

Frequency-based Dissociation of Symbolic and Nonsymbolic Numerical Processing during Numerical Comparison

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Abstract

Recent evidence suggests that during numerical calculation, symbolic and nonsymbolic processing are functionally distinct operations. Nevertheless, both roughly recruit the same brain areas (spatially overlapping networks in the parietal cortex) and happen at the same time (roughly 250 msec poststimulus onset). We tested the hypothesis that symbolic and nonsymbolic processing are segregated by means of functionally relevant networks in different frequency ranges: high gamma (above 50 Hz) for symbolic processing and lower beta (12–17 Hz) for nonsymbolic processing. EEG signals were quantified as participants compared either

symbolic numbers or nonsymbolic quantities. Larger EEG gamma-band power was observed for more difficult symbolic comparisons (ratio of 0.8 between the two numbers) than for easier comparisons (ratio of 0.2) over frontocentral regions. Similarly, beta-band power was larger for more difficult nonsymbolic comparisons than for easier ones over parietal areas. These results confirm the existence of a functional dissociation in EEG oscillatory dynamics during numerical processing that is compatible with the notion of distinct linguistic processing of symbolic numbers and approximation of nonsymbolic numerical information. ■

INTRODUCTION

It has been suggested that the ability to process different numerical representations (e.g., symbolic such as “1,” “2,” “three,” or nonsymbolic such as a group of 12 dots) acts as the basis for high-level mathematical skills (Nieder & Dehaene, 2009; for a review, see, e.g., De Smedt, Noël, Gilmore, & Ansari, 2013). Evidence shows that humans have two different mechanisms for processing different types of numerical representations. One cognitive system is for processing nonsymbolic numerical representations (e.g., groups of dots that represent quantities), termed here the “nonsymbolic system” (e.g., Mazzocco, Feigenson, & Halberda, 2011; Piazza et al., 2010; Landerl, Fussenegger, Moll, & Willburger, 2009). Another numerical cognitive system involves the processing of symbols that represent numbers (e.g., “1,” “7,” “ten”), termed here the “symbolic system” (e.g., Vanbinst, Ansari, Ghesquière, & De Smedt, 2016; Kolkman, Kroesbergen, & Leseman, 2013; Sasanguie, Van den Bussche, & Reynvoet, 2012; Vanbinst, Ghesquière, & De Smedt, 2012; Lonnemann, Linkersdörfer, Hasselhorn, & Lindberg, 2011; De Smedt, Verschaffel, & Ghesquière, 2009; Holloway & Ansari, 2009). Recently, it has been suggested that learnt numerical symbols do not acquire their numerical meaning from the nonsymbolic numerical system (e.g., Reynvoet & Sasanguie, 2016) and that the exact symbolic system is behaviorally distinct from the approximate

nonsymbolic one (Sasanguie, De Smedt, & Reynvoet, 2017; Lyons, Ansari, & Beilock, 2012). Yet, and despite the fact that these two numerical systems may be behaviorally separate, it has been shown that the horizontal segment of the intraparietal sulcus (IPS; Piazza, Pinel, Le Bihan, & Dehaene, 2007), in close cooperation with posterior and/or middle parts of the IPS (Eger et al., 2009), constitutes the neuronal correlate of processing both symbolic and nonsymbolic numerical information (for a review, see Eger, 2016). In addition to both symbolic and nonsymbolic numerical processing taking place at approximately the same neural location, it has also been suggested that they occur at almost the same time (in the first few hundred milliseconds after onset of the incoming numerical information, e.g., Smets, Gebuis, & Reynvoet, 2013; Libertus, Woldorff, & Brannon, 2007; Temple & Posner, 1998).

This raises the following question: How can functionally distinct processes (i.e., the processing of different numerical representations at different levels of numerical analysis) take place at the same time (roughly, in the first few hundredths of a millisecond after stimulus onset) and at spatially overlapping neural networks in the parietal cortices. In other words, what is the neuronal dynamics that modulates the behavioral distinction between symbolic and nonsymbolic numerical information? Here, we aimed to test the hypothesis that symbolic and nonsymbolic processing are segregated by means of activation pattern of functionally relevant networks in different frequency ranges.

Symbolic and Nonsymbolic Numerical Systems: Behavioral

Symbolic and nonsymbolic numerical systems are typically discussed distinctively. The nonsymbolic system is considered to have evolutionary roots (Hauser, Tsao, Garcia, & Spelke, 2003; Dehaene, Dehaene-Lambertz, & Cohen, 1998) that rely mostly on visuospatial cognitive abilities (Anobile, Turi, Cicchini, & Burr, 2015; Gallistel & Gelman, 2000) and involve approximate quantity processing (e.g., 100 dots that are presented briefly can be estimated as 90 and not as exactly 100; Lyons, Ansari, & Beilock, 2015; Barth, Beckmann, & Spelke, 2008). Estimation of numbers or quantities is related to the cognitive process employed when a stimulus is composed of a large number of items and is presented briefly (Pavese & Umiltà, 1998). In contrast, the symbolic system involves accurate and exact processing of numbers (e.g., the written number “100” will be considered exactly “100” and not “90”—as possible in the nonsymbolic system; De Smedt et al., 2013) and is influenced by language and culture (Gunderson, Spaepen, & Levine, 2015; Bender et al., 2014).

It is yet debatable, however, whether symbolic and nonsymbolic numerical processing continuously interact behaviorally and overlap. For example, some argue that symbolic and nonsymbolic numerical processing enhance one another over the course of math education (e.g., Piazza, Pica, Izard, Spelke, & Dehaene, 2013) and that the approximate numerical system possibly acts as foundational for math skills (Szkudlarek & Brannon, 2017). However, a review (De Smedt et al., 2013) as well as a meta-analysis (Schneider et al., 2017) and scientific investigations (Sasanguie, Defever, Maertens, & Reynvoet, 2014) have shown that the processes measured by nonsymbolic numerical tasks in scientific labs are not critical for school-relevant mathematics.

Symbolic and Nonsymbolic Numerical Systems: Neural Substrates

Thus, most behavioral evidence suggests that symbolic and nonsymbolic systems are functionally distinct operations (Schneider et al., 2017; Sasanguie et al., 2014; De Smedt et al., 2013). Nevertheless, it seems that both recruit roughly the same brain areas. Indeed, many studies have examined neural anatomical locations of the brain related to nonsymbolic (e.g., Ansari & Dhital, 2006; Cantlon, Brannon, Carter, & Pelphrey, 2006; Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004) and symbolic numerical systems (e.g., Notebaert, Nelis, & Reynvoet, 2011; Cohen Kadosh, Cohen Kadosh, Kaas, Henik, & Goebel, 2007). It has been suggested that symbolic and nonsymbolic numerical systems draw from the same neural populations (Santens, Roggeman, Fias, & Verguts, 2010). Furthermore, a meta-analysis (Arsalidou & Taylor, 2011) suggested that the IPS is consistently activated during arithmetic, indicating

that abstract representation is important for symbolic learnt arithmetic. The notion of spatial neural overlap (in the IPS) between symbolic and nonsymbolic numerical systems has also received support from a simulation study (but with nonsymbolic quantities being only partially recycled by the symbolic numbers; Verguts & Fias, 2004). Interestingly, a recent meta-analysis (Sokolowski, Fias, Mousa, & Ansari, 2017) showed that, in addition to the IPS, other brain regions throughout the parietal cortex are also engaged in both symbolic and nonsymbolic numerical systems.

Indeed, a common observation is that the brain areas involved in the different types of processing (i.e., symbolic and nonsymbolic) tend to be largely spatially overlapping. Lyons, Ansari, et al. (2015), for example, found that the IPS is involved in processing numerical information regardless of format. However, the way in which symbolic and nonsymbolic numbers are encoded is different (i.e., because no association was found between the neural activity evoked by symbolic numbers and the activity by the corresponding nonsymbolic numerical systems). Similarly, Bulthé, De Smedt, and Op de Beek (2014) found a significant involvement of the same brain areas in the decoding of both symbolic and nonsymbolic stimuli (with larger involvement in decoding nonsymbolic than symbolic number-specific representations). Moreover, in an fMRI adaptation paradigm (a method that allows investigation of stimulus related processes without requiring participants to respond to the stimuli presented), Cohen Kadosh et al. (2011) showed that, as magnitudes changed, both dots (nonsymbolic) and digits (symbolic) activated the same intraparietal regions. However, they found no crossnotation adaptation from nonsymbolic to symbolic numbers, suggesting that several different mechanisms within the same parietal regions are involved in numerical representation. Recently, the results of a repetitive transcranial magnetic stimulation study indicated that this neural spatial overlap might be because symbolic numbers can be associated with nonsymbolic numbers in the parietal lobe but only when relevant for the task. The authors suggested that this symbolic to nonsymbolic mapping is not a requirement for all symbolic number processing tasks (Sasanguie, Göbel, & Reynvoet, 2013). In contrast, it should be noted that, using multivoxel pattern analysis, Bulthé et al. (2014) observed no neural overlap between Arabic numerals and dot representations. Moreover, there was also no neural indication of the symbolic distance effect (i.e., better performance when comparing two numerically distant vs. two numerically close numbers; Pinel, Dehaene, Rivière, & Le Bihan, 2001; Buckley & Gillman, 1974; Moyer & Landauer, 1967). The distance effect is typically suggested to act as a signature for numerical processing, because it is assumed to originate from an overlap in the representation of numerical stimuli on a mental number line (e.g., Cohen Kadosh et al., 2005). Thus, multivoxel pattern analysis (Bulthé et al., 2014) did not directly show no overlap of numerical processing of symbolic versus nonsymbolic.

To summarize, most findings point to a neural spatial overlap between the processing of symbolic and nonsymbolic numerical systems; however, the type of interactions between the different modalities has not been fully proven (for a review, see Reynvoet & Sasanguie, 2016; for meta-analysis, see Sokolowski et al., 2017), and relatively little is known about the neural generators of the combined neural signature.

Symbolic and Nonsymbolic Systems: Neural Timing

The notion of a spatial neural overlap between symbolic and nonsymbolic numerical systems has also received support from recorded EEG ERP data. For example, Gebuis, Kenemans, de Haan, and van der Smagt (2010) found equal processing time (i.e., P3 waveform; showing the largest peak within the time window of 300–800 msec after stimulus presentation), reflecting stimulus evaluation, for both symbolic as well as nonsymbolic numerical presentations, beginning from fourth grade (Gebuis, Herfs, Kenemans, de Haan, & van der Smagt, 2009). Gómez-Velázquez, Berumen, and González-Garrido (2015) also found equal neural activations for both symbolic as well as nonsymbolic numerical systems in 8- to 10-year-old children with low, average, and high levels of mathematical achievement. Specifically, and similar to Gebuis et al. (2009), Gómez-Velázquez et al. reported no main effect of format in their analysis of the positive component between 440 and 560 msec (P3) found in both symbolic and nonsymbolic tasks. Indeed, previous studies have also found that the main effect of numerical distance is observed in the P2p waveform in both the symbolic and nonsymbolic formats (e.g., Libertus et al., 2007; Temple & Posner, 1998; but see also the P2p in numerical processing when only the nonsymbolic format was investigated [Smets et al., 2013; Hyde & Spelke, 2012] or when only symbolic numbers were investigated [Dehaene, 1996]; however, see Soltész & Szűcs, 2014). The P2p usually peaks at around 230 msec, and it is found at temporo-occipital and inferior parietal electrode groups (Smets et al., 2013). Hence, this early P2p ERP component has been proposed to “reflect an abstract and notation-independent neural activation that is invoked for both symbolic and nonsymbolic numerical processing” (Libertus et al., 2007, p. 13).

The review above suggests that the separate behavioral processes of symbolic and nonsymbolic systems take place at the same neural time and in spatially overlapping neural networks. Thus, here we aimed to search for the distinct neural dynamics that underlies these two possibly distinct behavioral processes.

EEG Oscillations and Cognition

In the past two decades (e.g., Cohen, 2017), general agreement has gradually increased among neuroscientists that

the neuronal oscillations commonly observed in the ongoing scalp EEG can be taken to be a system-level image of latent changes in neuronal coherence (see also Bastiaansen, Mazaheri, & Jensen, 2012; Varela, Lachaux, Rodriguez, & Martinerie, 2001). The argument is that neuronal oscillations affect the probability of spiking, such that action potentials have a greater chance of occurring during episodes of interregional oscillatory unity (Voytek & Knight, 2015). That is, brain regions activated by cognitive operations show increased coherence (neuronal cooperation) within certain frequency bands, depending on the nature and difficulty of the task (e.g., Uhlhaas, Roux, Rodriguez, Rotarska-Jagiela, & Singer, 2010; Ward, 2003). It is argued that every mental operation is accompanied by characteristic coherence patterns (e.g., for a review, see Bastiaansen et al., 2012). These insights can lead to the establishment of an empirical relationship between event-related changes in EEG oscillations, on the one hand, and aspects of cognition, on the other.

The application analysis to EEG data concentrated on particular phases of oscillatory cycles during numerical processing may prove a relevant tool for investigating rhythmic neural activity accompanying numerical function. Yet, and to the best of our knowledge, only a handful of studies on a similar topic (i.e., using EEG analysis) have been performed in numerical cognition studies (e.g., Hsu & Szűcs, 2012; Berger, 2011; Tzur, Berger, Luria, & Posner, 2010; Tzur & Berger, 2007).

Specific EEG Oscillations and Numerical Cognition: Beta and Gamma Bands

Within this context, a number of studies have focused on the relationship between oscillatory EEG dynamics and cognitive functions that may also be related to numerical cognition. For example, beta-band activity (12–30 Hz in humans) in parietal electrodes has been found to play a significant role in visuospatial processing, such as in RTs during maze learning (Caplan, Madsen, Raghavachari, & Kahana, 2001) and in the integration of visual features (Costa, Duarte, Martins, Wibrál, & Castelo-Branco, 2017). In addition, there is a growing consensus that beta oscillations are involved in time estimations (Wiener, Parikh, Krakow, & Coslett, 2018; Kononowicz & van Rijn, 2015). For example, Kononowicz and van Rijn (2015) have shown an increase in beta oscillation in central and parietal electrodes 600 msec poststimulus. Using MEG, time–frequency analysis showed an increase in beta band (16–32 Hz) when even only looking at numbers compared with nonnumerical stimuli over frontal and parietal regions for up to 700 msec. This pattern begins at stimulus onset (Peyton, Rubin, Pantanowitz, Kleks, & Teicher, 2016). Importantly, beta signature was also found during temporal counting (the task was to assess the quantity of discrete items) in a working memory task, within and across sensory modalities (visual, auditory, and tactile). Hence, beta oscillations were suggested to reflect the degree to which quantities were

estimated (Spitzer, Fleck, & Blankenburg, 2014). Similarly, upper beta-band amplitude (20–30 Hz) was modulated when participants estimated which of two sequentially presented vibrotactile stimuli had a higher frequency (Herding, Spitzer, & Blankenburg, 2016).

Together, these studies suggest a role for neuronal patterns of activation within the beta band in visuospatial processing and in time, as well as in numerical estimations. Hence, it may be relevant to study beta-band activity during the processing of nonsymbolic numerical information, because the nonsymbolic numerical system has been suggested to rely mostly on visuospatial cognitive abilities (Gallistel & Gelman, 2000) and to involve quantity approximations (e.g., Lyons, Ansari, et al., 2015; Barth et al., 2008). In addition, it has been suggested that time and numerical estimations are cognitively linked (Walsh, 2003).

To formulate our neural hypotheses for linguistic processing, we looked at EEG investigations of reading and language. Here, studies suggest a link between gamma band (above 30 Hz) and language (Hauk, Giraud, & Clarke, 2017; Mainy et al., 2008; Crone, Boatman, Gordon, & Hao, 2001), specifically with sublexical, phonological, lexical (e.g., Van Berkum, Zwitserlood, Bastiaansen, Brown, & Hagoort, 2004), and syntactic information (for a review, see Kösem & van Wassenhove, 2017), in addition to the ongoing semantic unification operations (Bastiaansen & Hagoort, 2006). For example, an increase in gamma power (40–60 Hz/60–70 Hz) was found across semantically correct (vs. incorrect) sentences (Bastiaansen & Hagoort, 2015; Rommers, Dijkstra, & Bastiaansen, 2013). Importantly, Salillas, Barraza, and Carreiras (2015) found that the type of initial language learning has an effect on basic numeric representations by showing that gamma-band (43–46 Hz) synchronization appears 150–250 msec after Basque–Spanish bilinguals compare pairs of Arabic numerals linked through the Basque base-20 wording system, but not when the pairs are related through the base-10 system. This gamma activity appeared only in bilinguals who learned math in Basque and not in equivalent proficiency bilinguals who learned math in Spanish.

In summary, then, there is considerable evidence in the literature that gamma-band frequencies are predominantly related to semantic or linguistic operations. As mentioned earlier, it is suggested that the numerical symbolic system is influenced by language and culture (Gunderson et al., 2015; Bender et al., 2014). Within the language domain and based on previous findings (Vanbinst et al., 2016), it is suggested here that basic symbolic numerical comparisons involve early cognitive linguistic processes that are analogous, for example, to phonological awareness while reading. Hence, it may be highly reasonable to test the links between gamma-band neural activation and symbolic processing.

It is therefore intriguing to relate these findings to the question that we addressed earlier: How does the brain segregate the processes of symbolic and nonsymbolic

numerical systems, given that both cognitive systems (symbolic and nonsymbolic) appear to be subserved by largely overlapping neuronal tissue (in the parietal lobes) and that they occur roughly in the same time frame (within a few hundred milliseconds after stimuli presentation)? Tentatively, we therefore propose a frequency-based segregation of symbolic and nonsymbolic systems with a specific focus on beta band, which is hypothesized to be predominantly related to visuospatial and numerical estimation processing while gamma band is hypothesized to be related to semantic or linguistic operations. Establishing such a frequency-based segregation would constitute an important step toward understanding the neural underpinnings of numerical processing.

The Current Study

In this article, we report a within-participant behavioral and electrophysiological investigation of the effects of symbolic (i.e., Arabic numerals) and nonsymbolic (i.e., dot arrays) numerical processing. A within-participant study of basic symbolic versus nonsymbolic numerical processing is generally uncommon in the field of numerical cognition and specifically in EEG studies. Here, we administered the well-known measures of nonsymbolic and symbolic magnitude comparison, during which typically developing university students compared smaller versus larger ratios of either two Arabic numerals or two dot arrays, under otherwise identical experimental conditions.

One major signature of numerical representations is that comparisons are subject to a ratio (minimum/maximum) limit: Accuracy decreases while RT increases as the ratio of the compared numbers approaches 1 (for a review, see, e.g., Cantlon, Platt, & Brannon, 2009). It is suggested that when the ratio between two numerals is closer to 1, the numbers to be compared share more cognitive representational overlap compared with numbers that are further apart (e.g., Vogel, Goffin, & Ansari, 2015) and hence may act as a signature of the mental number line. Therefore, it is harder to compare or calculate numbers with ratios closer to 1 (e.g., a comparison of 35 and 41, with a ratio of 0.85, is more difficult than a comparison of 15 and 21, with a ratio of 0.7; e.g., Vogel et al., 2015). However, when the ratio is closer to 0 (i.e., cognitively further apart), an approximate strategy can be utilized (Dehaene & Changeux, 1993). In contrast to previous investigations (e.g., Bulthé et al., 2014) and to tap approximate versus exact/linguistic processing, we used large quantities (ranging from 3 to 90). Thus, here we included an analysis of numerical ratio to investigate whether neural activations elicited by the EEG analysis are sensitive to the linguistic versus approximate dimensions of numerical magnitudes for both stimulus formats.

Using wavelet analysis, we studied oscillatory EEG signals to test the hypothesis that symbolic and nonsymbolic numerical processing are segregated by means of

frequency ranges: gamma (50 Hz and up) for exact linguistic processing and beta (10–17 Hz) for approximate processing. If our proposal is correct, we would expect relatively larger beta power for larger (0.8) nonsymbolic numerical ratios than for smaller (0.2) nonsymbolic numerical ratios. Similarly, we would expect relatively larger gamma power for large symbolic ratios compared with small symbolic ratios. It is important to note that, even though the ERP/EEG methodology has poor spatial resolution, current findings may also suggest or at least point to symbolic and nonsymbolic processing that is segregated by means of spatial location. Finally, neuronal oscillations are considered latent changes in neuronal coherence (Bastiaansen et al., 2012; Varela et al., 2001), which affect the probability (Voytek & Knight, 2015) of mental operations (e.g., for a review, see Bastiaansen et al., 2012) such as numerical processing. Hence, we assume that both the currently hypothesized beta and gamma effects would appear earlier than the P2p ERP component, which is typically found in both symbolic and nonsymbolic numerical comparisons (Gómez-Velázquez et al., 2015) and is suggested to indicate fast and automatic processing of numerical magnitudes (Dehaene, 1996).

METHODS

Participants

In previous neural analyses of basic numerical processing with adults, researchers used 24 participants (Smets et al., 2013; Gebuis & Reynvoet, 2012). Gebuis and Reynvoet (2012) found a medium effect size for numerosity on P2p at parietal areas ($\eta_p^2 = .24-.39$). Using G*Power 3.1.9.2, we calculated that, at the current setup, with an expected effect size f of 0.4 (a conservative view instead of the effect size f of 0.56 reported by Gebuis & Reynvoet, 2012), a sample size of 23 would be sufficient. As we expected that 10% of participants would drop at analysis, we recruited 26 participants.

Thus, 26 right-handed female university students participated in the experiment in exchange for a fee or course credits. All reported normal or corrected-to-normal vision, with no history of neurological problems. Two participants were rejected because of excessive noise on high frequencies. Thus, behavior and ERPs from 24 participants (mean age = 26.5 years, $SD = 4.96$ years) were analyzed.

Ethics Statement

The recruitment, payment, tasks, and overall procedure were authorized by the Research Ethics Committee of Haifa University and by the Research Ethics Committee of the Faculty of Education. All methods and experimental protocol were approved by the Research Ethics Committee of Haifa University (#123/09) and by the Research Ethics Committee of the Faculty of Education

(#144/14) and were carried out in accordance with the approved guidelines. In addition, informed consent was obtained from all participants.

Procedure—General

Participants performed numerical comparisons presented as arrays of dots (nonsymbolic) or Arabic numerals (symbolic). The numerical comparisons task (symbolic and nonsymbolic) was administered while both behavioral measures (accuracy rates [ACC] and RTs) as well as EEGs were recorded. All materials were computerized and presented with E-Prime 2.0 (Psychological Software Tools) on an HP computer, using a Samsung S23A950D 23-in. screen display with a resolution of 1024×768 .

Numerical Comparisons: General Description of Both Tasks (Symbolic and Nonsymbolic)

We conducted nonsymbolic and symbolic numerical comparison tasks developed on the basis of the widely used numerical comparison task (e.g., with manipulation of numerical ratio [Sasanguie et al., 2017; Price & Fuchs, 2016] or manipulation of numerical distance [Xenidou-Dervou, Molenaar, Ansari, van der Schoot, & van Lieshout, 2017]).

Here, the ratio between the two compared numerosities was manipulated. It should be noted that previous studies investigating the links between number comparison and brain activation frequently used numerical distance (e.g., Gebuis et al., 2009; Pinel et al., 2001) rather than numerical ratio as an independent variable. However, because the current main research question involves a comparison between symbolic and nonsymbolic representations and because manipulation of ratio is the only possible course of action in the case of large nonsymbolic quantities, we manipulated ratio and not distance. Importantly, numerical ratio and distance are highly correlated (e.g., Bugden, Price, McLean, & Ansari, 2012). Similarly, in this study, the average numerical distance was 38 for the small ratio trials and 6 for the large ratio trials. Consistent with this, the correlation between ratio and distance for the trials used was very high, $r(80) = -.674, p < .001$.

As in other recent studies (Sasanguie et al., 2017; Price & Fuchs, 2016), in the current study two types of ratio were used, small (0.2) and large (0.8), which allowed us to model the effect of symbolic and nonsymbolic numerical ratios on the oscillations' response; ratios of 0.4 and 0.6 were used as fillers, a common practice in the EEG literature (e.g., Núñez-Peña & Suárez-Pellicioni, 2014).

Thus, each experimental task consisted of 80 experimental trials and 80 fillers. Feedback on accuracy was provided only during practice trials. In each trial, the participant saw two numerosities (i.e., either two Arabic numerals in the symbolic task or two dot arrays in the nonsymbolic task), 0.5° to the right and the left side of the screen (see Figure 1).

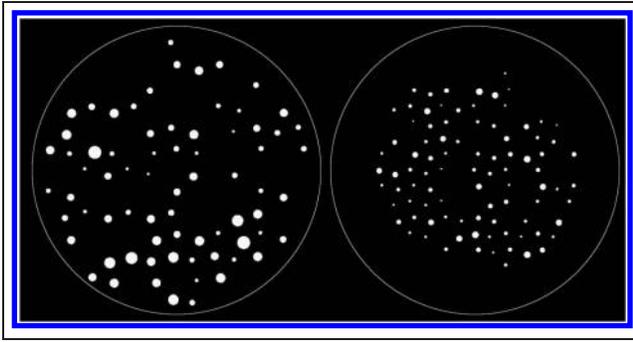


Figure 1. An example of a nonsymbolic comparison.

Before each task (symbolic and nonsymbolic), the participant completed eight practice trials. In both the practice and experimental tasks, participants were asked to identify which numerosity was larger by pressing the left or right button on a response box situated in front of them. In half of the trials, the larger numerosity was presented on the right side of the screen and in the other half, on the left. Participants were instructed to respond as correctly and as fast as possible.

Each condition began with a fixation circle (we avoided the use of a cross “+” or asterisk “*” to prevent association with addition or multiplication) for 500 msec, followed by an intertrial interval of 200–250 msec to prevent contingent negative variation (Tecce, 1972). The response interval lasted until an answer was provided, followed by an intertrial interval of 700 msec.

Nonsymbolic Numerical Comparisons

As depicted in Figure 1, the nonsymbolic stimuli were composed of two dot arrays (white on a black background) presented simultaneously. There were five options for each amount, selected randomly. Each picture’s size was 196 × 196 pixels. Both pictures were presented within a visual angle of 7.6°.

Nonsymbolic task: Control of continuous visual properties. It should be noted that each nonsymbolic stimulus has, in addition to its numerical value, continuous visual properties. The continuous visual properties consist of convex hull (the contour of the smallest polygon built around the dots), total dots, surface, average dot size, density, and contour (the smallest circle containing all the dots).

The continuous visual properties of dot arrays are usually correlated with each other (Leibovich & Henik, 2014). In some cases, this correlation can result in multicollinearity. Multicollinearity is commonly assessed using three tests (Meyers, Gamst, & Guarino, 2006): cross-correlation > .8, variance inflation factor (VIF) > 10, and tolerance < 0.1 (Leibovich & Henik, 2014). Multicollinearity can

yield regression weights that are poor reflections of variable relationships and complex results that are hard to interpret (Mason & Perreault, 1991). As no indication of multicollinearity was available in our data (see Tables 1 and 2), we performed a stepwise regression to check for effects of continuous properties on RT and accuracy.

Two multiple stepwise regressions were performed to evaluate whether ratio and continuous properties are able to predict RT and ACC. The regression was conducted in two blocks; in the first block, the ratio was entered and found significant, $r = .681$, $F(1, 116) = 100.448$, $p < .001$. Approximately 46.4% of the variance in the RT was due to the change in ratio. In the second block, all five continuous properties were entered using stepwise conditioning ($p < .05$ for enter, $p > .1$ for remove), and total dot surface was the only one found to have significant added value, $F(2, 115) = 54.764$, $p < .001$, with added variance explaining 2.4%, for a total of 48.8% of the explained variance in RT.

In the first block, ratio was entered to predict accuracy. Ratio was strongly correlated with accuracy, $r = .573$, $F(1, 116) = 56.737$, indicating that ratio can explain 32.8% of the variance in accuracy. In the second block, average dot size was found to have a significant added value of 5.8%, $F(2, 115) = 36.217$, for a total of 37.6% of the total variance explained. These tests indicate that participants responded primarily based on numerical ratio and not based on the visual continuous properties.

Symbolic Numerical Comparisons

The symbolic comparison task was identical to the nonsymbolic task, with the key difference being that the corresponding Arabic numerals now replaced the dot stimuli. All stimuli were presented in Courier New size 36.

Table 1. Cross-correlation between Continuous Visual Properties

	1	2	3	4	5
1. Convex hull	—	.701**	-0.171	.218*	.771**
2. Total dot surface		—	.402**	.550**	.544**
3. Density			—	.215*	-.224*
4. Average dot size				—	.216*
5. Contour					—

$n = 118$. A significant correlation was found between convex hull and total dot surface, average dot size, and contour; total dot surface and density, average dot size, and contour; density and average dot size and contour; and average dot size and contour. Although continuous visual properties are cross-correlated, no correlation exceeds the value of .8. Thus, cross-correlation analysis reveals no sign of multicollinearity.

* $p < .05$.

** $p < .01$.

Table 2. Tolerance and VIF Analysis of Continuous Visual Properties

	1		2		3		4		5	
	Tolerance	VIF								
1. Convex Hull	—	—	0.402	2.486	0.272	3.681	0.216	4.621	0.224	4.470
2. Total dot surface	0.322	3.106	—	—	0.343	2.914	0.222	4.503	0.152	6.579
3. Density	0.556	1.800	0.877	1.140	—	—	0.414	2.414	0.400	2.502
4. Average dot size	0.682	1.466	0.874	1.144	0.638	1.567	—	—	0.588	1.699
5. Contour	0.460	2.173	0.391	2.560	0.402	2.488	0.384	2.603	—	—

Tolerance values range from 0.152 to 0.682; none dips below 0.1. VIF scores range from 1.14 to 6.579; none exceeds a value of 10. Tolerance and VIF analysis of the continuous visual properties reveal no sign of multicollinearity.

Data Acquisition and Analysis

EEG Recording

The EEG analog signals were recorded continuously (from DC with a low-pass filter set at 100 Hz) from 64 Ag–AgCl pin-type active electrodes mounted on an elastic cap (Biosemi, www.biosemi.com/headcap.htm), according to the extended 10–20 system. All electrodes were referenced during recording to a common mode signal electrode between POz and PO3 and were subsequently re-referenced digitally (see Data Processing section below). Eye movements, as well as blinks, were monitored using bipolar horizontal and vertical EOG derivations via two pairs of electrodes, with one pair attached to the external canthi and the other to the infraorbital and supraorbital regions of the right eye. Both EEG and EOG were digitally amplified and sampled at 512 Hz, using a Biosemi Active II system (www.biosemi.com).

Data Processing

Data were analyzed using Brain Vision Analyzer software (Brain Products). Raw EEG data were initially 0.5 Hz high-pass and 30 Hz low-pass filtered (24 dB) and re-referenced off-line to the digital average of the 64 electrodes. For the wavelet analysis, a 100-Hz low-pass filter with 50-Hz notch was used on the raw data, instead of the 30-Hz low-pass on the raw data. EEG deflections resulting from eye movements and blinks were corrected using an independent component analysis procedure (Jung et al., 2000). Remaining artifacts exceeding ± 100 μ V in amplitude, a voltage step of over 50 μ V, or low activity of under 0.5 μ V change over 100 msec were rejected.

Analysis

Behavioral Analysis

Similar to previous studies (Pfister, Schroeder, & Kunde, 2013; Kiesel & Vierck, 2009), for the RT analysis, incorrect trials and outliers were omitted. Trials were counted as outliers when the RT deviated from the corresponding task–ratio mean by more than 2.5 SDs, calculated separately

for each participant. The number of omitted outlier trials ranged from 6 to 11 per participant. Accuracy rates (ACC) were defined as the amount of correct trials per ratio, regardless of RTs. A repeated-measures ANOVA with Task (symbolic, nonsymbolic) and Ratio (0.2 and 0.8) was performed to determine the effect of ratio on RT and ACC.

ERP Analysis

For reasons of focus and based on prior scientific findings such as the work of Smets et al. (2013) (as well as Gebuis & Reynvoet, 2012; Dehaene, 1996, see Introduction), we investigated the involvement of P2p waveform with symbolic and nonsymbolic numerical comparisons (e.g., Gómez-Velázquez et al., 2015). Based on Gebuis and Reynvoet (2012) and Smets et al. (2013), we analyzed parieto-occipital electrodes: O1, O2, PO3, PO4, PO7, and PO8 (see Figure 2).

Accordingly, ERPs were analyzed in two separate analyses of a mixed design three-way ANOVA, Task (2) \times Ratio (2) \times Electrode (6). One analysis included latencies as within-participant variables, and the other included amplitude. The averaged segments were baseline-corrected to 200 msec before stimulus onset. For each participant, the peak of the P2p was determined as the most positive peak between 180 and 300 msec. Subsequent visual scrutiny ensured that this value represented real peaks rather than end points of the epoch (Foti, Hajcak, & Dien, 2009; Campanella et al., 2002).

Wavelet Analysis

Data were segmented into epochs, starting from 500 msec before stimulus onset until 1000 msec poststimulus. A continuous wavelet transform with a standardized Morlet complex ($c = 5$) was chosen (Van der Lubbe & Utzerath, 2013)—for the high frequencies, 30 steps ranging from 30 to 80 Hz in logarithmic steps, and for the low frequencies, 18 steps ranging from 12 to 30 Hz in logarithmic steps. Gabor normalization was used in both cases (Van der Lubbe & Utzerath, 2013). Channels were baseline-corrected based on the 200 msec before stimulus and normalized

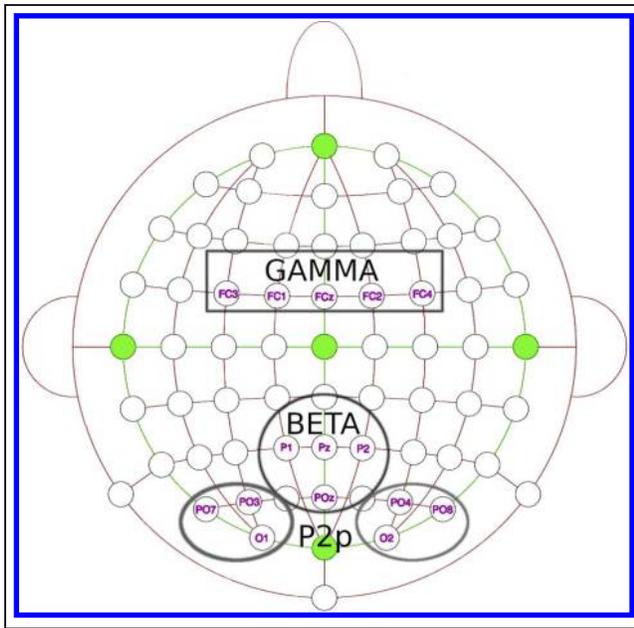


Figure 2. Layout of electrode used.

based on the -500 to -200 msec time window (Van der Lubbe & Utzerath, 2013). Please note that the baseline correction and normalization cannot be done on the same time points as a baseline function and set the total of the values in the defined time domain to 0, and if a normalization function were to be performed at the same time, it would try to classify this 0 total as 100%. The wavelet analysis was performed on single trials, and the resulting single-trial spectrograms of the absolute values were averaged. These averages thus include the activity that is phase locked to the stimulus (Yuval-Greenberg, Tomer, Keren, Nelken, & Deouell, 2008). For the high-frequency analysis and based on Schadow et al. (2007) and Völker et al. (2018), as well as based on a meta-analysis of fMRI studies that compared symbolic and nonsymbolic numbers (Sokolowski et al., 2017), the following electrodes, FC1, FC2, FC3, FC4, and FCz (i.e., frontocentral cluster), with a time range of 140–180 msec poststimulus were selected. Please note that wavelet analysis on four to five electrodes is a common practice (e.g., Yuval-Greenberg et al., 2008; Demiralp et al., 2007). The use of these specific electrodes as well as this specific time window was ultimately data driven yet is also supported by previous neural oscillation findings with schizophrenic patients (Koychev, El-Deredy, Mukherjee, Haenschel, & Deakin, 2012; Koychev, Deakin, Haenschel, & El-Deredy, 2011). We extracted Layers 17–30 (51–80 Hz). For the low-frequency analysis and based on previous studies (e.g., Erickson, Albrecht, Robinson, Luck, & Gold, 2017), we analyzed a parietal cluster, including the P1, P2, Pz, and POz electrodes (similar clusters can be found in Avancini, Soltész, & Szűcs, 2015; Szűcs & Soltész, 2008), with a data-driven optimized time window of 75–150 msec poststimulus presentation. Namely, given that

each participant showed a P2p peak that ranged between 180 and 300 msec and because we are looking for frequency-based activation, before P2p wave (based on the current research question), we chose a second and more narrow time window ranging between 75 and 150 msec poststimulus presentation.

We extracted Layers 1–4 (12–17 Hz; for analysis of a broader time window and frequency range, see Appendices A1 and A2).

As mentioned above, part of the preprocessing included a 50-Hz notch. This digital suppression of frequencies can result in misinterpretation of the data. Hence, many studies (Karch et al., 2016; Minzenberg, Yoon, Cheng, & Carter, 2016; Ball et al., 2008) analyzed only the upper gamma (frequency $> 51/55/60$ Hz) or lower (frequency $< 40/45/49$). Here, we focus on higher cognitive functions; therefore, we chose to focus on the high gamma frequencies (Uhlhaas, Pipa, Neuenschwander, Wibral, & Singer, 2011; Mainy et al., 2008).

A three-way ANOVA with the factors of Task (symbolic, nonsymbolic), Ratio (0.8, 0.2), and Electrodes (4 for beta/5 for gamma) was conducted on the average power.

Bayesian Statistics

We followed up the results using Bayesian statistics. Specifically, we computed Bayes factors (BF), which express the ratio between the evidence in favor of the hypothesis relative to the null hypothesis. BFs were calculated according to Dienes, Coulton and Heather (2018) using a half-normal model of H1.

For the behavioral results, we used priors taken from Lyons et al. (2012, Experiment 1). For the P2p, priors were taken from Libertus et al. (2007, Experiment 1 for symbolic P2p and Experiment 2 for nonsymbolic P2p). As no priors could be achieved for the beta- and gamma-band analysis, we used JASP 0.9.1 (JASP Team, 2018), with default values (Arciuli & Bailey, 2019; Trueblood et al., 2018). See Table 3 for BF calculations.

RESULTS

Behavioral

RT

A repeated-measures ANOVA was performed to determine the effect of ratio on RT. Results revealed a significant main effect for Ratio, $F(1, 23) = 33.038, p < .001, \eta_p^2 = .59, BF_{10} = 88.76$ (see Figure 3A) and Task \times Ratio interaction, $F(1, 23) = 7.838, p < .01, \eta_p^2 = .254, BF_{10} = 3.62$, with no main effect for Task, $F(1, 23) = 3.007, ns, BF_{10} = 2.38$.

Post hoc t tests on the different tasks revealed a significant increase in RT in both symbolic, $t(23) = 11.291, p < .001, BF_{10} > 100,000$, and nonsymbolic conditions, $t(23) = 4.244, p < .001, BF_{10} = 14.53$, between the 0.2 ratio (sym: $M = 571.219, SE = 17.059$; nonsym: $M = 509.232$,

Table 3. BF Calculations

	Priors	Sample Mean	Sample SE	BF ₁₀
<i>RT</i>				
Ratio	56.5	358	62	88.76
Task	34.5	126	73	2.38
Ratio × Task	69	377	134	3.62
Symbolic	41	170	15	> 100,000
Nonsymbolic	72	546	129	14.53
<i>ACC</i>				
Ratio	10.7%	9.4%	0.8%	> 100,000
Task	9.4%	5.9%	1.2%	16,557.37
Ratio × Task	20.5%	10.4%	1.5%	> 100,000
Symbolic	0.4%	4.2%	0.7%	215.7%
Nonsymbolic	20.9%	14.6%	1.4%	> 100,000
<i>P2</i>				
Ratio	0.95	1.192	0.242	42,798.21
Task	0.016	1.455	0.365	867.57
Ratio × Task	0.7	0.06	0.51	0.63
Symbolic	1.3	1.222	0.330	311.21
Nonsymbolic	0.6	1.162	0.373	35.22

$SE = 17.059$) and the 0.8 ratio (sym: $M = 741.133$, $SE = 21.086$; nonsym: $M = 1055.713$, $SE = 141.409$). A BF of more than 3 is considered substantial evidence for H1, whereas a BF of less than 1/3 is considered substantial evidence for the null hypothesis (Jeffreys, 1961). The Bayesian analysis confirms that the probability that ratio affected RTs is over 100,000 times more likely for the symbolic stimuli and 14 times for the nonsymbolic than the null hypothesis.

Accuracy Rates

A repeated-measures ANOVA was performed to determine the effect of ratio on accuracy rates. Results revealed a significant main effect for Ratio, $F(1, 23) = 124.92$, $p < .001$, $\eta_p^2 = .845$, $BF_{10} > 100,000$ (see Figure 3B); task, $F(1, 23) = 22.504$, $p < .001$, $\eta_p^2 = .495$, $BF_{10} = 16,557.37$; and Task × Ratio interaction, $F(1, 23) = 48.623$, $p < .001$, $\eta_p^2 = .679$, $BF_{10} > 100,000$.

Post hoc t tests on the different tasks revealed the typical ratio effect, as indicated by a significant decrease in accuracy in both symbolic, $t(23) = 6.156$, $p < .001$, $BF_{10} = 215.74$, and nonsymbolic conditions, $t(23) = 10.17$, $p < .001$,

$BF_{10} > 100,000$, between the 0.2 ratio (sym: $M = 99.58\%$, $SE = 0.169\%$; nonsym: $M = 98.92\%$, $SE = 0.834\%$) and the 0.8 ratio (sym: $M = 95.38\%$, $SE = 0.678\%$; nonsym: $M = 84.29\%$, $SE = 1.814\%$). BF confirms that ratio was the main reason for the difference in accuracy rates.

ERP Data

Repeated-measures ANOVAs of mean amplitudes and latency of parieto-occipital electrode groups in the 180–300 msec poststimulus time windows (P2p), revealed a significant effect for Ratio on both amplitude and latency (amplitude: $F(1, 23) = 24.217$, $p < .001$, $\eta_p^2 = .513$, $BF_{10} = 42,798.21$; latency: $F(1, 23) = 25.126$, $p < .001$, $\eta_p^2 = .522$; Figure 4) as well as Task (amplitude: $F(1, 23) = 15.929$, $p < .001$, $\eta_p^2 = .409$, $BF_{10} = 867.57$; latency: $F(1, 23) = 20.366$, $p < .001$, $\eta_p^2 = .470$), with no interaction (amplitude: $F(1, 23) < 1$, ns ; latency: $F(1, 23) < 1$, ns , $BF_{10} = 0.63$).

Because of the a priori hypothesis, as well as based on previous literature (e.g., Gebuis & Reynvoet, 2012; Libertus et al., 2007) and current behavioral findings, we calculated the different ratios in each task separately. Repeated-measures ANOVA found a significant effect for Ratio in both tasks (symbolic: amplitude, $F(1, 23) = 13.731$, $p < .001$, $\eta_p^2 = .374$, $BF_{10} = 311.21$; latency, $F(1, 23) = 8.594$, $p < .01$, $\eta_p^2 = .272$; nonsymbolic: amplitude, $F(1, 23) = 9.732$, $p < .01$, $\eta_p^2 = .297$, $BF_{10} = 35.22$; latency, $F(1, 23) = 12.996$,

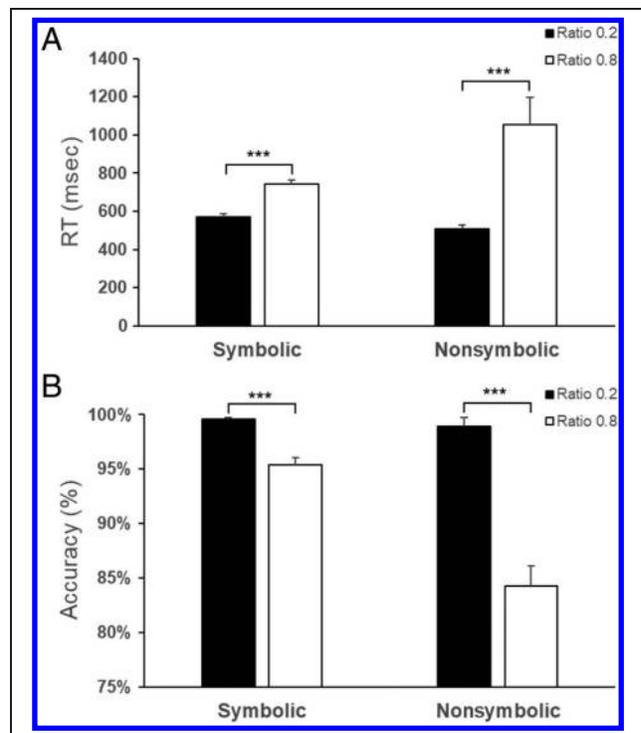


Figure 3. Behavioral effects: RT and accuracy rates in the comparison tasks. (A) RT in msec, significant effect for task, ratio, and interaction. Significant effect for ratio in both symbolic and nonsymbolic tasks. (B) Accuracy rates, significant effect for Task, Ratio, and interaction. Significant effect for Ratio in both tasks. *** $p < .001$.

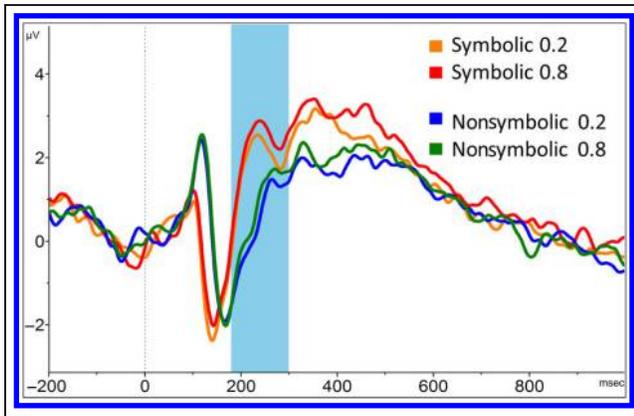


Figure 4. P2p wave. Figure 4 shows average ERPs for symbolic and nonsymbolic tasks in 0.2 and 0.8 ratios. A significant main effect for Task and Ratio (amplitude: $p < .001$; latency: $p < .001$). Significant effect for Ratio in both tasks (amplitude: $p < .001$; latency: $p < .001$).

$p < .001$, $\eta_p^2 = .361$), with higher ratios in each of the tasks, resulting in a more positive delayed peak.

In addition, a significant effect for Electrode (amplitude: $F(1, 23) = 9.874$, $p < .001$, $\eta_p^2 = .3$, $BF_{10} > 100,000$; latency: $F(1, 23) = 4.099$, $p < .01$, $\eta_p^2 = .151$, $BF_{10} = 0.476$), Electrode \times Task only in amplitude (amplitude: $F(1, 23) = 4.0316$, $p < .01$, $\eta_p^2 = .149$, $BF_{10} = 3.588$; latency: $F(1, 23) = 1.038$, ns , $BF_{10} = 0.017$), and Electrode \times Ratio (amplitude: $F(1, 23) = 2.583$, $p < .05$, $\eta_p^2 = .1$, $BF_{10} = 0.068$; latency: $F(1, 23) = 3.997$, $p < .01$, $\eta_p^2 = .148$, $BF_{10} = 0.118$), with no Electrode \times Task \times Ratio interaction (amplitude: $F(1, 23) < 1$, ns , $BF_{10} < 0.000001$; latency: $F(1, 23) < 1$, $BF_{10} < 0.000001$). Overall, despite difference between the electrodes, when looking at the effect sizes and Bayesian factors together, none of the interaction seems to point in a certain direction.

Wavelet Data

Gamma Band

Repeated-measures ANOVA of the average high-gamma power revealed a significant effect for Ratio, $F(1, 23) = 9.293$, $p < .01$, $\eta_p^2 = .288$, $BF_{10} = 1,226.198$ (see Figure 5A), as well as Task \times Ratio interaction, $F(1, 23) = 5.374$, $p < .05$, $\eta_p^2 = .189$, $BF_{10} = 22.732$, with no main effect for Task, $F(1, 23) = 1.556$, ns , $BF_{10} = 1.022$. No main effect for Electrode, $F(4, 92) < 1$, ns , $BF_{10} = 0.014$, or interactions were present (Task: $F(4, 92) < 1$, ns , $BF_{10} = 0.017$; Ratio: $F(4, 92) = .098$, ns , $BF_{10} = 0.013$; Task \times Ratio: $F(4, 92) = .735$, ns , $BF_{10} < 0.001$).

Post hoc tests revealed that the source of the interaction was a significant difference in the symbolic task, $F(1, 23) = 9.839$, $p < .01$, $\eta_p^2 = .3$, $BF_{10} > 100,000$, as the higher (symbolic) ratios elicit an increase in the gamma power. In contrast, no such difference (of ratios) was found in the nonsymbolic task, $F(1, 23) < 1$, ns , $BF_{10} = 0.222$. The BF analysis indicates that the Task \times Ratio interaction is 22.732 times more likely than the null hypoth-

esis. In the symbolic condition, a BF greater than 100,000 (i.e., over 100,000 times more likely than the null hypothesis) was found, whereas in the nonsymbolic condition, the BF was 0.222. Hence, the Bayesian analysis clearly provides substantial evidence for a ratio effect for the symbolic but not for nonsymbolic ratios in the gamma band.

Beta Band

Repeated-measures ANOVA of the average low-beta power revealed a significant effect for Task, $F(1, 23) = 9.378$, $p < .01$, $\eta_p^2 = .29$, $BF_{10} = 9648.012$ (see Figure 5B), as well as Task \times Ratio interaction, $F(1, 23) = 4.745$, $p < .05$, $\eta_p^2 = .171$, $BF_{10} = 5.756$, with no effect for Ratio, $F(1, 23) = 2.553$, ns , $BF_{10} = 0.253$.

In addition, over this parietal cluster, there was a significant effect for Electrode, $F(3, 69) = 59.042$, $p < .001$, $\eta_p^2 = .72$, $BF_{10} > 100,000$. Pz showed lower beta power compared with POz ($p < .05$), and both showed lower power compared with P1 and P2 ($p < .05$). However, all interactions with electrodes were not significant (task: $F(3, 69) = 1.417$, ns , $BF_{10} = 0.08$; ratio: $F(3, 69) = 1.956$, ns , $BF_{10} = 0.07$; Task \times Ratio: $F(3, 69) = 1.947$, ns , $BF_{10} < 0.001$). This finding suggests that despite global power difference, the electrode in the parietal cluster respond similarly under the different conditions (e.g., note the BF ranging from 0.08 to 0.001).

Post hoc tests revealed that the source of the interaction is a significant difference of ratios in the nonsymbolic task, $F(1, 23) = 6.448$, $p < .05$, $\eta_p^2 = .219$, $BF_{10} = 3.703$, with higher ratios showing a significant increase in the beta power. In contrast, no such difference was found in ratios of the symbolic task, $F(1, 23) < 1$, ns , $BF_{10} = 0.223$.

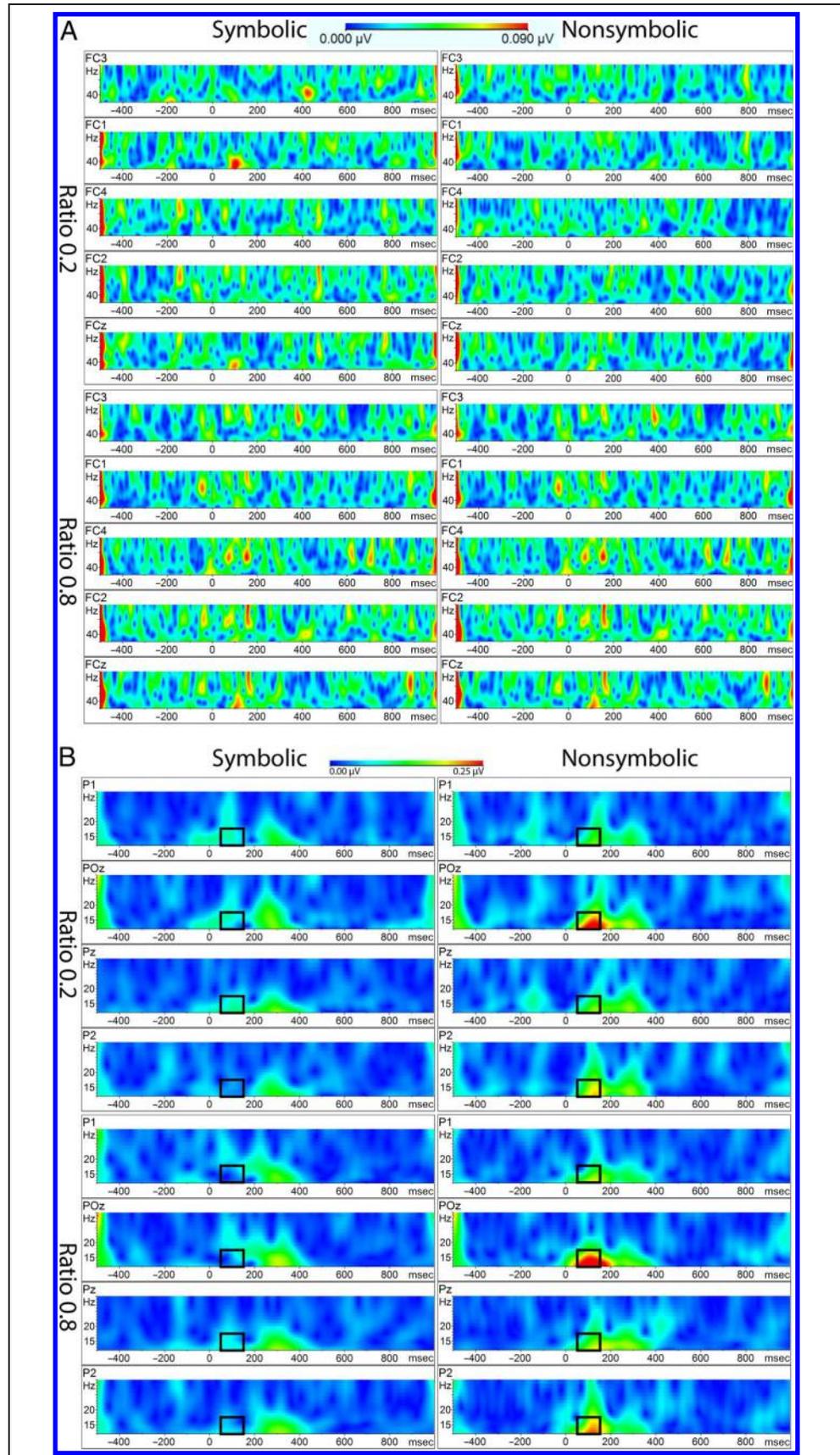
The BF analysis indicates that the Task \times Ratio interaction revealed a BF of 5.756. Whereas in the symbolic task, the BF was 0.223, in the nonsymbolic task, the BF was 3.703. Therefore, the Bayesian analysis supports the significant evidence for a ratio effect for the nonsymbolic but not for symbolic ratios in the beta band.

Exclusivity of Effects? Analyzing Gamma-band Power Changes over the Parietal Cluster and Beta-band Power Changes over the Frontocentral Cluster

Repeated-measures ANOVA on the average high-gamma power in the parietal cluster revealed no significant effect for Task, $F(1, 23) < 1$, ns ; ratio, $F(1, 23) = 1.113$, ns ; nor Task \times Ratio interaction, $F(1, 23) < 1$, ns . We found a significant effect for Electrode, $F(3, 69) = 3.334$, $p < .05$, $\eta_p^2 = .127$; however, all interactions with electrodes were not significant (task: $F(3, 69) < 1$, ns ; ratio: $F(3, 69) = 1.289$, ns ; Task \times Ratio: $F(3, 69) < 1$, ns).

A similar pattern was found in the frontocentral beta analysis. Repeated-measures ANOVA on the average low-beta power revealed no significant effect for Task, $F(1, 23) < 1$,

Figure 5. Wavelet analysis.
 (A) Increased gamma oscillations in the 0.8 ratio in the symbolic task at frontocentral cluster, $p < .01$. (B) Increased beta oscillations in the 0.8 ratio in the nonsymbolic task at parietal cluster, $p < .05$.



ns; ratio, $F(1, 23) < 1$, *ns*; nor Task \times Ratio interaction, $F(1, 23) < 1$, *ns*. We found a significant effect for Electrode, $F(4, 92) = 2.918$, $p < .05$, $\eta_p^2 = .113$, with all interactions with electrodes not significant (task: $F(4, 92) < 1$, *ns*; ratio: $F(4, 92) < 1$, *ns*; Task \times Ratio: $F(4, 92) < 1$, *ns*).

Gamma and Beta-band Latencies Compared with P2p

Four single-sample *t* tests were conducted on the average P2p latency (i.e., separately for symbolic and nonsymbolic tasks in ratios 0.2 or 0.8; see Appendix B) compared with the end point of the relative wavelet analysis time frame (180 msec symbolic gamma, 150 msec nonsymbolic beta). All *t* tests were significant (symbolic 0.2: $t(23) = 9.062$, $p < .001$, $BF_{10} > 100,000$; symbolic 0.8: $t(23) = 10.29$, $p < .001$, $BF_{10} > 100,000$; nonsymbolic 0.2: $t(23) = 10.982$, $p < .001$, $BF_{10} > 100,000$; nonsymbolic 0.8: $t(23) = 9.56$, $p < .001$, $BF_{10} > 100,000$). These findings clearly show that both beta and gamma oscillations came before the P2p wave.

DISCUSSION

Symbolic and nonsymbolic numerical processing, which play a crucial part in arithmetic skills (e.g., De Smedt et al., 2013), have been shown to be behaviorally distinct operations (e.g., Sasanguie et al., 2017; Lyons et al., 2012). Nevertheless, both take place at roughly the same neural place (in spatially overlapping parietal networks, e.g., Eger, 2016; as well as in additional brain regions, e.g., Sokolowski et al., 2017) and at the same time (in the first few hundred milliseconds after onset of the incoming numerical information; e.g., Smets et al., 2013; Libertus et al., 2007; Temple & Posner, 1998). Similar findings were also replicated in the current study showing the P2p ERP component during both symbolic and nonsymbolic numerical comparisons. Specifically, this is indicated by the main and simple effects of Ratio with no Task (symbolic/nonsymbolic) \times Ratio interaction (a nonsignificant interaction that was also supported by a Bayesian analysis, showing anecdotal evidence that there is no effect). The P2p ERP component is considered an electrophysiological signature of symbolic as well as nonsymbolic numerical processing and, specifically, of the symbolic and nonsymbolic ratio or distance effects (Libertus et al., 2007). Here, we aimed to search for the distinct neural dynamics that underlies the separate behavioral processes of symbolic and nonsymbolic numerical information known, so far, to take place at the same neural time and in spatially overlapping neural networks.

The current analysis was primed by earlier results from studies addressing modulation of gamma-band power in linguistic tasks (e.g., Hauk et al., 2017; Mainy et al., 2008; Crone et al., 2001) versus modulation of beta-band power in visuospatial (Costa et al., 2017; Caplan et al., 2001), numerical (Spitzer et al., 2014), or time (Wiener et al., 2018;

Kononowicz & van Rijn, 2015) estimations. Thus, here we tested the hypothesis that numerical linguistic and quantity estimations are segregated by means of neuronal frequencies of functionally relevant neural networks (frontocentral for linguistic vs. parietal for approximation) in different frequency ranges: gamma (50 Hz and up) for exact linguistic processing and lower beta (10–17 Hz) for quantity estimations. In the analysis of power changes across (symbolic or nonsymbolic) numerical comparisons, larger EEG gamma-band power was observed for difficult comparisons within the symbolic numerical system (ratio of 0.8) than for numerically easier symbolic ones (ratio of 0.2). Similarly, beta-band power was larger for nonsymbolic numerically difficult comparisons (ratio of 0.8) than for nonsymbolic numerically easier ones (ratio of 0.2). Thus, we argue that the effects of early beta- and gamma-band power reflect a rapid context-based analysis of exact linguistic (symbolic) or quantity estimation (nonsymbolic).

Interestingly, observed beta- and gamma-band effects began 75 and 140 msec and finished 150 and 180 msec after stimulus onset (respectively), that is, both processes ended significantly earlier than the P2p ERP component. Hence, current findings suggest that gamma and beta neural oscillations act as latent and distinct mechanisms, which act as “translators” of symbolic and nonsymbolic stimuli, for a later process of numerical processing.

The current findings suggest that numerical analysis of symbolic and nonsymbolic information occurs through a common mechanism (e.g., a mental number line) as behaviorally indicated by the ratio or distance effect, and neurophysiology by the P2p ERP waveform. Yet, results also indicate that early differences in oscillations of specific frequency bands reflect the format (symbolic or nonsymbolic) of the incoming information. Note, that when we conducted additional beta and gamma analysis at the time window of the P2p, results showed insignificant effects of task, ratio, or interaction (see Appendices A3 and A4), which suggests an early neural analysis (before P2p).

Indeed, neuronal oscillations are considered latent changes in neuronal coherence (Bastiaansen et al., 2012; Varela et al., 2001), which affect the probability (Voytek & Knight, 2015) of mental operations (e.g., for a review, see Bastiaansen et al., 2012). Against this background, it is found here that both beta and gamma effects appear earlier than the P2p ERP component, which is typically found in both symbolic and nonsymbolic numerical comparisons (Gómez-Velázquez et al., 2015) and has been suggested to indicate fast and automatic processing of numerical magnitudes (Dehaene, 1996) or, as we interpret it here, an early context-based analysis of the numerical meaning.

Possible Role of Beta Frequency Range in Quantity Comparisons

In our view, our data strengthen the notion that beta-band power is related to numerical structure building at the nonsymbolic numerical level, revealing itself

behaviorally as estimation and cognitively as the nonsymbolic ratio effect. To a certain degree, the observed effects in the beta frequency range essentially replicate previously reported results with visuospatial (Costa et al., 2017; Caplan et al., 2001), numerical (Spitzer et al., 2014), and time (Wiener et al., 2018; Kononowicz & van Rijn, 2015) estimations and are in line with the hypothesis that beta-band neuronal power is related to nonsymbolic quantity estimations. Current beta-band results further extend previous findings by indicating that different nonsymbolic numerical ratios elicit different levels of beta-band power. Namely, beta-band power increases during difficult nonsymbolic numerical comparisons (ratio of 0.8) compared with easier comparisons (ratio of 0.2). This suggests that when the nonsymbolic numerical system is confronted with a difficult quantitative analysis between two to-be-compared quantities (larger ratios), EEG beta power increases. Yet, beta power augmentation was absent for nonsymbolic quantitative relations that can be established more easily (smaller ratios). Taking the contrast between the ratio conditions as our prime marker for nonsymbolic numerical cognitive representation (for a review, see Cantlon et al., 2009; e.g., Vogel et al., 2015), we interpret this pattern as increased efforts to estimate the more difficult comparisons (larger ratios) compared with the easier ones.

The current finding, linking beta-band activation and nonsymbolic numerical comparisons, is similar to the pattern observed in a study of parametric oscillatory working memory activity reported by Spitzer et al. (2014). They found that prefrontal beta modulations are linked to numerical estimation of discretely presented items (in either the visual, auditory, or tactile modality). It should be noted, however, that there were differences in both electrodes and specific frequencies inside the beta band. We have no ready explanation for this difference beside the diverse focus of the research questions and the experimental paradigm. However, in terms of quantity estimations, both studies show the same pattern of effects, namely, a relatively increased beta power for more difficult quantity estimations (larger discrete quantities in Spitzer's study and larger ratio between two to-be-compared quantities in the current study). This pattern is exactly what one would expect for an effect related to the incremental building of a numerical structure of nonsymbolic information in the visual scene.

Further evidence for the notion of a link between beta-band power and the nonsymbolic numerical system stems from two relevant observations: (1) Behaviorally, the nonsymbolic numerical system relies mostly on visuospatial cognitive abilities (Gallistel & Gelman, 2000) and involves quantity approximations (e.g., Lyons, Ansari, et al., 2015; Barth et al., 2008). Moreover, time and numerical estimations have been suggested to be cognitively linked (Walsh, 2003). Thus, and because visuospatial (Costa et al., 2017; Caplan et al., 2001), numerical (Spitzer et al., 2014), and time (Wiener et al., 2018; Kononowicz & van Rijn, 2015)

estimations have all been scientifically linked with beta-band power modulations, the current findings add further support to the role of neuronal activation patterns in the beta-band frequency in numerical estimations. (2) Current control analysis of continuous visual properties (convex hull, dot surface, density, size, and contour) of the dots, which represent nonsymbolic information, revealed that continuous magnitudes are not a predictive cue of responses. That is, participants responded primarily based on numerical ratio, which is strongly linked with beta-band oscillations.

Thus, this study links beta power enhancement only to nonsymbolic rather than to general numerical comparisons and specifically to the nonsymbolic ratio effect. That is, beta power may be linked to the accumulative visuospatial building of nonsymbolic numerical information on a mental number line. This is supported by the idea that the ratio effect presents a number in an approximate and compressed way on a mental number line, resulting in the typical behavioral findings that quantities are discriminated based on their given numerical ratio (e.g., Dehaene, 2001). This idea has received additional support from single cell recording studies in monkeys (Nieder, 2016; Nieder & Dehaene, 2009). Namely, Nieder and Dehaene (2009) and Nieder (2016) found single neurons (i.e., "number neurons") that showed maximum activity for a particular number (i.e., the preferred numerosity). These "number neurons" showed a gradual decrease of activity that was dependent on the ratio between the presented numerosity and the preferred numerosity. Hence, our data may point to a link between beta-band power and the formation of the nonsymbolic mental number. This electrophysiological link displays itself behaviorally as estimation, and cognitively as the ratio effect.

The Possible Role of the Gamma Frequency Range in Processing Numerical Symbols

In line with our hypothesis, EEG gamma-band power was larger for symbolic numerically difficult comparisons (ratio of 0.8) than for symbolic numerically easier ones (ratio of 0.2). The frequency range in which this effect occurs is clearly distinct from that in which we observed effects related to nonsymbolic processing. Our data extends previous reports indicating that gamma-band neuronal frequencies play an instrumental role in binding the semantics of individual lexical items within a sentence (Rommers et al., 2013; Wang, Zhu, & Bastiaansen, 2012) to the level of numerical cognition. For example, Hald, Bastiaansen, and Hagoort (2006) found an increase in gamma power in response to a highly expected word presented in a sentence context. This gamma increase was eliminated when the word in the same position in the sentences was semantically anomalous. Similarly, Peña and Melloni (2012) found that gamma power increased only when Spanish or Italian monolinguals listened to sentences in their

own language, not when they listened to sentences spoken in a phonologically related or unrelated language. As such, current findings are in line with the hypothesis that gamma-band neuronal activation patterns are involved in the manipulation of symbolic numbers, possibly based on individuals' familiarity and fluency with these learnt and linguistically based numbers. Based on both empirical evidence and a computational model (Van Opstal, Gevers, De Moor, & Verguts, 2008; Verguts & Van Opstal, 2005), in the numerical field it was suggested that response selection mechanisms are sensitive to the relative frequency with which humans encounter different numbers (frequencies that were calculated to match those found in human lexical corpora). That is, individuals' familiarity and the fluency with which they can manipulate symbolic numbers may serve as the crucial link between basic numerical skills (such as number comparison) and more complex math abilities (see also Lyons, Nuerk, & Ansari, 2015). Thus, in our view, our data strengthen the notion that gamma-band power is related to the creation of numerical mental representation (e.g., mental number line) at the symbolic level. As mentioned earlier, studies suggest a link between gamma oscillations and different aspects of language, including sublexical, phonological, lexical, as well as syntactic information (e.g., Van Berkum et al., 2004; for a review, see Kösem & van Wassenhove, 2017). Therefore, within the language domain and based on previous findings (Vanbinst et al., 2016), it is suggested here that basic symbolic numerical comparisons (studied in the current research) involve cognitive sublinguistic processing that are analogous, for example, to phonological awareness in reading. As the link between gamma band and symbolic numerical information is very novel, we suggest exploring, for example, hemispheric differences in future studies to explore the possible link between phonological awareness and gamma signature.

Frequency-based Segregation of Symbolic and Nonsymbolic Numerical Processing?

In the current within-participant between modality design, we replicated and extended the results of previous, mostly nonnumerical cognition studies. Namely, here we show evidence that gamma-band neuronal activations are related to the symbolic level in numerical cognition, whereas beta-band activations are related to the nonsymbolic numerical cognition.

Furthermore, as we hypothesized in the Introduction, we observed the (theoretically motivated) pattern of increasing beta power in the more difficult nonsymbolic numerical comparisons, reflecting closer quantities on the nonsymbolic mental number line. We did not observe such an increase across the nonsymbolic comparisons for gamma power. Oscillations at beta and gamma frequencies are claimed to be particularly effective for engaging discrete neuronal populations in supporting the transfer of packets of specific information among relevant

neuronal assemblies (da Silva, 2013). In this case, there might be overlapping neuronal assemblies in the frontocentral and parietal cortex. Hence, the current data are compatible with the hypothesis of frequency-based segregation of symbolic and nonsymbolic processing in a frontoparietal numerical network. These data provide support for the view that, during numerical processing, nonsymbolic and symbolic information is being processed at different frequencies. As mentioned in the Introduction, the necessity for such a frequency-based segregation stems in part from previous observations that neural networks for symbolic and nonsymbolic numerical processing are largely spatially overlapping (Sokolowski et al., 2017; Lyons, Ansari, et al., 2015; Arsalidou & Taylor, 2011; Santens et al., 2010; Eger et al., 2009; for a review see Eger, 2016). However, the presently observed gamma and beta effects have clearly distinct scalp topographies (see the topographical maps in Figure 2). Hence, it should be noted that though our study supports the notion of distinct neural dynamics, it also points at dissociation in location, in disagreement with the spatially overlapping neural networks notion, presented at length in the Introduction. gamma-band effects appear over the frontocentral region, which is strongly compatible with the notion that symbolic numerical processing is the result of a dynamic interplay between parietal regions (Ansari, Garcia, Lucas, Hamon, & Dhital, 2005) and frontal areas involved in executive functions, memory, and language. fMRI findings have shown that during human development and during the acquisition of symbolic numerical knowledge, there is a neural shift from a strong involvement of frontal areas during childhood to increasing engagement of parietal regions during adulthood. This shift is possibly the result of the increased automaticity in the processing of symbolic numerical information, which in turn requires less recruitment of frontal areas that are typically associated with memory and executive functions. The current findings show that, even in adulthood, frontal activation possibly still exists in the form of neural induced gamma-band responses.

The beta-band effects, instead, have a maximum effect around the parietal lobe, which is strongly compatible with the notion that nonsymbolic numerical processing is involved with approximation. The different scalp topographies seem to suggest different underlying neuronal dipoles. However, it is difficult to relate scalp topographies to underlying source locations, as it has been well established that electrical potentials from different sources mix at the level of scalp EEG recordings and that small changes in source orientation can have a large impact on scalp topographies. Thus, EEG, with its spatial vagueness, is not the method of choice for obtaining the sources of the effects. Replication of the present findings with methods that are well suited for source reconstruction, such as MEG, would thus be important for revealing the sources underlying the beta and gamma power increases.

In addition future studies could use methodologies that will enable the analysis of neural synchronization. Neuronal synchronization is a mechanism in which neurons with similar properties can coordinate their discharges (Uhlhaas et al., 2010; Ward, 2003). Thus, it could be that brain regions activated by symbolic versus nonsymbolic numerical information show increased neuronal synchronization within certain frequency bands.

Conclusions

Our data demonstrate the existence of a functional dissociation in the oscillatory dynamics of the EEG during numerical processing: Power increases in the gamma frequency range are observed only during symbolic numerical comparisons. In contrast, power increases in the beta frequency band are observed only during nonsymbolic comparisons. This functional dissociation is compatible with the notion of a frequency-based segregation of symbolic and nonsymbolic numerical systems. During numerical processing, symbolic and nonsymbolic processing is represented by groups of neurons that are activated at different frequencies to transiently couple into functionally distinct networks.

APPENDIX A: EXTERNAL STATISTICAL ANALYSIS

Appendix A1: The Entire Pre-P2p Time Window and Beta Spectrum: Analysis of the Parietal Cluster in a Broad Time (0–180) and Frequency (12–30 Hz) Window

Repeated-measures ANOVA of the average beta power revealed a significant effect for Task, $F(1, 23) < 16.693$, $p < .001$, $\eta_p^2 = .421$, $BF_{10} > 100,000$, as beta power was higher in the *ns* task. This finding suggests that under a broad time window and frequency range (i.e., compared with the original more narrow analysis that can be found in the Results section), the strength of the Task effect increases as well. That is, BF rises from 9648 to over 100,000.

Nevertheless, no effect for Ratio, $F(1, 23) < 1$, *ns*, $BF_{10} = .445$, or interaction between Task \times Ratio, $F(1, 23) < 1$, *ns*, $BF_{10} = .18$, were found.

Appendix A2: Gamma Power: Analysis of Frontal Cluster in a Broad Time (0–180) Window

Repeated-measures ANOVA of the average gamma power revealed a significant Task \times Ratio interaction, $F(1, 23) < 6.139$, $p < .05$, $\eta_p^2 = .211$, $BF_{10} = 4.663$, with no effect for Task, $F(1, 23) < 1$, *ns*, $BF_{10} = .142$, or Ratio, $F(1, 23) = 1.189$, *ns*, $BF_{10} = .659$.

Post hoc tests revealed that the source of the interaction is a significant Ratio effect in the symbolic task, $F(1, 23) < 4.315$, $p < .05$, $\eta_p^2 = .158$, $BF_{10} = 41.975$, with greater gamma power in the 0.8 ratio ($ME = 172.756$, $SE = 6.041$) compared with the 0.2 ratio ($ME = 159.338$, $SE = 7.344$). In contrast, no Ratio effect was found in the nonsymbolic task, $F(1, 23) < 1$, *ns*, $BF_{10} = .167$.

Appendix A3: Analysis of Parietal Cluster during P2p Time Window

Gamma

Repeated-measures ANOVA of the average gamma power revealed no significant effect for Task, $F(1, 23) = 1.216$, *ns*, $BF_{10} = .147$; ratio, $F(1, 23) < 1$, *ns*, $BF_{10} = .413$; or interaction, $F(1, 23) < 1$, *ns*, $BF_{10} = .158$.

Beta

Repeated-measures ANOVA of the average beta power revealed no significant effect for Task, $F(1, 23) = 2.107$, *ns*, $BF_{10} = 26.761$; ratio, $F(1, 23) < 1$, *ns*, $BF_{10} = .137$; or interaction, $F(1, 23) < 1$, *ns*, $BF_{10} = .187$.

Appendix A4: Analysis of Frontocentral Electrodes during P2p Time Window

Gamma

Repeated-measure ANOVA of the average gamma power revealed no significant effect for Task, $F(1, 23) = 1.751$, *ns*, $BF_{10} = .105$; ratio, $F(1, 23) < 1$, *ns*, $BF_{10} = .102$; or interaction, $F(1, 23) < 1$, *ns*, $BF_{10} = .181$.

Beta

Repeated-measures ANOVA of the average beta power revealed no significant effect for Task, $F(1, 23) < 1$, *ns*, $BF_{10} = .133$; Ratio, $F(1, 23) < 1$, *ns*, $BF_{10} = .1$; or interaction, $F(1, 23) < 1$, *ns*, $BF_{10} = .142$.

APPENDIX B: P2p AVERAGE LATENCY AND AMPLITUDE PER PARTICIPANT

Table B1. P2p—Amplitude

<i>Participant ID</i>	<i>Symbolic Ratio: 0.2 Amplitude</i>	<i>Symbolic Ratio: 0.8 Amplitude</i>	<i>Nonsymbolic Ratio: 0.2 Amplitude</i>	<i>Nonsymbolic Ratio: 0.8 Amplitude</i>
106	-1.178	-0.771	1.957	2.176
107	0.715	2.451	1.269	2.600
108	-0.768	3.264	3.833	6.597
109	1.205	1.274	2.151	2.012
110	1.054	2.078	4.343	5.126
114	4.400	3.062	2.713	9.653
117	5.534	6.962	5.040	8.652
118	3.252	3.674	4.117	4.168
119	0.581	4.091	3.791	6.821
120	2.533	3.379	1.532	3.520
121	-0.902	2.511	2.118	3.167
122	4.554	5.100	8.015	8.802
124	6.247	6.442	5.267	5.994
126	1.150	3.742	4.537	3.830
130	4.276	7.192	7.537	9.071
131	-1.287	2.828	-0.611	-1.784
134	-0.154	-0.080	0.543	3.295
135	-0.761	1.272	1.916	4.523
140	3.350	2.364	3.622	3.197
142	2.600	2.699	3.559	4.435
143	6.471	5.424	3.216	2.202
145	0.333	1.656	3.474	2.573
148	2.785	2.263	3.260	4.194
149	0.944	3.380	5.380	5.645

Table B2. P2p—Latency

<i>Participant ID</i>	<i>Symbolic Ratio: 0.2 Latency (msec)</i>	<i>Symbolic Ratio: 0.8 Latency (msec)</i>	<i>Nonsymbolic Ratio: 0.2 Latency (msec)</i>	<i>Nonsymbolic Ratio: 0.8 Latency (msec)</i>
106	253	248	222	222
107	150	145	164	224
108	239	170	170	234
109	262	274	211	215
110	246	246	231	235
114	295	271	204	326
117	254	254	195	233
118	272	276	247	280
119	177	297	258	285
120	209	287	177	200
121	249	280	228	208
122	233	259	201	200
124	244	316	225	222
126	255	313	248	261
130	206	253	191	203
131	240	326	169	258
134	276	340	240	269
135	263	248	257	256
140	299	299	274	278
142	265	329	241	263
143	265	267	230	235
145	265	290	209	243
148	245	239	205	248
149	201	247	233	222

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REFERENCES

- Anobile, G., Turi, M., Cicchini, G. M., & Burr, D. C. (2015). Mechanisms for perception of numerosity or texture-density are governed by crowding-like effects. *Journal of Vision, 15*, 4.
- Ansari, D., & Dhital, B. (2006). Age-related changes in the activation of the intraparietal sulcus during nonsymbolic magnitude processing: An event-related fMRI study. *Journal of Cognitive Neuroscience, 18*, 1820–1828.
- Ansari, D., Garcia, N., Lucas, E., Hamon, K., & Dhital, B. (2005). Neural correlates of symbolic number processing in children and adults. *NeuroReport, 16*, 1769–1773.
- Arciuli, J., & Bailey, B. (2019). An acoustic study of lexical stress contrastivity in children with and without autism spectrum disorders. *Journal of Child Language, 46*, 142–152.
- Arsalidou, M., & Taylor, M. J. (2011). Is $2 + 2 = 4$? Meta-analyses of brain areas needed for numbers and calculations. *Neuroimage, 54*, 2382–2393.
- Avancini, C., Soltész, F., & Szűcs, D. (2015). Separating stages of arithmetic verification: An ERP study with a novel paradigm. *Neuropsychologia, 75*, 322–329.
- Ball, T., Demandt, E., Mutschler, I., Neitzel, E., Mehring, C., Vogt, K., et al. (2008). Movement related activity in the high gamma range of the human EEG. *Neuroimage, 41*, 302–310.
- Barth, H., Beckmann, L., & Spelke, E. S. (2008). Nonsymbolic, approximate arithmetic in children: Abstract addition prior to instruction. *Developmental Psychology, 44*, 1466–1477.
- Bastiaansen, M., & Hagoort, P. (2006). Oscillatory neuronal dynamics during language comprehension. *Progress in Brain Research, 159*, 179–196.
- Bastiaansen, M., & Hagoort, P. (2015). Frequency-based segregation of syntactic and semantic unification during

- online sentence level language comprehension. *Journal of Cognitive Neuroscience*, *27*, 2095–2107.
- Bastiaansen, M., Mazaheri, A., & Jensen, O. (2012). Beyond ERPs: Oscillatory neuronal dynamics. In S. J. Luck & E. S. Kappenman (Eds.), *The Oxford handbook of event-related potential components* (pp. 31–50). New York: Oxford University Press.
- Bender, A., Beller, S., Overmann, K. A., Everett, C., Gagne, D., Coppola, M., et al. (2014). The role of culture and language for numerical cognition. In *Proceedings of the Annual Meeting of the Cognitive Science Society* (Vol. 36). Available from <https://escholarship.org/uc/item/0qd5z9v8>.
- Berger, A. (2011). Electrophysiological evidence for numerosity processing in infancy. *Developmental Neuropsychology*, *36*, 668–681.
- Buckley, P. B., & Gillman, C. B. (1974). Comparisons of digits and dot patterns. *Journal of Experimental Psychology*, *103*, 1131–1136.
- Bugden, S., Price, G. R., McLean, D. A., & Ansari, D. (2012). The role of the left intraparietal sulcus in the relationship between symbolic number processing and children's arithmetic competence. *Developmental Cognitive Neuroscience*, *2*, 448–457.
- Bulthé, J., De Smedt, B., & Op de Beeck, H. P. (2014). Format-dependent representations of symbolic and nonsymbolic numbers in the human cortex as revealed by multi-voxel pattern analyses. *Neuroimage*, *87*, 311–322.
- Campanella, S., Gaspard, C., Debatisse, D., Bruyer, R., Crommelinck, M., & Guerit, J.-M. (2002). Discrimination of emotional facial expressions in a visual oddball task: An ERP study. *Biological Psychology*, *59*, 171–186.
- Cantlon, J. F., Brannon, E. M., Carter, E. J., & Pelphrey, K. A. (2006). Functional imaging of numerical processing in adults and 4-y-old children. *PLoS Biology*, *4*, e125.
- Cantlon, J. F., Platt, M. L., & Brannon, E. M. (2009). Beyond the number domain. *Trends in Cognitive Sciences*, *13*, 83–91.
- Caplan, J. B., Madsen, J. R., Raghavachari, S., & Kahana, M. J. (2001). Distinct patterns of brain oscillations underlie two basic parameters of human maze learning. *Journal of Neurophysiology*, *86*, 368–380.
- Cohen, M. X. (2017). Where does EEG come from and what does it mean? *Trends in Neurosciences*, *40*, 208–218.
- Cohen Kadosh, R., Bahrami, B., Walsh, V., Butterworth, B., Popescu, T., & Price, C. J. (2011). Specialization in the human brain: The case of numbers. *Frontiers in Human Neuroscience*, *5*, 62.
- Cohen Kadosh, R., Cohen Kadosh, K., Kaas, A., Henik, A., & Goebel, R. (2007). Notation-dependent and -independent representations of numbers in the parietal lobes. *Neuron*, *53*, 307–314.
- Cohen Kadosh, R., Henik, A., Rubinsten, O., Mohr, H., Dori, H., van de Ven, V., et al. (2005). Are numbers special? The comparison systems of the human brain investigated by fMRI. *Neuropsychologia*, *43*, 1238–1248.
- Costa, G. N., Duarte, J. V., Martins, R., Wibrál, M., & Castelo-Branco, M. (2017). Interhemispheric binding of ambiguous visual motion is associated with changes in beta oscillatory activity but not with gamma range synchrony. *Journal of Cognitive Neuroscience*, *29*, 1829–1844.
- Crone, N. E., Boatman, D., Gordon, B., & Hao, L. (2001). Induced electrocorticographic gamma activity during auditory perception. *Clinical Neurophysiology*, *112*, 565–582.
- da Silva, F. L. (2013). EEG and MEG: Relevance to neuroscience. *Neuron*, *80*, 1112–1128.
- Dehaene, S. (1996). The organization of brain activations in number comparison: Event-related potentials and the additive-factors method. *Journal of Cognitive Neuroscience*, *8*, 47–68.
- Dehaene, S. (2001). Précis of the number sense. *Mind & Language*, *16*, 16–36.
- Dehaene, S., & Changeux, J.-P. (1993). Development of elementary numerical abilities: A neuronal model. *Journal of Cognitive Neuroscience*, *5*, 390–407.
- Dehaene, S., Dehaene-Lambertz, G., & Cohen, L. (1998). Abstract representations of numbers in the animal and human brain. *Trends in Neuroscience*, *21*, 355–361.
- Demiralp, T., Bayraktaroglu, Z., Lenz, D., Junge, S., Busch, N. A., Maess, B., et al. (2007). Gamma amplitudes are coupled to theta phase in human EEG during visual perception. *International Journal of Psychophysiology*, *64*, 24–30.
- De Smedt, B., Noël, M.-P., Gilmore, C., & Ansari, D. (2013). How do symbolic and nonsymbolic numerical magnitude processing skills relate to individual differences in children's mathematical skills? A review of evidence from brain and behavior. *Trends in Neuroscience and Education*, *2*, 48–55.
- De Smedt, B., Verschaffel, L., & Ghesquière, P. (2009). The predictive value of numerical magnitude comparison for individual differences in mathematics achievement. *Journal of Experimental Child Psychology*, *103*, 469–479.
- Dienes, Z., Coulton, S., & Heather, N. (2018). Using Bayes factors to evaluate evidence for no effect: Examples from the SIPS project. *Addiction*, *113*, 240–246.
- Eger, E. (2016). Neuronal foundations of human numerical representations. *Progress in Brain Research*, *227*, 1–27.
- Eger, E., Michel, V., Thirion, B., Amadon, A., Dehaene, S., & Kleinschmidt, A. (2009). Deciphering cortical number coding from human brain activity patterns. *Current Biology*, *19*, 1608–1615.
- Erickson, M. A., Albrecht, M. A., Robinson, B., Luck, S. J., & Gold, J. M. (2017). Impaired suppression of delay-period alpha and beta is associated with impaired working memory in schizophrenia. *Biological Psychiatry: Cognitive Neuroscience and Neuroimaging*, *2*, 272–279.
- Foti, D., Hajcak, G., & Dien, J. (2009). Differentiating neural responses to emotional pictures: Evidence from temporal-spatial PCA. *Psychophysiology*, *46*, 521–530.
- Gallistel, C. R., & Gelman, I. I. (2000). Non-verbal numerical cognition: From reals to integers. *Trends in Cognitive Sciences*, *4*, 59–65.
- Gebuis, T., Herfs, I. K., Kenemans, J. L., de Haan, E. H. F., & van der Smagt, M. J. (2009). The development of automated access to symbolic and non-symbolic number knowledge in children: An ERP study. *European Journal of Neuroscience*, *30*, 1999–2008.
- Gebuis, T., Kenemans, J. L., de Haan, E. H. F., & van der Smagt, M. J. (2010). Conflict processing of symbolic and non-symbolic numerosity. *Neuropsychologia*, *48*, 394–401.
- Gebuis, T., & Reynvoet, B. (2012). Continuous visual properties explain neural responses to nonsymbolic number. *Psychophysiology*, *49*, 1649–1659.
- Gómez-Velázquez, F. R., Berumen, G., & González-Garrido, A. A. (2015). Comparisons of numerical magnitudes in children with different levels of mathematical achievement: An ERP study. *Brain Research*, *1627*, 189–200.
- Gunderson, E. A., Spaepen, E., & Levine, S. C. (2015). Approximate number word knowledge before the cardinal principle. *Journal of Experimental Child Psychology*, *130*, 35–55.
- Hald, L. A., Bastiaansen, M., & Hagoort, P. (2006). EEG theta and gamma responses to semantic violations in online sentence processing. *Brain and Language*, *96*, 90–105.
- Hauk, O., Giraud, A.-L., & Clarke, A. (2017). Brain oscillations in language comprehension. *Language, Cognition and Neuroscience*, *32*, 533–535.
- Hauser, M. D., Tsao, F., Garcia, P., & Spelke, E. S. (2003). Evolutionary foundations of number: Spontaneous representation of numerical magnitudes by cotton-top

- tamarins. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 270, 1441–1446.
- Herding, J., Spitzer, B., & Blankenburg, F. (2016). Upper beta band oscillations in human premotor cortex encode subjective choices in a vibrotactile comparison task. *Journal of Cognitive Neuroscience*, 28, 668–679.
- Holloway, I. D., & Ansari, D. (2009). Mapping numerical magnitudes onto symbols: The numerical distance effect and individual differences in children's mathematics achievement. *Journal of Experimental Child Psychology*, 103, 17–29.
- Hsu, Y.-F., & Szűcs, D. (2012). The time course of symbolic number adaptation: Oscillatory EEG activity and event-related potential analysis. *Neuroimage*, 59, 3103–3109.
- Hyde, D. C., & Spelke, E. S. (2012). Spatiotemporal dynamics of processing nonsymbolic number: An event-related potential source localization study. *Human Brain Mapping*, 33, 2189–2203.
- JASP Team. (2018). JASP (Version 0.9.0.1) [Computer software]. Retrieved from <https://jasp-stats.org/>.
- Jeffreys, H. (1961). *Theory of probability* (3rd ed.). Oxford, UK: Clarendon Press.
- Jung, T.-P., Makeig, S., Humphries, C., Lee, T.-W., McKeown, M. J., & Iragui, V. (2000). Removing electroencephalographic artifacts by blind source separation. *Psychophysiology*, 37, 163–178.
- Karch, S., Loy, F., Krause, D., Schwarz, S., Kiesewetter, J., Segmiller, F., et al. (2016). Increased event-related potentials and alpha-, beta-, and gamma-activity associated with intentional actions. *Frontiers in Psychology*, 7, 7.
- Kiesel, A., & Vierck, E. (2009). SNARC-like congruency based on number magnitude and response duration. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 35, 275–279.
- Kolkman, M. E., Kroesbergen, E. H., & Leseman, P. P. M. (2013). Early numerical development and the role of non-symbolic and symbolic skills. *Learning and Instruction*, 25, 95–103.
- Kononowicz, T. W., & van Rijn, H. (2015). Single trial beta oscillations index time estimation. *Neuropsychologia*, 75, 381–389.
- Kösem, A., & van Wassenhove, V. (2017). Distinct contributions of low- and high-frequency neural oscillations to speech comprehension. *Language, Cognition and Neuroscience*, 32, 536–544.
- Koychev, I., Deakin, J. F. W., Haenschel, C., & El-Deredy, W. (2011). Abnormal neural oscillations in schizotypy during a visual working memory task: Support for a deficient top-down network? *Neuropsychologia*, 49, 2866–2873.
- Koychev, I., El-Deredy, W., Mukherjee, T., Haenschel, C., & Deakin, J. F. W. (2012). Core dysfunction in schizophrenia: Electrophysiology trait biomarkers. *Acta Psychiatrica Scandinavica*, 126, 59–71.
- Landerl, K., Fussenegger, B., Moll, K., & Willburger, E. (2009). Dyslexia and dyscalculia: Two learning disorders with different cognitive profiles. *Journal of Experimental Child Psychology*, 103, 309–324.
- Leibovich, T., & Henik, A. (2014). Comparing performance in discrete and continuous comparison tasks. *Quarterly Journal of Experimental Psychology*, 67, 899–917.
- Libertus, M. E., Woldorff, M. G., & Brannon, E. M. (2007). Electrophysiological evidence for notation independence in numerical processing. *Behavioral and Brain Functions*, 3, 1.
- Lonnemann, J., Linkersdörfer, J., Hasselhorn, M., & Lindberg, S. (2011). Symbolic and non-symbolic distance effects in children and their connection with arithmetic skills. *Journal of Neurolinguistics*, 24, 583–591.
- Lyons, I. M., Ansari, D., & Beilock, S. L. (2012). Symbolic estrangement: Evidence against a strong association between numerical symbols and the quantities they represent. *Journal of Experimental Psychology: General*, 141, 635–641.
- Lyons, I. M., Ansari, D., & Beilock, S. L. (2015). Qualitatively different coding of symbolic and nonsymbolic numbers in the human brain. *Human Brain Mapping*, 36, 475–488.
- Lyons, I. M., Nuerk, H.-C., & Ansari, D. (2015). Rethinking the implications of numerical ratio effects for understanding the development of representational precision and numerical processing across formats. *Journal of Experimental Psychology: General*, 144, 1021–1035.
- Mainy, N., Jung, J., Baciú, M., Kahane, P., Schoendorff, B., Minotti, L., et al. (2008). Cortical dynamics of word recognition. *Human Brain Mapping*, 29, 1215–1230.
- Mason, C. H., & Perreault, W. D., Jr. (1991). Collinearity, power, and interpretation of multiple regression analysis. *Journal of Marketing Research*, 28, 268–280.
- Mazzocco, M. M. M., Feigenson, L., & Halberda, J. (2011). Impaired acuity of the approximate number system underlies mathematical learning disability (dyscalculia). *Child Development*, 82, 1224–1237.
- Meyers, L. S., Gamst, G., & Guarino, A. J. (2006). *Applied multivariate research: Design and interpretation*. Thousand Oaks, CA: Sage Publications.
- Minzenberg, M. J., Yoon, J. H., Cheng, Y., & Carter, C. S. (2016). Sustained modafinil treatment effects on control-related gamma oscillatory power in schizophrenia. *Neuropsychopharmacology*, 41, 1231–1240.
- Moyer, R. S., & Landauer, T. K. (1967). Time required for judgements of numerical inequality. *Nature*, 215, 1519–1520.
- Nieder, A. (2016). The neuronal code for number. *Nature Reviews Neuroscience*, 17, 366–382.
- Nieder, A., & Dehaene, S. (2009). Representation of number in the brain. *Annual Review of Neuroscience*, 32, 185–208.
- Notebaert, K., Nelis, S., & Reynvoet, B. (2011). The magnitude representation of small and large symbolic numbers in the left and right hemisphere: An event-related fMRI study. *Journal of Cognitive Neuroscience*, 23, 622–630.
- Núñez-Peña, M. I., & Suárez-Pellicioni, M. (2014). Less precise representation of numerical magnitude in high math-anxious individuals: An ERP study of the size and distance effects. *Biological Psychology*, 103, 176–183.
- Pavese, A., & Umiltà, C. (1998). Symbolic distance between numerosity and identity modulates Stroop interference. *Journal of Experimental Psychology: Human Perception and Performance*, 24, 1535–1545.
- Peña, M., & Melloni, L. (2012). Brain oscillations during spoken sentence processing. *Journal of Cognitive Neuroscience*, 24, 1149–1164.
- Peyton, G., Rubin, D. M., Pantanowitz, A., Kleks, A., & Teicher, M. (2016). Analysis of MEG signals for selective arithmetic tasks. In E. Kyriacou, S. Christofides, & C. Pattichis (Eds.), *XIV Mediterranean Conference on Medical and Biological Engineering and Computing 2016* (vol. 57). Cham, Switzerland: Springer.
- Pfister, R., Schroeder, P. A., & Kunde, W. (2013). SNARC struggles: Instant control over spatial-numerical associations. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 39, 1953–1958.
- Piazza, M., Facoetti, A., Trussardi, A. N., Berteletti, I., Conte, S., Lucangeli, D., et al. (2010). Developmental trajectory of number acuity reveals a severe impairment in developmental dyscalculia. *Cognition*, 116, 33–41.
- Piazza, M., Izard, V., Pinel, P., Le Bihan, D., & Dehaene, S. (2004). Tuning curves for approximate numerosity in the human intraparietal sulcus. *Neuron*, 44, 547–555.
- Piazza, M., Pica, P., Izard, V., Spelke, E. S., & Dehaene, S. (2013). Education enhances the acuity of the nonverbal approximate number system. *Psychological Science*, 24, 1037–1043.

- Piazza, M., Pinel, P., Le Bihan, D., & Dehaene, S. (2007). A magnitude code common to numerosities and number symbols in human intraparietal cortex. *Neuron*, *53*, 293–305.
- Pinel, P., Dehaene, S., Rivière, D., & Le Bihan, D. (2001). Modulation of parietal activation by semantic distance in a number comparison task. *Neuroimage*, *14*, 1013–1026.
- Price, G. R., & Fuchs, L. S. (2016). The mediating relation between symbolic and nonsymbolic foundations of math competence. *PLoS One*, *11*, e0148981.
- Reynvoet, B., & Sasanguie, D. (2016). The symbol grounding problem revisited: A thorough evaluation of the ANS mapping account and the proposal of an alternative account based on symbol–symbol associations. *Frontiers in Psychology*, *7*, 1581.
- Rommers, J., Dijkstra, T., & Bastiaansen, M. (2013). Context-dependent semantic processing in the human brain: Evidence from idiom comprehension. *Journal of Cognitive Neuroscience*, *25*, 762–776.
- Salillas, E., Barraza, P., & Carreiras, M. (2015). Oscillatory brain activity reveals linguistic prints in the quantity code. *PLoS One*, *10*, e0121434.
- Santens, S., Roggeman, C., Fias, W., & Verguts, T. (2010). Number processing pathways in human parietal cortex. *Cerebral Cortex*, *20*, 77–88.
- Sasanguie, D., Defever, E., Maertens, B., & Reynvoet, B. (2014). The approximate number system is not predictive for symbolic number processing in kindergarteners. *Quarterly Journal of Experimental Psychology*, *67*, 271–280.
- Sasanguie, D., De Smedt, B., & Reynvoet, B. (2017). Evidence for distinct magnitude systems for symbolic and non-symbolic number. *Psychological Research*, *81*, 231–242.
- Sasanguie, D., Göbel, S. M., & Reynvoet, B. (2013). Left parietal TMS disturbs priming between symbolic and non-symbolic number representations. *Neuropsychologia*, *51*, 1528–1533.
- Sasanguie, D., Van den Bussche, E., & Reynvoet, B. (2012). Predictors for mathematics achievement? Evidence from a longitudinal study. *Mind, Brain, and Education*, *6*, 119–128.
- Schadow, J., Lenz, D., Thaerig, S., Busch, N. A., Fründ, I., & Herrmann, C. S. (2007). Stimulus intensity affects early sensory processing: Sound intensity modulates auditory evoked gamma-band activity in human EEG. *International Journal of Psychophysiology*, *65*, 152–161.
- Schneider, M., Beeres, K., Coban, L., Merz, S., Schmidt, S. S., Stricker, J., et al. (2017). Associations of non-symbolic and symbolic numerical magnitude processing with mathematical competence: A meta-analysis. *Developmental Science*, *20*, e12372.
- Smets, K., Gebuis, T., & Reynvoet, B. (2013). Comparing the neural distance effect derived from the non-symbolic comparison and the same–different task. *Frontiers in Human Neuroscience*, *7*, 28.
- Sokolowski, H. M., Fias, W., Mousa, A., & Ansari, D. (2017). Common and distinct brain regions in both parietal and frontal cortex support symbolic and nonsymbolic number processing in humans: A functional neuroimaging meta-analysis. *Neuroimage*, *146*, 376–394.
- Soltész, F., & Szűcs, D. (2014). Neural adaptation to non-symbolic number and visual shape: An electrophysiological study. *Biological Psychology*, *103*, 203–211.
- Spitzer, B., Fleck, S., & Blankenburg, F. (2014). Parametric alpha- and beta-band signatures of supramodal numerosity information in human working memory. *Journal of Neuroscience*, *34*, 4293–4302.
- Szűcs, D., & Soltész, F. (2008). The interaction of task-relevant and task-irrelevant stimulus features in the number/size congruency paradigm: An ERP study. *Brain Research*, *1190*, 143–158.
- Szkudlarek, E., & Brannon, E. M. (2017). Does the approximate number system serve as a foundation for symbolic mathematics? *Language Learning and Development*, *13*, 171–190.
- Tecce, J. J. (1972). Contingent negative variation (CNV) and psychological processes in man. *Psychological Bulletin*, *77*, 73–108.
- Temple, E., & Posner, M. I. (1998). Brain mechanisms of quantity are similar in 5-year-old children and adults. *Proceedings of the National Academy of Sciences, U.S.A.*, *95*, 7836–7841.
- Trueblood, J. S., Holmes, W. R., Seegmiller, A. C., Douds, J., Compton, M., Szentirmai, E., et al. (2018). The impact of speed and bias on the cognitive processes of experts and novices in medical image decision-making. *Cognitive Research: Principles and Implications*, *3*, 28.
- Tzur, G., & Berger, A. (2007). When things look wrong: Theta activity in rule violation. *Neuropsychologia*, *45*, 3122–3126.
- Tzur, G., Berger, A., Luria, R., & Posner, M. I. (2010). Theta synchrony supports Weber–Fechner and Stevens’ Laws for error processing, uniting high and low mental processes. *Psychophysiology*, *47*, 758–766.
- Uhlhaas, P. J., Pipa, G., Neuenschwander, S., Wibral, M., & Singer, W. (2011). A new look at gamma? High- (> 60 Hz) γ -band activity in cortical networks: Function, mechanisms and impairment. *Progress in Biophysics and Molecular Biology*, *105*, 14–28.
- Uhlhaas, P. J., Roux, F., Rodriguez, E., Rotarska-Jagiela, A., & Singer, W. (2010). Neural synchrony and the development of cortical networks. *Trends in Cognitive Sciences*, *14*, 72–80.
- Van Berkum, J. J. A., Zwitserlood, P., Bastiaansen, M., Brown, C. M., & Hagoort, P. (2004). So who’s “he” anyway? Differential ERP and ERSP effects of referential success, ambiguity and failure during spoken language comprehension. *Supplement to the Journal of Cognitive Neuroscience*, *16*, 70.
- Vanbinst, K., Ansari, D., Ghesquière, P., & De Smedt, B. (2016). Symbolic numerical magnitude processing is as important to arithmetic as phonological awareness is to reading. *PLoS One*, *11*, e0151045.
- Vanbinst, K., Ghesquière, P., & De Smedt, B. (2012). Numerical magnitude representations and individual differences in children’s arithmetic strategy use. *Mind, Brain, and Education*, *6*, 129–136.
- Van der Lubbe, R. H. J., & Utzerath, C. (2013). Lateralized power spectra of the EEG as an index of visuospatial attention. *Advances in Cognitive Psychology*, *9*, 184–201.
- Van Opstal, F., Gevers, W., De Moor, W., & Verguts, T. (2008). Dissecting the symbolic distance effect: Comparison and priming effects in numerical and nonnumerical orders. *Psychonomic Bulletin & Review*, *15*, 419–425.
- Varela, F., Lachaux, J.-P., Rodriguez, E., & Martinerie, J. (2001). The brainweb: Phase synchronization and large-scale integration. *Nature Reviews Neuroscience*, *2*, 229–239.
- Verguts, T., & Fias, W. (2004). Representation of number in animals and humans: A neural model. *Journal of Cognitive Neuroscience*, *16*, 1493–1504.
- Verguts, T., & Van Opstal, F. (2005). Dissociation of the distance effect and size effect in one-digit numbers. *Psychonomic Bulletin & Review*, *12*, 925–930.
- Vogel, S. E., Goffin, C., & Ansari, D. (2015). Developmental specialization of the left parietal cortex for the semantic representation of Arabic numerals: An fMR-adaptation study. *Developmental Cognitive Neuroscience*, *12*, 61–73.
- Völker, M., Fiederer, L. D. J., Berberich, S., Hammer, J., Behncke, J., Kršek, P., et al. (2018). The dynamics of error processing in the human brain as reflected by high-gamma activity in noninvasive and intracranial EEG. *Neuroimage*, *173*, 564–579.

- Voytek, B., & Knight, R. T. (2015). Dynamic network communication as a unifying neural basis for cognition, development, aging, and disease. *Biological Psychiatry*, *77*, 1089–1097.
- Walsh, V. (2003). A theory of magnitude: Common cortical metrics of time, space and quantity. *Trends in Cognitive Sciences*, *7*, 483–488.
- Wang, L., Zhu, Z., & Bastiaansen, M. (2012). Integration or predictability? A further specification of the functional role of gamma oscillations in language comprehension. *Frontiers in Psychology*, *3*, 187.
- Ward, L. M. (2003). Synchronous neural oscillations and cognitive processes. *Trends in Cognitive Sciences*, *7*, 553–559.
- Wiener, M., Parikh, A., Krakow, A., & Coslett, H. B. (2018). An intrinsic role of beta oscillations in memory for time estimation. *Scientific Reports*, *8*, 7992.
- Xenidou-Dervou, I., Molenaar, D., Ansari, D., van der Schoot, M., & van Lieshout, E. C. D. M. (2017). Nonsymbolic and symbolic magnitude comparison skills as longitudinal predictors of mathematical achievement. *Learning and Instruction*, *50*, 1–13.
- Yuval-Greenberg, S., Tomer, O., Keren, A. S., Nelken, I., & Deouell, L. Y. (2008). Transient induced gamma-band response in EEG as a manifestation of miniature saccades. *Neuron*, *58*, 429–441.