The neural basis of counting sequences

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A R T I C L E   I N F O

A B S T R A C T

Sequence processing is critical for complex behavior, and counting sequences hold a unique place underlying human numerical development. Despite this, the neural bases of counting sequences remain unstudied. We hypothesized that counting sequences in adults would involve representations in sensory, order, magnitude, and linguistic codes that implicate regions in auditory, supplementary motor, posterior parietal, and inferior frontal areas, respectively. In an fMRI scanner, participants heard four-number sequences in a $2 \times 2 \times 2$ design. The sequences were *adjacent* or not (e.g., 5, 6, 7, 8 vs. 5, 6, 7, 9), *ordered* or not (e.g., 5, 6, 7, 8 vs. 8, 5, 7, 6), and were spoken by a *voice* of consistent or variable identity. Then, neural substrates of counting sequences were identified by testing for the effect of consecutiveness (ordered nonadjacent versus ordered adjacent, e.g., 5, 6, 7, 9 > 5, 6, 7, 8) in the hypothesized brain regions. Violations to consecutiveness elicited brain activity in the right inferior frontal gyrus (IFG) and the supplementary motor area (SMA). In contrast, no such activation was observed in the auditory cortex, despite violations in voice identity recruiting strong activity in that region. Also, no activation was observed in the inferior parietal lobule, despite a robust effect of orderedness observed in that brain region. These findings indicate that listening to counting sequences do not automatically elicit sensory or magnitude codes but suggest that the precise increments in the sequence are tracked by the mechanism for processing ordered associations in the SMA and by the mechanism for binding individual lexical items into a cohesive whole in the IFG.

1. Introduction

Complex sequence processing is ubiquitous in human learning and behavior, such as baking a baguette, playing the piano, and reading this paper. Since Lashley (1951) raised the problem of serial order, sequence processing has been explained not only by associative mechanisms between successive items in a sequence but also by mechanisms that build hierarchical relations between those items. More recently, sequence processing has been theorized in terms of neural mechanisms underlying transition and timing knowledge, chunking, ordinal knowledge, algebraic patterns, and nested tree structures (Dehaene et al., 2015).

Among sequences that we learn over a lifetime, counting sequences (one, two, three, … in English) occupy a unique position in human culture for several interrelated reasons. First, unlike other common verbal sequences, counting sequences refer to entities that represent abstract concepts (i.e., natural numbers). Second, items in a counting sequence are primarily defined by their relations in a unidimensional and potentially infinite structure. Third, counting sequences are extensively learned from infancy and remain an integral part of our lives. No other set of verbal sequences contains all of these rich underlying properties.

Considering these unique properties, counting sequences serve as an excellent testbed to study how abstract thinking arises from a verbal sequence. However, very little is known about the neural substrates for counting sequences. Counting has been used as an occasional incidental task in neuroimaging research (e.g., Šveljo et al., 2010), and is involved in more widely studied enumeration (Cutini et al., 2014; Knops et al., 2014; Piazza et al., 2002; Sathian et al., 1999; Vuokko et al., 2013; Zago et al., 2010). However, the knowledge of counting sequences should be distinguished from the act of enumeration as explained by Fuson (1988). Enumeration, the act of quantifying a set, involves visual, attentional, and cognitive processes in addition to one's knowledge about the counting sequence. Thus, previous studies targeted to investigate the process of enumeration, often in contrast to subitizing, do not provide a clear insight into the neural basis of counting sequences.

Theorization of the neural representation of sequences by Dehaene and colleagues (2015) may serve as a good starting point to construct hypotheses about the neural representation of counting sequences. However, the five levels of cerebral mechanisms for sequence coding proposed by Dehaene and colleagues (2015)—transitions and timing knowl-

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edge, chunking, ordinal knowledge, algebraic patterns, and nested tree structures—do not seem to well explain the representations of counting sequences. At the surface level, counting sequences may seem to reflect *ordinal knowledge* or *algebraic patterns*. However, ordinal knowledge as described in the taxonomy concerns the representations about which items in an arbitrarily and temporally ordered list comes first, second, third, etc. (Barone and Joseph, 1989; Inoue and Mikami, 2006; Ninokura et al., 2004; Tanji and Shima, 1994), whereas counting sequence depends on a list of items with an absolutely defined order in long-term memory. In other words, counting cannot be easily explained by, say, neurons maximally firing to ordinal position in a list (i.e., when hearing 4–5–6–7, would 4 activate the ordinal neurons associated with "fourth," in accordance with the global count sequence or "first" because it is first in this local list?). Counting sequence may be considered as following an algebraic pattern, following the pattern where each number in correct counting-up is equal to the previous number plus one. However, algebraic patterns typically are based on features of the stimuli made into a sequence through statistical learning (Marcus et al., 1999; Saffran et al., 1996), whereas the algebraic pattern underlying counting sequences is based on the abstract numerical values the number words refer to.

This lack of fit between counting sequences and the taxonomy proposed by Dehaene and colleagues (2015) invite a different framework for explaining the neural representation of counting sequences. Here, we hypothesize that counting sequences are split into multiple representation that are processed concurrently across the brain. These representations are 1) sensory, 2) order, 3) magnitude, and 4) linguistic. In a violations-of-expectation paradigm, we thus predict that listening to violated counting sequences (e.g., 5, 6, 7, 9) compared with valid counting sequences elicits activation in specific brain regions that implicate these representations. In the following sections, we discuss our rationale for each representation and the associated regions we predict.

1.1. Sensory representations

At its core, the counting sequence, like all verbal sequences, is a series of sounds. Yet, unlike daily spoken language, where words and sounds are organized into countless combinations, there is only one set of valid combinations of sounds that make up the counting sequence. Children are trained extensively on this sequence and are corrected when they make errors (Fuson, 1988; Gelman and Gallistel, 1986). For that reason, we predict that hearing numbers in the count sequence builds a sensory expectation of what sound will follow. For example, hearing "two, three, four" will create a sensory expectation of hearing the phoneme /f/ (i.e., the first sound of "five". This aligns with the taxonomy's *transition and timing knowledge* category, where the replacement of the expected stimulus causes a distinct response (Dehaene et al., 2015).

Transition and timing knowledge has been most often studied using violations-of-expectation paradigms (Dehaene et al., 2015). In this paradigm, participants become accustomed to hearing a series of stimuli, such as tones, at specific intervals. After becoming habituated to the stimuli, a spontaneous change (that violates the expectations) causes a distinct neural response called the mismatch response (MMR). The MMR is often measured as an ERP: a fronto-central negative deflection approximately 200 ms after the surprising stimulus appears (Näätänen et al., 2007). In fMRI studies, this low-level sensory effect has been localized primarily to the bilateral superior temporal gyri (Molholm et al., 2005) and also to the inferior frontal gyrus, although this latter effect has not been widely measured (see Deouell, 2008). The MMR in the temporal cortex does extend to unexpected phonemic categories (Shestakova et al., 2002) and speech sounds (Näätänen, 2001). Therefore, it is reasonable to expect that phonemic representations that generate MMRs will localize to similar regions as pitch violations (Molholm et al., 2005).

1.2. Order representations

As mentioned, ordinal knowledge described by Dehaene and colleagues (2015) is not directly applicable to explaining the structure of counting sequence. Nonetheless, counting sequences are still defined by ordered association between items, so neural mechanisms for processing ordered items must be engaged in representing counting sequences. Processing of ordered associations has been heavily studied in the motor control literature (Doyon et al., 2018; Hardwick et al., 2013; Hikosaka et al., 2002), with converging evidence suggesting that the supplementary motor area (SMA), consisting of the SMA proper and the pre-SMA, is crucial for movement and action sequences (for a review, see Nachev et al., 2008). Growing amount of evidence also suggests that the SMA, despite being named a motor area, is engaged in domain-general sequence processing (Cona and Semenza, 2017; Nachev et al., 2008). A large body of work implicates the SMA in both motor and non-motor functions, including perception, attention, memory, decision making, and language comprehension (Chen et al., 2019; Della Sala et al., 2002; Fischer and Zwaan, 2008; Gerloff et al., 1997; Longcamp et al., 2006; Marvel et al., 2019; Strick et al., 2009; Sul et al., 2011) Furthermore, in the context of numerical cognition, increasing the number of operands in simple arithmetic creates a procedural sequence, and this has been shown to increase activation in the SMA (Menon et al., 2000). Based on these developments, we hypothesize that SMA is recruited for counting sequences, particularly as a mechanism for representing ordered associations between items within a sequence.

Our operational definition of order representation hinges upon the idea of ordered associations, but such a mechanism should be distinguished from processes involved in numerical order (or ordinality) processing that is widely studied in the field (e.g., Lyons et al., 2016). Ordinality processing has been primarily tested using the ordinal judgement task (Lyons and Beilock, 2013; Sasanguie et al., 2017; Vogel et al., 2015, 2019). Typically, this task requires a binary yes or no judgement about whether three numbers are presented in order, from left to right. It may be tempting to say that mental processes underlying ordinal judgment are equivalent to order representation hypothesized to underlie counting sequences in this study. However, we argue for a conceptual difference between the two. Namely, ordinality is a category in which counting sequences are situated: All counting sequences are ordinal in nature, but not all ordinal sequences are counting. Thus, in this context, ordered association between items is a more fundamental mechanism than processes that underlie ordinality judgment.

When we consider this framework, it is not surprising to observe that, in addition to the intraparietal sulcus (IPS) which is implicated in magnitude processing broadly, SMA is the other most frequently activated region in response to ordinal judgement (Fias et al., 2007; Knops and Willmes, 2014; Lyons and Beilock, 2013; Marshuetz et al., 2000; Schubotz and von Cramon, 2001; Wang et al., 2015; Zorzi et al., 2011). None of these studies have addressed the role of the SMA in performing this task, perhaps because of the seemingly distal relationship between ordinality processing and motor functions. Our hypothesis, if true, would implicate that SMA activity represents a mechanism for processing ordered associations between number words in a counting sequence and thus could help resolve the conundrum concerning the role of SMA in numerical ordinal judgment.

1.3. Magnitude representations

A primary feature and purpose of a counting sequence is to understand and track magnitude and quantity. For that reason, we expect counting sequences to contain magnitude representations, even if the context of the sequence does not involve enumeration. Arabic numerals appear to automatically activate an internal magnitude representation (Dehaene, 1992; Dehaene et al., 1993; Dehaene and Akhavein, 1995). Girelli et al. (2000) performed a numerical Stroop task, in which participants identified the numerically larger number of a pair of Ara-

bic numerals that were presented in different sizes (i.e., a congruent trial matched the smaller magnitude with the smaller physical symbol). Specifically, they were looking to see how these responses were affected across development. Older children and adults were more susceptible to interference in incongruent trials than younger children, showing that these automatic connections to internal magnitude develop over time. These magnitude representations are also automatically activated for verbal number words, not only Arabic numerals, even when the words were task-irrelevant (Dehaene and Akhavein, 1995).

As mentioned above, the most common brain region targeted in numerical cognition is the IPS and the posterior parietal cortex (PPC) in general. The PPC is widely regarded as a key area for magnitude representation (for reviews, see Ansari, 2008; Eger, 2016; Nieder and Dehaene, 2009). Thus, it is a reasonable expectation that the PPC will track the numerical magnitude of the words in adult counting sequences.

1.4. Linguistic representations

The last kind of representation contained in counting sequences is a linguistic representation. After all, counting is a linguistic activity. Dehaene and colleagues (2015) write extensively about the interaction between sequence processing and language processing. Namely, language is supported by nested tree structures that allow for a sequence of words to be organized into meaning through abstract syntactical rules. However, the role of nested tree structures in a counting sequence is theoretically debatable. In its base form, when a child first learns to count, the sequence is devoid of meaning and prone to having an unstable order (Fuson, 1988; Gelman and Gallistel, 1986), suggesting that they may not be represented in a nested structure, but rather a linear form. Moreover, unlike complex number words (i.e., numerals composed of combinations of simplex number words, such as seven, and multiplicative morphemes, such as -ty, hundred, or thousand) that can be represented as a nested tree, it is unclear whether simplex number words that make up the first nine items in the counting sequence (one, two, … nine) engages a nested tree structure (but see Hurford, 1975; Watanabe, 2017). Nevertheless, as adults, we understand the meaning of the items in the counting sequence as well as the relationship between those items. That said, there must be a mechanism to represent the lexical items in a count sequence in an integrative manner.

It is uncontroversial that the left inferior frontal gyrus (IFG) is central to language processing, but its specific role remains unclear. Some authors have suggested the IFG to subserve some specific aspects of sentence processing while others have suggested it to serve a more general function such as verbal working memory and cognitive control (for a review, see Rogalsky and Hickok (2011)). Nevertheless, one potential line of convergence is that the IFG provides computations necessary for the integration, maintenance, and control of verbal items. One specific proposition worth noting in this context is the Memory, Unification, and Control (MUC) model by Hagoort (2005). Under this model, language comprehension and production are the process of pulling word information from memory, and binding (unifying) this information together. Going beyond the longstanding theoretical framework of linguistic Merge (Chomsky, 2014), the MUC model explains not only syntactic binding but also phonological and semantic binding, subserved by overlapping regions across the pars opercularis (pOper), pars orbitalis (pOrb), and pars triangularis (pTri) within the IFG (Hagoort, 2013; Willems et al., 2007; Zaccarella et al., 2017). Under this idea, the representation of counting sequences, which requires integration of verbal items into a meaningful set, may be best explained by this unification mechanism underpinned by the IFG, as posited in the MUC model. Note that the left IFG is primarily discussed in these propositions, but similar linguistic and nonlinguistic integration mechanisms are observed in the right hemisphere as well (e.g., Cheung et al., 2018; Menenti et al., 2009; Snijders et al., 2010; Willems et al., 2016).

1.5. The present study

This study aims to establish an overview of the neural basis of counting sequences using fMRI. Following our rationale stated above, we hypothesized that counting sequences contain *sensory, order, magnitude*, and *linguistic* representations. These hypotheses are tested using a sequence of four auditorily presented numbers. In a $2 \times 2 \times 2$ stimulus design, participants heard four-number sequences that varied orthogonally in *adjacency, orderedness*, and *voice identity* (Fig. 1). The four numbers could either be all adjacent (e.g., 4, 5, 6, 7) or non-adjacent (i.e., the last number is one number greater than what would have made adjacent numbers, e.g., 4, 5, 6, 8). The same numbers could be ordered (e.g., 4, 5, 6, 8) or unordered (i.e., scrambled such that there are no ascending pairs, e.g., 8, 4, 6, 5). Lastly, voice speaking the numbers was consistent across all four numbers or was different at the last number.

Using this design, we employed a violation-of-expectation paradigm, as is established in the sequence processing literature (Dehaene et al., 2015). This design is built on the assumptions that 1) the brain is employing predictive mechanisms on all of the aforementioned levels, 2) passive listening can activate these representations, and 3) short (4-item) sequences are sufficient to generate a violation-of-expectation response. As for the first assumption, there is ample evidence that responses to violations occur on sensory levels (e.g. Molmolm et al., 2005) and on higher order levels, such as linguistic (Kutas and Federmeier, 2011) or arithmetic (Niedeggen and Rösler, 1999). For the second assumption, MMRs are shown to appear in response to unattended acoustic environments (Winkler et al., 1996) and even to violated arithmetic statements played auditorily during sleep (Strauss and Dehaene, 2019). Lastly, while a longer sequence may yield a much larger effect size, there is some proof-of-concept for four-number sequences that are violated at the final number resulting in an MMR (Lang and Kotchoubey, 2002). Furthermore, due to the constraints of fMRI research, including lengthier sequences would be difficult without sacrificing statistical power.

Our primary interest was to test the effect of contrast between ordered non-adjacent sequences (e.g., 3, 4, 5, 7; henceforth referred to as *non-consecutive*) versus ordered adjacent sequences (e.g., 3, 4, 5, 6; henceforth referred to as *consecutive*) as a way to identify the brain regions that are crucial for representing counting sequences. In addition to this primary contrast of interest, we tested for the effect of orderedness by contrasting ordered sequences versus unordered sequences as a way to identify brain regions that track the ascending structure of a sequence. The effect of voice identity was also tested by contrasting conditions in which the last voice was different (mismatch) with conditions in which the voices were consistent (match). This voice identity factor served as a proof of concept for our violation-of-expectation paradigm and as a means to assess the specificity of the effects of consecutiveness or orderedness. These contrasts were evaluated both at the whole-brain level and within smaller regions of interest (ROIs) derived from our specific hypotheses about whether violations in consecutiveness recruit the auditory cortex (for sensory representations), supplementary motor area (for order representations), the posterior parietal cortex (for magnitude representations), or the inferior frontal area (for linguistic representations). Specifically, hypothesized brain regions were evaluated in the whole brain under the contrasts of consecutiveness, orderedness, and voice identity with a stringent statistics threshold in order to provide a comprehensive analysis of this relatively novel study. ROI analyses were conducted in anatomical masks defined based on our original hypotheses, when greater statistical power was needed.

2. Materials and methods

2.1. Participants

A total of 40 participants were recruited from the University of Massachusetts Amherst campus though flyers and online postings. Inclusion
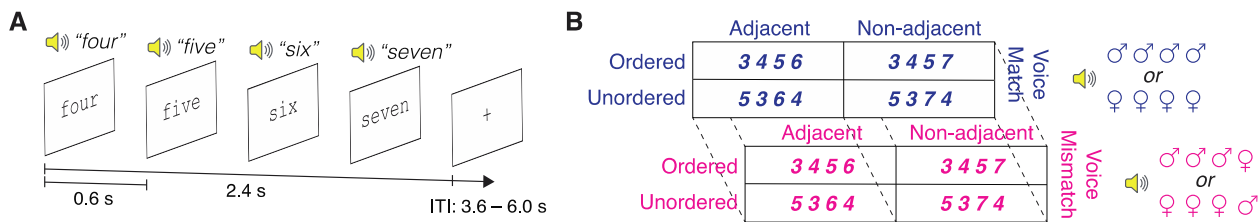
Fig. 1. Experimental paradigm and design. A) Sequence of stimuli in a single trial. Four numbers were presented visually and verbally at a rate of 0.6 s per number, followed by a variable inter-trial interval (ITI). Participants were asked to pay attention to the stimuli and press a button when one of the four auditorily-presented numbers did not match its corresponding visually-presented number, which happened occasionally throughout each run. Stimuli are not presented in scale. B) Schematic of 2 × 2 × 2 factorial design across the factors of Voice Identity (voice match/mismatch), Orderedness (ordered/unordered), and Adjacency (adjacent/non-adjacent). Numbers were visually presented in words and spoken by female and male computer voices. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

criteria were a) having normal or corrected to normal vision, b) age range of 18–29 years old, c) no history of neurological disorders (e.g., epilepsy, agnosia), 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). One participant was dropped as he/she did not meet the inclusionary criteria. Thus, the final sample included 39 participants (female = 25; mean age = 20.8 years, range = 18–27). Each participant completed one 2-hour session, for which they were compensated 30 USD. Some participants completed a behavioral experiment after the scan, unrelated to this study. Each participant gave their written informed consent, and all procedures were approved by the University of Massachusetts Institutional Review Board (IRB).

2.2. Procedure

The experiment consisted of six 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). The stimuli were generated using the Psychophysics Toolbox (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997) on MATLAB (r2015a; The Math Works, Inc., 2015) and were presented on an MRI-compatible monitor screen positioned behind the scanner (60 Hz, 1920 × 1080 resolution), made visible to the participant using a mirror attached to the head coil. 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 in the trial, making the trial duration 4.8 s (= 0.6 s × 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 and the placement of which within a run was randomly determined at the beginning of each run, resulting in a total scan length of 297.6 s.

2.3. Stimuli and task

The sequence of four numbers in each trial was constructed to match a 2 × 2 × 2 condition matrix (Fig. 1B), where the conditions were 1) adjacency, 2) orderedness, and 3) voice identity. The numbers ranged from 1 to 10. Inside the adjacency factor, stimuli were either four numbers from a consecutive count sequence (adjacent; e.g., 4, 5, 6, 7) or four numbers from a count sequence in which the first three numbers were consecutive and the last number was exactly two numbers away from the largest of the three consecutive numbers (non-adjacent; 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, 7 in that order or 4, 6, 5, 8 in that order). In the unordered 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 identity 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). All three factors were orthogonal to each other. The two levels of adjacency factor, by design, had different distributions of the number stimuli. To be specific, the numbers 1, 2, 3, 5, 6, and 10 were presented more for about 17% in the non-adjacent trials compared to the adjacent trials. In contrast, the numbers 4 and 7 were presented about 14%, the number 8 for about 29%, and the number 9 for about 71% more in the adjacent than in the non-adjacent trials. The auditory stimuli were computer generated in the Mac OS X system. Samantha had the speech rate of 170 words/min, and Alex had the speech rate of 200 words/min. The two voices were generated in a different speech rate in order to roughly equate the overall duration of the sound clips of the words used in the experiment.

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 its corresponding visually-presented number. The position of the mismatch within the trial was random. Participants were instructed to press any button on an MR-safe button box when they detected this audiovisual mismatch. No positive or negative feedback was given, 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 numbers, 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.

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 response time, because the task was incidental to our experimental question and thus no emphasis was given about the quickness of participant's response. Specifically, button presses within three seconds of the onset of the mismatch stimulus in a catch trial were considered hits. In a small number of cases, button presses were not recorded accurately due to a technical error, and those cases were excluded from the behavioral analysis. Average hit rate across participants was $M = 91.2\%$ ($SD = 10.8\%$), indicating a reasonable amount of attention given to the stimuli. False alarm rate (button presses during non-catch trials) was very low ($M = 0.775\%$, $SD = 0.463\%$) suggesting that the hit rate was not due to a generally high response rate.

2.4. Image acquisition parameters

Image data were 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 = 1200 ms, TE = 30 ms, flip angle = 69°, FOV = 210 mm, number of axial slices = 48, simultaneous multi-slice factor = 3, voxel size = 3.0 mm × 3.0 mm × 2.5 mm). T1 weighted MPRAGE images were collected after the third (out of six) functional run (TR = 2000 ms, TE = 2.13 ms, flip angle = 9°, FOV = 256 mm, number of saggital slices = 208, voxel size = 1.0 mm × 1.0 mm × 1.0 mm).

2.5. 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). 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 the 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 FSL) greater than 0.5 mm in more than 10% of volumes within a single run (Power et al., 2012). Average frame displacement across all runs and across all participants was 0.13 mm. Through this method, one participant was modeled with four of six runs.

2.6. Plan of analysis

Our goal was to test the neural correlates of counting sequences through the effect of *consecutiveness* (i.e., 5, 6, 7, 9, vs 5, 6, 7, 8). Secondary to this analysis, we were interested in the effect of *orderedness* (i.e., 5, 6, 7, 8, vs 5, 7, 6, 8). Our design also allows for testing of *voice identity*, which was critical in testing specificity: Can a given region's sensitivity to consecutiveness be explained by a response to a low-level sequence violation? We hypothesized four levels of representation for consecutive counting sequences (sensory, order, magnitude, and linguistic) that would relate to specific brain areas (STG, SMA, IPS, and IFG, respectively)

We first performed a whole-brain analysis on the effects of consecutiveness, orderedness, and voice identity. This whole-brain analysis allowed us not only to localize the effects of consecutiveness, orderedness, and voice identity in the hypothesized regions at a statistically stringent level but also to identify those effects in non-hypothesized regions. Next, we performed anatomically-defined region-of-interest (ROI) analyses within our hypothesized brain regions in order to measure specific effects that did not survive the stringent whole-brain analysis. The whole-brain and ROI analyses were both driven by a single set of a priori hypotheses, although the selection of the ROIs was guided by the contrasts orthogonal to the effect of investigation, as described in Section 3.2.

2.7. Estimation of neural activity

The General Linear Model (GLM) was employed to estimate the magnitude of neural activity (via hemodynamic response) associated with the eight different experimental conditions (2 × 2 × 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 0.5 mm was coded as a covariate of no-interest in the model. Finally, six motion parameters (head translation and rotation) were entered as a covariates of no-interest. A high pass filter (128 s) and an autoregressive AR(1) model was employed. In the second-level random-effects analysis, beta values from the individual-level GLMs were entered into a 2 × 2 × 2 full factorial ANOVA which was comprised of the three factors: adjacency, orderedness, and voice identity.

We examined the neural substrates for the different levels of sequential representations in a full factorial ANOVA. Neural correlates of basic (i.e., non-numerical) sensory expectations were tested by the main effect of voice identity (voice mismatch > voice match). Brain regions tracking ordered sequences were identified by the main effect of orderedness in the contrast of ordered versus unordered sequences. Central to our hypothesis, brain regions sensitive to the structure of consecutive count list were identified by contrasting ordered non-adjacent sequences (e.g., 2 3 4 6) against ordered adjacent sequences (e.g., 2 3 4 5), which indicates a violation of counting sequence. In the whole-brain univariate analyses, a clusterwise multiple comparisons correction with a cluster-defining threshold of $p < .001$ controlling for false discovery rate was considered for statistical inferences. When small volume correction within a region of interest was applied, a voxel-level inference was made with a correction using family-wise error rate. Reported coordinates are in the MNI space.

From these analyses, we made forward inferences (Henson, 2006) on whether or not the different levels of sequence representations (voice identity, orderedness, and consecutiveness) rely on the same neural mechanism. We then made a set of theory-driven, anatomically-constrained reverse inferences (Poldrack, 2006) on the effect of consecutiveness (or violation in the counting sequence), which are useful and effective in updating our evidence-based beliefs about the mechanisms underlying counting sequences and in generating novel hypotheses.

2.8. Data and code availability statement

All toolsets used in the processing and analysis pipeline are publicly available. Data and code are not available on a public repository but will be made available upon written request to the corresponding author, after clearance from the Institutional Review Board.
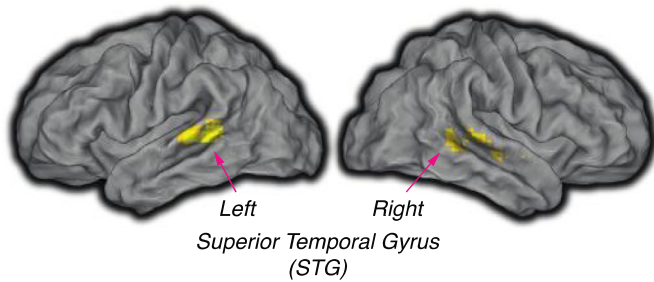
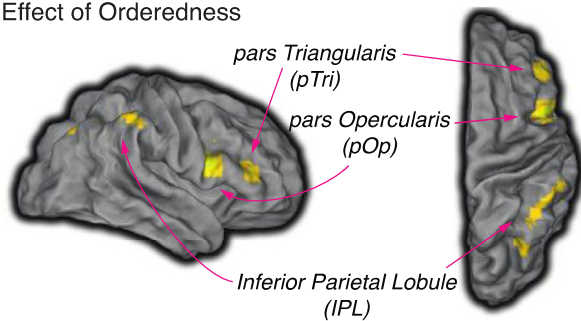## 3. Results

3.1. Whole-brain analysis

We first identified brain regions showing the effects of voice identity, orderedness, and consecutiveness of the counting sequence in a 2 × 2 × 2 full factorial ANOVA on a univariate, whole-brain level. As elaborated in Methods, the effect of voice identity served as a proof of concept in our violation-of-expectation paradigm and allowed us to examine the specificity of the other effects tested in the study. The contrast of voice mismatch versus voice match, as shown in Fig. 2A, revealed significant clusters centered around the right ($q_{FDR} < 0.001$) and left ($q_{FDR} < 0.001$) superior temporal areas, with no significant activations for the reverse contrast (Table 1). These regions were mostly identified as the superior and middle temporal gyrus according to the Automated Anatomical Labeling atlas (AAL; Tzourio-Mazoyer et al., 2002). For simplicity, these regions are henceforth referred to as the bilateral superior temporal gyrus (STG).

As shown in Fig. 2B, the effect of orderedness (ordered > unordered) resulted in four significant clusters: two clusters in the right inferior frontal gyrus (IFG) and two other clusters in the right inferior parietal

A Effect of Voice Identity

Left   Right

Superior Temporal Gyrus
(STG)

B Effect of Orderedness

pars Triangularis
(pTri)

pars Opercularis
(pOp)

Inferior Parietal Lobule
(IPL)

C Effect of Consecutiveness

Z=55
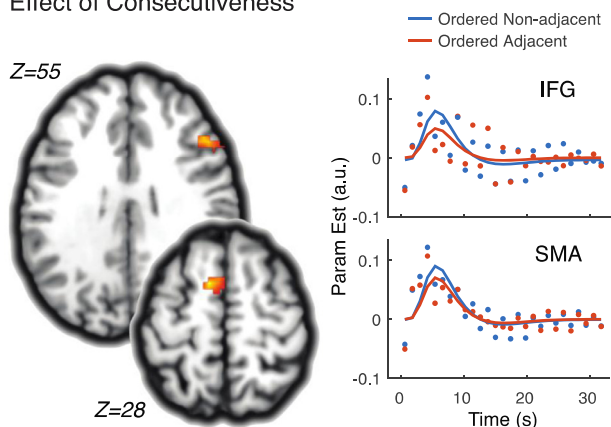
Z=28

— Ordered Non-adjacent
— Ordered Adjacent

IFG

SMA

Fig. 2. Results of whole-brain and regions-of-interest analyses. A) Significant effects of voice mismatch > match, at cluster-level qFDR < 0.05 using a cluster-defining threshold of $p < .001$. B) Significant effects of ordered > unordered sequences in the right frontal-parietal regions, with the same statistical threshold. C) Significant effects of consecutiveness (i.e., violation in the counting sequence) surviving small volume correction (pFWE < 0.05) within anatomically pre-defined right inferior frontal gyrus (IFG) and supplementary motor area (SMA), along with, for illustration purposes, grand averaged peristimulus time histogram with fitted hemodynamic response curve from identified local peaks at [45, 23, 28] in IFG and at [−9, 5, 55] in SMA. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

lobule (IPL) (Table 1). According to the AAL atlas, the posterior of the two IFG clusters ($q_{FDR} < 0.001$) was identified mostly in the pars opercularis (pOp) although some portion of it was in the pars triangularis, and the anterior of the two IFG clusters ($q_{FDR} = 0.003$) was identified largely in the pars triangularis (pTri), extending to the middle part of the middle frontal gyrus. The anterior of the two IPL clusters ($q_{FDR} = 0.002$) was identified partly in the supramarginal gyrus and the inferior parietal gyrus. The posterior of the two IPL clusters ($q_{FDR} = 0.022$) was largely identified in the angular gyrus with some portion of it in the middle and superior occipital gyri. Unlike the identified pOp and pTri that are spatially segregated from each other, the two IPL clusters together showed

elongated activity patterns from the anterior to posterior axis along the intraparietal sulcus typically associated with magnitude processing in previous fMRI studies on numerical cognition. Furthermore, the two IPL clusters made up a single cluster with a liberal cluster-defining threshold ($p < .005$). Thus, the two clusters were henceforth singly referred to as IPL. No other suprathreshold clusters were identified. The reverse contrast (unordered > ordered) did not result in any significant activations.

Finally, the effect of consecutiveness (i.e., violation in the counting sequence) was evaluated by contrasting ordered non-adjacent sequences (e.g., 2, 3, 4, 6) against ordered adjacent sequences (e.g., 2, 3, 4, 5). This contrast did not reveal any suprathreshold clusters at the whole-brain level, except a statistically weaker effect in the supplementary motor area ($q_{FDR} = 0.095$).

So far, the results from the whole-brain analysis indicate that the right inferior frontal and parietal areas are recruited for ordered numerical sequence and that regions in and around the bilateral auditory cortices encode low-level auditory properties of the presented sequence. The effect of consecutiveness, however, did not survive the statistical threshold in the whole-brain analysis. To address our central hypotheses about the representation of consecutive sequences, we thus followed up with more targeted analyses in regions of interest using small volume correction.

3.2. Regions of interest analyses

Our whole-brain analysis identified the right inferior frontal gyrus (IFG) and inferior parietal lobule (IPL) to be recruited for processing orderedness in a counting sequence (Fig. 2B). Although the recruitment of IFG and IPL was for orderedness, these brain regions were consistent with our original hypotheses about the representation of count sequence in magnitude and linguistic codes. We therefore reasoned that the same general areas in the fronto-parietal network 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 the consecutiveness of counting sequences. Thus, we performed a targeted analysis in a smaller search space within anatomically defined regions of interest (ROIs) from the AAL atlas. Even though the observed effect of orderedness was localized in the right hemisphere (see Discussion for our interpretations on this), our search included both the left and right fronto-parietal regions because we had no strong predictions about the lateralization of activities. The ROI in the IFG included pars opercularis and par triangularis. The ROI in the IPL included the supramarginal, angular, and inferior parietal gyri. In addition, as a means to test our hypothesis about the sensory representation, the bilateral auditory cortex was defined from the superior and middle temporal gyri from the same atlas. Finally, to test our hypothesis about the order representation, the supplementary motor area (SMA; including both pre-SMA and SMA proper) was defined likewise. Note that the definition of these anatomical ROIs followed the principles of our a priori hypotheses, but the selection of the specific masks was guided by the results of the whole-brain contrasts (orderedness and voice identity) orthogonal to the contrast of primary interest (consecutiveness).

The effect of violation in the counting sequence (consecutiveness) was tested in those targeted ROIs using small volume correction. A significant effect was observed in left SMA ($p_{FWE} = 0.022$ at [−9, 5, 55]) and in right IFG ($p_{FWE} = 0.022$ at [45, 23, 28]) (Fig. 2C). The IFG peak was identified in the pars triangularis according to the AAL atlas and was located between the pOp and pTri peaks observed in the previously reported effect of orderedness (see Fig. 2B). No other ROIs showed any suprathreshold effect. It should be noted that ordered adjacent and ordered non-adjacent sequences have slight unequal distributions of the number stimuli (see Methods). This difference in stimuli, however, is unlikely to play a role in the observed consecutiveness effect in SMA and IFG. First, it is difficult to explain why differences in the stimuli cause such an effect only in SMA and IFG but not in other ROIs. Sec-

Table 1

Statistics on the clusters of the effect of Voice Identity (Mismatch vs. Match) and Orderedness (Ordered vs. Unordered) in a whole-brain analysis with a cluster-defining threshold of $p < .001$. .

Condition	Anatomical region	Coordinates (MNI)			Peak Z-score	q_{FDR} (Cluster level)	Number of voxels
		x	y	z			
Voice Mismatch > Match	R. superior temporal gyrus	57	−34	7	6.11	< 0.001	242
	L. superior temporal gyrus	−69	−31	7	6.48	< 0.001	174
Ordered > Unordered	R. pars opercularis	48	11	22	5.68	< 0.001	194
	R. pars triangularis	42	35	16	4.33	.001	75
	R. intraparietal lobule	57	−31	49	4.18	.001	88
	R. intraparietal lobule	33	−61	37	4.34	.015	38

ond, if differences in the stimuli were to drive the effect in SMA and IFG, then the contrast between unordered adjacent and unordered non-adjacent should yield similar differences. However, that contrast did not result in any suprathreshold activity within SMA and IFG at the cluster-defining threshold of $p = .001$, nor across the whole brain. Even with the extremely liberal cluster defining threshold of $p = .05$, no meaningful peak was observed in the two ROIs ($p_{FWE} > 0.909$).

3.3. Post hoc Bayes factor analyses

Following some null effects of consecutiveness in several brain regions, we conducted some post hoc Bayes Factors (BF) analyses. BFs were computed from activation levels (i.e., parameter estimates from the GLM) at given peak locations, in order to provide the weight of the evidence in favor of the null or the alternative hypotheses. Following the default in JASP (JASP Team, 2020), the null hypothesis was modeled as a Cauchy prior centered on zero with scale = 0.707. When BF10 < 1, BF01 is reported for ease of interpretation.

The first analysis concerned the lack of the consecutiveness effect in the bilateral auditory cortex, which we had originally hypothesized based on the sensory code of counting sequences. First, peak coordinates in the left and right superior temporal gyrus were identified from the voice mismatch > match conditions (see Table 1), and a sphere with a radius of 5 mm was defined from each of the two peaks (19 voxels in a sphere). In each participant, parameter estimate values from the contrast of consecutive versus non-consecutive were averaged across the voxels within each sphere. These summarized values of activation levels entered the Bayesian analysis. The rationale was that if violations in consecutiveness were to activate the bilateral auditory cortex, its effect should be most pronounced in the regions where response was maximized for the effect of voice identity. The results indicated a moderate evidence for the null effect in the left superior temporal gyrus peak (−69 −31 7; BF01 = 3.690) and no evidence in either direction in the right superior temporal gyrus peak (57 −34 7; BF01 = 1.209). A similar Bayesian analysis was performed to assess the lack of the consecutiveness effect in the right IPL defined by the effect of orderedness (57 −31 49). The results indicated a moderate evidence for the null effect (BF01 = 5.655), suggesting that the IPL treats consecutive and non-consecutive sequences in a similar way.

We then tested to what extent SMA and IFG were selectively sensitive to the violation of counting sequence and not to other types of experimental manipulations. First, we examined the effect of orderedness in SMA. No suprathreshold voxels were observed for the effect of orderedness in SMA. Second, we examined the effect of voice identity in SMA and IFG. Again, no suprathreshold voxels were observed in either regions. These null effects were again followed-up with a Bayesian analysis. We first obtained the BF based on activation levels computed from the orderedness effect in the SMA peak defined from the effect of consecutiveness. There was a moderate evidence for the null effect (BF01 = 3.51), suggesting that the processing of ordered and unordered counting sequences is comparable in SMA. We then obtained the BFs based on activation levels computed from the voice identity effect in the IFG and SMA peaks defined from the effect of consecutiveness. There

was a moderate evidence for the null effect in both SMA (−9 5 55; BF01 = 5.747) and IFG (45 23 28; BF01 = 3.086). For comparison, the BF for the consecutiveness contrast in SMA was BF10 = 235.0. These results indicate that the brain response to the effect of consecutiveness in SMA and IFG cannot be explained by violations in low-level auditory properties of the sequence.

4. Discussion

Despite the large literature on the neural basis of numerical cognition with the majority of focus on cardinality or numerical magnitude (Ansari, 2008; Nieder and Dehaene, 2009) and to a lesser degree on ordinality (Lyons et al., 2016), there have been no studies targeted to investigate the neural representation of counting sequences. Here, we used a violation-of-expectation fMRI paradigm to investigate the neural substrates of counting sequences. We had hypothesized that counting sequences are represented in sensory, order, magnitude, and linguistic codes characterized by brain activities in the auditory cortex, the supplementary motor area (SMA), the posterior parietal area (PPC), and the inferior frontal gyrus (IFG), respectively. Our results demonstrated that violations in the counting sequence (e.g., 3 4 5 7 vs. 3 4 5 6) modulate brain activities in the SMA and the right IFG but not in the PPC and the auditory cortex (Fig. 2C).

Counting is the gateway to the acquisition of number concepts, which is arguably the simplest abstract idea that the human mind can conceptualize (Wiese, 2007). Number words signify abstract natural numbers that are used to identify a broad range of (nominal, ordinal, and cardinal) properties in "empirical objects." Furthermore, numbers are used to refer to not only concrete objects but also actions and events (three jumps), units of measurement (four hours), and concepts (two ideas). Critically, number words in a counting sequence as signifiers are primarily defined by their relations with each other, as opposed to their relations to the signified, making them a quintessential example of a symbolic system (Deacon, 1997; Wiese, 2007).

Arguably, no other verbal sequence contains these unique properties all together. Consider another overlearned sequence: the alphabet. Each element of the alphabet has no "meaning" and is arbitrarily and historically positioned in a sequence with no relationship with each other. It is therefore not surprising to find that ordering or comparing letters is substantially more difficult and slower than ordering or comparing numbers (e.g., Sasanguie et al., 2017). Such qualitative differences between counting sequences and other verbal sequences make it difficult to directly compare them with each other. Moreover, as described in Introduction, counting sequences do not appear to fall squarely under any single categorization in the sequence taxonomy proposed by Dehaene and colleagues (2015). Considering how unique the counting sequence is, yet how little is known about its neural basis, our goal was to characterize different levels of representations in a counting sequence at the neural level.

Counting is a sequential process that at the initial stage may not differ from other verbal sequences we learn in infancy such as nursery rhymes. This rudimentary knowledge of counting sequences exists as a memorized sequence connected simply by perceptual cues (Fuson, 1988).

Such sequential knowledge may exist in terms of transition probability postulated by Dehaene and colleagues (2015) even in adults who have long mastered the count list. To that end, we hypothesized that counting sequences are represented in an auditory code. However, we failed to find evidence supporting this hypothesis; violation of counting sequence (e.g., 3 4 5 7 > 3 4 5 6) did not show any suprathreshold activation in the bilateral STG. Bayes factors even suggested evidence favoring the null hypothesis in the STG, especially in the left hemisphere. At least under the current paradigm in our sample of participants, our results suggest that counting sequences do not automatically create phonetic expectations for the next number word in the correct counting sequence, different from the sensory expectations built online in a typical mismatch response study (Näätänen et al., 2007). One plausible hypothesis stemming from these results is that conceptual expectations override perceptual expectations in the adult brain. This allows us predict that children who rely more on perceptual cues to generate and comprehend count sequences may show an effect of phonetic expectations in the auditory cortex.

The rationale for our hypothesis concerning order representations comes from the large body of literature in neurobiology of motor control, as mechanisms for representing and processing ordered association between items have been extensively studied to understand movement and action sequences (Hikosaka et al., 2002; Hardwick et al., 2013; Doyon et al., 2018). The literature now suggests that not only motor sequence processing but also domain-general sequence processing, even in auditory modality, is subserved by the SMA (Cona and Semenza, 2017; Della Sala et al., 2002; Gerloff et al., 1997; Hikosaka et al., 1996; Lima et al., 2016; Nachev et al., 2008; Tanji and Shima, 1994). Thus, we hypothesized that the SMA would be sensitive to violations in the counting sequence. We indeed found a significant effect of consecutiveness in SMA. Previous studies have shown the involvement of SMA across a variety of different numerical tasks (Chochon et al., 1999; Dehaene et al., 1996; Dormal et al., 2010; Dormal and Pesenti, 2009; Fias et al., 2007; Hanakawa et al., 2002; Knops and Willmes, 2014; Lyons and Beilock, 2013; Marshuetz et al., 2000; Menon et al., 2000; Park et al., 2013; Schubotz and von Cramon, 2001; Wang et al., 2015; Zorzi et al., 2011). Many of these previous studies, however, did not provide interpretations about the role of SMA in those numerical tasks. Those that did suggested a wide variety of explanations. For instance, some earlier studies interpreted the involvement of SMA as motor preparation (e.g., Menon et al., 2000) or working memory and executive attention (e.g., Chochon et al., 1999). Other studies suggested that SMA activity underlies mental operation of numerical values (e.g., Hanakawa et al., 2002). While many of these interpretations may be plausible depending on the particular task used, a more parsimonious idea based on the current results is that the involvement of SMA is driven by the sequential nature (specifically, ordered associations) of numbers used in various numerical tasks. This idea is consistent with the findings by Lyons & Beilock (2013) who showed that symbolic, but not nonsymbolic, number ordering recruits the left premotor cortex including SMA. Importantly, however, our results show that mere ordinal nature of the counting sequence (i.e., orderedness) elicits negligible SMA activity (cf. Dehaene et al., 2015). Instead, a robust SMA activity is observed only when the precise incremental structure of the sequence is expected and violated. Moreover, SMA activity was observed in the absence of an explicit numerical task or working memory demand (as we used an incidental oddball detection task). Thus, our results suggest that the SMA spontaneously keeps track of the precise ordered associations between numbers in the counting sequence.

Our next hypothesis concerned the magnitude representation within the counting sequence in the posterior parietal cortex, since number words in a counting sequence track magnitude and refer to specific numerical values. Extensive research now implicates the posterior parietal cortex (PPC) as the core brain region for both symbolic and nonsymbolic number processing (Piazza et al., 2007; Dastjerdi et al., 2013; Piazza et al., 2004). Thus, we predicted that violations in the counting

sequence (i.e., consecutiveness) would elicit posterior parietal activity. However, contrary to our hypothesis, the right inferior parietal lobule (IPL) did not show an effect of consecutiveness. Our Bayesian analysis even indicated evidence for the null hypothesis, further suggesting that listening to counting sequences does not engage magnitude representations. Lack of IPL response for the violation of the counting sequence could be due to the incidental and passive-listening nature of our paradigm. Had we asked the participants to actively process the meaning of the numbers (although our primary intention was to study counting sequences in their most natural form—rote counting), we might have found an effect of consecutiveness in the IPL. What is intriguing, however, is that the IPL was still sensitive to ordinality under this incidental paradigm without an explicit numerical task, unlike previous studies that involved explicit ordinal judgments (Fias et al., 2007; Knops and Willmes, 2014; Lyons and Beilock, 2013; Marshuetz et al., 2000). Thus, these results in turn provide powerful evidence that numerical ordinality processing is subserved by the PPC.

Counting sequences are not only numerical but also linguistic in nature. Linguistic analysis of numerals has long suggested that complex numerals are syntactically organized in a nested tree structure (Hurford, 1975). While counting sequences in this study are made up of a list of simplex numerals and therefore do not form a phrasal structure, it is reasonable to posit that the representation of a counting sequence as a whole is underpinned by the mechanism that also govern linguistic structure building. Indeed, research in neurolinguistics has proposed several potential mechanisms underlying linguistic structure building subserved by the left IFG. For example, one account explains that a linguistic representation is constructed by a unification of constituents (Hagoort, 2005). More domain-general accounts argue for the role of cognitive control (specifically the selection of representations among competing alternatives; Thompson-Schill et al., 2005) or working memory (Fiebach et al., 2005) in linguistic structure building.

As in these accounts, the representation of a count sequence is likely to be constructed by binding elements stored in memory together into a cohesive whole. Our results indeed show that the IFG is sensitive to violations in orderedness and consecutiveness of a counting sequence. These results may be interpreted based on Hagoort's (2005) account: Number words are processed sequentially but unified as a whole into a sequence based off their matching to a long-term memory structure. When a number word that is not able to be unified into established representation of the counting sequence (either in its ordered nature or the consecutive structure), an adjustment must be made, leading to a change in neural response in the IFG. It is worth reiterating that, unlike the IFG, the IPL did not respond to violations in the counting sequence, which suggests that the representation of a counting sequence is qualitatively different from the representation of ordered numbers.

Our study also elucidates larger questions about general sequence processing within the framework proposed by Dehaene and colleagues (2015). An outstanding set of competing hypotheses raised (Dehaene et al., 2015; Wang et al., 2019) is whether one of the five systems described in the taxonomy chooses the best model for an incoming sequence or whether all systems operate independently of each other to represent relevant aspects of the incoming sequence. The current findings lend support to the latter hypothesis, as the results demonstrate that the general order of numbers and specific increments in the counting sequence are processed in different regions. The SMA activity—unique to processing valid counting sequences—indicates an independent system predicting the number that will come next in the sequence and eliciting a response when that number does not appear. In addition, it is interesting to note that the auditory cortex, a frequent target for basic sensory sequence processing, did not appear to respond to ordered number or correct counting sequences, against our initial hypotheses, raising the possibility that lower-level sequence processing activity may have been inhibited by higher-level sequence processing.

One intriguing finding is the predominantly right lateralized activity in the effect of orderedness and consecutiveness of the counting se-

quence. This is in stark contrast with the left lateralized activities found in the neurolinguistics literature. Theories about neural reuse or recycling (Anderson, 2010; Dehaene and Cohen, 2007) provide a plausible explanation. While neuroimaging studies in adults with a range of numerical and mathematical tasks overall do not show a strong laterality in PPC activity, developmental studies in infants and children mostly show right lateralized activity for magnitude processing (Cantlon et al., 2006; Hyde et al., 2010; Izard et al., 2008; Park, 2018; Park et al., 2014). Furthermore, spatial and temporal processing, which together with numerical processing make up the basis for general magnitude processing, primarily engages the right PPC (Walsh, 2003). These findings are in line with the idea that the right parietal cortex is the neural hub for the evolutionarily older system for magnitude, while other regions get recruited as a result of learning more advanced numerical concepts and operations.

Such an idea has gained empirical support in the cortical basis of visual numeral processing. In contrast to the left-lateralized neural activity for visual word forms presumably due to its direct anatomical connections with the left lateralized language network (Bouhali et al., 2014; Dehaene et al., 2005; Schlaggar and McCandliss, 2007; Thiebaut de Schotten et al., 2014), Arabic numerals and written number words have been shown to recruit the right visual cortex (Park et al., 2012; Shum et al., 2013), which may be due to its direct anatomical connections to the right PPC for numerical cognitive processes. Consistent with this view, Park et al. (2012) demonstrated that the laterality of visual cortical activation for numerals correlate with the laterality of parietal activation for numerical operations across participants. Following the theoretical framework of neural reuse or recycling, right lateralized IFG activity for consecutiveness and for orderedness may have been driven by the ontogenetically more primitive, right lateralized activities for numerical processing in the PPC.

In sum, the current results demonstrate a clear right fronto-parietal engagement for processing ordinality in a count sequence. Further, our results show that the representation of mere ordinality and the representation of the precise incremental steps of the counting sequence rely on different mechanisms. This latter representation, which is the essence of elementary number knowledge, is processed across cortical regions known for processing ordered associations between items in the supplementary motor area (SMA) and linguistic structural binding in the inferior frontal gyrus (IFG). The involvement of the SMA for representing violations in counting sequence provides novel evidence for the engagement of order code for counting sequences even in the absence of a need for action or mental operations. The recruitment of the right IFG provides a novel insight in terms of how the concept of number may be developed from structural building of individual elements into a cohesive whole and how this mechanism may be subserved by the right hemisphere. The finding that the IPL tracks the numerical order associated with the number words but not the precise increments in the count sequence structure provides new insights into the functional mechanism of that brain region. The findings all together demonstrate how multiple neural systems operate together to represent the sequential knowledge that is fundamental to mathematical thinking.

Credit authorship contribution statement

Eli Zaleznik: Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. **Joonkoo Park:** Methodology, Formal analysis, Writing – original draft, Writing – review & editing, Visualization, Supervision, Funding acquisition.

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Data and code availability statement

All toolsets used in the processing and analysis pipeline are publicly available. Data and code are not available on a public repository but will be made available upon written request to the corresponding author, after clearance from the Institutional Review Board.

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