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## Research Report

# Overlapping but separate number representations in the intraparietal sulcus—Probing format- and modality-independence in sighted Braille readers



Maria Czarnecka <sup>a,\*</sup>, Katarzyna Rączy <sup>a,b</sup>, Jakub Szewczyk <sup>a,c</sup>,  
Małgorzata Paplińska <sup>d</sup>, Katarzyna Jednoróg <sup>e</sup>, Artur Marchewka <sup>f</sup>,  
Guido Hesselmann <sup>g</sup>, André Knops <sup>h,1</sup> and Marcin Szwed <sup>a,\*\*,1</sup>

<sup>a</sup> Institute of Psychology, Jagiellonian University, Krakow, Poland

<sup>b</sup> Biological Psychology and Neuropsychology, University of Hamburg, Hamburg, Germany

<sup>c</sup> Department of Psychology, University of Illinois, Urbana Champaign

<sup>d</sup> The Maria Grzegorzewska University, Warsaw, Poland

<sup>e</sup> Laboratory of Language Neurobiology, Nencki Institute of Experimental Biology, Polish Academy of Sciences, Warsaw, Poland

<sup>f</sup> Laboratory of Brain Imaging, Nencki Institute of Experimental Biology, Polish Academy of Sciences, Warsaw, Poland

<sup>g</sup> Department of General and Biological Psychology, Psychologische Hochschule Berlin, Berlin, Germany

<sup>h</sup> UMR CNRS 8240, Laboratory for the Psychology of Child Development and Education, University of Paris, Paris, France

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## ABSTRACT

The Triple-Code Model stipulates that numerical information from different formats and modalities converges on a common magnitude representation in the Intraparietal Sulcus (IPS). To what extent the representations of all numerosity forms overlap remains unsolved. It has been postulated that the representation of symbolic numerosities (for example, Arabic digits) is sparser and grounded in an existing representation that codes for non-symbolic numerosity information (i.e., sets of objects). Other theories argue that numerical symbols represent a separate number category that emerges only during education. Here, we tested a unique group of sighted tactile Braille readers with numerosities 2, 4, 6 and 8 in three number notations: Arabic digits, sets of dots, tactile Braille numbers. Using univariate methods, we showed a consistent overlap in activations evoked by these three number notations. This result shows that all three used notations are represented in the IPS, which may suggest at least a partial overlap between the representations of the three notations used in this experiment. Using MVPA, we found that only non-automatized number information (Braille and sets of dots) allowed successful number classification. However, the numerosity of one notation could not be predicted above chance from the

\* Corresponding author.

\*\* Corresponding author.

E-mail addresses: [mhczarnecka@gmail.com](mailto:mhczarnecka@gmail.com) (M. Czarnecka), [m.szwed@uj.edu.pl](mailto:m.szwed@uj.edu.pl) (M. Szwed).

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brain activation patterns evoked by another notation (no cross-classification). These results show that the IPS may host independent number codes in overlapping cortical circuits. In addition, they suggest that the level of training in encoding a given type of number information is an important factor that determines the amount of exploitable information and needs to be controlled for in order to identify the neural code underlying numerical information *per se*.

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## 1. Introduction

In modern societies, numerical capacities are of central importance. Low numerical skills reduce a person's chances for succeeding in their professional career, often causing economic issues, such as higher risk for mortgage default (Gerardi et al., 2013). In general, lower numeracy levels (i.e., the ability to solve basic mathematical problems) have been shown to result in lower income (Estrada-Mejia et al., 2016) and to affect medical decision making (Reyna et al., 2009). Most of these skills crucially rely on the processing of symbolic numerical information, of which Arabic digits are the most common notation. The importance of numerical skills is reflected by the length of the formal education that individuals receive to ensure they master a circumscribed range of number-related concepts and procedures. Despite their importance, there remain a number of questions concerning the cognitive and neural mechanisms underlying the processing of numerical information that have stimulated vivid debates. Two central lines of research revolve around the questions of (1) how symbols such as Arabic digits are connected to their semantic content, and (2) whether numerical information from different modalities, formats (e.g., non-symbolic numerical information such as sets of objects vs. symbolic numerical information such as Arabic digits) and notations (e.g., Arabic digits vs. number words) converge on a unitary mental and neural representation.

According to the Triple Code Model (TCM; Dehaene, 1992; Dehaene & Cohen, 1997), numerical information is concurrently represented in different codes that rely on different cortical areas, depending on the type of sensory input. While phonological and visual number input codes can be considered asemantic (that is, they do not carry the cardinal information), a semantic magnitude code represents the cardinal information in an abstract manner, regardless of its input modality (Molko et al., 2003). The bilateral intraparietal sulcus (IPS) has been identified as the key cortical region for processing cardinal information. Studies have shown that the IPS activates specifically for numerical information, in both symbolic and non-symbolic formats (e.g., Arsalidou & Taylor, 2011; Piazza et al., 2006). While non-symbolic numerosity information is represented in an approximate fashion if a number exceeds three or four (e.g., “about twenty, more or less”), the symbolic system is more precise (a 19 is always a 19). The symbolic system is culturally acquired during formal education (De Smedt et al., 2013). Some researchers assume that symbolic representations are mapped onto evolutionarily

older, broader, and approximate representations of non-symbolic numbers (reviewed, for example, in Cantlon, 2012). In this process, a subset of neurons that formerly represented only non-symbolic numerosities (“about twenty, more or less”) would acquire additional sensitivity to the corresponding exact symbol (“19”). These neurons would then become precisely tuned to the specific number symbol, but they would preserve the responsiveness to the non-symbolic numerosity that the symbol corresponds with. This has been implemented in a computational model of numerical magnitude representation (Verguts & Fias, 2004). Eger et al. (2009) used multivariate pattern analysis (MVPA) to decode symbolic and non-symbolic numerosities in the parietal cortex during a magnitude comparison task. Interestingly, the classifier trained with Arabic digits generalized to non-symbolic numerosities, but the reverse generalization (from non-symbolic numerosities to Arabic digits) was not observed. One of the possible explanations for this is that the processing of Arabic digits takes place in a subset of a larger system of neurons that codes sets of dots. An algorithm trained on a subset is still able to recognize a broader pattern because the subset is a part of it, but the opposite is impossible. This suggests that the number representation is at least partially independent of the notation (Eger et al., 2009). Moreover, a number of studies report notation-independent modulation of neural activity in the IPS; this implies abstract coding of cardinal information (Naccache & Dehaene, 2001; Notebaert et al., 2010; see Knops, 2017 for a review).

Finally, modality-independent activity of the IPS was observed in studies that presented participants with numerical information in the visual and the auditory modality (e.g., Eger et al., 2003; Piazza et al., 2006). Eger et al. (2003) compared the processing of numbers, letters, and colors. Numbers were presented in both the visual and the auditory modality. They found a bilateral activation in the IPS only in response to numbers regardless of the modality. IPS activity has been interpreted as reflecting access to the abstract supramodal representation of numbers (Eger et al., 2003). Piazza et al. (2006) identified a right-lateralized, fronto-parietal network of increased activation for numerosity estimation of numbers presented in the visual and auditory modalities. This activation was not modulated by the modality of the stimuli (Piazza et al., 2006). Together, these studies support the TCM notion that the IPS represents magnitude information regardless of the modality, format, or notation. Yet, the abstract nature of the mental magnitude representation and its neural correlate in the IPS are subject to vivid debate.

In regards to the idea of supramodal number representation, more studies have addressed the question of whether the IPS hosts format-independent information. Lyons et al. (2015) postulated that symbolic and non-symbolic numbers, although both are coded in the IPS, are coded in fundamentally different ways without falling into the same abstract numerosity category. Bilateral IPS showed sensitivity to numerosity, regardless of whether a given number was presented symbolically or non-symbolically. Behavioral results showed that numerosity (i.e., the number of dots in a set) predicts the speed and accuracy in the matching task, but symbolic numbers do not. Using Representational Similarity Analysis (RSA), the authors showed that the similarity of the activation patterns for numerosities increased with decreasing numerical distance. In the case of symbolic numbers (Arabic digits), however, the patterns of cortical activation did not show a systematic relation with each other as a function of numerical distance. These results suggest that symbolic and non-symbolic quantities are not jointly represented by neural populations that are governed by overlapping principles (Lyons et al., 2015). Other decoding experiments have also shown significantly different classification accuracies for symbolic and non-symbolic numbers, with non-symbolic magnitudes leading to significantly higher classification accuracies, compared to symbolic ones (Bulthé et al., 2014, 2015). Furthermore, a recent high-field fMRI study reported topographically organized neural populations in the frontal cortex and the IPS that were tuned to visual and haptic non-symbolic numerosity information (Hofstetter et al., 2021). These maps did, however, overlap only partially. These studies support the idea that different notations have markedly different cortical representations. In contrast, a recent meta-analysis revealed overlapping bilateral activity in areas along the intraparietal sulcus (Sokolowski, et al., 2017); this indicates a common set of cortical regions that code for non-symbolic as well as symbolic number information. Most importantly, the common set of intraparietal regions was conserved when restricting studies, that entered the analysis, to passive designs that were not subject to response-related or attentional processes (Eliassen et al., 2003; Göbel et al., 2004; Schumacher & Jiang, 2003; Sokolowski, et al., 2017). Part of the evidence from behavioral and neuroimaging experiments does not fit easily into the model of abstract numerical representation (revised in Cohen Kadosh & Walsh, 2009; Eger et al., 2009; Lyons et al., 2015; Bulthé et al., 2014; 2015; Hofstetter et al., 2021). In sum, whether or not symbolic and non-symbolic numerical information converges on a common abstract neural representation still remains debated.

One factor that is consistently confounded when investigating the neural correlates of symbolic and non-symbolic number information is the amount of training that participants have received. That is, most participants in fMRI studies that investigated the processing of symbolic number information have undergone years, if not decades, of intense training that allows them to automatically extract the semantic content of the shown symbols. This automatic nature of the reading process putatively also leads to a large reduction of the attentional and neural resources that are deployed to accomplish the extraction of the semantic content of numbers. In contrast, the deliberate extraction of numerical

content from non-symbolic displays may be automatic and intuitive, but it is associated with more pronounced activity of the parietal cortex (Sokolowski et al., 2021).

Training participants in the perception of tactile number symbols (Braille) represents an interesting experimental approach to alleviate these confounds and investigate the extent to which numerical information from different modalities, notations, and formats converges on a common representation. There have been only a few attempts to investigate how tactile number information is processed in the human brain. In these experiments, tactile numbers were non-symbolic and were mostly presented sequentially (Cohen et al., 2014; Krause et al., 2013; Sixtus et al., 2020). Krause et al. (2013) asked participants to compare tactually presented numerosities (i.e., simultaneous stimulation of one to four fingers via piezoelectric Braille cells) with visually presented symbolic numbers (Arabic digits). They found a cross-modal numerical distance effect (i.e., the larger the distance between two numbers to be compared, the better the performance), which indicates at least a partial representational overlap between those two notations (Krause et al., 2013). Two recent experiments conducted with a group of sighted Braille readers used tactile Braille (symbolic) numbers. In a behavioral experiment, Rączy and colleagues (2020a) demonstrated cross-modal priming between Braille numbers and visually presented number words. Detailed analyses revealed, however, that the observed priming was most likely due to non-semantic repetition priming and did not reflect full-blown semantic access to the numerical prime (Rączy, Czarnańska, Zaremba, et al., 2020). In a follow-up repetition-suppression fMRI experiment, however, Rączy and colleagues (2020b) revealed semantic tactile-to-visual number priming at the neural level. The activity in the IPS was modulated by the numerical distance between tactile Braille primes and visually presented Arabic digit targets. This suggests some degree of semantic priming and at least a partial representational overlap between symbolic numbers from different modalities (i.e., tactile vs. visual; Rączy, Czarnańska, Papińska, et al., 2020). However, these studies are inconclusive with respect to the question of whether tactile primes elicit semantic priming in the first place. It has been argued that these priming effects do not provide sufficient evidence for semantic processing (Kunde et al., 2003). Rather, they could be a result of task-specific and asemantic action triggers that reflect associative learning during the course of an experiment. This question is important since it speaks to the central assumption of the TCM, which stipulates an abstract numerical magnitude representation in the IPS.

The current study investigates (1) whether Braille numbers elicit identifiable and distinct neural representations in a region that has been identified as pivotal in representing numerical magnitude information, namely the parietal cortex; (2) to what extent neural representations of Braille and visually presented symbolic numbers are characterized by a systematic overlap; (3) if this overlap exists, we attempt to determine if it exhibits similar patterns that allow for cross-classification between numbers of different modalities and formats using multi-voxel pattern analysis. We reasoned that an activation overlap observed by the classic analysis methods (GLM), would indicate a representational overlap between those categories.

Whereas, in MVPA cross-classification an identified activation pattern associated with one category, is used to predict activations in another category. Therefore If this prediction is accurate, it suggests that activation patterns are the same, rather than simply overlapping. The possible cross-classification between tactile and visual numerosities would provide evidence for a shared semantic system of representation in the parietal cortex.

## 2. Methods

No part of the study procedures or analyses was preregistered prior to conducting the research. We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

### 2.1. Participants and Braille training

Twenty-five healthy individuals (all female; median age = 25, range = 22–32) participated in the experiment. All participants were right-handed and monolingual, with normal or corrected-to-normal vision. Participants were students or graduates with a minimum of 3 years of higher education (median years of higher education = 5; range = 3–12). The study was approved by the local ethical committee (Komisja ds. Etyki Badań Naukowych) at Jagiellonian University, Kraków. Written consent was obtained from each participant.

The subjects were recruited from the participants of two previous projects. In these projects, participants underwent a nine-month tactile Braille reading course, during which they learned tactile recognition of Braille letters in the Polish alphabet (for details, see Bola et al., 2016; Matuszewski et al., 2021; Siuda-Krzywicka et al., 2016). For the purpose of the current experiment, participants attended an additional 3-week course that focused specifically on reading Braille numbers. This additional course took place either one or two years after the main nine-month course. It was designed and conducted by an experienced Braille teacher who had also co-designed the previous course (M.P., a co-author of this article). Since numbers in the Braille alphabet are letter symbols from A to J preceded by a number indicator, participants needed only three weeks to automatize their recognition of Braille numbers (for details, see Rączy, Czarnicka, Zaremba, et al., 2020; 2020b).

Braille readers were tested before and after the 3-week course. The pre-test included four tasks: (1) silent word reading speed in the Latin alphabet; (2) tactile Braille reading of single signs; (3) tactile Braille word reading; (4) tactile Braille number reading on an electronic Braille display. Participants were seated in a quiet place. In the silent word reading task (1), we used a test designed by Bola et al. (2016). Participants were instructed to read a 400-word text excerpt printed on paper. The overall time needed to read the text was measured. Reading comprehension was checked by 10 multiple-choice questions that were presented to participants after they had read the text. The tactile Braille reading of single signs (2) was measured in two separate tests: reading of single letters and

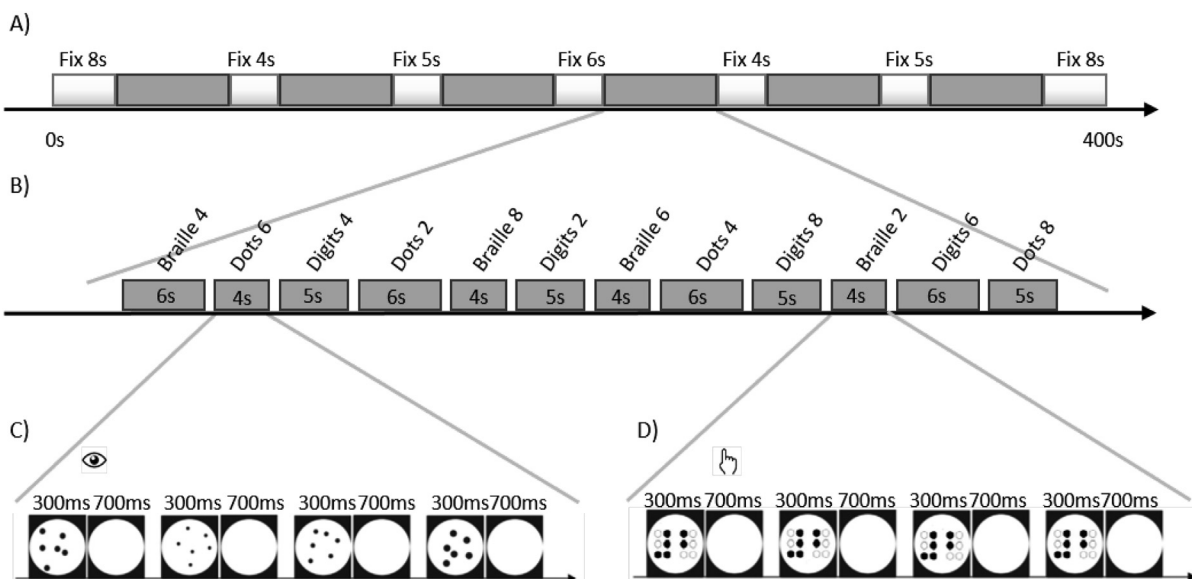
reading of single digits. Participants were instructed to read aloud as many letters as possible from a list in the first test, and as many digits as possible in the second test. The lists of letters and digits were printed in tactile Braille. The numbers of letters and digits correctly read in 60 s were measured separately. The tactile Braille word reading test (3) was carried out analogously, and the number of 4–6-letter-long tactile Braille words correctly read in 60 s was measured. In the last test (4), participants used a tactile Braille display (BraillePen Touch 12 <http://www.harpo.com.pl/>). The display was programmed to present 20 Braille digits (range 0–9) in a pseudo-random order in three separate runs. The digits were presented every 1 s: in the first try for 900 ms (followed by 100 ms break); in the second try for 600 ms (followed by 400 ms break); and in the last try for 300 ms (followed by 700 ms break). The accuracy of number recognition was measured for each run. After the Braille numbers course, participants were tested for the second time. This second testing session included 3 tasks from the first session, excluding the silent reading speed test in the Latin alphabet.

Before testing, participants were asked to declare their preferred reading hand and reading finger; they were instructed to use only the declared reading finger throughout the testing, Braille course, and fMRI session. Despite being right-handed, 10 of the 25 subjects read with their left hand. This preference for reading Braille with the non-dominant hand is a common and well-described phenomenon in blind persons (Millar, 1997; Rinaldi et al., 2020). It is most probably related to the right-hemispheric dominance in attention and has also been reported in sighted Braille readers (Bola et al., 2016).

### 2.2. Task and stimuli

Numerosities were presented visually and tactually (Fig. 1). Visual numbers were presented as images of size 400 × 400 pixels as either Arabic digits (visual symbolic) or sets of dots (visual non-symbolic); they were identical to those used by Bulthé et al. (2014). The stimuli were positioned approximately 100 cm from participants' eyes and were visible via a mirror attached to a head coil. Both formats consisted of centered white circles on a black background. Numerosities 2, 4, 6, and 8 were used in the experiment. The visual, symbolic condition consisted of Arabic digits. To avoid effects of adaptation to low level features, position of the digits on the screen and their size varied across trials. The visual non-symbolic condition consisted of sets of dots that were controlled for possible visual feature classification (total luminance and total area spanned by the dots; individual item size and inter-item spacing). Visual parameters pseudo-randomly varied across the dot displays.

As mentioned before, Braille numbers were presented in the standard form used by blind individuals: as the corresponding letter symbol preceded by the number indicator (for example, number 4 is represented by the letter D, preceded by a number indicator, ⠠⠙). They were presented on a 5-character electronic Braille display (fMRI-compatible Braille display, Neurodevice, <http://neurodevice.pl/>). To avoid sensory adaptation, they were presented pseudo-randomly on the first, second or third slot of the Braille display. For



**Fig. 1 – Overview of the experimental design. The numerosities 2,4,6 and 8 were presented as visual Arabic digits, visual sets of dots, and tactile Braille numbers. (A) Each run lasted approximately 400 s and contained 6 stimulus sequences separated by fixation. Each sequence (B) contained 12 blocks of stimuli. Each block contained 4–6 trials of the same kind; for example, (C) non-symbolic representations of numerosity 6 or (D) symbolic Braille representation of numerosity 2. In each block, subjects had to indicate whether the presented numerosity was higher or lower than 5 by pressing one of the two buttons on the response pad.**

behavioral testing and practice, we used a portable digital Braille Display (BP Touch 12 <http://www.harpo.com.pl>). Stimulation was controlled by Presentation Software (<https://www.neurobs.com/>). Legal copyright restrictions do not permit us to publicly archive the full set of stimuli used in this experiment. Readers seeking access to the stimuli are advised to contact the corresponding author of the [Bulthé et al. \(2014\)](#) publication.

### 2.3. fMRI task design

The design was similar to the one used by [Bulthé et al. \(2014\)](#), except for the addition of Braille numbers ([Fig. 1](#)). Participants were presented with numerosities 2, 4, 6, and 8 in the form of visual and tactile symbols (i.e., Arabic digits & Braille) or visual numerosities (i.e., sets of dots). Stimuli were presented in a rapid block design. A run lasted 6 min 40 s, starting with an 8-s presentation of a fixation cross. A run consisted of 72 blocks (6 presentations of each condition) and 5 fixations lasting randomly 4–6 s, one every 12 blocks. Each block included 4–6 stimuli of the same condition (but different visual features for visual stimuli or different spacing on the Braille display for tactile stimuli to avoid adaptation). One stimulus lasted 1 s and included 300 ms of number presentation and 700 ms of centered white circles on a black background. Each participant performed 8 runs. We used a magnitude comparison task in which each of the numbers (2, 4, 6, and 8) had to be compared to the fixed reference number-5. Comparison to a fixed standard required access to the underlying magnitude information, but it also allowed us to control for context-dependent effects on the number representations in the comparison. Participants were instructed to evaluate whether the

presented numerosity was smaller or larger than 5 each time the number and/or the notation changed. Responses were given by pressing the corresponding button on the response pad. Participants responded with the non-reading hand (see [Participants and Braille training](#) section above).

### 2.4. Data acquisition

MRI data were acquired with a 3 T S MAGNETOM Trio scanner. Functional MR scans were collected using an EPI sequence (48 slices,  $2.1 \times 2.1$  mm in plane voxel size, slice thickness 2 mm, interslice gap 1 mm, repetition time (TR) = 3000 ms, echo time (TE) = 30 ms, flip angle =  $90^\circ$ ,  $104 \times 104$  matrix). 3D T1-weighted MPRAGE images (176 slices, resolution  $1 \times 1 \times 1$  mm, TR = 2530 ms, TE = 3.32 ms,  $256 \times 256$  acquisition matrix) were also acquired for each subject. A 32-channel head coil was used. The data generated during the current study are available at: <https://openneuro.org/datasets/ds004400>

### 2.5. Data analysis

Behavioral data were analyzed in IBM SPSS Statistics 22 package ([http://www.psimgopro.pl/index\\_pl.html](http://www.psimgopro.pl/index_pl.html)) and in R (version: 4.0.2; R Core Team, 2020). The general linear model of a binomial family in R was fitted using the `glmer()` function from the `lme4` package (Bates et al., 2015). Prior to the analysis, categorical predictors (distance and number notation) were coded using `contr.sum()` function.

fMRI data were analyzed using the SPM12 software package (<https://www.fil.ion.ucl.ac.uk/spm/software/spm12>) with SPM Anatomy Toolbox version 3.0 with the JuBrain atlas (

[www.fz-juelich.de/](http://www.fz-juelich.de/)) for the labelling of anatomical locations. First, manual AC-PC correction of the anatomical images was applied. In the pre-processing for GLM, all the acquired functional volumes were corrected to the first slice for EPI distortion and slice acquisition time; they were subsequently realigned using rigid body transformations in order to correct for head movements. Data were segmented, then normalized to the standard adult template (MNI space, same voxel size) and smoothed (5 mm FWHM Gaussian kernel) using the DARTEL-based VBM. Then, the hemodynamic activity for each condition (for numbers 2, 4, 6, 8 in three conditions: Braille, Arabic digits, numerosities) and six estimated movement parameters were modelled as regressors in the first-level analysis. Blocks with incorrect answers were not excluded from the analysis. Subsequent analyses were performed using t-statistics resulting from the contrast of each condition versus implicit baseline. Activations in response to all three experimental conditions were also assessed using a conjunction approach based on the “conjunction null” hypothesis.

For decoding, the pre-processing consisted of slice timing correction, realignment, coregistration, and normalization. Then, the hemodynamic activity for each of the 12 conditions (for numbers: 2, 4, 6, 8, in: Braille, Arabic digits, numerosities) and the six estimated movement parameters were modelled as regressors in the first-level analysis. The decoding was performed using The Decoding Toolbox version 3.997 (Hebart et al., 2015; <https://sites.google.com/site/tdtdecodingtoolbox>). We used a support vector machine (SVM) with a radial basis function kernel ( $\gamma = 1$ ) as the decision function for classification. The type of the classification algorithm was C-SVC, with C set to 1. The classification was performed with feature selection that chose the set of 1500 voxels with a filter method. The selected filter uses a grid search algorithm to select those voxels with the highest classification weights in the training set. We performed classifications in native space, separately for each participant. During the training of the linear SVM, the data from 7 runs was used to construct the hyperplane that best separated the two conditions' data; the performance of the classifier was tested on the data of the remaining 1 run. This procedure was repeated 8 times per pair-wise classification, each time using data from a different functional run as the testing set (leave-one-out approach). SVM is a binary classifier that separates data points into two classes. Any multiclass classification is divided into multiple binary classifications. The pairwise classification was hence calculated in all 6 possible pairs without the reversed pairs: 2vs4, 2vs6, 2vs8, 4vs6, 4vs8, 6vs8. On the basis of the decision values from the binary classifications, overall multi-class accuracy is calculated and the confusion matrix is constructed. Every time a tie occurs (the algorithm does not find features to categorize a testing item as one of the classes) that item is automatically assigned to the first class. Lower accuracy translates to more undecided pairs, which hence results in larger biases towards first classes. In our classification, that creates a bias towards smaller numerosities because in all pairwise classifications the smaller number was entered as the first class. To assess accuracy of the classifier, 1000 permutations were carried out for each participant. In each iteration the labels in the training set were randomly assigned

within runs—*run-stratified permutation* (dependencies that existed in the original set were kept). Each iteration was averaged across participants. The group level accuracy was tested against 1000 averaged permutations by Fisher's  $p$ -value test.

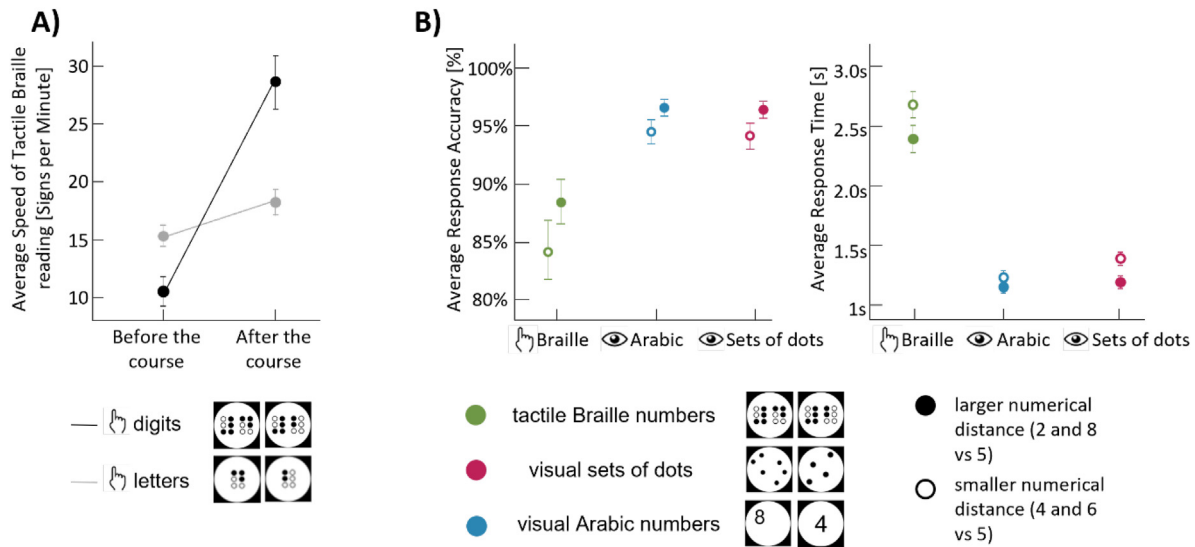
To investigate the distribution of voxels that were the most informative for the classification between numbers within each of the modalities, we ran a multivariate searchlight analysis (SA). This analysis was performed in a sphere with a 3-voxel radius that sequentially moved across all voxels within a mask that included the parietal region only. The mask was generated using the SPM Anatomy Toolbox version 3.0 with the JuBrain atlas (<https://www.fz-juelich.de/>). As a result, we obtained a classification accuracy for each voxel in the center of the sphere in which the local classification pattern had been identified. These values were used to create a map showing the performance of each classifier. The resulting participants' maps, restricted to the parietal region, were analyzed at the group level, adopting a standard random-effects approach. The analysis was performed separately for all three conditions (Braille, Arabic digits, sets of dots).

### 3. Results

#### 3.1. Reading speed and comprehension; Braille number reading training

To track participants' improvement in Braille number reading, we tested them before and after the number Braille reading course in five different tasks (see Methods). In the Latin alphabet silent reading speed task (1), participants read the 400-word text excerpt in an average of 2:27 min (SE = 0:08 min), which represents an average reading speed of 163 words per minute (WPM); this is a standard result for visual reading in skilled adults (e.g., Bola et al., 2016).

The most important measurement was the tactile Braille reading test on single letters and numbers (Fig. 2A). This test determined if the 3-week course in reading numbers in tactile Braille had improved the recognition of numbers. Before the course, participants were able to read an average of  $M = 15.4$  letters per minute (SE = .92) and  $M = 10.6$  numbers per minute (SE = 1.24). After the course, their performance had improved to an average of  $M = 18.3$  letters per minute (SE = 1.12) and  $M = 28.6$  numbers per minute (SE = 2.32). We performed a two-way repeated-measures (time point  $\times$  symbol type tested) ANOVA on these outcomes. The results suggest that all symbols, letters and numbers were better recognized in the post-test, regardless of their type ( $F_{(1, 24)} = 76.61, p < .001$ ). Importantly, we found an interaction between the factors ( $F_{(1, 24)} = 67.28, p < .001$ ), which suggests that the letters were significantly better recognized before the course, but the numbers were better recognized after it. This result shows that participants automatized the recognition of the numbers in tactile Braille. We also observed a significant difference ( $t_{(24)} = -4.32, p < .001$ ) in the tactile Braille word reading test (3). In the pre-test, participants reached an average speed of 4.78 WPM (SE = .60), whereas in the post-test they reached a reading speed of 6.09 WPM (SE = .67).



**Fig. 2 – (A) Results of the tactile Braille single letter and number reading test before and after the tactile Braille number reading course. (B) Accuracy and reaction times in the number comparison task in the scanner for smaller (4 and 6 vs 5) and larger (2 and 8 vs 5) numerical distances. All error bars represent SE.**

Since differences between reading Braille on paper vs. on a digital display exist, for the purpose of the main experiment we additionally tested participants' ability to recognize Braille numbers on a digital Braille Display (4). Before the course, participants were not able to recognize numbers on the Braille display, even when displayed for the longest period of 900 ms. After the course, participants recognized an average of 87.6% (SE = 2.28) of Braille numbers when displayed for 900 ms; 73% (SE = 3.37) of Braille numbers when displayed for 600 ms; and 71.6% (SE = 2.75) of Braille numbers when displayed for 300 ms.

### 3.2. Behavior in the MRI scanner

In the MRI scanner, participants performed a number comparison task. They were instructed to evaluate whether the presented numerosity was smaller or larger than five (see Design, Fig. 1). For accuracy we performed a logistic regression, and for the reaction times we performed a two-way, repeated-measures (distance  $\times$  format) ANOVA (Fig. 2B).

For accuracy, there was a significant main effect of numerical distance ( $\chi^2 = 15.75, p < .01$ ), suggesting more accurate responses for larger distances (5 vs 2 and 8) than for smaller distances (5 vs 4 and 6). We also found a main effect of stimulus condition ( $\chi^2 = 348.49, p < .01$ ): responses to Arabic digits ( $M = 95.78\%$ , SE = .80) and sets of dots ( $M = 95.41\%$ , SE = .74) were significantly more accurate than to Braille numbers ( $M = 84.98\%$ , SE = 1.81). No distance  $\times$  condition interaction was found (Fig. 2B). In reaction times, we found a significant main effect of numerical distance.

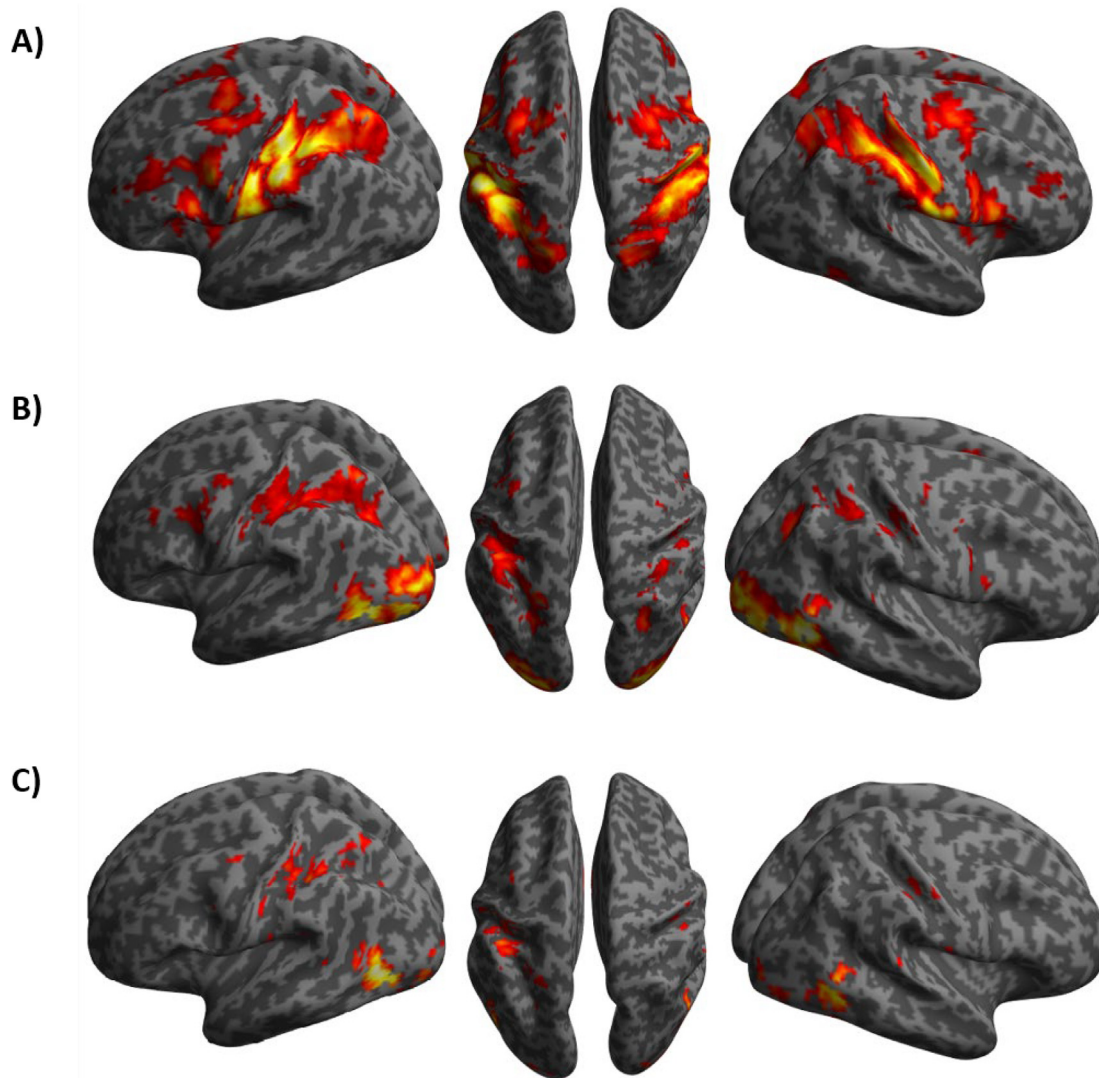
Participants responded faster to magnitudes that were numerically more distant from 5 (2 and 8) than to those which were less distant from 5 (4 and 6). There was also a significant main effect of stimulus condition ( $F_{(2, 48)} = 175.11, p < .001$ ), with shorter reaction times for Arabic digits ( $M = 1.19$  s, SE = .05) compared to sets of dots ( $M = 1.29$  s, SE = .05), both of which were processed significantly faster than Braille

numbers ( $M = 2.53$  s, SE = .10). We found a significant distance  $\times$  condition interaction ( $F_{(2, 48)} = 6.28, p < .05$ ), which indicated a larger distance effect for Braille numbers compared to the visual stimulus types (Fig. 2B).

### 3.3. General linear model—large spatial scale

Fig. 3 shows activations elicited by the task of comparing numerosities presented in three conditions with a fixed standard (5) relative to the implicit baseline. Comparison with numbers in form of the tactile Braille elicited massive bilateral activation that started in the superior parietal lobule and went anteriorly and inferiorly through the angular gyrus and the supramarginal gyrus down to the postcentral gyrus (Fig. 3A). We also observed activations in the precentral and frontal gyri (Table 1). When participants were presented with sets of dots, the activation in the parietal cortex was similar but sparser. As expected, we also observed additional activity of the visual cortex (Fig. 3B; Table 1). In the case of Arabic numbers, the activation in the parietal parts of the brain was mostly left lateralized, starting in the anterior part of the superior parietal lobule, going through the supramarginal gyrus, and ending in the postcentral gyrus. We also observed additional activity of the visual cortex (Fig. 3C; Table 1).

Fig. 4 shows further analysis of the activations evoked by the three conditions. Panel A shows the conjunction between tactile Braille numbers, sets of dots and Arabic numbers. The IPS activation that is common for the three conditions was bilateral but more pronounced in the left parietal cortex ( $t = 9.17, k = 1711$  MNI:-45;-38;41, FWE corr.  $P = .05$ ) compared to right IPL ( $t = 7.02, k = 159$  MNI:45;-27;39, FWE corr.  $P = .05$ ). Panel B shows the activation from the contrast: *small > large* numerical distance (i.e. 4 & 6 > 2 & 8 across conditions). All numbers were compared to "5". Therefore, in this comparison the numbers 4 and 6 are at a distance of 1, and numbers 2 and 8 are at a distance of 3. This activation can be interpreted as



**Fig. 3 – Statistical maps of brain regions that had significantly higher levels of activation during the comparison task (presented numerosities with set numerosity 5) relative to the implicit baseline. A) Tactile Braille numbers B) Visually presented sets of dots C) Visually presented Arabic numbers. All activations FWE corrected at  $p = .05$  on cluster level,  $p = .001$  on voxel level, cluster size 30.**

the cost of the decreasing numerical distance in the comparison task.

### 3.4. MVPA results—parietal cortex

To avoid classification based on the visual features of the visual stimuli or senso-motoric features of the tactile stimuli, we limited the current analysis to a region that is specific to number processing (Faye et al., 2019; Knops, 2017). Based on previous studies, we selected the bilateral parietal cortex as the region of interest.

For each condition, we trained the classifier to discriminate between the four possible numerosities: 2 vs. 4 vs. 6 vs. 8 (chance level: 25%). The results are shown in Fig. 5A. Within the parietal mask, visual non-symbolic numerosities were discriminated on average at 6.125% above chance level ( $t_{(24)} = 3.31, p = .002$ ). Patterns for Braille numbers were discriminated on average at 12.63% above chance level

( $t_{(24)} = 7.90, p < .001$ ). The mean accuracy for Arabic digits was not significantly different from chance (.38% above chance,  $t_{(24)} = .28, p = .389$ ).

The confusion matrices shown in Fig. 5 are calculated on the basis of the decision values of pairwise classifications between numbers 2, 4, 6, and 8 to show the overall accuracy between the four numbers. Panel B shows confusion matrices, whereas Panel C shows confusion matrices with ties excluded (undecided pairs) to correct the bias towards the smaller numerosities. Further calculations are performed on the unbiased matrices.

We investigated the unbiased confusion matrices for the distance effect by testing the difference between mean decoding accuracies for numerosities at a smaller distance to “5” (4 and 6), and a larger distance to “5” (2 and 8), separately for Braille numbers and sets of dots. We found a distance effect in the classification of tactile numbers, but we did not find a distance effect in the classification of sets of dots (Table 2).

**Table 1 – General Linear Model, statistical results of the whole-brain, group analysis ( $n = 25$ , thresholds: FWE corrected at  $P = .05$  on cluster level,  $P = .001$  on voxel level, cluster size  $k = 100$ .) Main effects were obtained by contrasting activations evoked by the experimental conditions with the implicit baseline. L—Left, R—Right.**

cluster size	t	MNI coordinates (x,y,z)			Region (SPM Anatomy Toolbox)
<b>A) Tactile Braille Numerosities</b>					
49,316	28.11	−59	−23	44	L: post central gyrus, supramarginal gyrus, superior parietal lobule, superior lateral occipital cortex
	25.12	56	−20	45	R: post central gyrus, supramarginal gyrus, superior parietal lobule, superior lateral occipital cortex
7158	19.69	26	−66	−24	R cerebellum
	19.31	−24	−65	−24	L cerebellum
719	7.81	36	35	21	R frontal pole
362	9.78	54	−59	−9	R inferior temporal gyrus
<b>B) Visual Sets of Dots</b>					
8259	24.15	47	−65	−6	R lateral occipital cortex
5671	19.98	−47	−72	−3	L lateral occipital cortex
5449	12.22	−47	−38	41	L IPS
1309	12.02	−44	6	32	L middle frontal gyrus
987	11.11	30	−63	29	R IPS
754	8.83	30	−47	44	R IPS
564	7.75	48	−30	44	R supramarginal gyrus
453	8.14	−17	−53	−21	L cerebellum
429	8.52	27	3	11	R putamen
293	8.53	−8	9	50	L paracingulate gyrus
287	7.67	−45	26	35	L middle frontal gyrus
264	7.11	45	9	20	R precentral gyrus
220	9.21	−26	−3	−12	L amygdala
118	9.59	9	−75	−20	R cerebellum
<b>C) Visual Arabic digits</b>					
1845	13.82	50	−65	−2	R lateral occipital cortex
1768	16.78	−42	−68	5	L lateral occipital cortex
1719	9.17	−45	−38	41	L IPS
472	9.28	−29	−87	−8	L lateral occipital cortex
471	8.26	21	−57	−20	R cerebellum
396	9.27	17	2	26	
329	7.54	−15	−56	−20	L cerebellum
232	7.48	42	−2	17	R central opercular cortex
191	7.56	−51	−21	18	L central opercular cortex
159	9.19	8	−77	−20	
159	7.02	45	−27	39	R IPL
153	7.5	−8	12	20	
146	7.56	−17	0	26	
140	7.79	−24	−2	−11	L putamen
131	6.53	−2	−62	−18	
114	9.07	69	−32	18	
112	7.01	29	−33	5	R superior temporal gyrus
106	8.18	27	3	9	

To further evaluate the distance effect we entered pairwise classification accuracies for the pairs with a distance of 1 (4 & 6) and 3 (2 & 8) steps into a linear regression analyses. Again, we only found a distance effect for Braille numbers ( $R^2 = .067$ ,  $F(1,148) = 10.666$ ,  $p = .001$ ) but not for sets of dots. Additionally, mean accuracy for each class was tested against the chance level (25%) to establish which numbers were classified significantly above chance.

### 3.5. Generalization across conditions

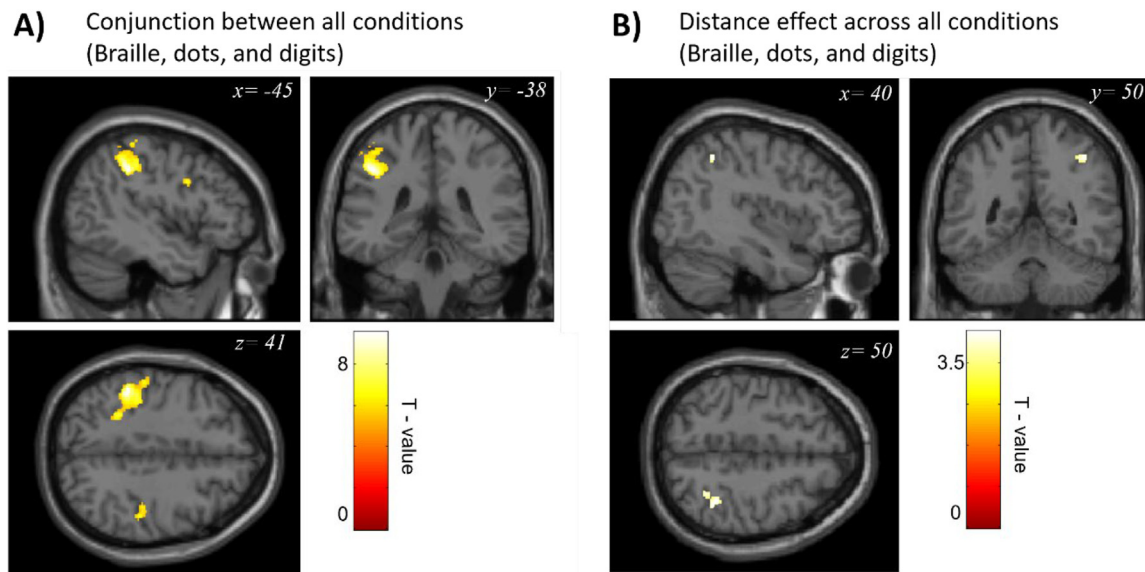
If the IPS codes for numerical information, irrespective of input modality, notation, or format, the activation pattern should be similar across our experimental conditions, which makes it possible to generalize the decoding from one condition to another. As within-category accuracy for Arabic digits

was below chance level, we did not consider them for further cross-classification analysis.

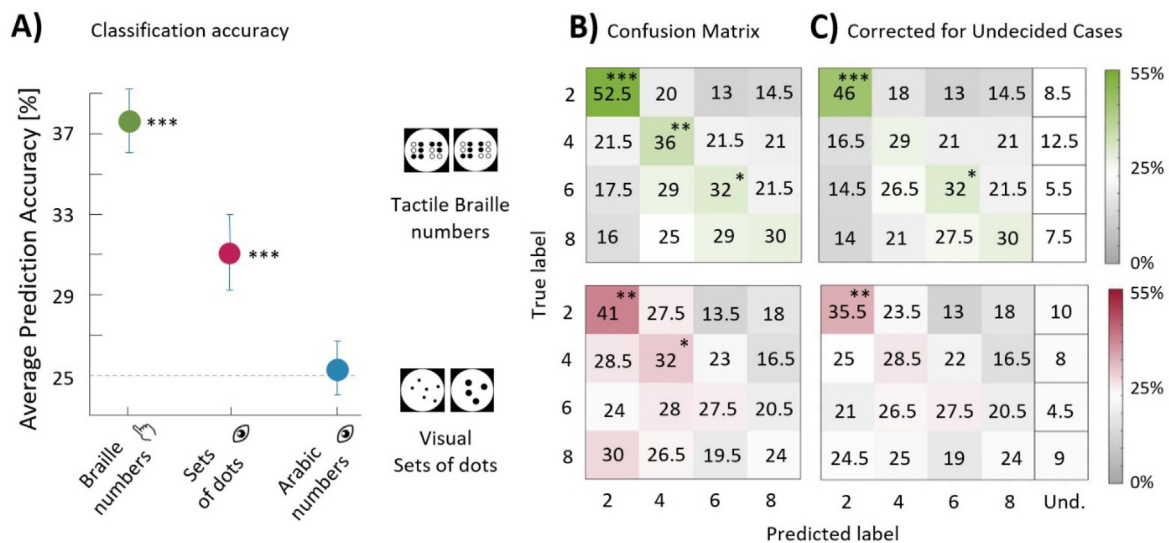
The generalization between Braille numbers and sets of dots did not reach significance level (trained on Braille numbers, tested on sets of dots – 1.63%,  $t_{(24)} = 1.34$ ,  $p = .096$ ; trained on sets of dots, tested on Braille numbers – .63%,  $t_{(24)} = .55$ ,  $p = .292$ ).

### 3.6. Small spatial scale, searchlight analysis

Fig. 6 Shows the group results of the searchlight analysis that was run in the parietal cortex of each participant separately. Significant clusters were obtained for Braille numbers and sets of dots, mirroring the earlier analysis. For Braille numbers, the classifier found local patterns of activation bilaterally in the parietal cortex, specifically in the intraparietal sulcus (Peak



**Fig. 4 – A)** Conjunction between the activations evoked by tactile Braille numbers, sets of dots and Arabic digits (FWE corrected at  $p = .05$  on cluster level,  $p = .001$  on voxel level, cluster size 30). **B)** Distance effect in the parietal cortex in all three conditions (contrast: distance 1 (4 & 6) > distance 3 (2 & 8) – across conditions,  $p = .001$  uncorrected, cluster size 30)



**Fig. 5 – Multi Voxel Pattern Analysis results for Braille, Arabic digits and sets of dots. A)** Mean within-category classification accuracies for the parietal ROI ( $n = 25$ , error bar represents standard error of the mean [SEM], statistical significance was established by testing against 1000 averaged permutations by the Fisher  $p$ -value test \*\*\* $p < .001$ , \*\* $p < .01$ , \* $p < .05$ ). **B)** Regular and **C)** corrected (excluding undecided (und.) pairs in the classification) confusion matrices, for Braille numbers and sets of dots. The diagonal row represents the accuracy for each numerosity (the values were tested for the difference of mean against the chance level: \*\*\* $p < .001$ , \*\* $p < .01$ , \* $p < .05$ )

MNI =  $-38$ ;  $-51$ ;  $52$ ,  $t(24) = 9.37$ , cluster-level extend threshold  $p < .001$ ; Peak MNI =  $-40$ ;  $-55$ ;  $54$ ,  $t(24) = 7.34$ , cluster-level extend threshold  $p < .001$ ) and the parietal lobule (superior and inferior). For sets of dots, the clusters with high classification accuracy were found mostly in the right hemisphere. The main cluster of high classification accuracy extended from the superior occipital gyrus (Peak MNI =  $29$ ;  $-68$ ;  $44$ ,  $t(24) = 8.43$ , cluster-level extend threshold  $p < .001$ ), through the angular gyrus (Peak MNI =  $33$ ;  $-66$ ;  $44$ ,  $t(24) = 7.03$ , cluster-

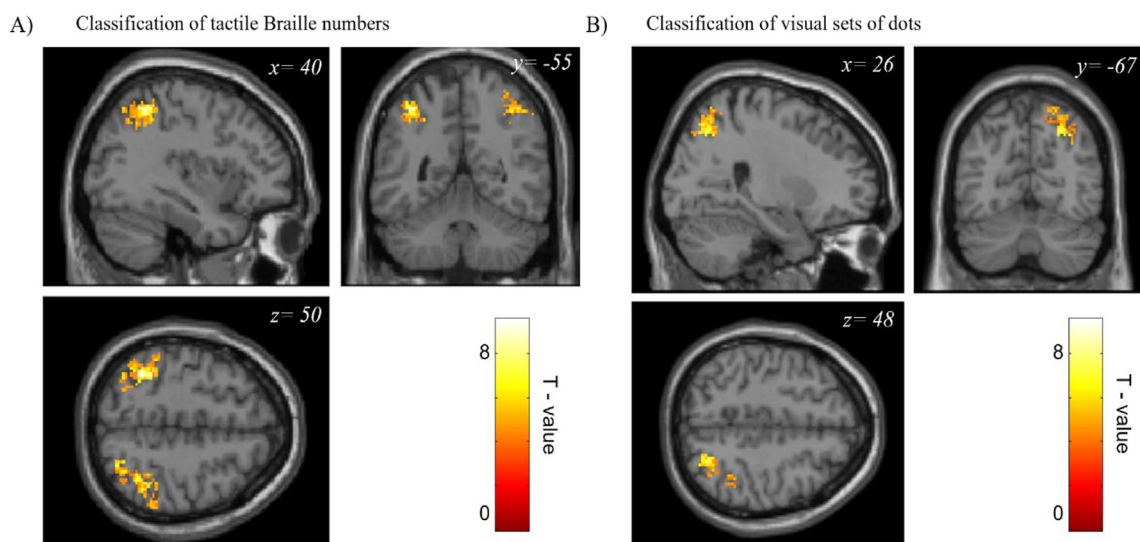
level extend threshold  $p < .01$ ), up to the intraparietal sulcus (Table 3).

#### 4. Discussion

The aim of the current study was to probe to what extent symbolic Braille numbers activate number-sensitive regions in the IPS, and to test the stipulated abstract nature of

**Table 2 – Results of statistical tests on unbiased confusion matrices (\*\* $p < .001$ , \*\* $p < .01$ , \* $p < .05$ ).**

	Mean small distance (4 and 6)	Mean large distance (2 and 8)	T-statistic	P value	df	sd
Tactile Braille	30.5	38	−2.25	.029	49	23.56
Sets of dots	28	29.75	−.56	.577	49	22.02
<b>Braille</b>						
Number	Mean accuracy	Chance level	T-statistic	P value	df	sd
2	46 ***	25	6.55	.000	24	16.02
4	29	25	1.09	.143	24	18.30
6	32 *	25	2.28	.016	24	15.34
8	30	25	1.63	.058	24	15.30
<b>Sets of dots</b>						
2	35.5 **	25	2.99	.003	24	17.56
4	28.5	25	1.27	.108	24	13.75
6	27.5	25	.76	.229	24	16.54
8	24	25	−.34	.630	24	14.84



**Fig. 6 – Statistical, group level results of the Searchlight Analysis, performed in the native space of each participant in the parietal mask, classifying numerosities in each condition (A) Clusters of significant classification of Braille numbers. (B) Clusters of significant classification of visually presented sets of dots. Thresholds:  $p < .001$  uncorrected, voxel-wise;  $p < .05$ , FWE cluster-wise ( $k = 30$ ).**

semantic number representation by probing whether or not activations in the IPS overlap for tactile Braille, visual sets of dots and visual Arabic numbers. We hypothesized that overlap would allow for a generalization of a multivariate classifier across modalities and formats. We observed (1) overlapping activations in the areas associated with the numerical processing for all three conditions. (2) We obtained above-chance accuracy classification for sets of dots but not for Arabic digits. (3) We were able to classify tactile Braille numbers despite their symbolic nature. (4) Using a searchlight analysis, we found that local patterns were right-lateralized for visual sets of dots but were bilateral for tactile Braille numbers.

The analysis showed that the semantic content of Braille numbers bilaterally activates large portions of the superior and inferior parietal cortex. In the case of the visual numerosities, we also found bilateral activation in the parietal cortex in the IPS: it was more left lateralized, and there were additional clusters in the visual cortex, as expected. Crucially, we observed overlapping activation for all three stimulus classes (dots, digits, Braille) in the bilateral parietal cortex. The

observed numerical distance effect in the bilateral parietal region provides evidence for the functional implication of the bilateral parietal cortex in processing the semantic content of numerical information from visual (digits, dots) or tactile (Braille) input. It should be noted that this effect emerged only when testing all three conditions together but for none of these conditions alone. This is in line with the idea that the IPS hosts cortical circuits that are sensitive to numerical information from different modalities, formats, and notations. It should be noted that the current study is among the first to jointly demonstrate this for non-symbolic visual (dots) and symbolic stimuli from two modalities: tactile (Braille) and visual (Arabic digits; see also Rączy, Czamecka, Paplińska, et al., 2020).

The visual conditions evoked less intense activations compared to symbolic tactile numbers (Braille). This was particularly pronounced for the Arabic digits (Table 3). The pronounced difference in the activations may be a consequence of the different levels of expertise in processing the numerical content of the different stimuli types. Learning to

**Table 3 – Statistical results of the group level analysis of the SA performed in the native space for each participant in the parietal mask, classifying numerosities in each condition ( $P < .001$  uncorrected, voxel-wise;  $P < .05$ , FWE cluster-wise ( $k = 30$ )). L—Left, R—Right.**

cluster size	t(24)	MNI coordinates (x,y,z)			Region (Anatomy Toolbox)
<b>Braille numbers</b>					
751	9.37	−38	−51	52	L Intraparietal Sulcus
	6.58	−36	−45	56	L Superior Parietal Lobule
	6.48	−42	−49	58	L Superior Parietal Lobule
778	7.34	40	−55	54	R Intraparietal Sulcus
	6.82	48	−39	46	R Intraparietal Sulcus
	6.44	21	−64	60	R Superior Parietal Lobule
<b>Sets of dots</b>					
314	8.43	29	−68	44	R Intraparietal Sulcus
	6.25	21	−64	62	R Superior Parietal Lobule
	6.05	27	−70	52	R Intraparietal Sulcus
63	7.06	44	−45	50	R Intraparietal Sulcus

read and process Arabic digits is the result of 16–26 years of training in our sample and is a skill that is commonly used in daily life. Compared to this high degree of automatization, explicitly comparing non-symbolic numerosities is less often practiced and therefore requires some extra effort, as evidenced by the significantly slower reaction times. Arguably, when processing non-symbolic information explicitly, participants would convert it to some symbolic format and continue processing in this format, thus strengthening symbolic number processing. Hence, we hypothesize that due to this overtraining, the activation evoked by Arabic digits is lower compared to other formats and modalities that are less frequently used (Fig. 3). Overtraining a skill leads to a decrease of its corresponding neural activations (Draganski et al., 2006; reviewed in Chein & Schneider, 2005). The Braille skills of our participants were roughly at the level of second-grade children. Reading speed in Braille numbers was considerably slower than for Arabic digits. The observed activation in frontal areas for Braille numbers may reflect the additional cognitive control that was needed while reading Braille numbers (Siuda-Krzywicka et al., 2016).

Braille numbers are composed of a number of elevated spots in a  $2 \times 3$  matrix. Recognizing the designated letter requires the processing of these spatial patterns. In a similar vein, visual word reading requires the processing of letters and their relative positions in words. IPS activity is related to the processing of letter position in a string (Ossmy et al., 2014). We can speculate that, unlike congenitally blind readers (who read with high proficiency), our subjects might still need to deliberately process each Braille dot's position in the matrix and thus strongly activate their IPS to integrate these individual elements in the sensory input. This could be an alternative explanation of why the level of their IPS activation for Braille numbers and dot patterns (which also need to be counted individually) is higher than for Arabic digits. The significant decodability of number two in Braille is reminiscent of the subitizing in the visual modality. However, we do not consider the latter to be at the origin of the observed classifier performance for two reasons. First, the empirical support for subitizing in the tactile domain remains controversial. For example, while Ferrand et al. (2010) did observe the typical behavioral signature in congenitally blind as well as in

sighted participants, Plaisier and Smeets (2011) observed reaction latencies that corresponded to an inverted U-shape over the range 1–8 items, implying that participants counted the smaller sets of either present or absent stimuli. Second, from a theoretical point of view, subitizing most likely reflects the parallel individuation of items in visual space that requires the deployment of spatial attention (Burr et al., 2010). The neural mechanisms that are underlying this function are not those deployed in representing tactile input from different fingers.

Together, the results at the network level support the idea of a joint hub for processing numerical content in the bilateral intraparietal cortex. The observed differences in activation strength may reflect the different level of expertise.

To investigate if the activation profiles of the different input modalities and formats adhere to the stipulated abstract nature, we used MVPA and tested whether we could (a) decode number information in the IPS and (b) generalize across input conditions.

Our results for visual inputs replicate the overall advantage in decoding accuracy of non-symbolic over symbolic notations. As shown in Fig. 5, sets of dots were decoded with significantly higher accuracy than Arabic digits, with the latter not reaching statistical significance. To test the functional relevance of the observed activation patterns, we reasoned that the behavioral distance effect should be reflected in the confusion matrices at the neural level. Yet, in the classification of the sets of dots we did not find the classic distance effect, even though it was significant in the behavioral analysis. This could be due to the overall low accuracy of this format. As concerns the tactile symbolic input (Braille), the classification accuracy was even higher compared to the sets of dots. Moreover, we found a regular distance effect in decoding the tactile Braille input.

One commonly proposed explanation for the higher decodability of sets of dots compared to Arabic digits relates to the underlying tuning function, which is broader and is characterized by a higher degree of overlap between adjacent numbers compared to symbolic numbers (Arabic), whose tuning functions are more focal (Bulthé et al., 2014, 2015; Damarla & Just, 2013; Eger et al., 2009). According to this view, activations evoked by symbolic numbers are thus discrete and

organized in more focused areas (Cantlon, 2012). Consequently, symbolic numerosities are decoded with much lower accuracy than non-symbolic ones due to their sparser representations. This explanation, however, is at odds with the findings of this study. As we show in Fig. 3, in our experiment the activation for Arabic digits was much sparser than for sets of dots, yet activation was much more pronounced for Braille numbers than for both visual inputs. The explanation for the lower decodability of Arabic digits may be much simpler and may come from lower activation due to overtraining. We were able to classify tactile symbolic numerosities, i.e., Braille numbers, regardless of their symbolic nature, with accuracy even higher than for the sets of dots (Fig. 4). We therefore argue that visual abstract numbers may be less decodable not because of their symbolic nature but rather due to their highly overtrained processing. This is consistent with results demonstrating that the weaker BOLD signal in response to weaker stimulus contrast led to less reliable decoding accuracies (Tong et al., 2012).

The lack of a significant distance effect in the dots condition in combination with the significant decoding of numerosity may reflect the categorical difference of enumeration mechanisms for numerosities within and outside the subitizing range. Unfortunately, the current data do not allow to further test this prediction since 2 was the only number from this range. Even if the classifier has picked up the distinction between these two numerosity regimes (Anobile et al., 2016), it should be noted that these mechanisms jointly operate over the entire number range to allow for processing numerical information. Future studies may include more stimuli from both ranges to further probe whether the classifier picks up a difference in processing mechanism or in numerosity.

We used a data-driven searchlight decoding analysis approach to validate the ROI-based decoding results. The searchlight analysis showed that the parietal cortex, especially sites in the vicinity of the intraparietal sulcus, is engaged in the processing of both visual and tactile number information. For Braille numbers, the classifier found local patterns of activation bilaterally in the intraparietal sulcus and the parietal lobule (superior and inferior). In the case of sets of dots, clusters of high classifier performance were more pronounced in the right hemisphere, including areas from the superior occipital gyrus through the angular gyrus up to the intraparietal sulcus.

The TCM stipulates an abstract representation of numerical meaning in the IPS, upon which numerical information from different modalities, formats or notations converge. However, previous studies, in particular behavioral and neuroimaging studies with tactile and visual symbolic number information, yielded contradicting results. While no semantic priming across modalities was observed in a behavioral study (Rączy, Czarnańska, Zaremba, et al., 2020), a subsequent fMRI study yielded evidence in favor of a common neural representation of numerical quantity in the IPS (Rączy, Czarnańska, Paplińska, et al., 2020). Sokolowski et al. (2021) recently reported dissimilar activations for visual symbols (digits) and non-symbolic numerosities (sets of dots), which undermines, according to these authors, the idea of grounding number symbols in the cortical system that processes non-symbolic quantities. The current results can be interpreted as

evidence against the idea of fully abstract system coding for numerical magnitude hosted in the IPS. Against the background of recently described partially overlapping topographically organized neural populations tuned to tactile and visual numerosities (Hofstetter et al., 2021), the possibility that an abstract representation still exists to some extent cannot be excluded. The lack of generalization across conditions in combination with the observed overlapping activity suggests that areas along the IPS contain separate but adjacent neural populations that are specialized to a given format and/or modality. However, the results of the current study also suggest that the different levels of expertise in processing numerical input from different input modalities and formats may modulate the overall strength of the activation, which in turn impairs more fine-grained analyses of the functional profiles.

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## 5. Conclusions and limitations

Together, our results show that the system that processes numerical information presented as tactile Braille numbers is located in regions that have previously been shown to be involved in number processing. This system may overlap partially with the system that processes numerical information presented as visual numerosities.

Our study has a number of limitations. First, it is important to remember that in this experiment we tested a very specific group of individuals, and we presented the numerosities to them in unnatural circumstances. Our subjects were slow readers, with skills roughly equivalent to second-grade children. To our knowledge, they are the only group of dual tactile-visual readers described so far, and it remains to be proven whether surpassing their skills is achievable. However, we cannot exclude the possibility that a different result would have been obtained in an imaginary and ideal population of sighted Braille readers with reading speeds approaching those of the Blind.

Second, because our design was optimized for MVPA analysis, we did not include a control condition but compared the activations against baseline. This method may not sufficiently control for non-numerical processes and task requirements such as attentional or response-related processes, or integration processes during the processing of Braille numbers. Therefore, we cannot exclude the possibility that the observed activations partly reflect these factors. It should be noted, though, that we sought to minimize this risk by integrating converging information from different number-related univariate and multivariate analyses. The block design used in this experiment also creates a possibility of losing the attention of the participant after the first read item. To prevent that, participants were instructed read each stimuli, even after they have given the response. Also blocks of numbers had differing quantity of items (4–6) with no break between blocks. Therefore participants were unable to predict when exactly the next block will begin.

It remains controversial whether the parietal activity reflects properties of neuronal representations themselves or is driven by decision- and response-related components (Cavdaroglu et al., 2015; Cavdaroglu & Knops, 2019; Shuman &

Kanwisher, 2004; Van Opstal et al., 2008). While some argue that parietal distance effects do not reflect representational overlap (Van Opstal et al., 2008) or are merely due to response-related processes (Shuman & Kanwisher, 2004), others argue that engagement in an active task amplifies the numerosity-specific signature in parietal activity (Cavdaroglu et al., 2015; Cavdaroglu & Knops, 2019). In our design, we used a fixed comparison task. Participants were asked to compare each presented number (2, 4, 6 or 8) with a fixed numerosity. One cannot look into the neural representations of numerical magnitudes without taking into account the context of the task used, which was a comparison task in our case. It is unclear if the decoding we captured in our experiment was possibly due to the use of a comparison task, the recognition of numerosity itself, or a combination of both. However, we do show that the information in the activity patterns evoked by numbers is specific enough to predict with significant accuracy the numerosity of visual, non-symbolic sets of dots and tactile symbolic Braille numbers.

The results of the current study do not replicate results of previous studies. In particular, in contrast to Bulthé et al. (2014), we not able to reliably decode numerical information conveyed by Arabic digits in all details—albeit adopting by and large the same design. This discrepancy may have its explanation in the lowered statistical power for each individual condition that was, in turn, due to the lowered number of repetitions of per condition. We chose to reduce this number to keep the time that participants would spend inside the scanner to a reasonable duration of 1 h while at the same time adding the Braille condition to the design. By focusing on selected conditions and thereby increasing statistical power, future studies may well be able to replicate the well-established above-chance classification of symbolic numerical information conveyed by Arabic digits (Bulthé et al., 2014, 2015; Damarla & Just, 2013; Eger et al., 2009).

Finally, the fact that we were neither able to decode visual symbolic number information nor generalize across conditions may be suggestive of a limit to the modality and format independence that the TCM stipulates. One possible architecture would comprise separate systems for different input formats, thus putatively overlapping at the meso-anatomical level. Another possible architecture would rely on a single system, of which the Arabic digits recruits only a small portion. Since our null result may result from the overall weak activation elicited by visual symbolic numbers, further studies are needed to examine the neural fate of the semantic information conveyed by Arabic digits.

### Author Contributions

Maria Czarnecka: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Visualization, Writing – original draft, Writing – review & editing; Katarzyna Rączy: Conceptualization, Data curation, Formal analysis, Investigation, Project administration, Writing – review & editing; Jakub Szewczyk: Formal analysis, Investigation, Methodology, Writing – review & editing; Małgorzata Paplińska: Conceptualization, Project administration, Resources; Katarzyna Jednoróg: Conceptualization,

Writing – review & editing; Artur Marchewka: Conceptualization, Writing – review & editing; Guido Hesselmann: Conceptualization, Methodology, Writing – review & editing; André Knops: Conceptualization, Investigation, Methodology, Supervision, Writing – review & editing; Marcin Szwed: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – original draft, Writing – review & editing

### Open practices

The study in this article earned Open Data badge for transparent practices. The data this study are available at: <https://openneuro.org/datasets/ds004400>.

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