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Counting Sequences Are Processed Across Multiple Levels Of Cortical Hierarchy

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Counting Sequences Are Processed Across Multiple Levels Of Cortical Hierarchy

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**COUNTING SEQUENCES ARE PROCESSED ACROSS MULTIPLE LEVELS
OF CORTICAL HIERARCHY**

A Thesis Presented

by

ELI ZALEZNIK

Submitted to the Graduate School of the
University of Massachusetts Amherst in partial fulfillment
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Psychological and Brain Sciences

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OF CORTICAL HIERARCHY**

A Thesis Presented

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ABSTRACT

COUNTING SEQUENCES ARE PROCESSED ACROSS MULTIPLE LEVELS OF CORTICAL HIERARCHY

SEPTEMBER 2022

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Learning the count list (one, two, three, ...) is a critical stepping-stone for the acquisition of number concepts. Most research about counting, however, is done in the behavioral domain, and little is known about the neural representations underlying counting sequences. Here, we test the hypothesis that transitional knowledge within a counting sequence exist both at sensory and conceptual (ordinal and magnitude) levels. To test this hypothesis, we employed a passive-listening violation-to-expectation fMRI paradigm where adult participants heard auditory count sequences that were correct (4 5 6 7) or violated at the end (4 5 6 8; consecutiveness) and, orthogonally, that were ordered or unordered (orderedness). Another orthogonal dimension was the manipulation of sensory sequence violation where the voice speaking the numbers was consistent throughout the trial or could change on the last number (voice identity). This 2x2x2 factorial design was analyzed using univariate and multivariate pattern analyses. Three clusters in the right fronto-parietal network (BA44, BA46, and IPS) showed greater neural response to violations to orderedness. Of the three clusters, the anterior IFG (BA46) demonstrated the encoding of consecutiveness. Interestingly, the bilateral STG, which showed a robust effect to violations in voice identity, also demonstrated the encoding of consecutiveness. These results indicate that a right-lateralized fronto-parietal network activity can differentiate between a count list and random numbers, while BA46 and bilateral STG respond specifically to violations of the count sequence, suggesting specific mechanisms in the brain for processing consecutive numbers in both the perceptual and cognitive levels.

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CHAPTER 1

INTRODUCTION

Human learning and behavior rely on complex sequential processing. Lashley (1951) challenged notions of associative mechanisms underlying human behavior, stating that associations are insufficient to explain behavior across many systems, such as linguistic, motor, and rhythmic, and that underlying hierarchical structures were necessary to process complex sequences. Sequential processing can now be seen as spanning associations, such as statistical learning in language acquisition (Saffran et al., 1996), and hierarchical trees including underlying syntactic structures (Chomsky, 1956; Dehaene et al., 2015).

Sequences, both containing associative information and hierarchical information, also underly children's earliest interaction with the natural number system: counting. Counting is a sequential process, where one tracks magnitude using an ordered series of number words. In English, "one, two, three" become associated items that recur in a recursively and hierarchically organized system, allowing counting of "twenty-one, twenty-two, twenty-three" and "one thousand and one, one thousand and two, one thousand and three." In comparison, non-count numbers spoken in a sequence (e.g. "seven, eight, one") may contain associations with each other matching something held in long-term memory (i.e., a phone number area code) but do not contain hierarchical organization. Despite their importance in building uniquely human number processing, the neural bases of counting sequences, however, have never been directly studied.

Learning to count correctly is critical to numerical development, and behavioral numerical development has been studied extensively. Children first listen to, then repeat,

a series of “meaningless” words (i.e., they may understand that “five” is a number word, but do not know that it refers to a specific value (Fuson, 2012; Gelman & Gallistel, 1986; Wynn, 1992). These words slowly take on meaning as the child’s counting sequence becomes stable and correct, until they begin to associate a single word with an item and later induce that each word has a numeric value to represent a set (Carey, 2004; Fuson, 2012; Gelman & Gallistel, 1986). Mastery over being able to answer how many objects are in a set is related to fluency of accessing the count list (Sarnecka & Carey, 2008). Compare this to adult speakers of languages without words for number, who are only able to express quantity in terms resembling the approximate number system (Gordon, 2004). Although theories about child numerical development have disagreed about the origin of number knowledge, there is no doubt that a child’s numerical understanding begins with learning to count consistently and correctly from one to ten (Fuson, 2012; Gelman & Gallistel, 1986).

Even beyond mastering the basics of counting, research on the overall structure on the number system suggests that quick access to the counting concepts plays a role in mathematical development across the lifespan. The ordinal judgement task asks participants to judge whether a set of presented numbers are “in-order”—typically ascending from left-to-right, but sometimes descending too—and remains one of the best predictors of arithmetic fluency from second grade through adulthood (Goffin & Ansari, 2016; Lyons & Ansari, 2015; Lyons & Beilock, 2009; Sasanguie et al., 2017; Sasanguie & Vos, 2018; Vogel et al., 2017, 2019). While the exact nature of this relationship is unknown, the strength of the effect suggests that similar underlying concepts are being mentally engaged when doing arithmetic as when recognizing the order of numbers.

Ordinal judgement also shows a distinct response-time effect, where participants are fastest to respond to consecutive sets that mirror the count list (Lyons et al., 2014; Lyons & Ansari, 2015; Sasanguie et al., 2017; Turconi et al., 2006; Vogel et al., 2017), and responses to the consecutive sets are the strongest individual predictors amidst the task of arithmetic performance in children in second through sixth grade (Lyons & Ansari, 2015). Thus, not only is counting fundamental to learning the number system, but it relates to processes far beyond the simple act of reciting a list or enumerating objects. How the brain represents counting sequences, however, is largely unknown. Although there is a large body of behavioral literature and theory on the topic, counting has only ever been used as an incidental task in neuroimaging literature. To provide a framework for understanding counting sequences, we will review neural studies of ordinality, the incidental counting literature and neural processes that may underlie counting sequence processing.

Neural correlates of ordinality

Ordinality has been implicated in various brain regions, such as the intraparietal sulcus (IPS) and supplementary motor area (SMA). Primarily, imaging studies have focused on the IPS and show that the IPS plays a role in, but does not entirely underlie, ordinal processing. The IPS is targeted because it has been shown to be active in response to symbolic and non-symbolic numerical tasks alike (for a review, see De Smedt, Noël, Gilmore, & Ansari, 2013). However, Lyons and Beilock (2013a) found IPS activity in response to ordinal judgements to be no different from non-numerical control tasks, whereas Franklin and Jonides (2009) found IPS activity for ordinal judgements to be equal to the magnitude comparison task. In support of the IPS involvement, a

classification analysis of ordinal judgement data was able to distinguish between ordinal judgement trials involving numbers compared to letters based on responses in the horizontal segment of the IPS (Fias, Lammertyn, Caessens, & Orban, 2007; Zorzi, DiBono, & Fias, 2011). When not comparing to magnitude processing, a right-lateralized, fronto-parietal network, including the IPS, was found in response to ordinal processing in the context of performing arithmetic (Knops & Willmes, 2014). Altogether, the IPS has been shown to be active in most, but not all ordinal tests. The IPS supports ordinal processing but is not the only region underlying ordinality.

Additionally, the supplementary motor cortex, (SMC) consisting of the supplementary motor area (SMA) and pre-supplementary motor area (pre-SMA) may also play a role in ordinality. Besides the IPS, SMA is the other most frequently activated region in response to ordinal judgement (Fias et al., 2007; Knops & Willmes, 2014; Lyons & Beilock, 2013; Marshuetz et al., 2000; Schubotz & von Cramon, 2001; Wang et al., 2015; Zorzi et al., 2011). However, none of these studies address the role of the SMA in performing this task, perhaps because of the association between the SMC and motor functions, such as transcranial magnetic stimulation over this area causing errors in motor sequences (Gerloff et al., 1997), or lesions causing difficulties with motor programs (Della Sala et al., 2002). Single-cell recordings in macaques trained on a three movement sequence revealed that cells in the SMA showed preference for certain linked motions within a sequence (i.e., a given cell may be active in between push and pull movements, but not between push and turn), suggesting that the region is related to temporally structuring or linking the motions within the sequence (Tanji & Shima, 1994). Because of

its apparent involvement in sequential processing, it is not unreasonable to believe that the SMA may be involved in cognitively processing number order.

Counting as sequence processing

While the neural bases of counting sequences have not been directly studied, Dehaene et al. (2015) developed a general framework for sequences and their neural underpinnings into a taxonomy of increasing complexity. Among five levels within the taxonomy, those that are relevant to counting sequences include ordinal knowledge (knowledge of what comes first, second, third, etc.) and transition and timing knowledge (knowledge of the timing or identity of the upcoming item in a sequence). However, counting sequences do not neatly occupy any positions in the taxonomy proposed by Dehaene et al. (2015).

For example, ordinal knowledge may be a tempting categorization for counting sequences, but it fails to explain important aspects of counting sequences. Dehaene et al. (2015) defines ordinal knowledge only as applying to finite sequences, yet a count sequence could theoretically stretch on infinitely. The neurophysiological mechanism proposed for ordinal knowledge has populations of neurons in the IPS of monkeys that are sensitive to particular ordinal positions of items in a sequence (Nieder et al., 2006). This explanation is difficult to extrapolate to an infinitely long list. Any explanation of neural responses to counting sequences should consider that counting can start from any given number and that adult failures to count correctly will not stem from a lack of numerical knowledge, but from limitations such as working memory capacity. Thus, counting sequences do not fit ordinal knowledge well.

Another potential candidate to explain counting sequences is transition and timing knowledge. Lang and Kotchoubey (2002) measured ERP responses to four-number

sequences. The sequences would always begin with three consecutive numbers (e.g., 3 4 5) and end with either the next consecutive number (6) or a random incorrect ending to the consecutive sequence (12). They found that when a sequence was violated with a random number ending, there was a negative wave between 70-200ms in frontal sites, which they concluded resembled a mismatch negativity (MMN; Lang & Kotchoubey, 2002). MMN is a fronto-central ERP component: a negative deflection usually peaking between 150-250ms after stimulus onset (Sams, Paavilainen, Alho, & Näätänen, 1985, as cited by Näätänen, Paavilainen, Rinne, & Alho, 2007). The classic MMN response is elicited by auditory stimuli, and results from a violation of transition and timing knowledge which, as defined by this taxonomy, is limited to sensory stimuli (Dehaene et al., 2015). Count sequences, however, contain semantic and magnitude properties that goes beyond basic sensory information. To our knowledge, the effect that Lang and Kotchoubey (2002) found has not been tested outside of that work. As such, it is unclear whether they showed a classic, sensory MMN or if the effect merely resembled one. Regardless, they showed an organized neural response specific to violated counting sequences. Violating expectations is one of the most robust ways to measure neural encoding of sequences (Dehaene et al., 2015). Therefore, measuring the neural responses to violating counting sequences can help shed light on the underlying sequence processing.

The present study

Because the taxonomy is insufficient in explaining the complexities of counting sequences, we propose an alternative framework where counting knowledge has two components: sensory knowledge and conceptual knowledge. Count sequences lack all

concept at their origin, being a series of culturally bound, “meaningless” words, repeated by a child. They contain linguistic concepts only in that they are words; there is neither semantic nor syntactic information within initial counting sequences. Thus, they are purely perceptual in nature. As perceptual knowledge develops, and a child learns to repeat the sequence correctly, they begin to develop a conceptual understanding of the count sequence. For adults with fully formed counting knowledge, a perceptual understanding of counting sequences may be the expectation of hearing certain sounds following the pattern (like transitional probabilities). For example, after hearing “two three four,” if the following phoneme is /s/, that is the only sensory information needed to understand that the sequence is not correct. In contrast, a conceptual understanding would be the activation of the information “five” in response to the above sequence. A perceptual understanding alone may be sufficient to explain responses to violations. However, without a conceptual understanding, it is difficult to explain why ordinal judgement results in the distinct response time effect for consecutive numbers. Sensory data may facilitate the responses, but the goal-directed information (“press the button if the numbers are in order”) must be connected to a concept of “being in order” if one is to act on it. One possibility is the activation of magnitude information in response to the sequence, another may be linguistic representations. Because of the unique RDE appearing in ordinality and the MMN-like component in response to violated counting sequences, we hypothesized that counting sequences are processed at both perceptual and conceptual levels that would implicate different brain regions. For example, we would see activation in areas closely associated with sensory and perception processing (e.g.

superior temporal cortex), numeric processing (e.g. IPS) and cognition (e.g. prefrontal cortex).

To directly test neural responses to counting sequences, we used a violation-to-expectation paradigm with a sequence of auditorily presented numbers in an MRI scanner. We developed an orthogonal 2x2x2 stimulus design. Participants heard four-number sequences organized into three conditions: *consecutiveness*, *orderedness*, and *voice identity*. The four numbers could either be all consecutive (e.g. 4 5 6 7) or the last number could be one more than the expected number (e.g. 4 5 6 8). The same numbers can be all ascending (e.g. 4 5 6 8) or scrambled such that there are no ascending pairs (e.g. 8 4 6 5). Lastly, the numbers were spoken by a mix of male and female computer voices. In the voice identity match condition, the same voice spoke all four numbers, and in the voice identity mismatch condition, one voice spoke the first three numbers and the other voice finished the sequence. The purpose of the voice identity condition is to localize areas that are specifically related to expectations of sensory properties of stimuli to compare with responses related to number sequence violation.

We predicted activation in frontal and auditory cortex in response to number sequence violations. Directly comparing the effects of a mismatch (4 5 6 8) to a match (4 5 6 7) is invalid due to the difference in stimuli between these sequences. Therefore, we tested each of the main effects (consecutiveness, orderedness and voice identity) to localize regions sensitive to the paradigm, then ran an orthogonal multivoxel pattern analysis (MVPA) on those areas to test classification ability based on the interaction between orderedness and consecutiveness.

CHAPTER 2

METHOD

Participants

A total of 40 participants were initially recruited from the University of Massachusetts Amherst campus through flyers and online postings. Inclusion criteria were a) having normal or corrected to normal vision, b) no history of neurological disorders (e.g., epilepsy, agnosia), c) age range of 18-29 years old, d) no history of neuropsychiatric illness (e.g., ADD, ADHD, autism), e) not currently taking psychoactive medication and f) passing safety criteria for fMRI scanning (e.g., no ferrous implants, claustrophobia). Three participants were dropped: one did not meet the inclusionary criteria, and two had excessive motion leading to more than two dropped runs (see Preprocessing below). Thus, 37 participants (female = 26; mean age = 20.8 years, range = 18-27) were entered into the analysis. Each participant completed one 2-hour session, for which they were compensated \$30. Some participants completed a behavioral experiment after the scan, unrelated to this study. All procedures were approved by the University of Massachusetts Institutional Review Board (IRB).

Stimuli, task, and procedure

The experiment consisted of six 5-minute runs, each with 48 trials for a total set of 288 trials per subject. Each trial consisted of a sequence of four numbers, auditorily presented through MR-safe headphones and visually presented simultaneously with its corresponding number word (Fig. 1A). Each number within a trial was visually presented as its written word (e.g., five) for 600 ms on the center of the screen (Courier New; 102

pt) immediately followed by the next number, making the trial duration 2.4 s ($= 0.6 \text{ s} \times 4$ numbers). The onset of the auditory presentation was synchronized with the onset of the visual presentation for each number, and the auditory presentation lasted on average for 442.2 ms with the maximum duration of 563.4 ms. Each trial was followed by a jittered intertrial interval (ITI) of 3.6 s, 4.8 s or 6.0 s, the distribution of which was logarithmic.

The number stimuli were constructed to match a $2 \times 2 \times 2$ condition matrix (Fig. 1B), where the conditions were 1) consecutiveness, 2) orderedness, and 3) voice. Inside the consecutiveness factor, stimuli were either four numbers from a consecutive count sequence (consecutive; e.g. 4, 5, 6, 7) or four numbers from a count sequence in which the first three numbers are consecutive and the last number is exactly two numbers away from the largest of the three consecutive numbers (nonconsecutive; e.g., 4, 5, 6, 8). In the orderedness factor, the four presented numbers were all in ascending order (ordered; e.g. 4, 5, 6, 7 in that order or 4, 5, 6, 8 in that order) or were scrambled so that the sequence was neither ascending nor descending (unordered; e.g. 4, 6, 5, 8 in that order). In the latter case, the four numbers were scrambled such that there were never ascending pairs nor could a four-number sequence begin or end with a consecutive descending pair. In the voice factor, either all four numbers were presented in a “male” or “female” voice (voice match), or the first three were presented in one voice and the fourth number was presented in the other voice (voice mismatch). The auditory stimuli were computer generated in the Mac OS X system (Samantha with the speech rate of 170 words/min; Alex with the speech rate of 200 words/min). All three factors were orthogonal to each other.

Five catch trials appeared in each run (about 10%) pseudorandomly positioned to ensure that they are at least 8 but not beyond 16 trials away from each other. In these catch trials, one auditorily-presented number did not match the visually-presented number. The position of the mismatch within the trial was randomized. Participants were instructed to press any button on an MR-safe button box when they detected this audio-visual mismatch. No positive or negative feedback was given in this task, but the fixation cross turned white to provide feedback for the button press. The box was placed either on the participant's stomach or at their side, depending on the individual's choice, for comfort. The stimuli sets, ITIs, condition and catch trial status were all randomly generated at the beginning of each run. Prior to the scan, participants were instructed about the task and were given a short block of practice trials in the scanner.

Behavioral analysis

To test whether participants were monitoring the stimuli, we analyzed the behavioral data. Our interest was primarily in the hit rate (button press for audiovisual mismatch), rather than false alarms or response time, because the task was incidental to our experimental question. Due to a scripting error, button presses were not measured accurately. Experimenters were able to note manually to some degree when the computer detected an input that was not recorded by the script. Within the script, because the mismatch could appear at any position in a four-number sequence, button presses within 3 seconds of the onset of the audio in a catch trial were considered hits. Presses more than two seconds away from a mismatch were labelled false alarms. Overall, participants were accurate despite the computer error ($M = 91.2\%$, $SD = 10.8\%$), and no participants were excluded from analysis due to behavioral performance.

Image acquisition parameters

Image data was acquired on a 3T Siemens Skyra scanner housed in the Human Magnetic Resonance Center at the University of Massachusetts Amherst. BOLD T2* contrasts were detected with an echo planar imaging sequence (TR = 1200ms, TE = 30ms, flip angle = 69°, FOV = 210mm, number of axial slices = 48, voxel size = 3.0mm × 3.0mm × 2.5mm). T1 weighted MPRAGE images were collected in between the third and fourth run (TR = 2000ms, TE = 2.13ms, flip angle = 9°, FOV = 256mm, number of sagittal slices = 208, voxel size = 1.0mm × 1.0mm × 1.0mm).

Preprocessing

Images were processed primarily in SPM8 (Statistical Parametric Mapping; <http://www.fil.ion.ucl.ac.uk/spm/>) on MATLAB 2016b (MathWorks, Natick, MA, USA), but also using custom scripts that utilized other toolboxes and software packages such as FSL 6.0 (<http://fsl.fmrib.ox.ac.uk/fsl>), ArtRepair 4 (<https://cibsr.stanford.edu/tools/human-brain-project/artrepair-software.html>), and libsvm 3.24 (<https://www.csie.ntu.edu.tw/~cjlin/libsvm/>). If not indicated otherwise, default parameters in these software packages were used. In each participant, the functional volumes were realigned to the first volume of the first run. The high-resolution anatomical image was coregistered to the mean of the realigned functional images. Then, the anatomical image was segmented into gray and white matter, after which the gray matter was normalized into Montreal Neurological Institute (MNI) space. The normalization parameters were applied to the realigned functional images, with a resulting spatial resolution of 3 mm × 3 mm × 3 mm. Finally, the normalized functional images were spatially smoothed with a Gaussian kernel (FWHM = 8 mm). Individual

runs were excluded from the subsequent GLM analysis (see Activation Analysis below) if they had a frame displacement (identified using ArtRepair and FSL) greater than .5mm in more than 5% of volumes within a single run (Power et al., 2012). Through this method, two participants were modeled with four of six runs, and one participant with five of six. Two participants who had more than two runs removed through this method were excluded from the analysis entirely. The final sample was 37 participants.

Activation analysis

The General Linear Model (GLM) was employed to estimate the magnitude of neural activity associated with the eight different experimental conditions ($2 \times 2 \times 2$ design; see Fig. 1B). At the individual participant level, the GLM was constructed with separate regressors for each of the eight conditions, which were convolved with the canonical hemodynamic response function. In addition, a regressor for all the catch trials and another regressor for all the button responses were convolved and entered into the model. In order to account for spurious motion artifacts, each frame displacement greater than .5 mm was coded as a covariate of no-interest in the model. Finally, six motion parameters (head translation and rotation) were entered as covariates of no-interest. A high pass filter (128 sec) and an autoregressive AR(1) model was employed. Beta values from the individual-level GLMs were entered into a $2 \times 2 \times 2$ full factorial ANOVA which was comprised of the three factors: consecutiveness, orderedness, and voice. Unless otherwise stated, a clusterwise multiple comparisons correction with a height threshold of $p < .001$ implemented in SPM was considered for statistical inferences.

Multivoxel pattern analysis

Multivariate pattern analysis (MVPA) has been demonstrated to be substantially more sensitive to differences in experimental manipulations, compared with univariate analyses (Norman et al., 2006; Haynes & Rees, 2006). We utilized this technique by implementing a binary linear support vector machine (SVM) classifier, in order to evaluate how different experimental conditions, pertaining to a set of our key hypotheses, are distinguished by their patterns of neural activation. Specifically, we tested the degree to which neural activity patterns can decode violations in voice, orderedness, and consecutiveness in several functionally-defined regions of interest (ROIs). These ROIs were defined by suprathreshold clusters from the main effects of the factorial ANOVA in the univariate activation analysis. It is important to note that the contrast of the two classes entered in binary classification were in all cases orthogonal to the contrast used to functionally define the ROIs.

The linear SVM was implemented using libsvm (<https://www.csie.ntu.edu.tw/~cjlin/libsvm/>). The contrast map of interest from each run served as a single pattern in one class of the dataset. Thus, in most participants who has all six runs analyzed, the SVM classified between six patterns (from a total of six runs) of one class and six patterns of another class. Participants who ended up having four or five runs in the analysis (see Methods) resulted in four or five patterns, respectively, for each class. The data were first scaled to the range [-1 1] as recommended in the libsvm library. A linear binary classification with $C=1$ was employed with a leave-one-run-out crossvalidation procedure, and the resulting classification accuracy was taken as a measure of the distinctiveness of neural patterns between the two classes. Raw

performance measures (such as classification accuracy) of MVPA techniques are reported to be spurious and biased when the data are small in sample size and low in effect size, which is typical in fMRI data (Combrisson & Jerbi, 2015; Jamalabadi et al., 2016).

Therefore, as recommended in those reports, the statistical significance of classification accuracy was assessed using a non-parametric permutation procedure, rather than testing against the theoretical chance level. Namely, for each binary classification, the observed classification accuracy was tested against the null distribution that was constructed from 10,000 random permutations of class labels. One-sided p-value was computed from the proportion of the null distribution exceeding the observed classification accuracy.

CHAPTER 3

RESULTS

Activation analysis

The effects of consecutiveness, orderedness and voice of a numerical sequence on neural responses were tested using a $2 \times 2 \times 2$ full factorial ANOVA on a univariate, whole-brain level. As shown in Fig. 2B, the main effect of orderedness (ordered > unordered) resulted in two significant clusters in the right inferior frontal area: one more posterior ($q_{\text{FDR-corr}} = .001$) and the other more anterior ($q_{\text{FDR-corr}} = .010$). The posterior cluster was identified mostly in the pars opercularis although some portion of it was in the pars triangularis. The anterior cluster was identified largely in the pars triangularis and extending to the middle part of the middle frontal gyrus. A third significant cluster was found in the anterior portion of the right intraparietal sulcus ($q_{\text{FDR-corr}} = .033$). No other suprathreshold clusters were identified. The reverse contrast (unordered > ordered) did not result in any significant activations. The main effect of voice identity (voice match > voice mismatch) revealed significant clusters centered around the right ($q_{\text{FDR-corr}} < .001$) and left ($q_{\text{FDR-corr}} < .001$) superior temporal gyri (STG; Fig. 2A), with no significant activations for the reverse contrast. There was no significant main effect of consecutiveness.

In addition to testing these main effects, we had initially predicted that the brain, especially in the inferior frontal and intraparietal regions, would be sensitive to violations in a counting sequence. In other words, for a brain region that encodes a precise step-wise increment in a numerical sequence (e.g., 2, 3, 4, 5 in that order), a violation to that precise increment (e.g., 2, 3, 4, 6 in that order) would result in neural activation in that region.

This hypothesis was tested with the contrast of two contrasts—that is, the contrast between ordered consecutive sequence (e.g., 2 3 4 5) versus unordered consecutive sequence (e.g., 3 5 2 4) and ordered nonconsecutive sequence (e.g., 2 3 4 6) versus unordered consecutive sequence (e.g., 3 6 2 4), which is effectively the interaction between orderedness and consecutiveness. Note that the neural activity for the respective unordered sequences were contrasted from the ordered sequences in order to control for the differences in the actual identity of the presented numbers. This interaction between orderedness and consecutiveness did not result in any significant clusters, nor did any other interaction between the factors. Considering that the univariate analysis may not be powerful enough to reveal a subtle effect, we followed up testing this hypothesis regarding the neural encoding of counting sequences in a multivariate pattern analysis (see below).

In sum, the activation results collectively indicate that regions in the right fronto-parietal network (specifically the pars opercularis, pars triangularis, and IPS) are sensitive to the order of the presented numerical sequence and that regions in and around the bilateral auditory cortices encode low-level auditory properties of the presented sequence.

Multivoxel pattern analysis

To test for one of our primary hypotheses about the neural encoding of counting sequences with a more powerful approach, we performed a multivoxel pattern analysis (MVPA) on the neural activation patterns for the counting sequences. As stated above, direct comparison between a correct counting sequence (e.g., 3 4 5 6) and a violated counting sequence (e.g., 3 4 5 7) is not appropriate due to the difference in stimuli presented. Thus, the respective unordered sequences were first contrasted from ordered

consecutive sequences and ordered nonconsecutive sequences, leaving only neural responses to the violation without the effect of the specific stimuli presented. Thus, the contrast maps of ordered consecutive versus unordered consecutive (e.g., 3 4 5 6 > 3 5 4 6) and the contrast maps of ordered nonconsecutive versus unordered nonconsecutive (e.g., 3 4 5 7 > 3 5 4 7) served as two classes in a binary linear SVM.

Our activation analysis suggested that at least three clusters in the right fronto-parietal network (pars opercularis, pars triangularis, and IPS) are actively encoding the high-level structure of a numerical sequence in that they are sensitive to the violation of orderedness of a sequence. We reasoned that the same regions may be encoding even higher-level structure of a numerical sequence involving the precise incremental structure of the sequence, according to which those regions should be sensitive to correct versus incorrect counting sequences. Thus, we used the three suprathreshold clusters identified from the main effect of orderedness (Fig. 2B) as the functional regions of interest (ROIs) for the SVM analysis. Note that the contrast used to define the functional ROIs were orthogonal to the contrast of interest in the MVPA.

The degree of separability between the two classes of neural activation patterns (correct count sequence versus incorrect count sequence) was quantified using the classification accuracy measure of the binary linear SVM, separately in pars opercularis, pars triangularis, and IPS. The statistical significance of this measure was assessed using a non-parametric permutation procedure (see Methods). In pars triangularis, the classification accuracy was small but significantly above chance (CA = 50.69%, $p=.021$), indicating that this region is involved in encoding specific high-level properties of the

numerical sequence (i.e., counting). Neither pars opercularis (CA = 50.17%, $p=.077$) nor IPS (CA = 48.03%, $p=.36$) showed significant results.

We then followed up with the question whether such high-level properties of the numerical sequence would be identified in the low-level sensory cortices. On the one hand, counting sequence is derived from an abstract concept, which makes it implausible to assume the involvement of low-level sensory cortices in the encoding of the counting sequence. On the other hand, we are entrenched with the specific transitional probabilities of the phonetics in a count sequence from very early in life, which makes it plausible to assume the involvement of low-level sensory cortices. We addressed this question by using the binary SVM on the same two classes of neural activation patterns but in the left and right STG, functionally defined by the main effect of voice identity in the univariate activation analysis (Fig. 2A). Both the left (CA = 55.88%, $p<.0001$) and right (CA = 52.49%, $p<.009$) STG showed robust and significant classification accuracy measures, indicating that the low-level sensory regions are indeed involved in encoding the counting sequence.

These results so far suggest that specific properties of the numerical sequence are encoded both at high, conceptual levels in pars triangularis and in low, sensory levels in auditory cortices (STG). To test the specificity of these findings to numerical sequences, we tested discriminability in patterns of activity due to the voice match vs mismatch in these same ROIs. The results showed no significant patterns in pars opercularis (CA = 51.23%, $p = .021$), BA46 (CA = 50.69%, $p = .163$), or rIPS (CA = 52.25%, $p = .171$), only in the right (CA = 59.98%, $p = .012$) and left (CA = 67.28%, $p < .0001$) STG. This

is in line with previous work that shows pre-attentive sensory predictive coding happens only in sensory areas (Brattico et al., 2006; Näätänen, 2001).

CHAPTER 4 DISCUSSION

We used a violation-to-expectation paradigm to test neural responses to ordered, unordered and violated verbal counting sequences. When listening to ordered compared to unordered sequences, a right-lateralized fronto-parietal network, involving the right IPS, pars opercularis and pars triangularis, showed significant activity. Hearing a change in the identity of the voice speaking the sequence evoked activity in the bilateral STG. The bilateral STG and pars triangularis showed discriminable patterns of activity between hearing violated sequences and hearing correct counting sequences in an MVPA analysis. Together, the results suggest that order is processed in the IPS, IFG and auditory cortex, and violations to expectations in counting sequences are processed in frontal and sensory cortex, but not IPS.

We found a right-lateralized fronto-parietal network that preferentially responded to number sequences that were correctly ordered over scrambled, orderless sequences (i.e. 4 5 6 7 compared to 5 4 7 6). Specifically, regions involved were the IPS, pars opercularis and pars triangularis. This network alone cannot tell us much about the nature of counting sequences, since this comparison was done in relation to non-sequential stimuli, but it does localize a general order processing to this network. This finding is in line with Knops and Willmes (2014), who found a similar, right-lateralized fronto-parietal network shared between number ordering (using the ordinal judgement task) and arithmetic. We extend this work by showing this fronto-parietal network is not only responsive to order—independent to arithmetic—but so much so that it is active only from passive listening to ordered numbers. This shared network between counting,

ordinal judgement and arithmetic also suggesting that basic counting shares neural circuits with later developed arithmetic.

The critical finding of our study is a response to violated sequences compared to correctly completed sequences (e.g. 3 4 5 7 compared to 3 4 5 6, accounting for differences in stimuli) in pars triangularis and the STG. The responses in the frontal gyrus and auditory cortex support our hypothesis of distinct conceptual and perceptual processing of counting sequences. Transition and timing knowledge (Dehaene et al., 2015) may underly the sensory sequence aspect, in line with the finding of an MMN-like component that is detectable after the first syllable in the mismatched number word (Lang & Kotchoubey, 2002). Simple tones (Winkler et al., 1996) and complex auditory stimuli, like chords (Brattico et al., 2006), and phonemes (Shestakova et al., 2002) produce MMN in response to transitional violation, and we can extend this to number sequences as well. As a control, we tested sensitivity to the voice identity mismatch > match using MVPA and showed that voice identity mismatch was only processed in the STG, not frontal regions as well, in line with the wealth of literature localizing the auditory MMN to the auditory cortex (Brattico et al., 2006; Molholm et al., 2005; Shestakova et al., 2002). The sensory component of counting sequence processing can therefore be seen as distinct from the conceptual processing.

In the representations underlying counting sequences, one interesting finding is the apparent lack of IPS involvement in responding to sequence violations. The IPS is involved with all kinds of numerical tasks, including symbolic and non-symbolic magnitude comparison (Fias et al., 2003), and ordinal judgement (Fias et al., 2007; Franklin & Jonides, 2009), but there was no significant difference in patterns of

activation between hearing valid and violated counting sequences. The IPS plays a role in building the order of the sequence, but it does not actively respond to the violation of the sequence. The absence of the IPS may be attributed to the passivity of the task. It is possible that the IPS would have been activated if participants were asked to actively say the numbers on the screen and engage in the violation.

The only region we found associated with counting concept violation is right pars triangularis. This is interesting because the pars triangularis a segment of the right-side homologue to the classical linguistic neural region. The left IFG is frequently referred to as a site for binding operations, such as Chomsky's Merge (Chomsky, 2014; Pallier et al., 2011) or Hagoort's unification in Memory, Unification, Control (MUC; Hagoort, 2005). Hagoort's MUC model is particularly compelling to us in explaining these results. Although merge is applied fairly specifically to binding units in a syntactic structure, MUC is open to explaining domain-general relationships between elements stored in memory becoming bound together into a cohesive whole (Hagoort, 2005, 2019).

We suspect that the right IFG is performing similar operations: number words are entered into a space sequentially and unified into a counting sequence based off their matching to a long-term structure. When a number word that is not able to be unified into the counting sequence, an adjustment must be made, leading to a change in BOLD response. The larger IFG works together to build the sequence, but only a segment, the pars triangularis, performs an additional process in detecting violations. In this view, it is still an open question of the nature of the structure stored in long-term memory. One could argue that this structure is the natural number system acting like Dehaene and colleague's (2015) nested tree structures. However, this study only used the numbers 1

through 10. These sequences in their initial form are probably associative in nature, rather than hierarchical: children from ages 3 to 6 perform better at recalling lists of ordered triads (e.g. 3 4 5) compared to unordered triads (3 5 4)—a preference for count sequences even before the recursive and hierarchical natural number system has been established (Van Rinsveld et al., 2020). Still, there is the possibility that nested tree structures might underly counting processing in uncommon, complex numbers (e.g. 2431, 2432, etc.) or in adult counting of simple sequences. Regardless, there is the clear establishment of some kind of violable counting concept that may be linguistic and memory based with connections to later developed number processing.

There were two primary limitations to this study. The first is that the methods only entailed passive listening to counting sequences. We chose passive listening because of its connection to the initial steps of learning to count. Namely, children hear numbers counted before they are capable of repeating them (Fuson, 2012; Gelman & Gallistel, 1986). Our study cannot speak to neural processing underlying the active enumeration of objects or magnitudes, only the sequential processing of the natural number system. The second is that this study has only adult participants. Numerical development is protracted, and this study can only provide information on how counting sequences are represented in the brains of those who have mastered the natural number system. It is thus an open question of how these representations change over the course of learning complex numerals.

Conclusion

This study represents a first look at the adult neural representation of counting sequences and can provide a baseline with which to compare how that representation

changes across development. Counting sequences for adults are highly engrained. The difference in difficulty in counting from one compared to an arbitrary number is trivial. Compare this to children, who struggle with integrating the decades and hundreds into their count list throughout early grade school (Gould, 2017). How does the neural representation of counting sequences change as children develop mastery over the natural number system? This represents the first work to intentionally test neural responses to violations of counting sequences. We found that adults' brains are sensitive to counting sequences in their most basic form in passive listening. These sequences are represented in hierarchically organized brain regions, where auditory and cognitive areas respond to order and sequence violations.

Table 1. MNI coordinates and statistical details for analysis presented in fig. 2

Anatomical Region	Coordinates (MNI)			Mean	q_{FDR}	Number of Voxels
	X	Y	Z	Z-score		
rIFG – Opercularis	48	11	19	5.56	< .001	177
rIFG – Triangularis	42	35	14	4.20	.010	92
rIPS	57	-31	49	4.16	.033	56

Table 2. MNI coordinates and statistical details for analysis presented in fig. 3

Anatomical Region	Coordinates (MNI)			Mean	q_{FDR}	Number of Voxels
	X	Y	Z	Z-score		
ISTG	63	-31	7	6.17	< .001	190
rSTG	-66	-34	7	5.98	< .001	190

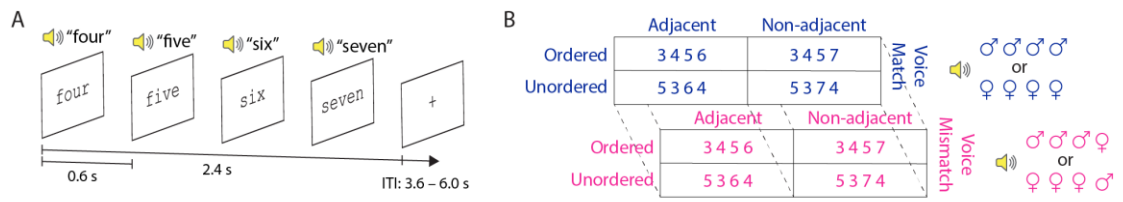
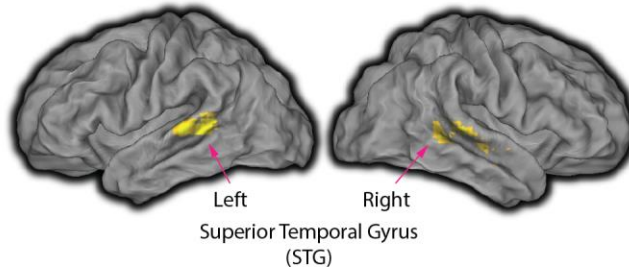


Figure 1. Schematics of procedure and design.

A Effect of Voice Identity



B Effect of Orderedness

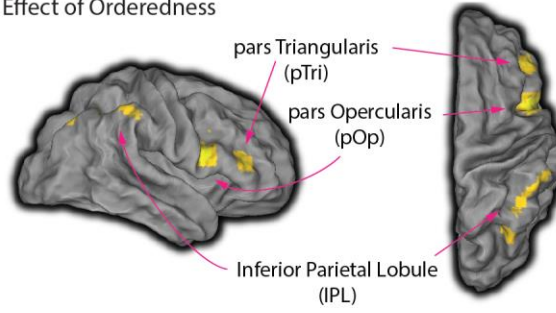


Figure 2. Effects of Voice Identity and Orderedness.

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