The neural representation of ordinal information: domain-specific or domain-general?

Lucie Attout [ab], Nathan Leroy [ab], & Steve Majerus [ab]

[a] Psychology and Neuroscience of Cognition Research Unit, University of Liège

[b] Fund for Scientific Research FNRS, 1000 Brussels, Belgium

Author note

Lucie Attout, https://orcid.org/0000-0002-4494-9379

Steve Majerus, https://orcid.org/0000-0002-8206-8097

We have no conflicts of interests to disclose

Correspondance concerning this article should be addressed to Lucie Attout, , Psychology and Neuroscience of Cognition Research Unit, Université de Liège; Boulevard du Rectorat, B33, 4000 Liège – Belgium; Tel: 0032 4 3663991; Email: lucie.attout@uliege.be

Running title: Neural representation of order

Abstract

Ordinal processing allows for the representation of the sequential relations between stimuli and is a fundamental aspect of different cognitive domains such as verbal working memory (WM), language and numerical cognition. Several studies suggest common ordinal coding mechanisms across these different domains but direct between-domain comparisons of ordinal coding are rare and have led to contradictory evidence. This fMRI study examined the commonality of ordinal representations across the WM, the number and the letter domains by using a multivoxel pattern analysis approach and by focusing on triplet stimuli associated with robust ordinal distance effects. Neural patterns in fronto-parietal cortices distinguished ordinal distance in all domains. Critically, between-task predictions of ordinal distance in fronto-parietal cortices were robust between serial order WM, alphabetical order judgment but not when involving the numerical order judgment tasks. Moreover, frontal ROIs further supported between-task prediction of distance for the luminance judgment control task, the serial order WM and the alphabetical tasks. These results suggest that common neural substrates characterize processing of ordinal information in WM and alphabetical but not numerical domains. This commonality, particularly in frontal cortices, may however reflect attentional control processes involved in judging ordinal distances rather than the intervention of domain-general ordinal codes.

200 words

Keywords: distance effect, neuroimaging, numerical cognition, serial order, working memory.

Introduction

Ordinal processing is the ability to deal with the sequential relation between stimuli in a set of stimuli. This capacity is a fundamental aspect of information processing and has been extensively studied in different domains such as working memory (WM) and numerical cognition. Representation of ordinal relations is necessary for the comparison of numbers, for the maintenance of the serial order of events and for the representation of long-term sequential relations between different types of stimuli such as numbers, the letters of the alphabet, the days of the week and so on. However, the nature and possible domain-generality of ordinal representations remains an open question. In this study, we assessed the hypothesis of domain-general codes for the representation of ordinal information across WM, numerical and alphabetical domains by assessing the neural similarity of voxel activity patterns associated with the ordinal distance effect.

A reverse distance effect, commonly called the ordinal distance effect, is considered to be a marker of ordinal-level representations and has been primarily studied in the numerical domain. While the standard distance effect corresponds to more accurate and faster performance in judging the magnitude of numbers that are farther apart (e.g. 3-8) as compared to numbers that are closer (e.g. 3-4) (Moyer and Landauer 1967), the ordinal distance effect generally leads to more accurate and faster judgment for close numbers (e.g. 3-4) when the order of numbers within a sequence has to be determined (Turconi et al. 2006; Franklin et al. 2009; Franklin and Jonides 2009; Sury and Rubinsten 2012; Lyons and Beilock 2013; Goffin and Ansari 2016; Vos et al. 2017). This faster judgment of ordinal information for close numbers is particularly observed when comparing numbers apart by a distance of 1 (consecutive pairs) relative to more distant numbers, and this mainly for numbers presented in ascending order (see for example Turconi et al., 2006). This specificity of the ordinal distance effect has been interpreted as reflecting the automatic retrieval of consecutive items from long-term memory (Franklin et al. 2009; Vos et al. 2017; Sella et al. 2020). Moreover, the ordinal distance effect seems to be more robust when participants need to judge the order of triplets (e.g. 2-3-4) rather than pairs (e.g. 3-4) (Jou and Aldridge 1999; Leth-steensen and Marley 2000; Turconi et al. 2006; Franklin et al. 2009; Lyons and Beilock 2013). This ordinal distance effect, although primarily explored in the numerical domain, has also been observed in other domains such as alphabetical or WM domains. A seminal neuropsychological study has shown evidence for cross-domain ordinal impairment: the Patient CO showed not only difficulties in accessing the ordinal meaning of numbers, but also exhibited deficits with judging the order of letters, days and months (Turconi and Seron 2002). Studies in healthy participants have also revealed similar ordinal distance effects for the judgment of letter stimuli and number stimuli (Jou and Aldridge 1999; Van Opstal et al. 2008; Attout et al. 2014; Goffin and Ansari 2019). Finally, in the WM domain, two previous studies found a standard distance effect characterized by faster judgment of the serial order of two memoranda when they were from distant rather than close serial positions in the memory list (for example, in the memory sequence *A B C D E*, the order of B-D is judged faster and more accurately than the order of B-C) (Marshuetz et al. 2000; Attout et al. 2014). Other studies found a standard distance effect with a larger amount of serial position exchange errors for items from close (adjacent) positions in the sequence as compared to further apart positions (Lee and Estes 1981; Nairne et al. 1991; McCormack et al. 2000; Majerus and Boukebza 2013). For a serial order probe recognition paradigm where participants were presented two probe items that were close or further apart in the memory list, Marshuetz et al. (2000) observed a standard distance effect for serial position distances 2 to 4, with more errors for small than larger distances. However, a reversed distance effect was observed for distance 1 relative to distance 2, item pairs stemming from immediately adjacent serial positions leading to less errors and being judged faster than items being separated by two serial positions. These studies appear to support the existence of domain-general ordinal processes, but very few of them have directly compared ordinal distance effect across domains and results are inconsistent. A few neuropsychological studies have indeed highlighted the possibility of dissociations for ordinal processing across different domains such as a months, days, letters and numbers in neglect patients (Zorzi et al. 2006; Zamarian et al. 2007).

At the neural level, most studies assessing ordinal processing observed activity foci in frontal and IPS areas across different domains. These domains involved serial order WM, numbers, letters and months (Fulbright et al. 2003; Fias et al. 2007; Ischebeck et al. 2008; Attout et al. 2014; Goffin and Ansari 2019). More precisely, the IPS appears to be sensitive to both, standard and ordinal distance effects with disctinct activation for far numerical/positional distances vs. close numerical/positional distances during number processing tasks (Nieder 2005; Franklin and Jonides 2009; Kaufmann, Vogel, Starke, Kremser, and Schocke 2009; Knops and Willmes 2013; Lyons and Beilock 2013; Matejko et al. 2019; Goffin et al. 2020) as well as in WM tasks (Marshuetz et al. 2000; Attout et al. 2014), respectively. Fias et al. (2007) directly compared distance effects for a number magnitude comparison task and a letter order judgment task showing the specific involvement of the horizontal segment of the IPS for both tasks. Moreover, they found a dissociation between the anterior and the posterior parts of the IPS, with the anterior IPS being directly related to the number and letter comparisons while the posterior IPS was involved in more general comparison processes as it was also recuited for the judgment of visual saturation. Finally, Attout et al. (2014) compared ordinal judgment across three domains and observed parametric modulation of the right IPS for ordinal distance effects in numerical, WM and alphabetical judgment tasks. Regarding the frontal part of the network commonly associated with ordinal processing tasks, although some studies have shown sensitivity to ordinal distance of middle and inferior frontal gyri, this seems to be the case only for ordinal judgment tasks requiring more explicit, controlled judgments (e.g. serial order WM and alphabetic ordinal judgment) but not in numerical ordinal judgment which can rely on the more automatic activation of numerical information (Fulbright et al. 2003; Attout et al. 2014, 2015).

Although these studies support the existence of common neural mechanisms for the representation of ordinal information, there is currently however no direct evidence. Showing activity in similar brain networks does not necessarily imply that the same information is processed in these networks across tasks and domains. Multivariate pattern analyses assessing the informational content of neural activity have indeed led to contradictory evidence regarding the existence of domain-general codes for the representation of serial order information. In a multivariate re-analysis of the data published by Fias et al. (2007), Zorzi et al. (2011) showed that neural activity patterns in the IPS were distinct for the magnitude number judgment task and the alphabetical order judgment task.

A critical aspect of the different studies mentioned is the use of pairs of stimuli versus longer sequences. When pairs of stimuli are used for ordinal processing, the ordinal and magnitude processing for numerical information can be confounded. This situation is most likely to occur when pairs of stimuli are used: when judging if 3-4 vs. 4-3 is in the correct numerical order, the participant can simply determine if the smaller number is the first one, hence using a magnitude judgment (see Lyons et al., 2016 for a review; see also Vos et al., 2017 for a recent discussion). Lyons and collegues suggested instead that ordinal information in triplets can only be determined based on an ordinal processing strategy: when judging if 3-4-5 vs. 3-5-4 is in the correct numerical order, the ordinal succession of all three numbers need to be judged. This distinction appears indeed to be a crucial element when assessing the commonality of processes involved in ordinal processing across domains. When using stimulus pairs, Franklin and Jonides (2009) found overlapping IPS activity for tasks considered to distinguish ordinal and magnitude judgment while specific neural signatures were observed for ordinal processing only when triplets were used (Lyons and Beilock 2013). Moreover, the reverse distance effect (faster judgment for closer distances) that characterizes ordinal processing, as compared to magnitude processing (faster judgment for larger distances) has rarely been reported in previous fMRI studies or has led to contradictory results (Fulbright et al. 2003; Fias et al. 2007; Attout et al. 2014; Goffin et al. 2020). For example, Franklin and Jonides (2009) observed both standard and reverse distance effects in the left IPS but it should be noted that they used number pairs instead of triplets. The studies using triplets however did not necessarily lead to a clearer pattern of results. While Fulbright et al. (2003) observed a standard instead of a reverse distance effect in parietal cortices by distinguishing near and far distances in letters, numbers and shapes, Matejko et al. (2019) reported a reverse distance effect for judging numbers. Moreover, with a different, implicit serial order processing paradigm, Goffin et al. (2020) observed IPS activity for processing both, number and letter sequences but only the numerical distance effect was associated with IPS activity. However, like all previous studies, this study did not use a more sensitive MVPA approach to assess sensitivity to ordinal processing. Hence, most of the studies reviewed here have used paradigms for which it is not ascertained that ordinal processes were really involved, and the studies using triplets and examining reverse distance effects led to contradictory results (e.g. Fulbright et al. 2003; Matejko et al. 2019; Fias et al., 2011).

In sum, while several studies support the possibility of domain-general neural codes for ordinal processing, direct and robust evidence is still lacking. First, the vast majority of studies used univariate analyses, highlighting overlapping neural networks for ordinal processing across domains but without directly showing that these networks code the same ordinal information across domains. The few studies that used multivariate techniques for determining the similarity of neural patterns across ordinal processing domains did not support the hypothesis of domain-general codes. Second, ordinal coding may have been confounded with magnitude coding for numerical judgment in many studies, partly due to the use of stimulus pairs rather than stimulus triplets. Third, the distance effects could also be explained by the differential levels of attentional control that are involved when comparing close to large distances: the ordinal distance effect is characterized by faster responses for closer distances and thus closer distances require less extended attentional control as they can be judged quicker as compared to further apart distances. And it is striking to observe that the fronto-parietal regions typically attributed to ordinal judgement overlap with the dorsal attention fronto-parietal network. This fronto-parietal attentional network supports goal-directed, top-down attention, monitoring of task-related behavior and temporary maintenance of internal representations (Culham and Kanwisher 2001; Corbetta and Shulman 2002; Majerus et al. 2016, 2018). All these processes are also involved when judging the ordinality of stimuli as this judgment requires to compare the presented stimuli to internal representations of ordinality, and both have to be in an active format in the focus of attention in order to reach a match-mismatch decision. This aspect has been rarely controlled in the numerical cognition literature as control conditions requiring differential levels of attentional control are often not included (but see Fias et al., 2007, Lyons & Beilock,2013; Matejko et al., 2019 as exceptions).

The present study used a multivariate pattern analysis approach in order to determine the commonality of ordinal processes across the number, letter and WM domains by examining the between-task predictability of neural patterns associated with ordinal processing. Furthermore, in all tasks, triplet stimuli were used in order to ensure reliable measuring of ordinal processing and differentiation from magnitude processing in the numerical domain. Participants had to assess ordinal information for triplets in alphabetical and number judgment tasks by determining if the triplet of numbers/letters was in alphabetical or numerical order; in an order WM task, participants were asked to determine if the letters in the probe triplet were in the same order as in the memory sequence or not. For each task, we manipulated the distance of the letters/numbers/positions within the triplet. We manipulated the two smallest distances as these have been shown to lead to the most robust ordinal distance effects (Turconi et al. 2006; Lyons and Beilock 2013). A final task was a luminance judgment task controlling for general task difficulty effects and associating differential attentional control requirements. In this task, participants had to determine if three grey-colored rectangles had the same brightness or not; there were two levels of luminance difference (a small one and a larger one) in order to control for the differences in task difficulty when judging closer and further apart distances in the ordinal judgment tasks. We adopted an ROI approach for this study by determining to which extent the different frontal and parietal ROIs considered to be associated with ordinal processing in previous studies actually represent information about ordinal distance, and this in a domain-specific or domain-general manner (Fulbright et al. 2003; Fias et al. 2007; Ischebeck et al. 2008; Franklin and Jonides 2009; Kaufmann, Vogel, Starke, Kremser, and Schocke 2009; Knops and Willmes 2013; Lyons and Beilock 2013; Attout et al. 2014, 2015; Goffin et al. 2020). Based on these studies, we distinguished anterior versus posterior portions of the bilateral IPS, as well as the middle and inferior frontal gyri. Finally, we also included the primary visual cortex area V1 as a control ROI, in order to examine the specificity of the parietal and frontal ROIs for ordinal processing. V1 was selected as this region has been shown to be sensitive to task difficulty in visual tasks as well as to visual features such as color and luminance, the latter being critical for the luminance control condition (Geisler et al. 2007; Dai and Wang 2012). If common ordinal codes support ordinal judgment in the three domains under investigation, then we should observe prediction of ordinal distance based on associated neural patterns between the WM, alphabetical and numerical judgment task, except for the luminance judgement task. On the other hand, if neural patterns distinguishing ordinal distance reflect the differential attentional control requirement of the two ordinals distances, then we should also observe prediction between the ordinal and luminance distance effects; in that case, between-task predictions of distance involving the numerical judgment task may also be less reliable given the less effortful nature of numerical judgment versus alphabetical and WM judgment.

Materials and Methods

Participants

Thirty-six right-handed French-speaking young adults with no history of neurological disorder, sensory impairment or learning difficulties were recruited for this study. They received 10 euros/hour for their participation. Data from 2 participants were excluded because of excessive movement in the scanner (i.e. see criteria below). The data from 34 participants (22 women) were retained for analysis (mean age = 23.30 ± 2.80 years old, age range = 19-33). Minimal number of years of education was 14. The ethics committee of the Faculty of Medicine of the University of Liège had approved the study. In line with the Declaration of Helsinki, all participants gave their written informed consent prior to inclusion in the study.

Task description

The Figure 1 illustrates the four judgement tasks.

Order WM task

The order WM task included three phases: (1) the encoding phase consisted of the presentation of a list of six letters (e.g., ‘B, D, E, F, C, A’) ordered horizontally (fixed duration: 2500 msec); (2) the maintenance phase consisted of the presentation of a fixation cross displayed for a variable duration (random Gaussian distribution centered on a mean duration of 6000 ± 2000 msec); (3) the retrieval phase consisted of the presentation of triplet of letters ordered vertically. The encoding and recognition phases were presented using horizontal and vertical displays, respectively, to avoid direct visual matching and recognition.

Participants indicated within 4000 msec if the order of the letters in the triplet matched the order of the same letters in the memory list (by pressing the button under the middle finger for 'yes' and by pressing the button under the index for 'no'). The presentation duration of each probe stimulus varied as a function of the participants' response time, with a maximum duration of 4000ms. In order to allow for the assessment of ordinal distance effects, the task assessed relative order. The participants were asked to judge whether the 3 letters of the probe list were presented in the same order as in the memory list, without necessarily being in direct succession. For example, for the memory list 'B, D, E, F, C, A, G', both 'B, D, E' and 'B, E, C,' were positive probes while differing in ordinal distance. We used letters from A to I which were the same letters as also used in the alphabetical order judgment task (see below). Before starting the practice trials, an example for each distance was given to participants to ensure perfect understanding of task requirements.

Alphabetical order judgment task

The alphabetical order judgment task consisted of the judgment of alphabetical order for a letter triplet displayed vertically. Participants had to decide within 4000 msec whether the letters within the triplet were displayed in correct alphabetical order or not (by pressing the button under the middle finger for 'yes' and by pressing the button under the index for 'no'). The correct order could be in ascending ('A B C') or descending order ('C B A') while the incorrect order was a mixed order ('A C B'). Again, in order to allow for the assessment of ordinal distance effects, the task assessed relative order. We asked to participant to judge whether 3 letters were in alphabetical order without being necessarily in direct succession with both ascending and descending order being correct. For example, both lists 'F G H' and 'A C E' were correct probes while differing in ordinal distance. In order to ensure fast and easy access to ordinal information, only the first nine letters of the alphabet were used; this furthermore maximized the comparability with the number judgment task which also only used the first nine numbers of the number chain (see below). Again, an example for each distance was given before starting the practice trials.

Numerical order judgment task

The numerical order judgment task followed the same design as the alphabetical order judgment task but involved the presentation of digit triplets dispayed from top to bottom. Participants had to determine if the numbers within the triplet were in correct numerical order, with both ascending and descending orders being considered as correct, and numbers not needing to be in direct successions, like for the alphabetical order judgment task. Again, an example for each distance was given before practice trials. The participants responded by pressing the button under their index finger for ‘no’ responses and the button under their middle finger for ‘yes’ responses. The distances varied from 1 to 2 as for the two previous tasks (e.g., ‘1 2 3’ for the distance 1 and ‘1 3 5’ for the distance 2).

Luminance judgment control task

The luminance judgment control task consisted of the presentation of a triplet of rectangles (grey vertical rectangles of 5.7° x 3.8°) with rectangles displayed at increasing/decreasing levels of luminance from left-to-right. Two rectangles were presented on each side of the center (at 11°) and one on the center. The participants had to decide within 4000 msec whether luminance was the same or not for all the rectangles within the triplet by pressing the button under their index finger for ‘no, they are different’ and the button under their middle finger for ‘yes, they are the same’. We manipulated two different photometric luminance levels (close distance = difference of 20 cd/m2 hue–saturation– brightness between each stimuli; far = difference of 40 cd/m2 hue-saturation-brightness between each stimuli) in order to mimick the contrast of two ordinal distances in the other tasks. For the negative trials of the luminance judgement task, all stimuli had the same luminance so that only a “different – not different” judgement was required and did not involve any ordinal judgment. For mixed trials to become negative, the judgment criterion would have been the ordered succession of luminance levels. Given that the luminance task was supposed to be a non-ordinal judgement task, we wanted to avoid this situation. Finally, given that spatial or ordinal coding processes were not expected to determine luminance processing and judgment, the display was kept in a standard horizontal direction.

< INSERT FIGURE 1 HERE >

General procedure

For each task there were 28 trials per ordinal distance for ‘in order’ stimuli and 16 trials for ‘not in order’ stimuli; for alphabetical and numerical ‘in order’ trials half were in ascending order and the other half in descending order; for the luminance judgment task, it was the same but with increasing and decreasing levels of luminance. The beginning of each trial was indicated by the appearance of an exclamation mark of 200 msec duration: the end of each trial corresponded to the moment of the participants’ button press response. If the participant did not respond within 4000 msec, ‘no response’ was recorded and the next trial began. Both response accuracy and response times were collected. The duration of the intertrial interval was variable (random Gaussian distribution centered on a mean duration of 7000+-1000 msec) and further varied as a function of the participants’ response times since the probe array disappeared immediately after a response was recorded.

The displays for the alphabetical and numerical tasks as well as for the WM encoding phase were presented vertically to avoid display-induced left-right spatialization of the target information (given the Mental Whiteboard hypothesis of ordinal coding, it was desirable to avoid display induced left-right spatial coding).

Each task was presented in a single run within the same fMRI session, and the order of the four runs within each session varied randomly between participants. A T1 structural brain scan was acquired after the first two blocks allowing the participants to rest (see below).

Finally, a practice session outside the scanner, prior to the start of the experiment, familiarized the participants with the specific task requirements and included the administration of 4 practice trials for each task. These practice trials could be repeated until the participants demonstrated full understanding of the different tasks. The tasks were presented on a workstation running Matlab 12 and the Cogent toolbox (UCL, http://www.vislab.ucl.ac.uk/cogent.php). Anonymized data are available on the Open Science Framework: osf.io/daf5s.

MRI acquisition

Functional MRI time series were acquired on a whole-body 3T scanner (Magnetom Prisma, Siemens Medical Solutions, Erlangen, Germany) operated with a 20-channel receiver head coil. Multislice T2*-weighted functional images were acquired with the multi-band gradient-echo echo-planar imaging sequence (CMRR, University of Minnesota) using axial slice orientation and covering the whole brain (32 slices, multiband factor = 2, FoV = 192x192 mm², voxel size 3x3x3 mm³, 25% interslice gap, matrix size 64x64x32, TR = 1174 ms, TE = 30 ms, FA = 90°). The five initial volumes were discarded to avoid T1 saturation effects. A gradient-recalled sequence was applied to acquire two complex images with different echo times (TE = 10.00 and 12.46 ms respectively) and generate field maps for distortion correction of the echo-planar images (EPI) (TR = 634 ms, FoV = 192x192 mm², 64x64 matrix, 40 transverse slices (3 mm thickness, 25% inter-slice gap), flip angle = 90°, bandwidth = 260 Hz/pixel). For anatomical reference, a high-resolution T1-weighted image was acquired for each subject (T1-weighted 3D magnetization-prepared rapid gradient echo (MPRAGE) sequence, TR = 1900 ms, TE = 2.19 ms, inversion time (TI) = 900 ms, FoV = 256x240 mm², matrix size = 256x240x224, voxel size = 1x1x1 mm³). Between 571 and 736 functional volumes were acquired during alphabetic, numerical and luminance tasks while between 1124 and 1351 functional volumes were acquired during order WM task. Head movement was minimized by restraining the participant's head using a vacuum cushion. Stimuli were displayed on a screen positioned at the rear of the scanner, which the participant could comfortably see through a mirror mounted on the standard head coil.

fMRI analyses

Image preprocessing

The functional images were preprocessed and analysed at the univariate level using SPM12 software (Wellcome Department of Imaging Neuroscience, www.fil.ion.ucl.ac.uk/spm) implemented in MATLAB (Mathworks, Inc., Sherbom, MA). EPI time series were corrected for motion and distortion using the Realign and Unwarp with default settings functions together with the FieldMap toolbox (implemented in SPM12) (Andersson et al. 2001; Hutton et al. 2002). A mean realigned functional image was then calculated by averaging all the realigned and unwarped functional scans and the structural T1 image was coregistered to this mean functional image (using a rigid body transformation optimised to maximise the normalised mutual information between the two images). The mapping from subject to MNI space was estimated from the structural image with the Unified segmentation approach (Ashburner and Friston 2005). The warping parameters were then separately applied to the functional and structural images to produce normalised images of resolution 2 × 2 × 2 mm3 and 1 × 1 × 1 mm3, respectively. Finally, the warped functional images were spatially smoothed with a Gaussian kernel of 4 mm FWHM to improve signal-to-noise ratio while preserving the underlying spatial distribution (Schrouff et al. 2012); this smoothing also diminishes the impact residual head motion can have on MVPA performance, even after head motion correction (Gardumi et al. 2016). We screened extreme head motion by excluding the *entire* data set of a participant if whole session movement was larger than 4 mm / 4° and/or if there was a peak movement exceeding 3 mm / 3° relative to initial head position. Note that we used a 4 mm / 4° threshold rather than the more common 3 mm / 3°

threshold for whole session movement (see for example, Franklin and Jonides 2009; Kaufmann, Vogel, Starke, Kremser, Schocke, et al. 2009; Holloway and Ansari 2010; Kalm et al. 2013; Matejko et al. 2019; Goffin et al. 2020; Sommerauer et al. 2020) because of the lengthy duration of the tasks in the scanner, increasing the likelihood of whole session movement. This resulted in the removal of the data of two participants.

Univariate analyses

Univariate analyses isolated BOLD signal variations associated with the distance effect in each task. For each participant, BOLD responses were estimated at each voxel, using a general linear model with epoch regressors and event-related regressors. For all tasks, the regressor ranged from the onset of the probe display to the participant's response; for the order WM task, this means that analyses were restricted to the retrieval stage in which ordinal distance was manipulated. On this basis, for each condition, two linear contrast were obtained. These contrasts were then entered in second-level analyses, corresponding to random effects models.

Paired t-tests for each judgment task were performed to assess univariate distance effects. For each model, the design matrix also included the realignment parameters to account for any residual movement-related effect. A high-pass filter was implemented using a cutoff period of 128 sec in order to remove the low-frequency drifts from the time series. Serial autocorrelations were estimated with a restricted maximum likelihood algorithm with an autoregressive model of order 1 (+ white noise). Statistical inferences were performed at the cluster level, using a significance threshold of $p < .05$ with FWE corrections for multiple comparisons across the whole brain or across volumes of interest (ROI analyses), and with a cluster-forming threshold of $p<.001$ uncorrected (Eklund et al. 2016). Note that for the univariate fMRI analyses we used a frequentist statistical approach in order to allow comparability with previous studies that investigated the nature and spatial extent of the univariate neural responses associated with ordinal processes. However, these univariate analyses need to be interpreted cautiously since conducting voxel-wise analysis in several small regions of interest increases the risk for Type 1 error. Subsequent multivariate analyses mainly used a Bayesian statistical approach (see below).

Multivariate analyses

Multivariate analyses were conducted using PRoNTo, a pattern recognition toolbox for neuroimaging (www.mlnl.cs.ucl.ac.uk/pronto; Schrouff et al., 2013). We trained classifiers to distinguish voxel activity patterns associated with distance 1 versus distance 2 in the preprocessed and 4-mm smoothed functional images for each order judgment task separately, using a binary support vector machine (Burges 1998). For within-task classification of distance, a leave-one-block-out (LOBO) cross-validation procedure was used. For between-tasks prediction of distance, a leave-one-run-out (LORO) cross-validation procedure was used, resulting in training the classifier on one task and testing the classifier on the other task. At the group level, classifier performance was tested by comparing the group-level distribution of classification accuracies to a chance-level distribution using Bayesian one sample t-tests. The Bayesian approach relies on a model comparison rationale and adopts a model selection strategy to select and quantify the strength of evidence associated with each model (Wagenmakers 2007; Dienes 2011; Morey and Rouder 2011). The Bayesian framework does not involve traditional *p*-values, thereby avoiding multiple testing problems such as alpha inflation or loss of power when adopting a stricter alpha level (Klugkist et al. 2011). Finally, the Bayesian approach has the advantage to not only give evidence in favour of the alternative model but also to appreciate evidence in favour of the null model, allowing to reject or not the null hypothesis more confidently (Wagenmakers 2007). The BF_{10} value represents the result of the likelihood ratio of the alternative model ($H1$) relative to the null model ($H0$) and the BF_{01} value represents the likelihood ratio of $H0$ relative to $H1$. The following classification of evidence strength was used (Jeffreys 1961; Lee and Wagenmakers 2014): A BF of 1 provides no evidence, 3>BF>1 provides anecdotal evidence, 10>BF>3 provides moderate evidence, 30>BF>10 provides strong evidence, 100>BF>30 provides very strong evidence, and BF>100 provides extreme/decisive evidence. Given the relatively subtle effect, the distance effect, Bayesian analyses were conducted with Version 0.10.2.0 of the JASP software package, using default settings for the Cauchy prior distribution (JASP Team, 2017, jasp-stats.org). A standard mask removing voxels outside the brain was applied to all images, and all models included timing parameters for hemodynamic response function delay (5 sec) and hemodynamic response function overlap (5 sec), ensuring that stimuli from different categories falling within the same 5 sec were excluded (Schrouff et al. 2013).

ROI analyses

The IPS areas were directly selected from the mean coordinates published in previous studies focusing on ordindal processing in alphabetical, numerical and WM domains (Majerus et al. 2006; Fias et al. 2007; Ischebeck et al. 2008; Franklin and Jonides 2009; Knops and Willmes 2013; Lyons and Beilock 2013; Attout et al. 2014). Based on previous studies, an anterior [44, -40, 36; -38, -46, 42] and a posterior IPS ROI [24, -64, 44; -30, -60, 48] were defined for each hemisphere. We also included two frontal ROIs, a middle frontal [50, 42, 20; -46, 22, 24] and an inferior frontal [44, 10, 30; -40, 26, 13] areas (Attout et al. 2015; Goffin et al. 2020). Given that some studies also suggest a role of hippocampal regions in short-term sequential processing (Fortin et al., 2002; Roberts et al, 2018; Hsieh et al., 2014), we also defined ROIs for the anterior [-30, -22, -14; 30, -14; -20] and posterior [-20, -34, 0; 26, -37, 0] hippocampus in both hemispheres (Kalm et al. 2013; Jenkins and Ranganath 2016; Roberts et al. 2018; Attout et al. 2019). These ROIs (see Figure 2) were constructed by generating a sphere of 10 mm radius around the coordinates of interest using the anatomical WFU PickAtlas Toolbox (Wake Forrest University 312 PickAtlas, http://fmri.wfubmc.edu/cms/software). Finally, we included visual area V1 as a control ROI defined using the IBASPM 116 atlas (http://www.thomaskoenig.ch/Lester/ibaspm.htm) with the WFU PickAtlas Toolbox to select Brodmann area 17 corresponding to the primary visual cortex V1.

< INSERT FIGURE 2 HERE >

Results

Behavioral analyses

Accuracies and median response times (for correct responses only) for each task and ordinal distance are presented in Table 1. The effect of ordinal distance was examined via Bayesian repeated measures ANOVA (Task x Distance) on response accuracy and response times. In line with previous studies, we expected an ordinal distance effect mainly for response times given that accuracy should be high for all task conditions (Lyons and Ansari 2015; Sasanguie et al. 2017). For accuracy, we observed strong evidence for a main effect of Distance (BF_{10}=88.35) and Task (BF_{10}=1.96E+17). The main effect of Distance was characterized by better performance for distance 1 than distance 2, reflecting an ordinal distance effect. Also, at the Task level, better performance was observed for the numerical order judgment task in comparison to the order WM task (BF_{10}=1.11E+3), to the alphabetical order task (BF_{10}=9.81E+3) and to the luminance task (BF_{10}=1.83E+10). Finally, lower performance was observed for the luminance task in comparison to the alphabetical and the oerder WM judgement tasks (respectively, BF_{10}=2175.58 and BF_{10}=3294.25) while these two last tasks did not differ from each other (BF_{10}=0.19). We also observed an interaction effect between Task and Distance (BF_{10}=8.25E+39), where a standard distance effect was observed only for the luminance judgment task (BF_{10}=2.83E+12) but not for the others (alphabetical: BF_{10}=0.19; numerical: BF_{10}=0.22; order WM: BF_{10}=1.62).

For response times, we used median response times in order to avoid bias by extreme response times. There was also strong evidence for a main effect of Task (BF_{10}=1.15E+51), faster response times being observed for the numerical order judgment task in comparison to the two other order tasks (alphabetical: BF_{10}=4.25E+9; order WM: BF_{10} =1.18E+11); furthermore the response times were similar for the order WM than the alphabetical task (BF_{10}=1.29); finally, the response times for the luminance task were faster than for all other tasks (numerical: BF_{10}=6.56; alphabetical: BF_{10}=3.74E+10; order WM: BF_{10}=4.06E+10). No evidence for a main effect of distance was observed (BF_{10}=1.45) but there was decisive evidence for the interaction between Task and Distance (BF_{10}=1.89E+60). While we observed an ordinal distance effect in all tasks, with distance 1 leading to faster reaction times than distance 2 (alphabetical: BF_{10}=2.10E+6; order WM: BF_{10}=3.07E+8; numerical: BF_{10}=4.40), we observed, as expected, a standard distance effect in the control task, with luminance distance 1 leading to slower response times than distance 2 (BF_{10}=2.24E+3).

< INSERT TABLE 1 HERE >

Neuroimaging - Univariate Analyses

A first set of neuroimaging analyses assessed the effect of distance on univariate neural activity changes in the order WM, ordinal numerical and ordinal alphabetical judgement tasks. We conducted paired t-tests for each order judgment task (see Table 2 and Figure 3). At whole brain level, no significant univariate effects were observed. For the order WM judgement task, we observed an ordinal distance effect (contrast of distance 2 minus distance 1) bilaterally in the anterior IPS and in the left posterior IPS. For the alphabetical order judgement task, the ordinal distance effect was associated with the bilateral posterior part of the IPS. For the ordinal numerical judgment task, the bilateral anterior and right posterior parts of the IPS were associated with the ordinal distance effect, as well as the bilateral middle frontal gyrus, the left inferior frontal gyrus. For the luminance judgment control task, no effect of luminance difference was observed at the whole-brain or ROI level. In sum, the ordinal distance effect in all ordinal processing tasks involved the unilateral or bilateral IPS, with higher activity peaks for distance 2 relatively to distance 1, as expected in the reverse distance effect, the distance 1 being easier than the distance 2, while the luminance distance effect only involved the occipital ROI and this for the reverse contrast than the ordinal tasks, the distance 1 activating more this brain area than the distance 2.

< INSERT TABLE 2 HERE >

< INSERT FIGURE 3 HERE >

Neuroimaging - Within-task classifications of ordinal distance

Next, we assessed multivariate patterns of activity associated with ordinal distance within each ROI (see Figure 4). For both the alphabetical and the order WM tasks, above chance-level classification of ordinal distance was observed in bilateral anterior and posterior IPS ROIs as well as in both frontal ROIs and the occipital ROI. For the numerical task, above chance-level classification of ordinal distance was observed only in the left posterior IPS ROI and in the right inferior frontal ROI. For the luminance control task, above-chance level classification of luminosity level was observed in the right posterior IPS, the right inferior frontal gyrus and the occipital ROI (see Figure 4 for BF values and means of accuracies classification). No above chance-level classification of ordinal distance was observed in the hippocampal ROIs.

< INSERT FIGURE 4 HERE >

Neuroimaging - Between-task predictions of ordinal distance

The final set of analyses examined the critical between-task predictions of ordinal distance within the different ROIs (see Figure 5). We observed robust evidence in favor of above-chance level prediction for ordinal distance between alphabetical judgment and order

WM, with reliable bidirectional prediction in the right posterior IPS; reliable bidirectional prediction was also observed in both frontal ROIs. For between-task predictions involving the numerical tasks, no reliable bidirectional predictions were observed in any ROI, although note that two unidirectional predictions (left anterior IPS and the right inferior frontal gyrus; see Figure 5) were above chance level. For latter between-task predictions, the majority of predictions were actually associated with positive evidence for the null hypothesis, with most BF_{01} values larger than 3. When considering between-task predictions involving the luminance judgment task controlling for potential differences in task difficulty associated with the two distance levels, evidence in favour of the null hypothesis, where there is no difference from chance-level prediction, was also observed (all $BF_{01} > 2.89$) (see Appendix). In line with results for within-task classification, no reliable between-task prediction was observed at the hippocampal level.

< INSERT FIGURE 5 HERE >

In order to assess in an appropriate manner the role of differential attentional control involvement in the robust between-task prediction of ordinal distance for the alphabetical and WM task, it is important to consider predictions between the luminance task and these two tasks by reversing the distance of the luminance task. Therefore, in order to compare distance effects between the luminance and the other tasks that share the same pattern of task difficulty (i.e., ‘harder’ distance vs. ‘easier’ distance), we exchanged labels for distance 1 and 2 in the luminance task. Indeed, for the ordinal judgment tasks, attentional control requirements are larger for distance 2 while the reverse is the case for the luminance where distance 1 judgments led to larger reaction times. Therefore, we ran additional between-task predictions by predicting distance 1 of the ordinal distance effects by distance 2 of the luminance distance effect and the distance 2 of the ordinal distance effects by distance 1 of the luminance distance effect. In this case, in agreement with a differential engagement of attentional control processes, we indeed, observed evidence for between-task prediction of distance between the luminance judgment and both the WM and alphabetical judgment tasks, and this mainly in the two frontal ROIs (right middle frontal gyrus for the alphabetical task and and the left inferior frontal gyrus for the WM task) (see Figure 6). Finally, when focussing on the V1 ROI, all between-task predictions remained at chance level (all $BF_{01} > 5.87$) supporting the specificity of fronto-parietal contributions to between-task prediction of ordinal distance in the serial order WM and the alphabetical judgement tasks (see Figures 5 and 6).

< INSERT FIGURE 6 HERE >

Discussion

We conducted a direct examination of the domain-generality hypothesis of ordinal codes, by assessing ordinal judgment across three domains, by using triplet stimuli maximizing ordinal processing and by determining the neural similarity of ordinal processing across domains in fronto-parietal cortices. At the behavioural level, we observed the expected reverse distance effect for ordinal judgement, demonstrated by quicker response times for smaller vs. larger ordinal distances in order WM, alphabetical and numerical tasks. Both univariate and multivariate analyses showed sensitivity to ordinal distance in fronto-parietal cortices for each task but not at the hippocampus level. Critically, however, between-domain prediction of ordinal distance was only reliable between the serial order WM and the alphabetical tasks, and this for neural patterns in the right posterior IPS, the right inferior frontal and the left middle frontal ROIs. Moreover, we observed evidence for between-task prediction of distance between the luminance judgment (standard distance effect) and both the WM and alphabetical judgment tasks (ordinal distance effect), and this mainly in the two frontal ROIs.

The present study supports the hypothesis of domain-general neural codes endorsing ordinal processing at least for WM and alphabetical domains, and further reveals important new information about the nature of these codes. The hypothesis of domain-general ordinal codes has been mainly supported in the literature by studies observing different levels of activity in fronto-parietal cortices for judging close versus larger ordinal distances across different domains such as numerical, alphabetical and WM domains (Fulbright et al. 2003; Fias et al. 2007; Ischebeck et al. 2008; Attout et al. 2014, 2015; Goffin et al. 2020). While our results support the domain-general implication of fronto-parietal cortices in ordinal judgment, they do however not support the hypothesis of domain-general ordinal codes per se. First, we observed a prediction of ordinal distance in fronto-parietal cortices only for the order WM and alphabetical tasks, but not for the numerical domain. Furthermore, this prediction was not specific to ordinal distance as luminance distance could also be predicted from ordinal distance in the WM and alphabetical judgment task. This is a critical result as it shows that the across domain prediction of ordinal distance in the WM and alphabetical tasks is not only driven by ordinal distance per se and this result supports the alternative hypothesis, namely that differences in attentional control requirements may drive, at least partially, the judgment of close versus larger ordinal distances.

Indeed, while judgment of distance 2 in comparison to distance 1 was more difficult in the alphabetical and WM tasks, as reflected by lower accuracy and increased response times, distance 2 was easier than the distance 1 in the luminance task, leading to no prediction of distance between the luminance and the other two tasks. However, when inverting the distance labels in the luminance task so that distance 2 is now also the more difficult condition, prediction between luminance and ordinal distance effects was observed, indicating that the neural processing supporting judgment of close versus larger distances reflects at least partly the ‘hard-vs-easy’ dimension of these distances and associates different levels of attentional control. Furthermore, the frontal ROIs that support prediction of distance effects between the luminance and the WM and alphabetical conditions are well known to be involved in top-down, attentional control processes (Culham and Kanwisher 2001; Corbetta and Shulman 2002; Majerus et al. 2016, 2018). More precisely, the inferior frontal gyrus has been associated with integration of information coming from the top-down, dorsal attention network and the bottom-up stimulus driven attention network (Corbetta and Shulman 2002; Asplund et al. 2010; Sebastian et al. 2016). The middle frontal gyrus, also less highlighted in prototyptical representations of the dorsal attention network, is very frequently co-activated with the attentional dorsal network and has been considered to be a core part of the dorsal attentional network too (Rypma et al. 1999; Serences et al. 2005; Chiu and Yantis 2009; Majerus et al. 2012, 2018; Kurth et al. 2016). This is also in line with a previous study observing hypoactivation of the same middle frontal gyrus area in adults with dyscalculia DD during alphabetical and WM order judgment tasks, and the association of this hypoactivation to difficulties in controlled, explicit processing of order information (Attout et al. 2015). This area has also been associated with the manipulation and monitoring of multiple stimuli (Champod and Petrides 2010).

We should however note that the posterior parietal ROI, although discriminating between ordinal distance, did not allow for prediction between luminance and ordinal distances, and hence may have a more specific role in ordinal processing. The right posterior IPS is part of the fronto-parietal dorsal attention network (Corbetta et al. 2000; Todd and Marois 2004; Majerus et al. 2012, 2018) but has also been associated with more specific, spatial attentional processes. These processes are particularly required during ordinal judgment, as the sequences need to be scanned from the left to the right and vice versa for determining their sequential order, while this kind of spatial processing is not required at all for the type of luminance judgment task as used in this study. A spatial-attentional role of the posterior IPS is supported by several brain-imaging studies showing differentiated neural signals for leftward versus rightward orientation of attention in this area (Yantis et al. 2002;

Silver and Kastner 2009; Vandenberghe and Gillebert 2009; Bressler and Silver 2010; Gillebert et al. 2011). The posterior IPS may provide an attentional spatial frame that allows to temporarily organize memoranda and letters on a horizontal line, ordered from left to right, with coarse or more refined spatial codes depending upon the level of ordinal resolution that is needed when comparing close vs. larger ordinal distances. This spatial ordinal processing strategy, also known as the *Mental whiteboard hypothesis* (Abrahamse et al. 2014, 2017), is based on the observation that information is organized spatially even in auditory-verbal WM, as illustrated by the fact that early WM list items are responded to faster with the left hand as they are presumably associated to the left part of the mental line, and more recent WM items are responded to faster with the right hand due to their association to the right part of the mental line (van Dijck and Fias 2011). At the brain level, one recent study has provided further evidence for an involvement of spatial attention mechanisms in serial order processing. Rasoulzadeh et al. (2021) showed that neurophysiological signatures of spatial attention in fronto-parietal cortices were indeed sensitive to the position of an item within a list of memoranda, as shown by posterior alpha suppression contralateral to the position of the item. Moreover, we should also note that we did not observe any neural responses to ordinal information in the hippocampal ROIs. While some studies observed a role for the hippocampus in the maintenance of temporal sequences (Fortin et al. 2002; Hsieh et al. 2014; Jenkins and Ranganath 2016; Roberts et al. 2018), other studies did not observe a specific response to serial order information in this area (Majerus et al. 2006, 2010; Papagno et al. 2017; Attout et al. 2019). Many studies reporting hippocampal involvement in ordinal processing used tasks that had also a consolidation and long-term memory component such as in Hebb learning paradigms (Kalm et al. 2013; Attout et al. 2020). The hippocampus may support episodic memory for ordinal information rather than ordinal information per se.

Finally, a further important result of this study is the fact that in the numerical domain, the ordinal distance effect appeared to elicit more specific neural patterns as small versus larger numerical ordinal distances could be decoded in fronto-parietal cortices, but the neural patterns associated with this distinction could not predict ordinal distance effects in the WM and alphabetical tasks or the luminance distance effect. A first possible interpretation is that this result reflects ordinal codes specific to the numerical domain. In a multivariate re-analysis of the results of Fias et al. (2007), Zorzi et al. (2011) indeed observed that the neural patterns in the IPS are specific to numerical judgment, relative to letter judgment. Also, neuropsychological studies demonstrated dissociations for ordinal processing between numbers and other domains such as a months, days and letters in neglect patients (Zorzi et al. 2006; Zamarian et al. 2007). Neurons in the IPS have furthermore been shown to be tuned to numbers and to demonstrate a topographic organisation as a function of numerosity in this area (Harvey et al. 2013; Matejko et al. 2019; Sommerauer et al. 2020). This is also in line with the work of Ginsburg et al. (2014; Ginsburg & Gevers 2015), suggesting that the numerical and WM domains differ by their recruitment of long-term vs. short-term representations. They indeed demonstrated in a series of experiments that the ordinal effects for numbers and WM content can arise simultaneously within the same task, suggesting that both effects stem from independent processes. Our results support this assumption and go further by highlighting the specificity of numerical order judgment as compared to several other judgment tasks such as alphabetical order judgement and luminance judgement, in addition to serial order WM. Furthermore, distance judgment in these three latter tasks involved neural patterns in a broader fronto-parietal brain network while numerical ordinal judgment was restricted to neural patterns in a more specific left posterior IPS part whose role in the representation of numerical information has been highlighted in several studies (e.g. Franklin and Jonides 2009; Attout et al. 2014).

Another possible interpretation is however that this neural differentiation also reflects differential attentional control involvement, but at a different level than for the other three tasks due to the more automatic and overlearned nature of numerical and associated ordinal processing. Indeed, a major difference between the numerical and the three other tasks is that numerical order judgment is likely to involve rapid activation of overlearned numerical ordinal knowledge allowing to reach a fast decision about the ordinality of triplet. For the serial order WM task, there is no long-term ordinal knowledge specific to individual memoranda that could be retrieved. However, as mentioned by the Mental whiteboard hypothesis, a general, left-right spatial template may be retrieved for structuring and fixing the serial order of the incoming memoranda. This is also the case for the alphabetic order judgment: although the alphabetic task also involved the retrieval of long-term ordinal information, this information is less overlearned particularly when the triplets do not involved the first three letters of the alphabet; hence ordinal information of letters needs to be reinstated (via recitation of the letter chain) and then temporarily represented for finalizing the comparison process. Hence, although in all tasks, the distance effects can be explained by differences in attentional control requirements, these attentional requirements are overall much more reduced in the numerical task than in the other three tasks; in other words, the level of attentional control for judging a distance-1 stimulus in the alphabetical and WM tasks is not the same as the attentional control needed for judging a distance-1 stimulus in the numerical task. This interpretation is supported by the important differences in response times between the tasks: ordinal judgment in the serial order WM and the alphabetical order tasks were, respectively, 1.49 and 1.61 times slower than for the numerical judgment task. Automatic and rapid access to long-term ordinal representations for numerical information is also supported by other studies directly showing that extensive use of the numerical sequence in daily life leads to implicit and direct access to these representations (Vos et al. 2017; Sella et al. 2020; Sommerauer et al. 2020).

To conclude, the present study shows, in line with previous studies, a domain-general involvement of a fronto-parietal network in the processing of ordinal distance but only for non-numerical ordering. However, contrary to these studies, this fronto-parietal network appears to reflect the differential involvement of top-down and spatial attentional ressources rather than domain-general coding of ordinal representations. The present study sheds new light on the nature and role of fronto-parietal cortices in processing ordinal information across domains.

Funding

This work was supported by a grant from Fonds de la Recherche Scientifique – FRS – FNRS (CR, FC 88264, Belgium).

Aknowledgments

We would like to thank all participants for their time and effort invested in this study. There is no conflict of interest in connection with this work.

References

[dataset] Attout, 2021, Neural representation of order, retrieved from osf.io/daf5s

Abrahamse EL, Dijck J Van, Majerus S, Fias W. 2014. Finding the answer in space : the mental whiteboard hypothesis on serial order in working memory. 8:1–12.

Abrahamse EL, van Dijck J-P, Fias W. 2017. Grounding Verbal Working Memory: The Case of Serial Order. Curr Dir Psychol Sci. 26:429–433.

Andersson JL, Hutton C, Ashburner J, Turner R, Friston K. 2001. Modeling geometric deformations in EPI time series. Neuroimage. 13:903–919.

Ashburner J, Friston KJ. 2005. Unified segmentation. Neuroimage. 26:839–851.

Asplund CL, Todd JJ, Snyder AP, Marois R. 2010. A central role for the lateral prefrontal cortex in goal-directed and stimulus-driven attention. Nat Neurosci. 13:507–512.

Attout L, Fias W, Salmon E, Majerus S. 2014. Common neural substrates for ordinal representation in short-term memory, numerical and alphabetical cognition. PLoS One. 9.

Attout L, Ordonez Magro L, Szmalec A, Majerus S. 2019. The developmental neural substrates of item and serial order components of verbal working memory. Hum Brain Mapp. 40:1541–1553.

Attout L, Ordonez Magro L, Szmalec A, Majerus S. 2020. The developmental neural substrates of Hebb repetition learning and their link with reading ability. Hum Brain Mapp. 41:3956–3969.

Attout L, Salmon E, Majerus S. 2015. Working memory for serial order is dysfunctional in adults with a history of developmental dyscalculia : Evidence from behavioral and neuroimaging data. Dev Neuropsychol. 40:230–247.

Bressler DW, Silver MA. 2010. Spatial attention improves reliability of fMRI retinotopic mapping signals in occipital and parietal cortex. Neuroimage. 53:526–533.

Burges CJC. 1998. A tutorial on support vector machines for pattern recognition. Data Min Knowl Discov. 2:121–167.

Champod AS, Petrides M. 2010. Dissociation within the frontoparietal network in verbal working memory: A parametric functional magnetic resonance imaging study. J Neurosci. 30:3849–3856.

Chiu YC, Yantis S. 2009. A domain-independent source of cognitive control for task sets: Shifting spatial attention and switching categorization rules. J Neurosci. 29:3930–3938.

Corbetta M, Kincade JM, Ollinger JM, McAvoy MP, Shulman GL. 2000. Voluntary orienting is dissociated from target detection in human posterior parietal cortex. Nat Neurosci. 3:292–297.

Corbetta M, Shulman GL. 2002. Control of goal-directed and stimulus-driven attention in the brain. Nat Rev Neurosci. 3:201–215.

Culham JC, Kanwisher NG. 2001. Neuroimaging of cognitive functions in human parietal cortex. Curr Opin Neurobiol. 11:157–163.

Dai J, Wang Y. 2012. Representation of surface luminance and contrast in primary visual cortex. Cereb cortex. 22:776–787.

Dienes Z. 2011. Bayesian versus orthodox statistics: Which side are you on? Perspect Psychol Sci. 6:274–290.

Eklund A, Nichols TE, Knutsson H. 2016. Cluster failure: Why fMRI inferences for spatial extent have inflated false-positive rates. Proc Natl Acad Sci U S A. 113:7900–7905.

Fias W, Lammertyn J, Caessens B, Orban GA. 2007. Processing of abstract ordinal knowledge in the horizontal segment of the intraparietal sulcus. J Neurosci. 27:8952–8956.

Fortin NJ, Agster KL, Eichenbaum HB. 2002. Critical role of the hippocampus in memory for sequences of events. Nat Neurosci. 5:458–462.

Franklin MS, Jonides J. 2009. Order and magnitude share a common representation in parietal cortex. J Cogn Neurosci. 21:2114–2120.

Franklin MS, Jonides J, Smith EE. 2009. Processing of order information for numbers and months. Mem Cognit. 37:644–654.

Fulbright RK, Manson SC, Skudlarski P, Lacadie CM, Gore JC. 2003. Quantity determination and the distance effect with letters, numbers, and shapes: a functional MR imaging study of number processing. Am J Neuroradiol. 24:193–200.

Gardumi A, Ivanov D, Hausfeld L, Valente G, Formisano E, Uludağ K. 2016. The effect of spatial resolution on decoding accuracy in fMRI multivariate pattern analysis. Neuroimage. 132:32–42.

Geisler WS, Albrecht DG, Crane AM. 2007. Responses of neurons in primary visual cortex to transient changes in local contrast and luminance. J Neurosci. 27:5063–5067.

Gillebert CR, Mantini D, Thijs V, Sunaert S, Dupont P, Vandenberghe R. 2011. Lesion evidence for the critical role of the intraparietal sulcus in spatial attention. Brain. 134:1694–1709.

Ginsburg V, Gevers W. 2015. Spatial coding of ordinal information in short- and long-term memory. Front Hum Neurosci. 9:1–10.

Ginsburg V, van Dijck J-P, Previtali P, Fias W, Gevers W. 2014. The impact of verbal working memory on number–space associations. J Exp Psychol Learn Mem Cogn. 40:976–986.

Goffin C, Ansari D. 2016. Beyond magnitude: Judging ordinality of symbolic number is unrelated to magnitude comparison and independently relates to individual differences in arithmetic. Cognition. 150:68–76.

Goffin C, Ansari D. 2019. How are symbols and nonsymbolic numerical magnitudes related? Exploring bidirectional relationships in early numeracy. Mind, Brain, Educ. 13:143–156.

Goffin C, Vogel SE, Slipenkyj M, Ansari D. 2020. A comes before B, like 1 comes before 2. Is the parietal cortex sensitive to ordinal relationships in both numbers and letters? An fMRI-adaptation study. Hum Brain Mapp. 41:1591–1610.

Harvey BM, Klein BP, Petridou N, Dumoulin SO. 2013. Topographic representation of numerosity in the human parietal cortex. Science (80-). 341:1123–1126.

Holloway ID, Ansari D. 2010. Developmental specialization in the right intraparietal sulcus for the abstract representation of numerical magnitude. J Cogn Neurosci. 22:2627–2637.

Hsieh LT, Gruber MJ, Jenkins LJ, Ranganath C. 2014. Hippocampal Activity Patterns Carry Information about Objects in Temporal Context. Neuron. 81:1165–1178.

Hutton C, Bork A, Josephs O, Deichmann R, Ashburner J, Turner R. 2002. Image distortion correction in fMRI: A quantitative evaluation. Neuroimage. 16:217–240.

Ischebeck A, Heim S, Siedentopf C, Zamarian L, Schocke M, Kremser C, Egger K, Strenge H, Scheperjans F, Delazer M. 2008. Are numbers special? Comparing the generation of verbal materials from ordered categories (months) to numbers and other categories (animals) in an fMRI study. Hum Brain Mapp. 29:894–909.

Jeffreys H. 1961. Theory of probability. Oxford, UK: Oxford, UK: Clarendon.

Jenkins LJ, Ranganath C. 2016. Distinct neural mechanisms for remembering when an event occurred. Hippocampus. 26:554–559.

Jou J, Aldridge JW. 1999. Memory representation of alphabetic position and interval information. J Exp Psychol Learn Mem Cogn. 25:680–701.

Kalm K, Davis MH, Norris D. 2013. Individual sequence representations in the medial temporal lobe. J Cogn Neurosci. 25:1111–1121.

Kaufmann L, Vogel SE, Starke M, Kremser C, Schocke M. 2009. Numerical and non-numerical ordinality processing in children with and without developmental dyscalculia: Evidence from fMRI. Cogn Dev. 24:486–494.

Kaufmann L, Vogel SE, Starke M, Kremser C, Schocke M, Wood G. 2009. Developmental dyscalculia: compensatory mechanisms in left intraparietal regions in response to nonsymbolic magnitudes. Behav Brain Funct. 5:35.

Klugkist I, van Wesel F, Bullens J. 2011. Do we know what we test and do we test what we want to know? Int J Behav Dev. 35:550–560.

Knops A, Willmes K. 2013. Numerical ordering and symbolic arithmetic share frontal and parietal circuits in the right hemisphere. Neuroimage. 84:786–795.

Kurth S, Majerus S, Bastin C, Collette F, Jaspar M, Bahri MA, Salmon E. 2016. Effects of aging on task- and stimulus-related cerebral attention networks. Neurobiol Aging. 44:85–95.

Lee CL, Estes WK. 1981. Item and Order Information in Short-Term Memory: Evidence for Multilevel Perturbation Processes. J Exp Psychol Hum Learn Mem. 7:149–169.

Lee MD, Wagenmakers E-J. 2014. Bayesian cognitive modeling: A practical course. Cambridge university press.

Leth-steensen C, Marley AAJ. 2000. A model of response time effects in symbolic comparison. Psychol Rev. 107:62–100.

Lyons IM, Ansari D. 2015. Numerical Order Processing in Children: From Reversing the Distance-Effect to Predicting Arithmetic. Mind, Brain, Educ. 9:207–221.

Lyons IM, Beilock SL. 2013. Ordinality and the nature of symbolic numbers. J Neurosci. 33:17052–17061.

Lyons IM, Vogel SE, Ansari D.On the ordinality of numbers: A review of neural and behavioral studies. In: Progress in Brain Research. Elsevier B.V. p. 187–221.

Majerus S, Attout L, D’Argembeau A, Degueldre C, Fias W, Maquet P, Martinez Perez T, Stawarczyk D, Salmon E, Van der Linden M, Phillips C, Balteau E, Argembeau AD, Degueldre C, Fias W, Maquet P, Perez TM, Stawarczyk D, Salmon E, Linden M Van

Der, Phillips C, Balteau E. 2012. Attention supports verbal short-term memory via competition between dorsal and ventral attention networks. Cereb Cortex. 22:1086–1097.

Majerus S, Boukebza C. 2013. Short-term memory for serial order supports vocabulary development: New evidence from a novel word learning paradigm. J Exp Child Psychol. 116:811–828.

Majerus S, Cowan N, Péters F, Van Calster L, Phillips C, Schrouff J. 2016. Cross-Modal Decoding of Neural Patterns Associated with Working Memory: Evidence for Attention-Based Accounts of Working Memory. Cereb Cortex. 26:166–179.

Majerus S, D'Argembeau A, Martinez Perez T, Belayachi S, Van der Linden M, Collette F, Salmon E, Seurinck R, Fias W, Maquet P. 2010. The commonality of neural networks for verbal and visual short-term memory. J Cogn Neurosci. 22:2570–2593.

Majerus S, Péters F, Bouffier M, Cowan N, Phillips C. 2018. The dorsal attention network reflects both encoding load and top-down control during working memory. J Cogn Neurosci. 30:144–159.

Majerus S, Poncelet M, Van der Linden M, Albouy G, Salmon E, Sterpenich V, Vandewalle G, Collette F, Maquet P. 2006. The left intraparietal sulcus and verbal short-term memory: focus of attention or serial order? Neuroimage. 32:880–891.

Marshuetz C, Smith EE, Jonides J, DeGutis J, Chenevert TL. 2000. Order information in working memory: fMRI evidence for parietal and prefrontal mechanisms. J Cogn Neurosci. 12:130–144.

Matejko AA, Hutchison JE, Ansari D. 2019. Developmental specialization of the left intraparietal sulcus for symbolic ordinal processing. Cortex. 114:41–53.

McCormack T, Brown GD, Vousden JI, Henson RN. 2000. Children's serial recall errors: implications for theories of short-term memory development. J Exp Child Psychol.

76:222–252.

Morey RD, Rouder JN. 2011. Bayes factor approaches for testing interval null hypotheses. Psychol Methods. 16:406–419.

Moyer RS, Landauer TK. 1967. Time required for judgements of numerical inequality. Nature. 215:1519–1520.

Nairne JS, Riegler GL, Serra M. 1991. Dissociative effects of generation on item and order retention. J Exp Psychol Learn Mem Cogn. 17:702–709.

Nieder A. 2005. Counting on neurons: the neurobiology of numerical competence. Nat Rev Neurosci. 6:114–177.

Papagno C, Comi A, Riva M, Bizzi A, Vernice M, Casarotti A, Fava E, Bello L. 2017. Mapping the brain network of the phonological loop. Hum Brain Mapp. 38:3011–3024.

Rasoulzadeh V, Sahan MI, van Dijck J-P, Abrahamse E, Marzecova A, Verguts T, Fias W. 2021. Spatial Attention in Serial Order Working Memory: An EEG Study. Cereb Cortex. 31:2482–2493.

Roberts BM, Libby LA, Inhoff MC, Ranganath C. 2018. Brain activity related to working memory for temporal order and object information. Behav Brain Res. 354:55–63.

Rypma B, Prabhakaran V, Desmond JE, Glover GH, Gabrieli JDE. 1999. Load-dependent roles of frontal brain regions in the maintenance of working memory. Neuroimage. 9:216–226.

Sasanguie D, Lyons IM, De Smedt B, Reynvoet B. 2017. Unpacking symbolic number comparison and its relation with arithmetic in adults. Cognition. 165:26–38.

Schrouff J, Kussé C, Wehenkel L, Maquet P, Phillips C. 2012. Decoding Semi-Constrained Brain Activity from fMRI Using Support Vector Machines and Gaussian Processes. PLoS One. 7:e35860.

Schrouff J, Rosa MJ, Rondina JM, Marquand AF, Chu C, Ashburner J, Phillips C, Richiardi J, Mourão-Miranda J. 2013. PRoNTo: pattern recognition for neuroimaging toolbox. Neuroinformatics. 11:319–337.

Sebastian A, Jung P, Neuhoff J, Wibral M, Fox PT, Lieb K, Fries P, Eickhoff SB, Tüscher O, Mobascher A. 2016. Dissociable attentional and inhibitory networks of dorsal and ventral areas of the right inferior frontal cortex: a combined task-specific and coordinate-based meta-analytic fMRI study. Brain Struct Funct. 221:1635–1651.

Sella F, Sasanguie D, Reynvoet B. 2020. Judging the order of numbers relies on familiarity rather than activating the mental number line. Acta Psychol (Amst). 204:103014.

Serences JT, Shomstein S, Leber AB, Golay X, Egeth HE, Yantis S. 2005. Coordination of voluntary and stimulus-driven attentional control in human cortex. Psychol Sci. 16:114–122.

Silver MA, Kastner S. 2009. Topographic maps in human frontal and parietal cortex. Trends Cogn Sci. 13:488–495.

Sommerauer G, Graß KH, Grabner RH, Vogel SE. 2020. The semantic control network mediates the relationship between symbolic numerical order processing and arithmetic performance in children. Neuropsychologia. 141:107405.

Sury D, Rubinsten O. 2012. Ordinal processing of numerical and non-numerical information. In: Breznitz Z,, Rubinsten O,, Molfese V,, Molfese D, editors. Reading, Writing, Mathematics and the Developing Brain: Listening to Many Voices. Springer Netherlands. p. 209–232.

Todd JJ, Marois R. 2004. Capacity limit of visual short-term memory in human posterior parietal cortex. Nature. 428:751–754.

Turconi E, Campbell JID, Seron X. 2006. Numerical order and quantity processing in number comparison. Cognition. 98:273–285.

Turconi E, Seron X. 2002. Dissociation between order and quantity meaning in a patient with

Gerstmann syndrome. Cortex. 38:911–914.

van Dijck JP, Fias W. 2011. A working memory account for spatial-numerical associations. Cognition. 119:114–119.

Van Opstal F, Gevers W, De Moor W, Verguts T. 2008. Dissecting the symbolic distance effect: Comparison and priming effects in numerical and nonnumerical orders. Psychon Bull Rev. 15:419–425.

Vandenberghe R, Gillebert CR. 2009. Parcellation of parietal cortex: Convergence between lesion-symptom mapping and mapping of the intact functioning brain. Behav Brain Res. 199:171–182.

Vos H, Sasanguie D, Gevers W, Reynvoet B. 2017. The role of general and number-specific order processing in adults’ arithmetic performance. J Cogn Psychol. 29:469–482.

Wagenmakers E-J. 2007. A practical solution to the pervasive problems ofp values. Psychon Bull Rev. 14:779–804.

Yantis S, Schwarzbach J, Serences JT, Carlson RL, Steinmetz MA, Pekar JJ, Courtney SM. 2002. Transient neural activity in human parietal cortex during spatial attention shifts. Nat Neurosci. 5:995–1002.

Zamarian L, Egger C, Delazer M. 2007. The mental representation of ordered sequences in visual neglect. Cortex. 43:542–550.

Zorzi M, Di Bono MG, Fias W. 2011. Distinct representations of numerical and non-numerical order in the human intraparietal sulcus revealed by multivariate pattern recognition. Neuroimage. 56:674–680.

Zorzi M, Priftis K, Meneghello F, Marenzi R, Umiltà C. 2006. The spatial representation of numerical and non-numerical sequences: Evidence from neglect. Neuropsychologia. 44:1061–1067.

Tables

Table 1. Descriptive statistics for behavioural performance in the different judgment tasks as a function of distance.

	Accuracy		Response times	
	M	SD	M	SD
Alphabetical D1	.90	.09	1977.02	505.60
Alphabetical D2	.90	.12	2260.88	556.86
Numerical D1	.98	.04	1283.94	282.53
Numerical D2	.98	.03	1344.62	321.49
Order WM D1	.92	.08	1745.45	330.60
Order WM D2	.88	.13	2177.22	330.60
Luminance D1	.66	.13	1275.93	419.63
Luminance D2	.92	.11	1072.15	345.29

Table 2. Univariate fMRI results.

	No. voxels	Left/ right	x	y	z	SPM Z - value
Ordinal distance effect for order WM (D2<D1)						
IPSa	26	L	-30	-44	44	3.79*
	50	R	46	-36	40	4.25*
IPSp	96	L	-28	-64	44	4.26*
Ordinal distance effect for ordinal alphabetical judgment (D2<D1)						
IPSp	43	L	-28	-64	44	4.24*
	11	R	30	-62	38	3.50*
Ordinal distance effect for ordinal numerical judgment (D2<D1)						
IPSa	69	L	-38	-44	40	3.81*
	28	R	38	-38	40	3.73*
IPSp	71	R	32	-60	46	4.00*
MFG	57	L	-48	22	22	3.98*
	18	R	46	40	22	3.89*
IFG	34	L	-36	28	20	4.06*

*= p < .05, small volume corrections

Figures

Figure 1. Description of the different judgement tasks.

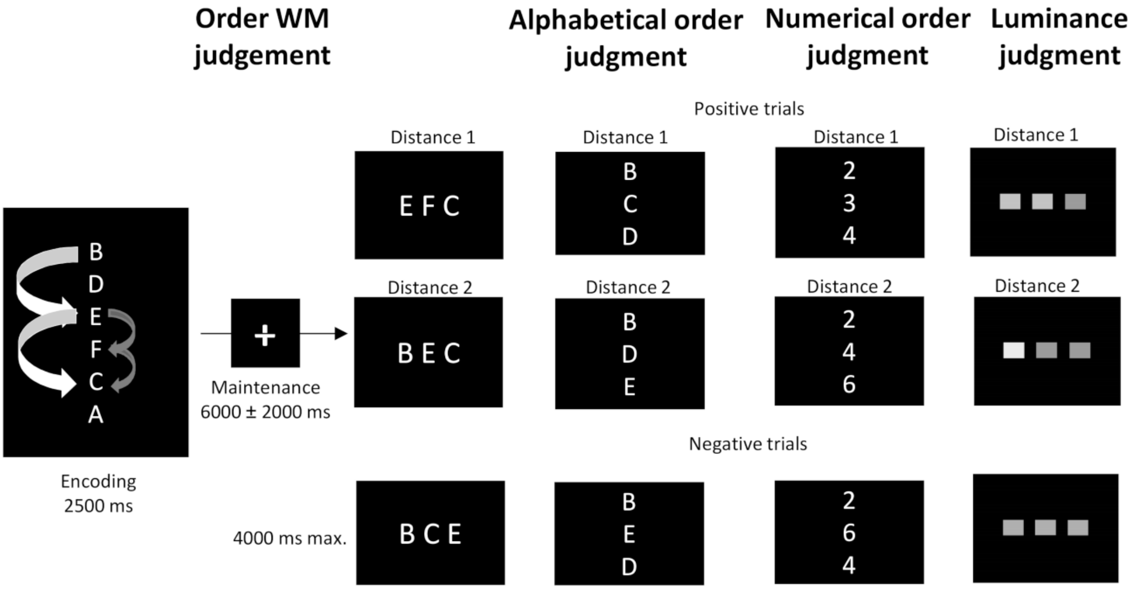

Figure 2. ROI used in the univariate and multivariate analyses. The upper panel shows the IPS ROIs, the middle panel shows the frontal ROIs and the lower panel shows the V1 ROI.

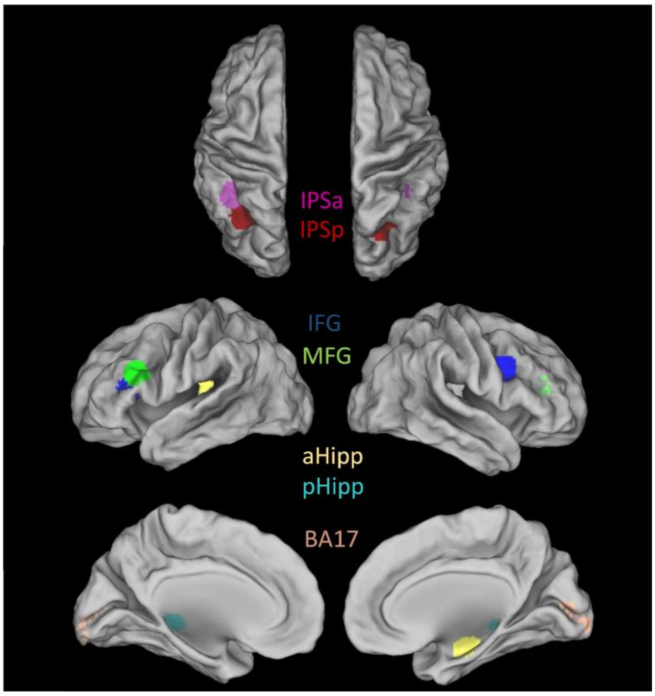

Figure 3. Displaying of univariate results at uncorrected level (p<0.001) for the three order judgement tasks.

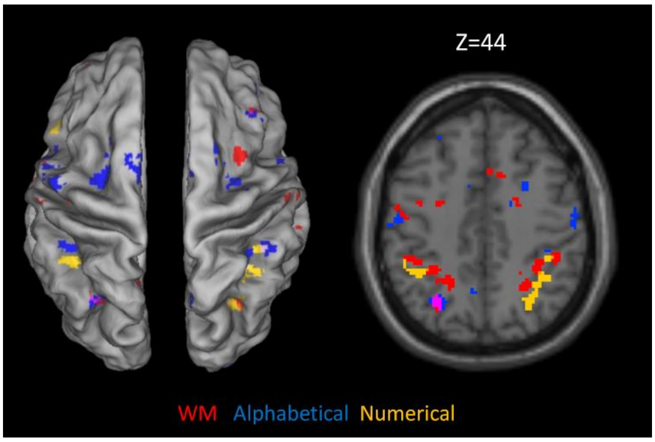

Figure 4. Classification rates for within-task predictions of distance between each ordinal judgment task for the different ROIs. BF_{10} values at the top of each column assess deviation from chance-level classification levels. Dark grey bars indicate above-chance level prediction of ordinal distance for the corresponding tasks.

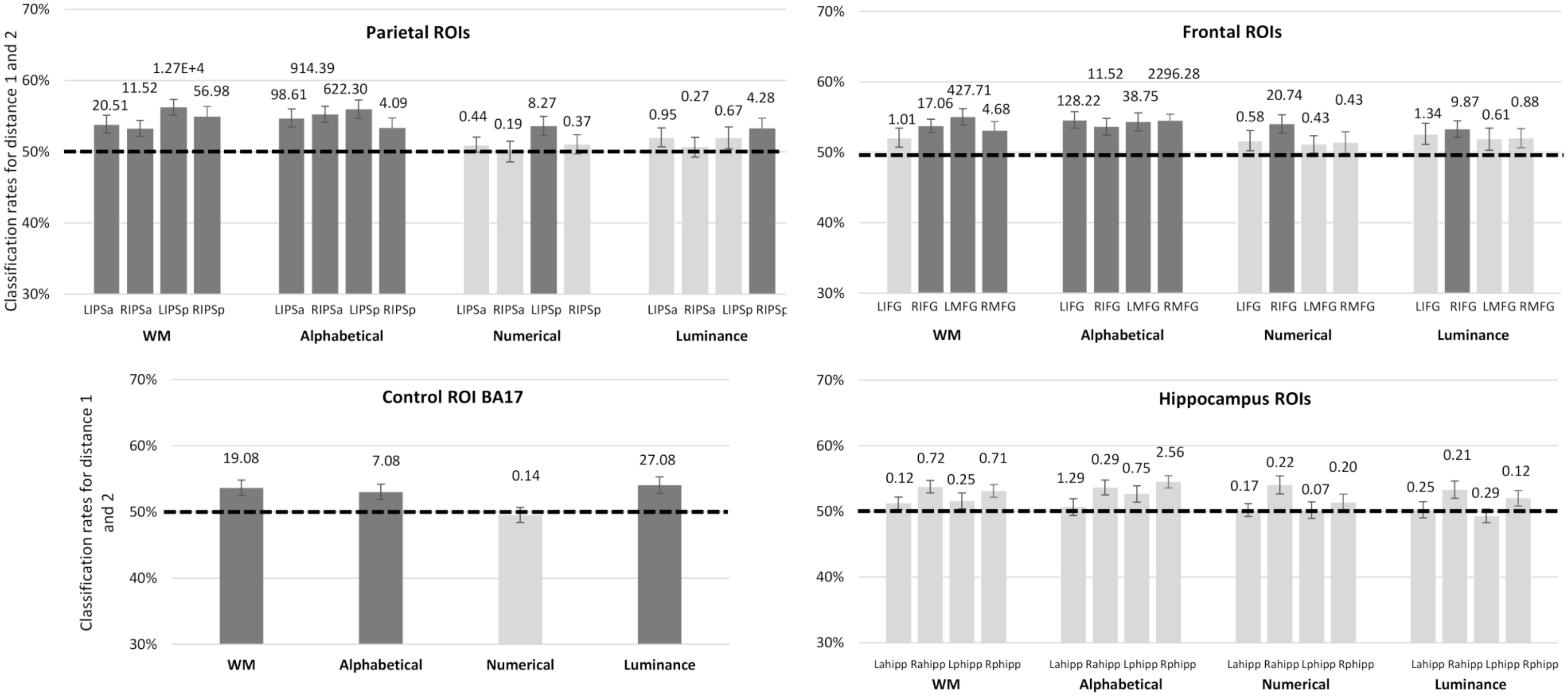

Figure 5. Classification rates for between-task predictions of distance between each ordinal judgment task for the different ROIs. BF$_{10}$ values at the top of each column assess deviation from chance-level classification levels. Dark grey bars indicate above-chance level prediction of ordinal distance in both directions for the corresponding tasks.

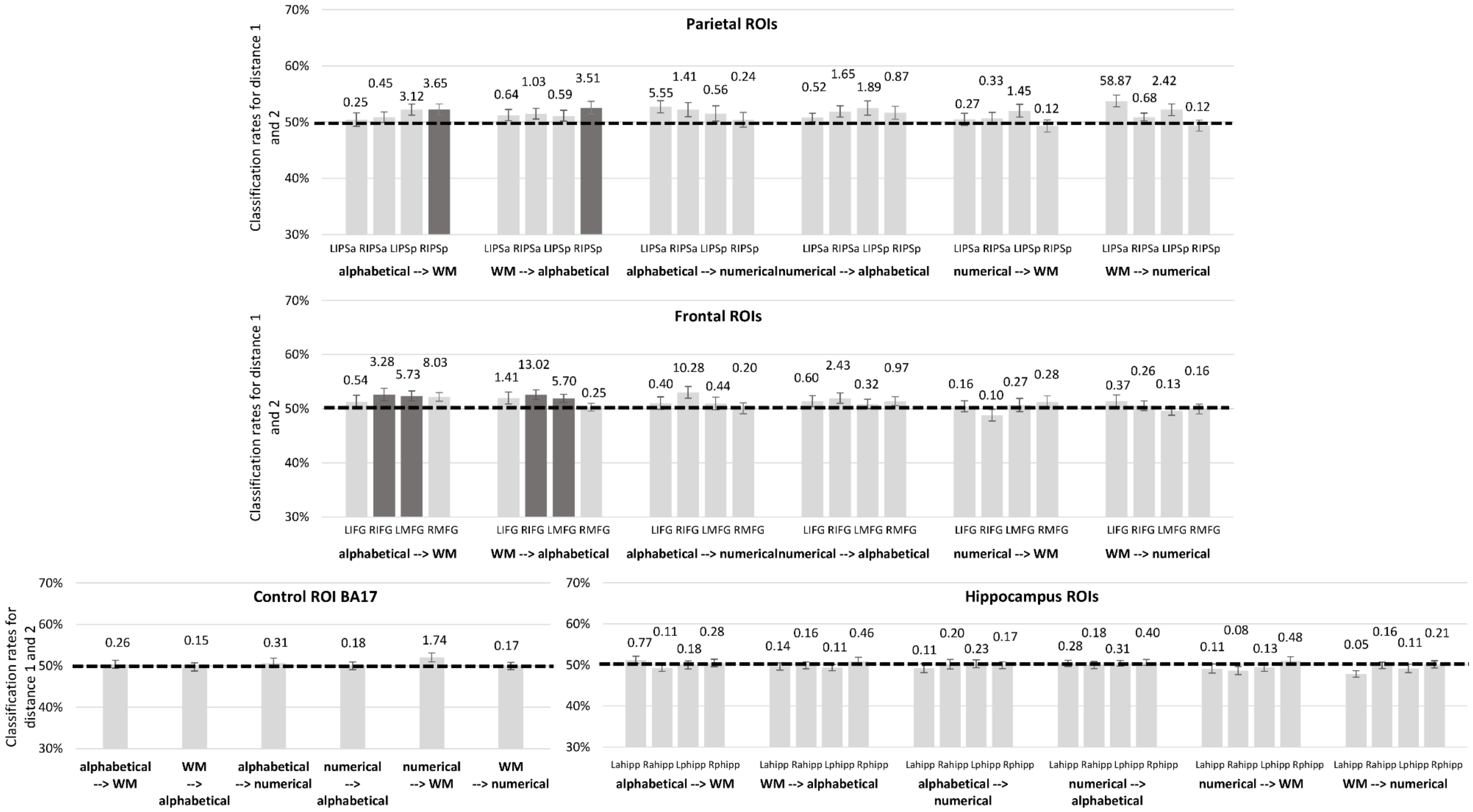

Figure 6. Classification rates for between-task predictions of distance between each ordinal judgment task and the luminance judgement task after reversing the distance of the luminance task, for the different ROIs. BF_{10} values at the top of each column assess deviation from chance-level classification levels. Dark grey bars indicate above-chance level prediction of ordinal distance in both directions for the corresponding tasks.