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Format-dependent representations of symbolic and non-symbolic numbers in the human cortex as revealed by multi-voxel pattern analyses☆

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Neuroimaging studies in the last 20 years have tried to unravel the neural correlates of number processing across formats in humans and non-human primates. Results point to the intraparietal sulcus as the core area for an abstract representation of numerical quantity. On the other hand, there exist a variety of behavioral and neuroimaging data that are difficult to reconcile with the existence of such an abstract representation. In this study; we addressed this issue by applying multi-voxel pattern analysis (MVPA) to functional Magnetic Resonance Imaging (fMRI) data to unravel the neural representations of symbolic (digits) and non-symbolic (dots) numbers and their possible overlap on three different spatial scales (entire lobules, smaller regions of interest and a searchlight analysis with 2-voxel radius). Results showed that numbers in both formats are decodable in occipital, frontal, temporal and parietal regions. However, there were no overlapping representations between dots and digits on any of the spatial scales. These data suggest that the human brain does contain an abstract representation of numerical magnitude.

Introduction

The neural mechanisms of numerical cognition have been intensively investigated in behavioral and neuroimaging research (for review see Ansari (2008); Nieder and Dehaene (2009)) due to the central role of numbers in daily life and education (Gerardi et al., 2013; Lipkus and Peters, 2009; Nelson et al., 2008; Reyna et al., 2009; Zikmund-Fisher et al., 2007). A core theme in this research deals with the question of representational overlap between symbolic (e.g. Arabic digits) and non-symbolic (e.g. arrays of dots) magnitudes. This issue has been approached by comparing brain activity during non-symbolic as well as symbolic tasks and by searching for regions that are commonly active while processing these two formats of numerical magnitudes. Both approaches have provided evidence in favor of the existence of an abstract representation of numerical magnitudes and the accumulating evidence suggests that the intraparietal sulcus (IPS) hosts a core module for processing numerical magnitude (Dehaene and Cohen, 1997; Eger et al., 2003; Pinel et al., 2001a).

More recently, it has been suggested that the multi-voxel pattern analysis (MVPA) of fMRI data might be an interesting method to probe the abovementioned question. This method provides a more fine-grained understanding of the nature of the activated numerical representations (Raizada et al., 2010). The existing body of data that has been interpreted in favor of an abstract representation of numerical magnitude is typically based on null results, indicating no differences between symbolic and non-symbolic formats in behavioral tasks and in activity in the IPS. Such null results are, however, difficult to interpret, as they can occur due to insufficient power to detect a difference. The present study attempts to overcome this issue by applying MVPA of fMRI data on regions of interest (ROIs) throughout the entire cortex (a) to test if symbolic and non-symbolic numerical magnitudes are processed in the same brain areas, and (b) to investigate the amount of representational overlap between both formats in those brain areas. Although MVPA has been applied to investigate numerical processing (Damarla and Just, 2012; Eger et al., 2009; Raizada et al., 2010), the present study extends the existing body of evidence in two important ways. First, this study is the first to apply MVPA not only in the IPS but also outside the parietal cortex. This allowed us to test the existence of a format-independent system for representing numerical magnitudes. Second, we also used MVPA searchlight analysis in the whole cortex to uncover other possible (common) areas for processing symbolic and non-symbolic magnitudes.

There has been a longstanding behavioral tradition in attempting to reveal the common representation of different numerical formats

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(Barth et al., 2003; Buckley and Gillman, 1974; Dehaene and Akhavein, 1995; Jaffe-Katz et al., 1989; Naccache and Dehaene, 2001; Shepard et al., 1975). One of the most important findings is the so-called numerical distance effect (Moyer and Landauer, 1967). The numerical distance effect is the observation that reaction times increase and accuracy rates decrease in number comparison tasks when numerical magnitudes are closer in distance than when they are further apart. This effect has been observed in children (Feigenson et al., 2004; Holloway and Ansari, 2010; Lonnemann et al., 2011; Sekuler and Mierkiewicz, 1977), adults (Dehaene, 1992; Dehaene et al., 1990; Moyer and Bayer, 1976; van Opstal and Verguts, 2011) and animals (Brannon et al., 2001; Nieder and Miller, 2003) and it has been contended that this indicates a similar way of representing numerical magnitudes across different species and ages. Moreover, this numerical distance effect seems to be similar for symbolic and non-symbolic stimuli, which suggests a common numerical magnitude system for different formats (Dehaene et al., 1990).

Neuroimaging studies in the last 20 years have tried to unravel the neural correlates of this numerical distance effect and number processing across formats in humans and non-human primates. Results have pointed to the IPS as the core area for the representation of numerical magnitude because of three main findings: (a) the IPS is involved in magnitude processing in humans (for a meta-analysis and review see Ansari (2008); Nieder and Dehaene (2009)) and primates (Nieder and Miller, 2003; Nieder et al., 2002; Sawamura et al., 2002); (b) the IPS activity correlates with the distance between numerical magnitudes in humans (Ansari et al., 2006; Cohen Kadosh et al., 2005; Piazza et al., 2007; Pinel et al., 2004); and (c) the IPS activity does not differ between formats in humans (Eger et al., 2003; Fias et al., 2003; Piazza et al., 2007).

Although these findings have been replicated with different paradigms and tasks, the abstract processing of numerical magnitudes and the function of the IPS as number module remain a debated issue. More specifically, some behavioral and neuroimaging observations are very difficult to reconcile with the abstract view on magnitude processing (for extensive discussion, see Cohen Kadosh and Walsh (2009)). For example, Gebuis and Reynvoet (2012a) have shown that the processing of non-symbolic magnitude is more grounded in low-level visual parameters than the processing of symbolic quantities. Lyons et al. (2012) found that comparing numerical magnitudes across formats is more difficult than comparisons within one format, suggesting that additional processing is required for cross-format comparisons. The experiments of Maloney et al. (2010) demonstrated that the distance effect of non-symbolic magnitudes is not correlated with that of symbolic magnitudes. Furthermore, children with developmental dyscalculia are more impaired in symbolic tasks compared to non-symbolic tasks (De Smedt and Gilmore, 2011; Iuculano et al., 2008; Landerl and Kölle, 2009; Rousselle and Noël, 2007). Finally, a recent review by De Smedt et al. (2013) on the association between numerical magnitude processing and individual differences in mathematics achievement indicated that in typically developing children, measures of symbolic but not non-symbolic number processing are reliable predictors of individual differences in mathematics achievement (De Smedt et al., 2013). In sum, these behavioral data are difficult to reconcile with an abstract representation of numerical magnitudes.

This abstract representation of numerical magnitudes has also been challenged by patient and neuroimaging studies. A study on patients with damage to the left supramarginal gyrus showed a dissociation between the processing of symbolic and non-symbolic magnitudes (Polk et al., 2001). Neuroimaging studies have demonstrated that the IPS contains an abstract representation of numerical order rather than numerical magnitude (Fias et al., 2007; Ischebeck et al., 2008) and that activity in the IPS while performing a numerical task was related to response-selection rather than numerical processing per se (Cappelletti et al., 2010; Göbel et al., 2004).

Whether or not numerical magnitudes are processed in an abstract way in the IPS has been subject to a continuing discussion in the numerical cognition domain (Cohen Kadosh and Walsh, 2009). One of the main issues in this debate is the fact that evidence for an abstract representation of numerical magnitudes is based on null results, indicating no differences across formats in activation in the IPS. It is crucial to point out that these null results emerge from fMRI studies that have used univariate methods to measure the overall regional activity for different conditions. Such data, however, limit our understanding of the information encoded by neural populations in that region. Recently, it has been suggested that the application of MVPA to fMRI might be one way to solve this issue (Ansari, 2008; Cohen Kadosh and Walsh, 2009; Dehaene, 2009).

MVPA allows to identify spatial patterns of brain activity of different stimuli in a certain region of interest (Norman et al., 2006). Two previous studies have used MVPA to relate the processing of symbolic and non-symbolic formats directly to each other. Damarla and Just (2012) showed that the neural codes for quantities of objects, e.g., a picture of three tomatoes or the digit 3 with a picture of one tomato, can be accurately decoded in the parietal cortex. Eger et al. (2009) compared the activation patterns evoked by dot patterns and digits (numbers 2, 4, 6 and 8) in the parietal cortex. The activation patterns non-symbolic and symbolic magnitudes were distinguishable at the individual level and they could be significantly decoded in the parietal cortex. However, the decoding was less accurate for symbolic compared to non-symbolic magnitudes. Eger et al. (2009) also applied cross-format generalization, showing significant generalization from symbolic to non-symbolic magnitudes but not from non-symbolic to symbolic. The studies of Damarla and Just (2012) and Eger et al. (2009) demonstrated that MVPA has the sensitivity that is required to investigate the representations of magnitudes. These data also suggested at least some commonality in symbolic and non-symbolic representations of magnitudes.

Similar to the study of Eger et al. (2009) we investigated the representation of numerical magnitude in the context of a comparison task. However, we extended their design in three important ways. First, given the growing literature, which shows that non-symbolic comparison tasks involve a lot of non-numerical processes (Gebuis and Reynvoet, 2012a,b; Gilmore et al., 2013), we implemented a whole-brain approach to define the relative importance of the different lobules. Our approach consisted of including a large set of ROIs and searchlight analysis. In these analyses we targeted the neural representations of number at multiple spatial scales: a large spatial scale (the entire cortex, frontal, parietal, occipital and temporal lobes), an intermediate spatial scale (ROIs in the four cortices) and a small scale (a whole-brain searchlight analysis with a radius of twice the voxel size). Second, Eger et al. (2009) only used ten subjects, but we aimed to replicate this in a larger sample of 16 subjects. Third, the paradigm of Eger et al. (2009) was an event-related fMRI design in which each trial involved the presentation of a sample number followed by a match number. Participants had to indicate whether the match number was smaller or larger than the sample number. We opted for a fixed comparison task in which each of the numbers (2, 4, 6 and 8) had to be compared to the fixed reference number 5 and control in this way for possible context-dependent effects on the number representations. The consequence of this fixed comparison task is that different from Eger et al. (2009) we cannot look into the neural representations of numerical magnitudes without the context of a comparison task.

We expected accurate decoding performance for both symbolic and non-symbolic magnitudes. If this decoding would be limited to the IPS, this would favor the existence of a format-independent module for representing numerical magnitudes. On the other hand, if decoding performance would be observed across various brain areas, this would suggest that the representation of magnitudes would be more widely distributed throughout the brain. We also predicted that a neural distance effect would occur for both formats in the regions with accurate decoding. The decoding performance for small distances should be lower than for large distances. Finally, we tested the generalization between the two numerical formats. Such generalization should occur if there is an abstract representation of number. However, the absence

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