ROI for visual stimuli. On the other hand, during the response period the classifier successfully decoded numerosity information in a parietal ROI for both visual and auditory numerosities. These results were further confirmed by support vector regression. In sum, our study does not support the involvement of the parietal cortex during estimation of sequential numerosity in the absence of an active task with a response requirement.

© 2015 Elsevier Inc. All rights reserved.

Introduction

The ability to comprehend and differentiate quantities is an essential cognitive capacity. We use this ability for simple automated acts such as calculating the grip aperture before we grasp a cup as well as when we are performing mathematical operations. Certain developmental or genetic disabilities can render people incapable of performing even very simple calculations or understanding quantities in general (Chu et al., 2013; Mazzocco, 2009; McCloskey, 1992). Therefore, over the last few decades a considerable amount of research has focused on the neural basis of numerical cognition. One of the most influential ideas in the field has been the triple-code model (TCM) of numerical cognition suggested by Dehaene (1992) and Dehaene and Cohen (1995). According to a recent update of the TCM (Arsalidou and Taylor, 2011), numerical information is represented by three interacting but distinct codes, each associated with separate cortical structures. The Arabic number code is used for multi-digit arithmetic operations. Visually presented Arabic digits are associated with activity in bilateral fusiform and lingual regions. The verbal number code is used for memorized arithmetic problems that

are phonologically coded, such as single-digit multiplication and addition. Memorized arithmetic facts are associated with activity in predominantly left-hemisphere perisylvian language areas and the left angular gyrus. The abstract magnitude code is used for non-verbal quantity and magnitude understanding. Tasks requiring magnitude processing are associated with activity in the horizontal aspect of the intraparietal sulcus (hIPS). Although they can function independently in certain tasks, these three components are thought to interact with each other for more complex numerical operations (Arsalidou and Taylor, 2011). Interestingly, while the temporal cortex and articulatory loop are involved in learned aspects of arithmetic (e.g., the acquisition of the Arabic digit system and memorization of simple calculation facts; see Arsalidou and Taylor, 2011 for a review), the parietal cortex (specifically the intraparietal sulcus-IPS) is thought to contain an innate mechanism that humans share with other species, often referred to as ‘number sense’ (Nieder and Dehaene, 2009). The number sense is thought to enable us to comprehend quantities in an abstract fashion, independent of notation (e.g., symbolic or non-symbolic), presentation format (e.g., simultaneous or sequential) or sensory modality (e.g., visual or auditory; Dehaene et al., 2004).

A number of studies have examined the role of the IPS in representing numerical information presented in different notations (symbolic or non-symbolic). Eger et al. (2009) used multivariate pattern analysis (MVPA) to

^{*} Corresponding author at: Rudower Chaussee 18, Room 1.222, 12489 Berlin, Germany. E-mail address: seda.cavdaroglu@hu-berlin.de (S. Cavdaroglu).

decode symbolic (Arabic digits) and non-symbolic (dot-arrays) numerosities in a parietal ROI during numerical comparison. Interestingly, the classifier trained with Arabic digits generalized to non-symbolic numerosities, although the reverse generalization (from non-symbolic numerosities to Arabic digits) was not observed, supporting only partial notation independence. Piazza et al. (2007) observed a similar asymmetry. Exploiting fMRI adaptation, they found that after adaptation to non-symbolic numerosities, deviant digits led to a strong recovery of signal in the left parietal cortex. Conversely, after adaptation to Arabic digits, non-symbolic deviants did not lead to a recovery of signal in the left parietal cortex. In the right parietal cortex, they found symmetric recovery-effects across presentation notations (Piazza et al., 2007). These results suggest complete notation independence for the right parietal cortex and partial for the left. In contrast, Cohen Kadosh et al. (2007) reported symmetric recovery effects in the left parietal cortex, but none in the right. In short, both studies (Cohen Kadosh et al., 2007; Piazza et al., 2007) support hemispheric asymmetry of notation independence, but with opposite lateralization. On the other hand, using dot-arrays, an earlier fMRI study failed to find a numerosity specific representation in the parietal cortex (Shuman and Kanwisher, 2004). Specifically, Shuman and Kanwisher (2004) demonstrated that 1) a numerical comparison task did not induce higher BOLD response in the parietal cortex compared to a non-numerical comparison task, 2) there were no adaptation effects for numerosity repetition in the parietal cortex, and 3) the difficulty-related BOLD increase in the parietal cortex was not higher for numerical tasks compared to non-numerical tasks. Furthermore, Cohen Kadosh et al. (2011) found greater recovery in parietal BOLD response for a notation change (e.g., dots to digits) compared to a magnitude change. Two recent studies also found qualitatively different parietal representations of numerosity in dot arrays and Arabic digits (Bulthé et al., 2014; Lyons et al., 2014). Taken together, the role of parietal cortices in representing symbolic and non-symbolic numerical information remains controversial.

The idea of an abstract number system ('number sense') stipulates the same mechanism for the representation of numerical information that was extracted from simultaneous (dot-array) and sequential (series of dots) stimuli. In other words, an abstract number sense should be format-independent. Results from neurophysiology support format-independency. Nieder et al. (2006) found neurons in primate region VIP that selectively responded to numerosities from one to four, whether presented simultaneously (dot-array) or sequentially (series of dots). However, during the sample period only 2 out of 228 recorded neurons (~1%) were tuned to the same numerosity for both simultaneous and sequential stimuli (e.g., responding maximally to both a series of three dots and an array of three dots). In humans, the neural underpinnings of simultaneous versus sequential visual numerosities have not been investigated in detail.

Although a number of studies suggest at least partial notation and format independence, the sensory modality independence of numerical magnitude remains unclear. Eger et al. (2003) found overlapping BOLD response in the parietal cortex during auditory and visual symbolic number tasks. Piazza et al. (2006) found overlapping BOLD response in the right IPS during estimation of auditory (beeps) and visual (dots) sequential non-symbolic stimuli. However, overlapping BOLD response does not necessarily mean that the auditory and visual numerical information converge onto the same neural circuitry. In the macaque brain, Nieder (2012) found neurons that coded numerosities from one to four in a sensory-modality independent (i.e., supramodal) fashion. In humans, although a supramodal number sense is thought to reside in the hIPS (Dehaene et al., 2004), the neural underpinning of supramodal numerosity representation has also not been investigated in detail.

Given the lack of unanimous evidence for supramodal numerosity representation in the human parietal cortex, we aimed at studying the neural representation of auditory and visual numerosities using an event-related fMRI paradigm. We conducted multivariate analyses using machine-learning methods (support vector classification-SVC

and support vector regression-SVR) that allowed us to investigate whether common representation for auditory and visual numerosities existed in selected regions of the brain.

Moreover, we designed our paradigm such that numerosity estimation and comparison could be separated. Similar bilateral IPS regions are activated for numerical tasks and response-selection (Eliassen et al., 2003; Göbel et al., 2004; Schumacher and Jiang, 2003). Interestingly, Göbel et al. (2004) found no increase in BOLD response in IPS during a numerical comparison task after they controlled for response-selection and reaction time. To overcome a potential confusion between task-related processes and numerosity estimation, we presented auditory and visual numerosities (5, 7, 11, 16) either as series of beeps or dots and only asked participants to make a comparison on 20% of trials (see the **Materials and methods** section). This design enabled us to keep participants attentive during the whole experiment, assess performance, separate numerosity estimation from task related processing, and optimize the number of estimation-only trials.

Materials and methods

Participants

14 healthy right-handed participants underwent fMRI scanning after giving written informed consent (4 males; mean age = 26.3 ± 6.29 years). They were recruited using a Humboldt University database. All had normal or corrected-to-normal vision and reported no history of neurological or psychiatric illnesses. The study was approved by the Berlin Center for Advanced Neuroimaging (BCAN, Nr. 112 and 117), and the Ethical committee of Humboldt Universität zu Berlin. Participants were reimbursed 24 € for their participation.

Stimuli and procedure

Participants engaged in a non-symbolic numerosity-processing task. The non-symbolic numerosities were presented either visually (series of dots) or auditorily (series of beeps). Four numerosities (5, 7, 11, and 16) outside the subitizing range were chosen. They had approximately equal distances from each other on logarithmic scale. Non-numerical sensory features of stimulus sequences were balanced using four different stimulus sets. Single dot/beep duration and total duration increased with numerosity in set 1 and decreased with numerosity in set 4. The interval between single dots/beeps (ISI) increased with numerosity in set 2 and decreased with numerosity in set 3. Frequency (numerosity divided by total duration) increased with numerosity in sets 3 and 4 and decreased with numerosity in sets 1 and 2. This way, we ensured that participants could not rely on a single sensory cue (i.e., duration, frequency, or ISI) to extract numerosity information. To prevent counting, the majority of individual beeps and dots lasted less than 270 ms. Only in set 4 did we use dot/beep durations longer than 270 ms as well. Otherwise it was not possible to have a set of trials where total duration decreased with numerosity. This threshold is consistent with previous studies showing that participants cannot rely on verbal strategies (e.g., counting) within that period (e.g., Piazza et al., 2006; Tokita and Ishiguchi, 2011). We introduced random jitters within the series of dots/beeps to prevent numerosity perception based on periodicity. The length of the jitter depended on the single dot/beep duration for that trial. It was calculated such that after the subtraction of the jitter, the duration of that dot/beep was 40 ms (i.e., jitter = [dot / beep duration - 40 ms]). This way, we made sure that 1) by the subtraction of the jitter, the single dot/beep did not become incomprehensible (i.e., too short to be perceived) and 2) when the duration of a single dot/beep was longer than 270 ms, subjects could not reliably use a counting strategy because they would miss stimuli that were too fast to count. The number of jitters inserted also increased with numerosity to keep periodicity constant. Supplementary Table S1 reports the average, minimum and maximum single dot/beep durations and total stimulus duration for each set and numerosity.

Download English Version:

<https://daneshyari.com/en/article/6024893>

Download Persian Version:

<https://daneshyari.com/article/6024893>

[Daneshyari.com](https://daneshyari.com)