



How are grammatical and arithmetic processing related in the brain? An ALE meta-analysis

Nurit Viesel-Nordmeyer^{a,b,c,*}, Johannes C. Ziegler^b, Jérôme Prado^c

^a Pôle Pilote pour la Recherche en Education et la Formation des enseignants (AMPIRIC), Aix-Marseille University, Inspé, 52, avenue Escadrille Normandie Niemen, Marseille 13013, France

^b Centre de Recherches en Psychologie et Neurosciences (CRPN), Aix-Marseille University, CNRS, 3, place Victor Hugo, Marseille 13331, France

^c Centre de Recherche en Neurosciences de Lyon, INSERM U1028 - CNRS UMR5292, Université de Lyon, 95, Bd Pinel, Bron 69500, France

ARTICLE INFO

Keywords:

Grammar
Arithmetic
Syntax
Neural overlap
Multiple-demand network
ALE meta-analysis

ABSTRACT

Grammatical and arithmetic skills are consistently associated, but the nature of this relationship remains debated. On the one hand, it may be due to shared linguistic processes. On the other hand, it may also come from domain-general abilities involved in extracting and applying abstract structured rules. To address this question, we investigated the neural basis of the relation between grammatical and arithmetic processing by conducting an activation likelihood estimation (ALE) meta-analysis of whole-brain fMRI studies of grammatical ($n = 50$ experiments) and arithmetic ($n = 70$ experiments) processing in healthy children and adults. Left perisylvian language regions were more consistently recruited for grammatical than arithmetic processing, whereas bilateral parietal regions were more consistently recruited for arithmetic than grammatical processing. The conjunction analysis revealed overlapping activation in four left-lateralized regions: the junction between the Inferior and Middle Frontal Gyrus, the Supplementary Motor Area, the Parietal Lobule, and the Anterior Insula. Together, these findings indicate that grammatical and arithmetic processing recruit both shared and domain-specific neural systems. The overlapping regions largely correspond to areas associated with the multiple-demand network, suggesting that both domains engage domain-general cognitive mechanisms involved in complex rule-based processing. In contrast, classical perisylvian language regions were selectively recruited during grammatical processing, whereas bilateral parietal regions were more consistently associated with arithmetic processing. These findings therefore suggest that the relation between grammar and arithmetic is better explained by the coexistence of shared domain-general mechanisms and domain-specific neural systems than by shared linguistic processes alone.

1. Introduction

A large body of research documents an association between language and mathematical skills (for reviews, see [Amland et al., 2025](#); [Peng et al., 2020](#)). This research notably suggests that the ability to produce and comprehend linguistic structures (i.e., *grammatical abilities*) is related to the ability to produce and comprehend numerical expressions (i.e., *arithmetic skills*). This association has been found in behavioral studies on typically developing children and adolescents (e.g., [Chow, Ekholm, 2019](#); [Kleemans et al., 2018](#)), as well as in groups showing either arithmetic (e.g., [Chow et al., 2021](#); [Shankweiler et al., 1995](#)) or grammatical impairments (e.g., [Kleemans et al., 2012](#); [Shankweiler](#)

[et al., 1995](#)).

Two main explanations have been proposed to account for the association between arithmetic and grammatical skills, and these explanations are not mutually exclusive. First, the association may stem from the fact that mathematical language itself involves linguistic meaning and structure (e.g., [Purpura and Logan, 2015](#); [Purpura and Reid, 2016](#); [Purpura et al., 2019](#)). For example, arithmetic learning involves the understanding of grammatical word forms such as comparatives (e.g., *small-er*; *clos-er*) and superlatives (e.g., *smallest*, *closest*), which are essential for comparing or relating quantities (e.g., [Spelke, 2017](#); [Viesel-Nordmeyer et al., 2022; 2021](#)). According to this view, grammatical and arithmetic skills may be related because both rely on the processing

* Corresponding author at: Pôle Pilote pour la Recherche en Education et la Formation des enseignants (AMPIRIC), Aix-Marseille University, Inspé, 52, avenue Escadrille Normandie Niemen, Marseille 13013, France.

E-mail addresses: nurit.viesel-nordmeyer@univ-amu.fr (N. Viesel-Nordmeyer), johannes.ziegler@univ-amu.fr (J.C. Ziegler), jerome.prado@cnrs.fr (J. Prado).

<https://doi.org/10.1016/j.neubiorev.2026.106925>

Received 25 May 2026; Received in revised form 3 August 2026; Accepted 24 August 2026

Available online 25 August 2026

0149-7634/© 2026 Elsevier Ltd. All rights are reserved, including those for text and data mining, AI training, and similar technologies.

of linguistic structures, including those carrying semantic content relevant to mathematical reasoning.

Second, arithmetic and grammatical skills may be associated because they share a common underlying syntactic structure (e.g., Hauser et al., 2002; Matsumoto and Nakai, 2023; Nakai and Okanoya, 2018). Indeed, processing both arithmetic equations and sentences requires the understanding, extraction, and application of hierarchical rules. Thus, the association between grammatical and arithmetic skills may reflect shared domain-general rule-processing abilities (e.g., Hauser et al., 2002; Viesel-Nordmeyer et al., 2022; 2021; 2019).

In the present study, we use evidence coming from the neural processing of grammar and arithmetic to determine whether the association between these skills may be driven by processes that are related to linguistic-semantic processing or domain-general rule-processing abilities. To address this question, we conducted an activation likelihood estimation (ALE) meta-analysis (see Eickhoff et al., 2016, 2012, 2009; Turkeltaub et al., 2012) of brain imaging studies on grammatical and arithmetic processing.

Previous work has distinguished brain regions specifically associated with linguistic meaning from domain-general brain regions belonging to a multiple-demand network that support various cognitive functions (even though these can be recruited during language tasks) (for reviews see e.g., Duncan, 2010; Duncan and Owen, 2000; Fedorenko et al., 2024; Friederici et al., 2011; Humphreys and Tibon, 2023). Building on this distinction, we aim to characterize both the shared and the domain-specific neural systems supporting grammatical and arithmetic processing. Specifically, we examine whether the observed neural overlap is more consistent with shared linguistic-semantic processes or with domain-general (i.e., meaning-independent) mechanisms, while also identifying the neural systems that distinguish the two domains.

In doing so, this meta-analysis aims to characterize how shared and domain-specific neural systems jointly contribute to grammatical and arithmetic processing, thereby providing new insights into why these skills are related while remaining functionally distinct. Below, we first define grammatical and arithmetic skills and the brain regions most commonly associated with them. We then review the existing behavioral and neuroimaging literature on the relation between grammatical and arithmetic processing.

1.1. The nature of grammar

Grammar is one of the fundamental components of language (e.g., Sioco, De Vera, 2018). It is commonly defined as “the way a language manipulates and combines words in order to form longer units of meaning” (Ur, 1991, p. 4; see also e.g., Thornbury, 1999; Ur, 1991), which cannot be conveyed by vocabulary alone. The construction of these units of meaning is determined by a system of rules present in all languages. These rules encompass both the ordering of words within sentences, referred to as syntax, and the internal structure of words, referred to as morphology (e.g., Payne, 2012).

The ordering of words within a sentence is hierarchically structured (e.g., Gazdar et al., 1985). As illustrated in Fig. 1, syntactic units called “phrases” are built around lexical heads such as nouns (N; e.g., “man”) and verbs (V; e.g., “eat”). Noun-Phrases (NP; e.g., “the man”) and verb-phrases (VP; e.g., “eats an apple”) are formed according to

language-specific syntactic rules. A key property of these rules is their capacity for recursive embedding of phrases within phrases (e.g., Hauser et al., 2002). Within NP, for example, nouns (e.g., “man”) are often accompanied by a “specifier” (e.g., “the”). Within VP, verbs (e.g., “eat”) are often accompanied by a complement (e.g., “an apple”), which itself may include another NP (“an apple”). Thus, phrase structure arises from recursively combining syntactic units into increasingly complex configurations (e.g., Gazdar et al., 1985). The hierarchical nature of these rules is commonly visualized by a so-called tree structures (e.g., Derrick and Archambault, 2009; Hunter, 2021; Johnson, 1998), which depict the overall syntactic organization of the whole sentence as well as the internal structure of its constituent phrases (for an example see Fig. 1).

To combine different words within sentences, morphological rules are needed (e.g., Holmberg and Roberts, 2013; Matthews, 1991). Morphology can be defined as the study of the structure and function of words (e.g., Zeige, 2015). Words consist of “roots” (e.g., *believe* as a verb; *registration* as a noun) that can be combined with an “affix” (e.g., *able* in *believable*; *pre* in *pre registration*) to form a “stem” (e.g., *believable*, *preregistration*). Affixes can be attached in front of the root (prefix; e.g., *pre* in *pre registration*) or to its end (suffix; e.g., *able* in *believable*) (e.g., Twain, 2013). Within sentences, affixes serve several grammatical functions. They can mark relational roles (e.g., the boy’s apple) or express comparative relations between different objects (e.g., the boy’s apple is larger than the girl’s apple). Moreover, word structure resembles syntactic structure in being hierarchical. For instance, adjectives may be formed through the sequential application of morphological rules (see Fig. 1). For example, an adjective can be formed by attaching a suffix (e.g. *able*) to a noun (e.g., *approach*). Further, a prefix (e.g., *un-*) may then be attached to this adjective that was formed before (e.g., *unapproachable*). Morphology also exhibits recursion, allowing complex structures to be built from repeated applications of the same rule (e.g., *apple-eater*; *apple-eater-eater*; *apple-eater-eater-eater*) (e.g., Holmberg and Roberts, 2013; Twain, 2013). Like syntactic structures, the hierarchical and recursive nature of word formation can be visualized using tree structures (see Fig. 1).

To summarize, grammatical rules of both syntax and morphology are necessary for expressing relations within sentences, such as relations between words (e.g., the words “man” and “apple”), contextual information (e.g., → “That is the man’s apple”), temporal relations (e.g., → “That is the man’s apple” or “That was the man’s apple”), or distinctions between singular and plural (e.g., → “That is the man’s apple” or “These are the man’s apples”) (e.g., Sioco, De Vera, 2018; Thornbury, 1999). Hence, syntax and morphology are fundamental for constructing meaning in language. Without grammatical structure, the ability to comprehend and communicate complex meanings would be severely limited.

Note that some definitions equate grammar directly with syntax, as in the notion of “universal grammar” proposed by Chomsky (e.g., Chomsky, 1957; Halle, 1962). In this framework, grammar is largely detached from context and meaning (e.g., Chomsky, 1957; 1981). Other definitions adopt a broader perspective, incorporating additional sub-systems of language such as “phonology” and “phonetics” (e.g., Payne, 2012; Meibauer et al., 2015). Still others include components describing the system of meaning, such as “semantics” or “pragmatics” (e.g., Payne, 2012; Meibauer et al., 2015).

In the present study, we adopt a definition of grammatical skills as a set of skills foundational for communicating in a language (e.g., Payne, 2012). Specifically, we follow accounts that define grammar as “system of rules for combining words and phrases in sentences into larger units of meaning” (Ur, 1991, p. 4; see also e.g., Hornby, 2000; Thornbury, 1999; Ur, 1991). This definition incorporates both syntax and morphology.

1.2. Brain areas involved in grammatical processing

Grammatical processing is cognitively demanding, as it requires the application of multiple hierarchical and rule-based operations.

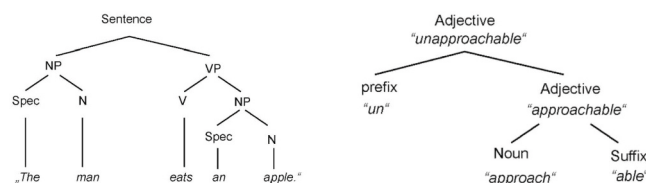


Fig. 1. Examples of a syntactic (sentence “The man eats an apple”) and a morphologic (adjective “unapproachable”) tree structure.

Neuroimaging research therefore consistently reports the engagement of distributed neural networks during grammatical processing (Menks et al., 2024). These networks include regions of the domain-specific language network (for reviews see Fedorenko et al., 2024; Friederici, 2011) but also brain regions associated with the domain-general multiple-demand network (for reviews see e.g., Duncan, 2010; Duncan and Owen, 2000; Humphreys and Tibon, 2023).

The domain-specific language network occupies a well-defined anatomical configuration (Fedorenko et al., 2024). In most individuals, it is strongly left-lateralized and includes areas of the inferior (IFG) and middle frontal gyri (MFG) as well as areas of the superior (STG) and middle temporal gyri (MTG) (see Fedorenko et al., 2024; Friederici, 2011; Friederici, 2019; Vigneau et al., 2006). Classical accounts often refer to these regions as “Broca’s area” (traditionally the posterior IFG, sometimes extending dorsally to adjacent portions of the MFG) and “Wernicke’s area” (posterior temporal cortex), although contemporary perspectives emphasize distributed functional specialization within this network (e.g., Hagoort and Indefrey, 2014; Poeppel and Hickok, 2004).

Within this system, the left IFG, particularly its opercular and triangular parts, has been most consistently associated with grammatical processing (for reviews, see Friederici, 2011; Friederici, 2019; Sakai, 2005). Activity in the posterior IFG in particular has been linked to hierarchical structure-building operations such as “Merge,” which combines linguistic elements according to language-specific rules. Simpler, adjacency-based combinatorial operations may engage the frontal operculum and the anterior superior temporal gyrus (ASTG), connected via a ventral white-matter pathway, whereas more complex hierarchical structures rely on a dorsal pathway (the arcuate fasciculus) linking the posterior IFG to the posterior superior temporal cortex (e.g., for reviews, see Friederici, 2011; 2012; Friederici, 2019).

Beyond these language-specific brain regions, a prior review on grammatical processing (Sakai, 2005) suggested that the left lateral premotor cortex (PMC) may also contribute to syntactic grammatical processing. Notably, the co-activation of the PMC and IFG persists even when controlling for working memory demands, leading to the proposal of a frontal “grammar center” specialized for syntactic computations (Sakai, 2005). Critically, compared to temporal regions that are strongly implicated in lexical-semantic processing, the left IFG appears to be more closely linked to structural, potentially meaning-independent grammatical operations (Fedorenko et al., 2012; Shain et al., 2024; Vigneau et al., 2006; Wang et al., 2024). This distinction is particularly relevant when considering accounts of grammar as a rule-based computational system (e.g., Chomsky, 1957, 1981).

It should be noted, however, that most evidence for functional specialization of grammatical processing comes from research from adult populations. In children, grammatical processing cannot be clearly dissociated from general lexical language processing before approximately 9–10 years of age (e.g., Fengler et al., 2016; Wang et al., 2024; 2023).

1.3. The nature of arithmetic

Arithmetic is a fundamental branch of mathematics that can be defined as the theory (e.g., Nagel and Newman, 2001; Wilson, 2020) or science of numerical calculations (e.g., Sophian, 2008). Like grammar, arithmetic relies on structured, rule-based operations. The operations of “addition,” “subtraction,” “multiplication” and “division” form the main calculations of arithmetic. “Addition” means combining two single numbers into a single quantity (e.g., “ $3 + 2 = 5$ ”), whereas “subtraction,” the inverse of addition, means separating a subset from a larger set (e.g., “ $5 - 2 = 3$ ”) (e.g., Verschaffel, De Corte, 1996; Wright et al., 2012). “Multiplication” can be conceptualized as repeated addition of the same number (e.g., “ $3 \times 2 = 6 = 2 + 2 + 2$ ”), and “division” is the inverse of this multiplication process (e.g., “ $6 \div 3 = 2$ ”) (e.g., Huber et al., 2013; Park and Nunes, 2001; Wright et al., 2012). Overall,

arithmetic skills can be defined as the knowledge and application of rules and procedures to combine, transform and manipulate numbers. Importantly, the understanding of these numerical relations (and quantities) is suggested to depend on the understanding of linguistic-semantic concepts, such as grammatical word forms of comparatives (e.g., smaller, larger) or superlatives (e.g., smallest, largest”) (e.g., Spelke, 2017; Viesel-Nordmeyer et al., 2022; 2021).

Further, multi-step calculations require the sequential application of learned algorithms (e.g., carrying or borrowing procedures), in which intermediate representations must be computed and integrated according to hierarchical constraints. Thus, similar to grammar, arithmetic involves combinatorial processes that operate over symbolic elements in a systematic manner. At the same time, arithmetic performance is not uniformly procedural. For many single-digit problems, skilled adults or adolescents appear to retrieve solutions directly from long-term memory (Barrouillet et al., 2008; Campbell and Xue, 2001; Siegler, 1988). Such retrieval has been proposed to rely, at least in part, on verbally encoded associations between operands and results (Dehaene et al., 2004). However, alternative accounts suggest that repeated procedural strategies may become automatized with practice in both children and adults (Fayol and Thevenot, 2012; Mathieu et al., 2016; Prado and Thevenot, 2026; Uittenhove et al., 2016). Arithmetic performance may therefore reflect both rule-based computation and memory-based retrieval processes (including verbal encoding).

To summarize, on the one hand arithmetic may engage language-related mechanisms in several ways. Understanding numerical relations and quantities (e.g., magnitude comparison) often depends on linguistic-semantic concepts (e.g., grammatical word forms). Also, arithmetic facts may be encoded in verbal form, and verbal working memory may support intermediate computations. On the other hand, arithmetic clearly entails structured transformations that are not inherently semantic, raising the possibility that domain-general rule-processing mechanisms contribute to arithmetic independently of linguistic meaning.

1.4. Brain areas involved in arithmetic processing

The operations, rules and strategies associated with arithmetic problem solving engage multiple neural processes. Prior research has identified different brain regions to be activated during arithmetic processing (e.g., Peters and de Smedt, 2018; Nieder, 2025; Vogel and de Smedt, 2021). Among these, the parietal cortex, including the bilateral intraparietal sulcus (IPS), the left angular gyrus (AG) are often implicated. The IPS has been argued to support the representation of symbolic and non-symbolic numerical quantities that underlie the manipulation of numbers during mental calculation (e.g., de Smedt, 2016; Nieder, 2016; Peters and de Smedt, 2018). In contrast, the left AG is typically activated when participants solve arithmetic problems that rely on retrieval of arithmetic facts from long-term memory (e.g., Zamarian et al., 2009), though there is a debate regarding whether this involvement is confounded by task difficulty (Prado and Thevenot, 2026). Additional evidence suggests that the left MTG might support the retrieval of arithmetic facts from long-term-memory due to its role in phonological processing (Prado, 2018; Prado et al., 2011; Prado et al., 2014; Suárez-Pellicioni and Booth, 2022). Furthermore, activations in the left IFG have also been observed, particularly during more demanding calculations that require substantial verbal working memory processes (de Smedt et al., 2011; Prado et al., 2011; Prado et al., 2014). Finally, studies with children suggest that the hippocampus might play a transient role in processing arithmetic fact and encoding arithmetic problems during early arithmetic learning (Cho et al., 2012; de Smedt et al., 2011).

1.5. Previous studies on the relation between grammar and arithmetic skills

Findings from both behavioral and neuroimaging research suggest that grammatical processing and arithmetic processing might be related. Behavioral studies on both typically developing children and adolescents (e.g., Chow and Ekholm, 2019; Kleemans et al., 2018) as well as children and adolescents with either arithmetic difficulties (e.g., Chow et al., 2021; Shankweiler et al., 1995) or language impairments (e.g., Kleemans et al., 2012; Shankweiler et al., 1995) consistently report associations between performance in the two domains. Critically, although many of these studies assess multiple language components, grammatical skills typically show the strongest association with arithmetic skills. For instance, Kleemans et al. (2018) examined typically developing 5th graders on a range of mathematical and language skills. They found that children's arithmetic skills were predicted by their receptive grammatical skills and phonological skills but not by their vocabulary skills. Interestingly, other mathematical skills included in the study, in particular fraction skills and geometric skills, were not directly predicted by grammatical skills. Importantly, these analyses controlled for working memory skills, which are involved in both mathematical and language processing (for reviews see Peng et al., 2020; Peng and Fuchs, 2016; Viesel-Nordmeyer et al., 2023).

Further supporting evidence comes from Chow et al. (2021), who compared children with arithmetic difficulties to typically developing children in their receptive syntax, morphology and vocabulary skills. Children with arithmetic difficulties were significantly impaired in syntax, but not in morphology or vocabulary. Notably, the authors also showed that these differences could not be attributed to group differences in verbal working memory.

Similar results were reported for children with specific language impairment (Kleemans et al., 2012), who were tested on their language (naming speed, phonological awareness, receptive grammar skills) and working memory skills (central executive, phonological loop, visual-spatial sketchpad) during their last year of preschool and on their arithmetic skills one year later (while they were in 1st grade). When controlling for working memory skills, receptive grammar and phonological skills in preschool predicted arithmetic skills in 1st grade, whereas vocabulary did not. Finally, Shankweiler et al. (1995) compared children with reading difficulties, arithmetic difficulties, combined difficulties and typically developing children on various language skills, including phonological awareness, morphology and syntax. Children with arithmetic difficulties showed the poorest performance in syntax, not only relative to typically developing peers but also relative to the group showing combined difficulties in both reading and arithmetic.

Neuroimaging research in adults provides converging evidence for a relationship between arithmetic and grammar skills. Indeed, studies that have examined both skills concomitantly tend to show overlapping brain areas in both types of tasks (e.g., Baldo and Dronkers, 2007; Makuuchi et al., 2012; Nakai and Okanoya, 2018; 2020; Nakai and Sakai, 2014). Notably, most of these studies relied on the idea that the hierarchical tree structure characteristic of syntax can be transferred to arithmetic processing (e.g., Fig. 2; for reviews see Friedrich and Friederici, 2009; Matsumoto and Nakai, 2023; Westbury et al., 2003). Accordingly, in most of these studies, arithmetic and language problems were designed with similar syntactic structures (Makuuchi et al., 2012; Nakai and Okanoya, 2018; 2020; Nakai and Sakai, 2014).

For instance, Nakai and Okanoya (2020) examined young adults performing both language and arithmetic tasks in an fMRI scanner. In the language task, participants had to judge whether the content of a single sentence of seven ordered words (e.g., "a kind woman saved a small kid") was consistent with the content of the probe stimulus that included a shortened sentence ending with a question mark (e.g., "Did a women save?"). In the arithmetic task, participants had to judge whether an arithmetic expression with seven elements [e.g., "4", "2", "-", "6", "2", "÷", "x" corresponding to "(4-2) x (6 ÷ 2)"] matched a

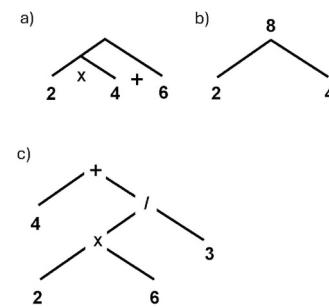


Fig. 2. Examples of a suggested tree-structure for arithmetic. Panel (a) illustrates a proposed structural correspondence between arithmetic tree structure and language tree structures, as suggested in Nakai and Okanoya (2020): e.g., “ 2×4 ” refers to a noun phrase (“The man”) and “ $+$ ” refers to a verb phrase (e.g. “eats”). Panel (b) shows an alternative arithmetic tree structure, as suggested in Nakai and Sakai (2014). Panel (c) shows an arithmetic tree structure of a more complex arithmetic problem “ $4 + [(2 \times 6)/3]$ ”, as suggested in Westbury et al. (2003). Together, these examples illustrate the theoretical basis for treating arithmetic as a rule-based system with hierarchical structure comparable to that of natural language grammar.

proposed result displayed in the probe (e.g., “ $= 6?$ ”). The authors found shared neural activation in the bilateral IFG in both language and arithmetic tasks. Notably, these results were obtained while controlling for participants’ general cognitive load and working memory.

Based on results of another study, Nakai and Okanoya (2018) provided evidence regarding the existence of a repetition suppression effect between both language and arithmetic processing (in both directions) that engaged shared neural resources within the bilateral IFG. Also, complementary behavioral studies in adults have reported cross-domain structural priming effects between both language and arithmetic, consistent with the idea of shared structural representations (e.g., Scheepers and Sturt, 2014; Scheepers et al., 2011; Pozniak et al., 2018).

Despite this converging evidence, several issues remain unresolved. First, studies on patients with both agrammatic aphasia (e.g., Bánrét, and Mészáros, 2019; Varley et al., 2005) or general aphasia (e.g., Gonzalez et al., 2021; Klessinger et al., 2007; Proios et al., 2021) challenge the idea that structure-dependent operations in language and arithmetic rely on a single shared syntactic system. For example, participants with severe grammatical impairments have been shown to perform accurately on exact calculations (Varley et al., 2005), and mathematical deficits in aphasia are not uniform across patients (e.g., Gonzalez et al., 2021; Klessinger et al., 2007; Proios et al., 2021). These findings raise the possibility that arithmetic may rely on partially independent mechanisms or that shared processing occurs at a more abstract, domain-general level.

Second, existing studies do not clearly show whether this association between grammar and arithmetic reflects a direct dependency of arithmetic processing on syntactic grammar skills or whether a third factor drives the relationship (such as executive control). Although some studies have controlled for working memory, not all studies have done so and it remains possible to attribute the association to this domain-general system. Furthermore, the few available brain imaging studies comparing directly grammatical processing to arithmetic processing (e.g., Baldo and Dronkers, 2007; Makuuchi et al., 2012; Nakai and Okanoya, 2018; 2020; Nakai and Sakai, 2014) predominantly found shared brain activation for syntactic language and arithmetic processing in the IFG. The left IFG involvement in arithmetic processing is generally consistent with a recent large-scale study linking structural properties of this region with individual differences in arithmetic skills (Viesel-Nordmeyer and Prado, 2023). However, while the left IFG is closely associated with language or phonological processing (e.g. for reviews Burton, 2001; Carter et al., 2019; Dapretto and Bookheimer, 1999; Friederici, 2011; Pollack and Ashby, 2018; Sakai, 2005), it is also implicated in domain-general functions such as working memory or

motor control (for reviews see Fedorenko et al., 2024; Liakakis et al., 2011). This makes it difficult to draw any definitive conclusion regarding the nature of the association between arithmetic and grammatical skills from these findings.

Third, the available neuroimaging studies are limited in scope. Many were conducted in Japanese, a language with structural properties that differ substantially from Indo-European languages, potentially constraining generalizability (for a review see Malik-Moraleda et al., 2022). Therefore, language-specific characteristics may modulate the relationship between syntax and arithmetic, and different association patterns cannot be ruled out for other languages (e.g., Tang et al., 2006; Yu et al., 2012). It is also worth noting that these neuroimaging studies were designed using language and arithmetic problems with similar syntactic structures, limiting the conclusions about the general relationship between grammatical and arithmetic processing with different syntactic structures.

Finally, all existing brain imaging studies were conducted with adults, making the findings less relevant for explaining the associations between grammatical and arithmetic skills in children.

Taken together, prior research suggests some association between grammatical (especially syntactic) skills and arithmetic performance. However, it remains unclear whether this association reflects shared linguistic-semantic processes, shared domain-general rule-processing mechanisms, or partially overlapping but distinct systems. A quantitative synthesis of the neuroimaging evidence is therefore necessary to clarify the neural basis of this relationship.

1.6. The present study

Given the limited number of brain imaging studies that have directly compared grammatical and arithmetic processing within the same experimental framework, we conducted an Activation Likelihood Estimation (ALE; see Eickhoff et al., 2016, 2012, 2009; Turkeltaub et al., 2012) meta-analysis to identify the brain regions that are the most consistently activated during grammatical and arithmetic processing across the literature. Specifically, we aimed to identify the brain regions that underlie both grammatical and arithmetic processing, in both children and adults.

Based on previous brain imaging studies on linguistic syntax and arithmetic processing in adults (see Baldo and Dronkers, 2007; Makuuchi et al., 2012; Nakai and Okanoya, 2018, 2020; Nakai and Sakai, 2014) as well as previous brain imaging studies on arithmetic processing in children and adolescents (e.g., Prado et al., 2011; Prado et al., 2014; De Smedt et al., 2011), we expected overlapping activation clusters between grammatical and arithmetic processing in the left lateral prefrontal cortex, including the left IFG but also extending dorsally into the MFG (IFG/MFG). Indeed, that area is implicated not only in language but also in the multiple-demand network associated with domain-general executive control (e.g., Duncan, 2010; Duncan and Owen, 2000; Fedorenko et al., 2024; Friederici, 2011; Humphreys and Tibon, 2023). Therefore, overlap in this region would be consistent with the hypothesis that the association between grammar and arithmetic reflects shared domain-general rule-processing demands.

In addition, we examined whether neural overlap would extend beyond the IFG/MFG to other perisylvian language regions. Indeed, previous brain imaging studies have shown that the left superior and middle temporal gyri (STG, MTG) are associated with linguistic-semantic processing (e.g., Fedorenko et al., 2024; Friederici, 2011). If arithmetic and grammatical processing show overlapping activation in these regions, this would suggest that their association is at least partly driven by shared linguistic-semantic mechanisms rather than purely domain-general processes.

By quantitatively synthesizing the available neuroimaging evidence, the present meta-analysis aims to clarify whether the neural overlap between grammar and arithmetic reflects shared domain-general cognitive control mechanisms engaged during rule-based tasks, shared

semantic-linguistic processes, or a combination of both.

2. Methods

The present meta-analysis was conducted in accordance with the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) Statement guidelines (see Page et al., 2021). We followed the PRISMA checklist (<https://www.prisma-statement.org/>) and provide a corresponding flow diagram summarizing the study selection process (see Fig. 3).

2.1. Study selection and inclusion criteria

Given that our primary objective was to identify overlapping brain areas of grammatical and arithmetic processing, we conducted two independent literature searches. First, we searched for studies on grammatical processing with the following search terms: “syntax” OR “grammar” AND “fMRI”. Second, we searched for studies on arithmetic processing using the search terms “arithmetic” OR “algebra” AND “fMRI”. Initial searches were conducted in September 2022 on PubMed and included all peer-reviewed articles that were published up to that date. These searches yielded 383 studies on grammatical processing as well as 778 studies on arithmetic processing. To ensure that the meta-analysis reflected the most up-to-date literature, we conducted a follow-up search in April 2025 using the same search terms and database. This additional search identified 28 additional studies on grammatical processing and 25 additional studies on arithmetic processing.

2.2. Data extraction and coding procedure

In accordance with the PRISMA guidelines, we implemented a screening and coding procedure that involved three main steps (see Fig. 3). First, studies were *title-screened* considering the search terms mentioned above. Specifically, studies were excluded at this stage if the title clearly indicated that the study was unrelated to grammatical or arithmetic processing or that fMRI was not used in this study. “Grammatical” or “arithmetic” processing were interpreted broadly at this stage. Specifically, studies with a title that referred to other language or

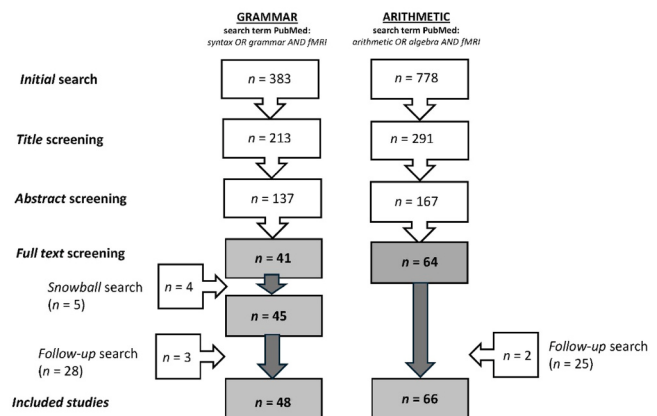


Fig. 3. PRISMA flow diagram of the systematic literature search and study selection process for the two independent meta-analyses on grammatical and arithmetic processing. The diagram shows the numbers of studies included at each step of the selection process (initial database search, title screening, abstract screening, full text screening, final inclusion). Note. ‘Snowball search’ refers to the identification of additional studies from the reference lists of articles retained during full-text screening, as well as from the reference lists of reviews and meta-analyses excluded at earlier stages. ‘Follow-up search’ refers to a second round of database searching (April 2025) conducted after the initial round (September 2022) to ensure that the meta-analysis reflected the most recent literature, followed by the same screening steps applied to the newly identified studies.

mathematical domains (e.g. algebra, reading) were retained for the abstract screening. In addition, studies were excluded if the title indicated that the article was a review, clinical trial, case study, or other meta-analysis. These exclusion criteria were applied consistently across the subsequent abstract and full-text screening stages.

Second, the *abstracts* of the remaining studies were screened with respect to the search terms and previously defined exclusion criteria. Studies were excluded if they (1) exclusively included clinical or otherwise unhealthy participants, (2) exclusively used brain imaging methods other than fMRI (e.g., EEG; structural MRI), (3) did not report whole brain analyses, (4) used unsuitable grammatical or arithmetic tasks (e.g. learning/training tasks, artificial grammar tasks), or (5) used arithmetic tasks that could not be dissociated from linguistic processing (e.g., arithmetic word problems, in which the mathematical operation is embedded in a sentential context). This last criterion ensured that observed neural overlap between grammatical and arithmetic processing could not be attributed to linguistic demands introduced by the arithmetic task itself.

Third, all studies that passed the abstract screening were *full text screened* using the same inclusion and exclusion criteria described above. In addition, we checked (1) that these studies actually included a grammar or arithmetic task performed in the fMRI scanner, and (2) that whole-brain functional activation results were reported for healthy participants. Also, previous studies indicate that children do not show separate brain networks of syntax and semantic processing before the age of 9–10 (e.g., Wang et al., 2023; 2024). Therefore, studies that focused on grammatical processing before that age were excluded from our meta-analyses on grammatical processing. Finally, because there was an imbalance between studies involving right- and left-handers (i.e., the vast majority of studies involved right-handers), we excluded the few studies that involved only left-handers (e.g., Tejavibulya et al., 2022).

The full-text screening procedure resulted in the inclusion of 41 studies on grammatical processing and 64 studies on arithmetic processing. All included studies were subsequently subjected to fine coding, as presented in Table 1. As part of this process, the reference lists of the included articles, as well as the excluded reviews and meta-analyses, were screened for additional relevant studies (“Snowball search”). This procedure yielded five additional studies on grammatical processing, four of which were included in the fine-coding procedure. In total, fine-coding was conducted for 45 grammatical processing studies and 64 arithmetic processing studies.

The entire screening and coding procedure was double-coded. Specifically, the first coding was conducted by the first author, and the second coding was conducted by the second author and a research engineer. Discrepancies were evaluated at two stages: (a) the general inclusion of the studies in the fine coding procedure, and (b) the fine coding procedure itself. For the study inclusion, the intercoder reliability was 93.5% for studies on grammatical processing and 95% for

studies on arithmetic processing. For the fine-coding procedure, the inter-coder-reliability was 92.3% for studies on grammatical processing and 97.5% for studies on arithmetic processing. All disagreements between the coders were resolved through discussion and by consulting the original articles.

The follow up search yielded three additional studies on grammatical processing ($n = 45 + 3 = 48$) and two additional studies on arithmetic processing ($n = 64 + 2 = 66$). The follow up coding procedure was conducted by all three authors. Intercoder-reliability for the inclusion of the studies was 96.4% for grammatical processing and 84.0% for arithmetic processing. After discussing the initial discrepancies, full agreement was reached for all inclusion decisions. Intercoder-reliability for the fine-coding procedure was 100% for studies on both grammatical and arithmetic processing. References for all included studies, as well as detailed information on each study can be found in the [Supplementary Materials](#). A descriptive summary of the included studies, including characteristics of participants, materials and contrasts, is shown in Table 2.

2.3. Meta-analytic procedure

In a first step, we conducted two separate ALE (see Eickhoff et al., 2016; 2012; 2009; Turkeltaub et al., 2012) meta-analyses (both including children and adults): one for grammatical processing and one

Table 2
Descriptive summary of the included studies.

	Grammar studies ($n = 50^1$)	Arithmetic studies ($n = 70^1$)
Participants		
Mean Sample size	18.4	26.4
<u>Languages</u>		
English	34.0%	44.3%
German	32.0%	14.3%
Dutch	6%	7.1%
Finnish	—	1.4%
Swedish	—	1.4%
French	4.0%	12.9%
Spanish	4.0%	—
Mandarin	6.0%	14.3%
Japanese	8.0%	—
English-Chinese	—	1.4%
Kaqchikel	2.0%	—
Unknown	—	1.4%
<u>Ages</u>		
< 14 years	4.0%	27.1%
14–18 years	—	8.6%
18–35 years	86.0%	65.7%
35–45 years	4.0%	—
> 45 years	4.0%	—
<u>Tasks</u>		
<u>Modality</u> ³		
Verbal/audio	66.0%	2.9%
Visual	44.0%	97.1%
<u>Contrasts</u> ³		
Stimuli vs. baseline/fixation	24.0%	25.7%
Production vs. stimuli repetition ³	6.0%	1.4%
Large vs. small problems (arithmetic only)	12.0%	29.8%
Stimuli vs. other tasks	78.0%	45.7%

Notes. ¹Sample sizes between included studies following the search procedure vs. studies included in the meta-analysis differ due to the fact that some studies conducted different experiments using different participants. ²While “production” refers to a higher cognitive process demand by a given stimulus (e.g., conversion of a given word in another word form), “repetition” refers to a simple repetition demand of the presented stimuli (e.g. oral repetition of the word in its presented form); ³Given that some studies included different modalities of stimuli presentations or different combinations of task contrasts, the percentage values do not sum to 100%. More detailed information for each study can be found in the supplemental file.

Table 1
Coding criteria in the fine-coding procedure.

Moderators	Levels and operation definitions
Title screening	1 = “yes”/ 2 = “not sure”/ 0 = “no”
Abstract screening	1 = “yes”/ 2 = “not sure”/ 0 = “no”
Full-text screening	1 = “yes”/ 2 = “not sure”/ 0 = “no”
Whole brain analyses	1 = “yes”/ 0 = “no”
fMRI task visual/verbal	1 = visual/ 2 = audio/verbal
fMRI Scanner	Name of the scanner
Statistical threshold	statistical threshold of the included contrasts
fMRI task	Short description of the task
Contrasts fMRI task	Contrasts
Coordinates fMRI task	MNI or Talairach values
Number of participants	Total number of participants
Country	Name of the country
Age span	Age span
Mean age	Mean age

for arithmetic processing. Note that two of the grammar studies (Heim et al., 2003; Obleser et al., 2011) and three of the arithmetic studies (Chang et al., 2016; Díaz-Barriga Yáñez et al., 2023; Matejko and Ansari, 2019) included separate experiments on different groups of participants. This led to the final inclusion of 50 studies in the meta-analysis of grammatical processing and 70 studies in the meta-analysis of arithmetic processing. With both sample sizes we met the suggested criterion for adequate power, which is ≥ 30 experiments (see Eickhoff et al., 2016; Yeung et al., 2023).

The BrainMap application GingerALE was used to run the meta-analyses (Version 3.02: Fox et al., 2013; <https://www.brainmap.org>). For each ALE meta-analysis, the following procedure was applied: First, all reported activation foci were converted into a common space (i.e., the Montreal Neurological Institute template). Next, each focus was modeled as a three-dimensional Gaussian probability distribution reflecting spatial uncertainty (e.g., Eickhoff et al., 2009). For each experiment, modeled activation maps were generated by combining the Gaussian distributions of all reported foci using the maximum probability approach, thereby accounting for within-experiment effects (e.g., Turkeltaub et al., 2012). ALE scores were then computed by combining modeled activation maps across experiments to identify regions showing consistent activation across studies. Results were thresholded at a voxel-level of $p < 0.05$ using family-wise error correction (FWE), which provides stringent control of false positives and prioritizes spatial specificity, and has been recommended for ALE meta-analyses with sufficiently powered datasets (see Eickhoff et al., 2016; Frahm et al., 2022). Given that both datasets substantially exceeded the recommended minimum of 30 experiments for adequately powered ALE analyses (Eickhoff et al., 2016), we chose voxel-level FWE over cluster-level FWE to prioritize spatial specificity over sensitivity. Statistical inference was performed by comparing the observed ALE values against a null distribution generated from 1000 permutations (e.g., Eickhoff et al., 2012; Marozzi, 2004). To avoid spurious clusters consisting of only a few voxels, we applied a minimum cluster size of 200 mm³ (e.g., Eickhoff et al., 2016), consistent with common practice in ALE-meta-analyses (e.g., Chai et al., 2025; Gavazzi et al., 2023; Kumar et al., 2016; Noferini et al., 2026).

In a second step, we conducted two additional analyses. First, we performed a conjunction analysis to determine brain areas that both support grammatical and arithmetic processing. This was done by using the results of the separate meta-analyses of grammatical and arithmetic processing (see Figure S1, Table S1 and S2), as well as a third dataset that pooled the foci from both grammatical and arithmetic studies (this dataset served as an empirical baseline, Fox et al., 2013). A new ALE map taking the voxel-wise minimum value from the two original thresholded maps was then created to determine areas of overlap across the two meta-analyses. Second, we conducted contrast analyses in both directions (grammatical > arithmetic; arithmetic > grammatical) to identify brain regions that were specific to each domain. Statistical inference for conjunction and contrast analyses was again based on 1000 permutations controlling for multiple comparisons applied at the voxel-level using a family-wise error-corrected threshold of $p < .05$ with minimum cluster size of 200 mm³ due to the reasons described above. All images were visualized using MRICroGL (Rorden and Brett, 2000).

Finally, because the main analyses described above included both children and adults, we repeated the procedure described above but this time only including studies on adult participants (grammar studies: $n = 48$; arithmetic studies: $n = 45$). This allowed us to evaluate the impact of including studies with children on the main findings.

3. Results

3.1. Brain regions involved in grammatical or arithmetic processing (separate meta-analyses)

Results of the separate meta-analyses for both grammatical and

arithmetic processing in children and adults can be found in the [Supplementary Materials](#) (see Table S2, Table S3, Figure S1). Briefly, these analyses indicate that studies on grammatical processing most consistently report activation of a left-lateralized brain network that involves the IFG/MFG, MTG and STG, the pre supplementary motor area (preSMA), and the parietal cortex (see Table S2 and Figure S1). Studies on arithmetic processing most consistently report activation of a bilateral network that includes the IFG, parietal cortex, insula, preSMA, and MFG (see Table S3 and Figure S1). These findings suggest both overlapping and distinct brain regions supporting grammatical and arithmetic processing. We then turn to conjunction and contrast analyses to formally test this claim.

3.2. Brain regions involved in both grammatical and arithmetic processing

Significant clusters identified in the conjunction analysis of grammatical and arithmetic processing in children and adults are shown in Fig. 4 and Table 3. The conjunction analysis between grammatical and arithmetic processing revealed four left-lateralized clusters. The largest cluster was identified at the border of the IFG and MFG (Brodmann Area [BA] 9). With a cluster volume of 1552 mm³, this cluster was more than twice as large as any of the other three clusters. The second cluster was located in the left SMA (BA 6; 776 mm³) and the third cluster in the left IPL (BA 40; 536 mm³). A smaller cluster of 256 mm³ was also found in the dorsal part of the left anterior Insula (BA 13). Thus, four left-lateralized regions showed consistent spatial overlap across studies of grammatical processing and arithmetic processing.

3.3. Brain regions more involved in grammatical than arithmetic processing

The contrast analysis comparing grammatical to arithmetic processing showed three left-lateralized clusters (see Table 4). The largest cluster (5816 mm³) was identified in the left IFG, encompassing the opercular and triangular parts corresponding to Broca's area (BA 44 and BA 45). The second cluster (1624 mm³) was located in the left temporal cortex, extending across the posterior STG (BA 22) and the dorsal MTG (BA 21), which are two regions traditionally associated with Wernicke's area. Beyond these perisylvian brain regions, a third cluster (1720 mm³) was identified in the left anterior SMA (BA 6), indicating additional frontal involvement specific to grammatical processing.

3.4. Brain regions more involved in arithmetic than grammatical processing

The contrast analysis comparing arithmetic to grammatical processing revealed a large number of clusters distributed across both hemispheres (see Fig. 4 and Table 5). The most prominent clusters were located bilaterally in the right IPS (6408 mm³) and left IPS (5512 mm³). Another cluster (2816 mm³) included parts of the left SMA and the left anterior cingulate cortex (BA 6; BA 32; BA 24). Two additional clusters were located in the anterior insula bilaterally, with one cluster in the left insula (2232 mm³) and the right insula (1888 mm³). Another cluster extended across the left MFG and parts of the precentral gyrus (BA 6; BA 9; 1720 mm³). Finally, three smaller clusters were found in the dorsolateral prefrontal cortex (BA 9; 440 mm³), the left SMA (BA 6; 688 mm³) and an additional region of the left intraparietal sulcus (BA 40; 312 mm³).

3.5. Control analyses only involving adult participants

The main analyses described above included studies involving both children and adults. Therefore, it is difficult to determine the impact of learning and development on our results. Unfortunately, there were not enough studies with children to perform reliable contrast analyses comparing adults to children (Müller et al., 2018). Nonetheless, we

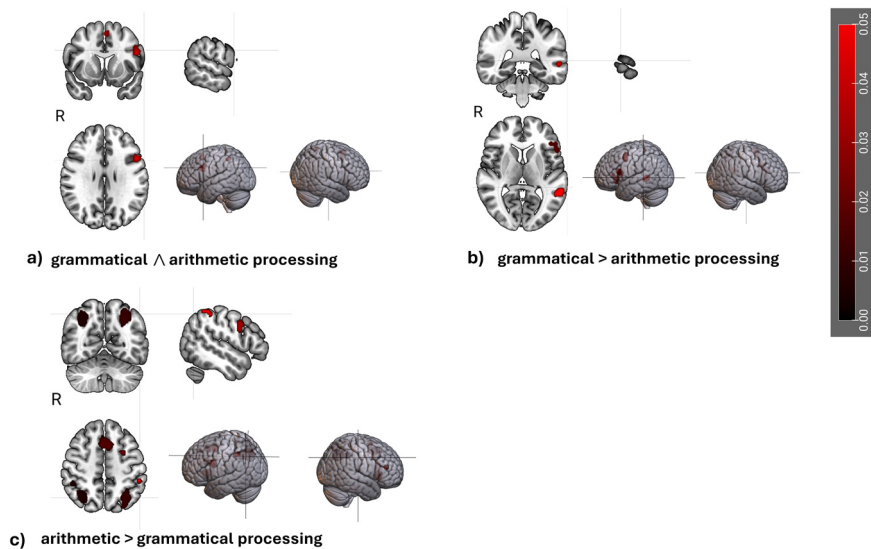


Fig. 4. Brain regions showing shared and dissociated activation between grammatical and arithmetic processing across studies including adults and children. Statistical maps are shown for (a) the conjunction analysis identifying regions commonly engaged in grammatical and arithmetic processing (grammatical $\wedge$ arithmetic), (b) the contrast analysis identifying regions more strongly engaged in grammatical than arithmetic processing (grammatical $>$ arithmetic), and (c) the contrast analysis identifying regions more strongly engaged in arithmetic than grammatical processing (arithmetic $>$ grammatical). All analyses used activation likelihood estimation (ALE; Eickhoff et al., 2016) with a voxel-level family-wise error-corrected threshold of $p < 0.05$ (based on 1000 permutations) and a minimum cluster size of 200 mm³. Color scale represents ALE values. Coordinates are reported in MNI space; "R" indicates the right hemisphere.

Table 3
ALE conjunction analysis of brain regions supporting grammatical and arithmetic processing in children and adults.

Cluster	MNI Coordinates			ALE value	Volume (mm ³)	Foci	Contributing studies
	x	y	z				
(1) Left Inferior and Middle Frontal Cortex (BA 9)	-48	12	26	.050	1552	28	A2, A7, A11, A12, A15, A33, A41, A43, A49, A52, A60, A66, G3, G7, G18, G24, G31, G34, G38, G40, G41, G50,
(2) Left Supplementary Motor Area (BA 6)	-2	14	54	.038	776	29	A2, A8, A9, A11, A12, A13, A15, A28, A29, A35, A36, A39, A41, A43, A49, A55, A61, A66, G31, G32, G37, G40, G46, G50,
(3) Left Inferior Parietal Lobule (BA 40)	-42	-44	48	.032	536	15	A14, A31, A45, A53, A56, A58, A68 G7, G19, G20, G26, G34, G41, G44
(4) Left Insula (BA 13)	-32	26	-2	.029	256	7	A7, A24, A43 G7, G32, G38, G40

Note. The table on the contributing studies including study details can be found in the Supplementary file in Table S1.

assessed the impact of studies involving children on our main findings by running our analyses once again, but this time only with adult studies. All figures and tables relative to these control ALE meta-analyses are available in the [Supplementary Materials](#) (see [Table S4-S8](#) and [Figure S1-S3](#)).

After excluding studies involving children, the conjunction analysis still again identified the same four overlapping clusters: left IFG/MFG (BA 9: $X = -48$, $Y = 12$, $Z = 28$; ALE=.0468; 1480 mm³), left SMA (BA 6: $X = -2$, $Y = 14$, $Z = 54$; ALE=.0375; 544 mm³), left IPL (BA 40: $X = -40$, $Y = -46$, $Z = 48$; ALE=.0314; 328 mm³) and the dorsal part of the left anterior Insula (BA 13: $X = -34$, $Y = 26$, $Z = -2$; ALE=.0259; 128 mm³). The Grammar $>$ Arithmetic contrast likewise replicated the main findings, revealing the same three clusters as in the primary analyses: the left IFG (BA 44, BA 45: $X = -50.5$, $Y = 19.9$, $Z = 6.8$; $p < .001$, $Z = 3.29$; 4952 mm³), left SMA (BA 6: $X = -43.7$, $Y = 1.9$, $Z = 51.2$; $p < .001$, $Z = 3.29$; 1528 mm³), and left STG/MTG (BA 22, BA 21: $X = -57.6$, $Y = -46.8$, $Z = 4.8$; $p < .001$, $Z = 3.29$; 1728 mm³). Similarly, the Arithmetic $>$ Grammar contrast reproduced the principal findings, including bilateral IPS clusters (right IPS: BA 40, BA 7: $X = 30.5$, $Y = -59.4$, $Z = 41.1$; $p = .013$, $Z = 3.29$; 3928 mm³; left IPS: BA 19, BA 39: $X = -25.6$, $Y = -63.3$, $Z = 40.1$; $p < .001$, $Z = 3.29$; 3560 mm³), SMA/ anterior cingulate cortex (BA6, BA 32, BA 24: from cluster#3/9:

2816 mm³ to cluster#5/7:1256 mm³), bilateral insula (right Insula: BA 13: cluster#5/9: 1888 mm³ to cluster#7/7: 664 mm³; left Insula: BA 13: cluster#4/9: 2232 mm³ to cluster#3/7: 1384 mm³), and inferior/middle frontal regions (BA 6, BA 9: cluster#6/9: 1720 mm³ to cluster#4/7: 1256 mm³). Thus, excluding studies involving children had little impact on the overall pattern of results.

4. Discussion

The overarching goal of our study was to shed light on the causes of the association between grammatical and arithmetic skills by identifying the brain regions that consistently support both grammatical and arithmetic processing in the literature. Specifically, we aimed to determine whether areas of overlap would be predominantly located in regions that may be involved in linguistic-semantic processing or in domain-general processes which underpin rule-processing mechanisms. We conducted separate ALE meta-analyses for both grammatical and arithmetic processing, followed by a conjunction analysis to identify shared brain regions and contrast analyses in both directions (grammar $>$ arithmetic; arithmetic $>$ grammar). Due to the small number of available brain imaging studies identified for grammatical processing in children, we conducted our main meta-analysis on both children and

Table 4
ALE contrast analysis of grammatical vs. arithmetic processing in children and adults.

Cluster	MNI Coordinates			p	z	Volume (mm ³)	Foci	Contributing studies
	x	y	z					
(1) Left Inferior Frontal Gyrus (BA 44, BA 45)	-50.8	19.1	7.9	<.001	>3	5816	48	G1, G2, G3, G7, G8, G9, G10, G11, G12, G14, G20, G22, G27, G29, G30, G31, G32, G34, G36, G37, G39, G41, G42, G43, G44, G46, G49
(2) Left anterior supplementary motor area (BA 6)	-42.3	2	50.2	<.001	>3	1720	18	G17, G19, G26, G27, G31, G32, G34, G40, G44, G46, G47, G48
(3) Left Middle/ Superior Temporal Gyrus (BA 21, BA 22)	-56.5	-44.9	4.4	<.001	>3	1624	13	G6, G8, G9, G17, G32, G38, G43, G44, G45, G46, G49

Note. The table on the contributing studies including study details can be found in the Supplementary file in Table S1.

adults and subsequently performed a control meta-analysis including only adult studies.

On the one hand, we found an overlap between grammatical and arithmetic processing in four left-lateralized brain clusters located in the IFG/MFG, the SMA, the IPS and the anterior Insula. On the other hand, we also found several clusters showing specificity for each domain. In particular, we identified clusters for grammatical processing in the left Perisylvian regions and clusters for arithmetic processing in various regions of the left hemisphere, as well as in the bilateral IPS. Together, these findings provide important insights into the neural architecture underlying the association between grammatical and arithmetic processing.

4.1. Brain regions showing overlapping activity between grammatical and arithmetic processing

Our main meta-analysis revealed four clusters of shared neural activation between grammatical and arithmetic processing, all located in the left hemisphere. Specifically, the largest cluster was identified at the border between the left IFG and left MFG (BA 9), while two clusters of comparable size were found in the left SMA (BA 6) and in the dorsal part of the left inferior parietal lobule (IPL, BA 40). A smaller cluster was detected in the dorsal part of the left anterior Insula (BA 13).

All four clusters are typically associated with the so-called “multiple-demand network” of cognitive processing (for reviews see Duncan, 2010; Duncan and Owen, 2000; Fedorenko et al., 2024; Humphreys and Tibon, 2023). The multiple-demand network notably comprises a set of frontal and parietal regions that are activated across a wide range of cognitive tasks. Activations in the multiple-demand network have been linked to domain-general cognitive processes, such as attention, perception, response selection, executive control, working memory, episodic memory or problem solving (e.g., Duncan, 2010; Duncan and Owen, 2000; Humphreys and Tibon, 2023). For instance, prior studies that contrasted task difficulty across diverse cognitive domains including language or mental arithmetic found neural activation in at the junction between the left IFG and left MFG (e.g., Jost et al., 2009; Kong et al., 2005; Gruber et al., 2001; Menon et al., 2000; Zago et al., 2001). Such complex cognitive processes are known to place high demands on executive function or working memory processes (e.g., Nee et al., 2012). Importantly, prior studies have shown that the area of the left IFG that extends dorsally into the MFG is typically associated with executive demands rather than language-specific processing (e.g., Fedorenko and Blank, 2020).

Similarly, studies show that the SMA is not only associated with the execution of motor processes but also with attention, inhibition or updating (e.g., Bhattacharjee et al., 2021; Hanakawa et al., 2002; Tanaka et al., 2005). The left parietal lobule (BA 40) has also been shown to support working memory (e.g. Koenigs et al., 2009), consistent with the fact that it exhibits long-range connectivity with lateral frontal executive control regions of the dorsolateral prefrontal cortex (for reviews see Humphreys et al., 2020; Humphreys and Tibon, 2023). Finally, the anterior Insula has been consistently associated with general goal-directed cognition (e.g., Chang et al., 2013; Duncan and Owen, 2000; Dosenbach et al., 2006; Yarkoni et al., 2009), including executive processing, inhibition, switching, or error-processing (for reviews see Chang et al., 2013; Menon and Uddin, 2010; Menon, 2024).

Notably, although the multiple-demand network is often activated during grammatical processing (e.g., sentence comprehension, sentence production, lexical decision or picture naming), it is not sensitive to linguistic meaning per se (e.g., Fedorenko et al., 2024). Instead, the network appears to be similarly engaged during the processing of different types of arithmetic problems, regardless of whether numerical problems are presented symbolically (e.g., $500 - 2 + 3 = ?$) or verbally (e.g., *subtract 2 from 500, then add 3*), indicating that the multiple-demand network operates largely independently of representational format or semantic content (see Fedorenko et al., 2024). Taken

Table 5

ALE contrast analysis of arithmetic vs. grammatical processing in children and adults.

Cluster	MNI Coordinates			<i>p</i>	<i>Z</i>	Volume (mm ³)	Foci	Contributing studies
	<i>x</i>	<i>y</i>	<i>z</i>					
(1) Right IPS (BA 40; BA 7)	33.1	-57.6	41.4	.013	>2	6408	65	A1, A2, A3, A5, A6, A9, A12, A13, A14, A15, A18, A20, A22, A24, A25, A28, A31, A33, A40, A41, A43, A45, A48, A49, A50, A51, A56, A57, A58, A60, A62, A63, A64, A68, A70
(2) Left IPS (BA 7; BA 19; BA 39)	-27.8	-63.2	43.4	<.001	>3	5512	67	A1, A2, A3, A4, A5, A6, A9, A11, A12, A13, A15, A18, A20, A23, A24, A25, A26, A27, A28, A31, A35, A36, A37, A39, A40, A42, A43, A45, A48, A49, A50, A51, A57, A58, A59, A60, A66, A67, A70
(3) Left Supplementary Motor Area / Cingulate Gyrus (BA 6; BA 32; BA 24)	2.3	13.4	45.4	<.001	>3	2816	38	A5, A6, A8, A9, A12, A13, A15, A18, A19, A27, A28, A29, A31, A33, A35, A36, A41, A43, A49, A50, A51, A52, A55, A58, A61, A62, A64, A66
(4) Left Claustrum/Left Insula (BA 13)	-31.2	18.7	3.53	<.001	>3	2232	35	A4, A5, A7, A8, A9, A10, A13, A16, A23, A24, A25, A36, A37, A39, A43, A51, A53, A55, A56, A59, A61, A66, A69, A70
(5) Right Insula/Right Claustrum (BA 13)	35.2	19.6	6.3	<.001	>3	1888	19	A3, A5, A7, A8, A11, A18, A20, A23, A37, A43, A50, A51, A53, A55, A56, A59, A61
(6) Left Precentral Gyrus/Left Inferior Frontal Gyrus/Left Middle Frontal Gyrus (BA 6; BA 9)	-50	2	30	<.001	>3	1720	25	A13, A18, A22, A33, A35, A36, A40, A41, A42, A43, A49, A50, A51, A55, A56, A59, A66, A70
(7) Left Supplementary Motor Area (BA 6)	-23	4.5	56.5	<.001	>3	688	7	A4, A9, A20, A23, A33, A41, A51
(8) Right Dorsolateral Prefrontal Cortex (BA 9)	45.6	36.3	22.9	<.001	>3	440	11	A9, A13, A15, A24, A31, A40, A50
(9) Left IPS (BA 40)	-50	-40	54	.007	>3	312	3	A52, A54, A56

Note. The table on the contributing studies including study details can be found in the Supplementary file [Table S1](#).

together, the shared activation in regions of the multiple_demand network for both grammatical and arithmetic processing does not provide strong support for the view that arithmetic processing primarily depends on linguistic-semantic representations. Rather, these findings are consistent with the view that both grammatical and arithmetic processing rely on domain-general processes supported by shared brain regions.

In a seminal review of grammatical processing in the brain (Sakai, 2005), the two main clusters that we identified in our conjunction analysis—namely the left IFG extending dorsally into the MFG (BA 9) and the left SMA (BA 6)—were proposed to form a putative “grammar center” reflecting the “universal nature of grammatical processing” (p. 817). These regions were argued to selectively process syntactic structures of grammar independently of (verbal) working memory demands. In this respect, it is worth noting that the shared activation of syntactic processing in language and arithmetic in the IFG reported by Nakai and Okanoya (2020) was observed while controlling for working memory processes. Likewise, most behavioral studies reporting an association between syntactic grammar and arithmetic skills controlled for working memory influences. Therefore, it is unlikely that the shared processing of grammar and arithmetic in these regions can be explained solely by shared working memory demands. Instead, it is possible that the left prefrontal cortex, left SMA, and anterior Insula may form a specific brain network supporting the processing of hierarchical, rule-based structures across domains, independently of linguistic meaning. Which higher cognitive functions may be required by this network (e.g., executive control, working memory, inhibition) cannot be answered with our study.

Interestingly, this proposed syntactic network may not be limited to language and mathematics. For instance, a recent meta-analysis on grammatical syntax and musical rhythm processing (Heard and Lee, 2020) reported the same three main clusters of overlapping brain regions (the SMA, left prefrontal cortex, and left anterior insula) for grammar and music that we identified for grammar and arithmetic. Indeed, the syntactic structure of language has been mapped not only onto arithmetic (e.g., Jeon, 2014; Tettamanti and Weniger, 2006), but also onto music (for a review, see Patel, 2003). This convergence may reflect the fact that music, like language and arithmetic, involve the perception and manipulation of discrete elements organized into

hierarchically structured sequences (Patel, 2003).

Note, however, that the brain regions identified here differ from those previously proposed to support general hierarchical processing across a variety of cognitive domains. Specifically, prior research suggested the pars opercularis (BA 44) as a core region for domain-general hierarchical processing beyond language, mathematic and music (for a review, see Jeon, 2014; Tettamanti and Weniger, 2006). In contrast, the pars opercularis is typically considered part of a core language network and has been shown to be sensitive to linguistic meaning (e.g., Fedorenko et al., 2024).

4.2. Brain regions more involved in grammatical than arithmetic processing

The contrast between grammatical and arithmetic processing revealed three clusters that were selectively engaged during grammatical processing, primarily within the classical perisylvian language network. These clusters included the opercular and triangular parts of the left IFG (BA 44/45), a smaller temporal cluster encompassing the posterior superior and dorsal MTG (BA 22/21), and an additional cluster in the left anterior SMA (BA 6). Together, this pattern indicates that domain-specific grammatical processing recruits both core language regions and adjacent frontal areas beyond the canonical perisylvian cortex.

Broca’s area (BA 44/45) has consistently been identified as a key region during syntactic processing (e.g., Ardila et al., 2016; 2017; Friederici, 2019; 2011; Malik-Moraleda et al., 2022, Sakai, 2005). Numerous neuroimaging studies have reported robust activation during a wide range of syntactic tasks, including sentence comprehension, morphosyntactic agreement, and syntactic complexity manipulations (e.g., Ben-Shachar et al., 2003; 2004; Bonhage et al., 2015; Bornkessel-Schlesewsky et al., 2009; Caplan et al., 2000; 2008; Dapretto and Bookheimer, 1999; Feng et al., 2015; Friederici et al., 2006; Henderson et al., 2016; Moro et al., 2001; Santi and Grodzinsky, 2007; Tyler et al., 2005). Importantly, activations of Broca’s area are often accompanied by co-activation in the anterior STG/dorsal MTG (“Wernicke’s Area”; BA 22, BA 21) and/or the left SMA (BA 6), mirroring the pattern observed in the present meta-analysis.

For instance, Feng et al. (2015) found activations in the left IFG, the

anterior STG/left dorsal MTG, and the left SMA while participants processed passive versus active sentences in a visually presented sentence-picture judgement task. Also, Tyler et al. (2005) showed activation in the left IFG and the anterior STG while participants processed regular versus irregular past tense forms in an orally presented same-different judgement task. Furthermore, Hashimoto and Sakai (2002) found selective activations in the left IFG and the left SMA for syntax processing using a visually presented judgement picture task. Notably, Hashimoto and Sakai (2002) directly contrasted syntax with working memory processes and found that SMA activation persisted for syntactic processing even when working memory was controlled.

In the context of the grammar versus arithmetic contrast, our findings are consistent with Sakai's (2005) proposal that the opercular and triangular parts of the IFG, together with the left anterior SMA, form a core network for syntactic processing. Importantly, in Sakai's account, this network supports grammatical structure building independently of linguistic meaning and cannot be reduced to verbal working memory demands. The present results extend this proposal by showing that this network is selectively recruited for grammatical processing relative to arithmetic, even though other regions of the SMA and IFG may participate in domain-general processing shared between the two domains. Structural connectivity findings linking BA 44 with premotor regions via the opercula-premotor fasciculus (Lemaire et al., 2013) further support the view that some parts of the SMA may contribute specifically to grammatical computations rather than general cognitive control underpinning multiple cognitive processes.

Prior reviews have already pointed out that Broca's area (BA 44/45) and the ventral premotor cortex (BA 6) may support general grammatical processing (see Friederici et al., 2006). In particular, it has been argued that the ventral premotor cortex (BA 6) supports the processing of local syntactic dependencies derived from sequential input, whereas Broca's area (BA 44/45) is more strongly involved in the processing of syntactic hierarchies at more abstract levels (see Friederici et al., 2006; Friederici, 2004). Based on our results, it is not possible to determine whether the grammar-specific cluster of the SMA (BA6) we identified reflects sensitivity to linguistic meaning or instead supports higher-order cognitive processes that are required for grammatical but not arithmetic processing. This question is further complicated by the fact that a different region of the SMA (BA 6) also emerged as part of the domain-general convergence network for grammar and arithmetic, suggesting functional heterogeneity within this region.

Finally, the smallest grammar-specific cluster, located in the Wernicke's area (BA 21; BA 22), is most plausibly interpreted as reflecting sensitivity to linguistic meaning. More specifically, previous studies (e.g., Fedorenko, et al., 2012; Shain et al., 2024) that examine the relative contributions of syntax and semantics within the language network found that grammar processing with and without lexical meaning (sentences vs. Jabberwockies) is present across many regions of the language network. However, the sensitivity to syntactic processing in the absence of meaning is weakest in the anterior STG and dorsal MTG compared to the other parts of the language network.

4.3. Brain regions more involved in arithmetic than grammatical processing

The contrast between arithmetic and grammatical processing revealed nine clusters that were selectively engaged during arithmetic processing. Specifically, two large clusters were identified in the right (BA 7; BA 40) and in the left IPS (BA 7; BA 19; BA 39). Furthermore, we found seven much smaller clusters distributed over both hemispheres. These clusters included the left and right Insula (BA 13), but also further parts of the left frontal gyrus (BA 6; BA 32; BA 24) and the left dorsolateral prefrontal cortex (BA 9).

The prominent bilateral involvement of the IPS is consistent with a large body of evidence identifying this region as a core substrate of numerical and arithmetic processing (e.g., Dehaene et al., 2004;

Escobar-Magariño et al., 2022; Xu and Spelke, 2000; Holloway et al., 2010; Ansari, 2016; Matejko and Ansari, 2019; Sokolowski et al., 2017). Specifically, the IPS is frequently found to be activated during the encoding and manipulation of symbolic and non-symbolic magnitudes (e.g., Cohen Kadosh et al., 2007; Piazza et al., 2007; Holloway et al., 2013; Knops, 2017; Nieder, 2025).

However, in addition to its hypothesized domain-specific role of magnitude processing, the IPS has also been associated with the multiple demand network (for reviews see Duncan, 2010; Duncan and Owen, 2000; Fedorenko et al., 2024; Humphreys and Tibon, 2023). Note that arithmetic tasks often impose substantial demands on domain-general cognitive resources, including working memory, executive control, and interference resolution. Consistent with this, we also found several smaller arithmetic-specific clusters that were located in other regions associated with the multiple-demand network, such as the dorsolateral prefrontal cortex, medial frontal cortex, supplementary motor area, and anterior insula. These regions have been implicated in attentional control, task switching, updating, and working memory maintenance (for reviews, see Chang et al., 2013; Cowan, 2011; Rottschy et al., 2012; Vogel and de Smedt, 2021). Notably, visual working memory processes, which have been shown to play a particularly important role in arithmetic problem solving, are strongly associated with fronto-parietal activation patterns overlapping with those observed here (for a review Li et al., 2022).

The recruitment of these domain-general regions during arithmetic processing likely depends on task demands, problem complexity, and individual expertise. Developmental and expertise-related studies have demonstrated a fronto-parietal shift in arithmetic processing across the lifespan, with greater reliance on frontal control regions during early learning or difficult problems and increased parietal specialization with automatization and expertise (e.g., Artemenko, 2021; Menon, 2010; Zamarian et al., 2009; Vogel and de Smedt, 2021). Note that, given that about 30% of the arithmetic studies (but only about 10% of the grammar studies) included in the present meta-analysis here focused on a contrast involving a difference in difficulty (e.g., larger versus small problems), the greater involvement of brain regions from the multiple-demand network in arithmetic than grammatical processing may be affected by a confound in task difficulty rather than a specificity of arithmetic processing compared to grammatical processing per se.

4.4. Limitations

The present meta-analysis is subject to several limitations that should be considered when interpreting the findings. First, due to the small number of studies that examined grammatical or arithmetic processing in children, it was not possible to run separate conjunction analyses and contrast analyses on grammatical and arithmetic processing for children and adults. Therefore, it remains unclear whether there are developmental differences in the neural association and distinctions between grammatical and arithmetic processing. Nonetheless, our control analyses indicate that the inclusion of studies involving children did not have a large effect on our main findings, as these were very similar when only adult studies were included. Given that it is unlikely that a sufficient number of developmental studies on grammatical processing will become available in the near future, further progress will depend on individual neuroimaging studies that directly compare grammatical and arithmetic processing across development within the same experimental framework.

Second, we were not able to perform separate analyses for different types of arithmetic operations or different kinds of grammar tasks, as the number of available studies did not allow for this. Previous studies have shown that arithmetic operations such as addition, subtraction, multiplication, and division can recruit partially distinct neural networks, often reflecting differences in strategy use, task complexity, and expertise (e.g., De Smedt et al., 2011; Fehr et al., 2007; for a review see Arsalidou and Taylor, 2011; Menon, 2010; Rosenberg-Lee et al., 2011).

Similarly, different grammar tasks, such as sentence comprehension, grammaticality judgement, or sentence-picture matching, may differentially engage working memory, visual processing, or control-related regions (e.g., Friederici et al., 2004, 2006). Therefore, the present results reflect commonalities across heterogeneous task designs rather than fine-grained distinctions between specific operations or task types.

Third, as pointed out earlier, about 30% of the arithmetic studies included in our meta-analysis focused on a manipulation difficulty, contrasting large to small problems. Such contrasts are known to robustly engage domain-general control regions, including working memory and executive function networks (e.g., Chang et al., 2013; Prado, 2018; Vogel and De Smedt, 2021). Thus, some of the arithmetic-specific activation observed in domain-general regions may reflect task-induced cognitive demands rather than arithmetic processing per se. Future studies examining the neural overlap and distinctions of grammatical and arithmetic processing should include tasks controlling for working memory or cognitive control to better disentangle shared domain-general processes from domain-specific mechanisms.

Fourth, the present meta-analysis relies on group-level activation coordinates, which raises general concerns about interindividual variability in the precise localization of functional brain regions (e.g., Bijsterbosch et al., 2018; Fedorenko, 2021; Shain et al., 2024). This clearly places limitations on the interpretability of group-averaged anatomical labels such as Brodmann areas. Although our interpretations draw on well-characterized functional networks identified through individual-level localization (e.g., the language network and the multiple-demand network), the assignment of specific cognitive functions to anatomically defined clusters should nevertheless be approached with caution. Accordingly, the present findings should be understood as reflecting probabilistic convergence across studies rather than definitive localization of cognitive processes.

Finally, coordinate-based meta-analyses such as ALE map spatial convergence of activation peaks across studies (e.g., Acar et al., 2018; Eickhoff et al., 2016) but cannot inform about the finer-grained computations implemented within those regions. Even when two tasks reliably activate the same macroscopic region, they may recruit functionally distinct neuronal populations, rely on different multivariate activity patterns, or engage different patterns of functional connectivity (e.g., Engel et al., 2021; Rasero et al., 2024). The present findings should therefore be understood as evidence of shared spatial convergence rather than shared neural computations. Methods with finer functional resolution (e.g., multivariate pattern analysis, representational similarity analysis, or subject-specific functional localization) will be needed to determine whether the overlapping regions identified here support common or distinct computations across grammatical and arithmetic processing.

4.5. Conclusion

The present meta-analysis found a neuronal overlap between grammatical and arithmetic processing in the left hemisphere, in particular at the junction between the left IFG and the left MFG, the SMA, the IPL and the anterior Insula. These brain regions are widely recognized as being part of the multiple-demand network, which supports complex cognitive processing across domains, including executive control, working memory, and attentional regulation. The observed neural overlap is therefore consistent with the hypothesis that the association between grammatical and arithmetic skills may reflect shared demands on domain-general mechanisms involved in understanding, extracting, and applying complex rule structures. Thus, the association between grammatical and arithmetic skills may reflect a shared neural architecture for structured, rule-based cognition rather than shared linguistic representations per se. By contrast, classical language regions selectively distinguished grammatical from arithmetic processing, further suggesting that arithmetic processing does not primarily rely on linguistic representations.

Funding

Parts of this research were funded by the Center of Excellence on Research in Education and Teacher Training (AMPIRIC) to N.V. and J.Z., a Heinrich Hertz Stiftung Scholarship of the Ministry of Culture and Science, North Rhine-Westphalia, Germany to N.V., the Institute of Language, Communication and the Brain (France 2030, ANR-16-CONV-0002) to J.Z., and a research grant from the eFRAN program (France 2030, ANR 22-FRAN-0004) to J.Z.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.neubiorev.2026.106925.

References

- Acar, F., Seurinck, R., Eickhoff, S.B., Moerkerke, B., 2018. Assessing robustness against potential publication bias in Activation Likelihood Estimation (ALE) meta-analyses for fMRI. *PLoS One* 13 (11), e0208177. <https://doi.org/10.1371/journal.pone.0208177>.
- Amland, T., Grande, G., Scherer, R., Lervåg, A., Melby-Lervåg, M., 2025. Cognitive factors underlying mathematical skills: a systematic review and meta-analysis. *Psychol. Bull.* 151 (1), 88–129. <https://doi.org/10.1037/bul0000457>.
- Ansari, D., 2016. Neural substrates. In: Berch, D.B., Geary, D.C., Koepke, K.M. (Eds.), *Mathematical Cognition and Learning: Vol. 2. Development of mathematical cognition: Neural substrates and genetic influences*. Elsevier, pp. 27–50.
- Ardila, A., Bernal, B., Rosselli, M., 2016. How localized are language brain areas? A review of Brodmann areas involvement in oral language. *Arch. Clin. Neuropsychol. Off. J. Natl. Acad. Neuropsychol.* 31 (1), 112–122. <https://doi.org/10.1093/arclin/acv081>.
- Ardila, A., Bernal, B., Rosselli, M., 2017. Should Broca's area include Brodmann area 47? *Psychosoma* 1 (29), 73–77. <https://doi.org/10.7334/psicothema2016.11>.
- Arsalidou, M., Taylor, M.J., 2011. Is 2+2=4? Meta-analyses of brain areas needed for numbers and calculations. *NeuroImage* 54 (3), 2382–2393. <https://doi.org/10.1016/j.neuroimage.2010.10.009>.
- Artemenko, C., 2021. Developmental fronto-parietal shift of brain activation during mental arithmetic across the lifespan: a registered report protocol. *PLOS ONE* 16 (8), 1–13. <https://doi.org/10.1371/journal.pone.0256232>.
- Baldo, J.V., Dronkers, N.F., 2007. Neural correlates of arithmetic and language comprehension: a common substrate? *Neuropsychologia* 45 (2), 229–235. <https://doi.org/10.1016/j.neuropsychologia.2006.07.014>.
- Bánrétí, Z., Mészáros, É., 2019. In: Gyuris, B., Mády, K., Recski, G. (Eds.), *Recursive calculation abilities in agrammatic aphasia: A pilot study*. MTA Nyelvtudományi Intézet, pp. 59–78. $K + K = 120$.
- Barrouillet, P., Mignon, M., Thevenot, C., 2008. Strategies in subtraction problem solving in children. *J. Exp. Child. Psychol.* 99 (4), 233–251. <https://doi.org/10.1016/j.jecp.2007.12.001>.
- Ben-Shachar, M., Hendler, T., Kahn, I., Ben-Bashat, D., Grodzinsky, Y., 2003. The neural reality of syntactic transformations: evidence from functional magnetic resonance imaging. *Psychol. Sci.* 14 (5), 433–440. <https://doi.org/10.1111/1467-9280.01459>.
- Ben-Shachar, M., Palti, D., Grodzinsky, Y., 2004. Neural correlates of syntactic movement: converging evidence from two fMRI experiments. *NeuroImage* 21 (4), 1320–1336. <https://doi.org/10.1016/j.neuroimage.2003.11.027>.
- Bhattacharjee, S., Kashyap, R., Abualait, T., Annabel Chen, S.-H., Yoo, W.-K., Bashir, S., 2021. The role of primary motor cortex: more than movement execution. *Nat. Neurosci.* 53 (2), 258–274. <https://doi.org/10.1080/00222895.2020.1738992>.
- Bijsterbosch, J.D., et al., 2018. The relationship between spatial configuration and functional connectivity of brain regions. *eLife* 7, e32992. <https://doi.org/10.7554/eLife.32992>.
- Bonhage, C.E., Mueller, J.L., Friederici, A.D., Fiebach, C.J., 2015. Combined eye tracking and fMRI reveals neural basis of linguistic predictions during sentence comprehension. *Cortex* 68 (68), 33–47. <https://doi.org/10.1016/j.cortex.2015.04.011>.
- Bornkessel-Schlesewsky, I., Schlewsky, M., Cramon, D.Y. von, 2009. Word order and Broca's region: evidence for a supra-syntactic perspective. *Brain Lang.* 111 (3), 125–139. <https://doi.org/10.1016/j.bandl.2009.09.004>.
- Burton, M.W., 2001. The role of inferior frontal cortex in phonological processing. *Cogn. Sci.* 25 (5), 695–709. [https://doi.org/10.1016/S0364-0213\(01\)00051-9](https://doi.org/10.1016/S0364-0213(01)00051-9).
- Campbell, J.I., Xue, Q., 2001. Cognitive arithmetic across cultures. *J. Exp. Psychol. General.* 130 (2), 299–315. <https://doi.org/10.1037/0096-3445.130.2.299>.
- Caplan, D., Alpert, N., Waters, G., Olivieri, A., 2000. Activation of Broca's area by syntactic processing under conditions of concurrent articulation. *Hum. Brain Mapp.* 9, 65–71.
- Caplan, D., Chen, E., Waters, G., 2008. Task-dependent and task-independent neurovascular responses to syntactic processing. *Cortex* 44 (3), 257–275. <https://doi.org/10.1016/j.cortex.2006.06.005>.
- Carter, B.T., Foster, B., Muncy, N.M., Luke, S.G., 2019. Linguistic networks associated with lexical, semantic and syntactic predictability in reading: a fixation-related fMRI study. *NeuroImage* 189, 224–240. <https://doi.org/10.1016/j.neuroimage.2019.01.018>.

- Chai, Q.Y., Song, A.Q., Zhao, Q.Y., Shen, Q.Q., Cui, L., 2025. An ALE meta-analysis on the effects of neural changes due to exercise on executive function in a healthy population. *Sci. Rep.* 15 (1), 34415. <https://doi.org/10.1038/s41598-025-17431-1>.
- Chang, T.-T., Metcalfe, A.W.S., Padmanabhan, A., Chen, T., Menon, V., 2016. Heterogeneous and nonlinear development of human posterior parietal cortex function. *NeuroImage* 126, 184–195. <https://doi.org/10.1016/j.neuroimage.2015.11.053>.
- Chang, L.J., Yarkoni, T., Khaw, M.W., Sanfey, A.G., 2013. Decoding the role of the insula in human cognition: functional parcellation and large-scale reverse inference. *Cereb. Cortex* 23 (3), 739–749. <https://doi.org/10.1093/cercor/bhs065>.
- Cho, S., Metcalfe, A.W.S., Young, C.B., Ryali, S., Geary, D.C., Menon, V., 2012. Hippocampal-prefrontal engagement and dynamic causal interactions in the maturation of children's fact retrieval. *J. Cogn. Neurosci.* 24 (9), 1849–1866. https://doi.org/10.1162/jocn_a.00246.
- Chomsky, N., 1957. *Syntactic structures*, 2nd ed. Mouton de Gruyter.
- Chomsky, N., 1981. Lectures on Government and Binding: The Pisa lectures (Studies in generative grammar /SGG; Vol. 9). De Gruyter. <https://doi.org/10.1515/9783110884166>.
- Chow, J.C., Ekholm, E., 2019. Language domains differentially predict mathematics performance in young children. *Early Child. Res. Q.* 46, 179–186. <https://doi.org/10.1016/j.jecresq.2018.02.011>.
- Chow, J.C., Majajika, C.E., Sheaffer, A.W., 2021. Language skills of children with and without mathematics difficulty. *J. Speech Lang. Hear. Res.* 64 (9), 1–7. https://doi.org/10.1044/2021_JSLHR-20-00378.
- 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 (2), 307–314. <https://doi.org/10.1016/j.neuron.2006.12.025>.
- Cowan, N., 2011. The focus of attention as observed in visual working memory tasks: making sense of competing claims. *Neuropsychologia* 49 (6), 1401–1406. <https://doi.org/10.1016/j.neuropsychologia.2011.01.035>.
- Dapretto, M., Bookheimer, S.Y., 1999. Form and content: dissociating syntax and semantics in sentence comprehension. *Neuron* 24 (2), 427–432. [https://doi.org/10.1016/S0896-6273\(00\)80855-7](https://doi.org/10.1016/S0896-6273(00)80855-7).
- de Smedt, B., 2016. Individual differences in arithmetic fact retrieval. In: Berch, D.B. (Ed.), *Development of mathematical cognition. Neural substrates and genetic influences*. Elsevier, pp. 219–244.
- de Smedt, B., Holloway, I.D., Ansari, D., 2011. Effects of problem size and arithmetic operation on brain activation during calculation in children with varying levels of arithmetical fluency. *NeuroImage* 57 (3), 771–781. <https://doi.org/10.1016/j.neuroimage.2010.12.037>.
- Dehaene, S., Molko, N., Cohen, L., Wilson, A.J., 2004. Arithmetic and the brain. *Curr. Opin. Neurobiol.* 14 (2), 218–224. <https://doi.org/10.1016/j.conb.2004.03.008>.
- Derrick, D., Archambault, D., 2009. TreeForm: explaining and exploring grammar through syntax trees. *Lit. Linguist. Comput.* 25 (1), 53–66. <https://doi.org/10.1093/lit/fqp031>.
- Díaz-Barriga Yáñez, A., Longo, L., Chesnokova, H., Poletti, C., Thevenot, C., Prado, J., 2023. Neural evidence for procedural automatization during cognitive development: intraparietal response to changes in very-small addition problem-size increases with age. *Dev. Cogn. Neurosci.* 64, 1878–9293. <https://doi.org/10.1016/j.dcn.2023.101310>. Article 101310.
- Dosenbach, N.U.F., Visscher, K.M., Palmer, E.D., Miezin, F.M., Wenger, K.K., et al., 2006. A core system for the implementation of task sets. *Neuron* 50 (5), 799–812. <https://doi.org/10.1016/j.neuron.2006.04.031>. Article 16731517.
- Duncan, J., 2010. The multiple-demand (MD) system of the primate brain: mental programs for intelligent behaviour. *Trends Cogn. Sci.* 14 (4), 172–179. <https://doi.org/10.1016/j.tics.2010.01.004>.
- Duncan, J., Owen, A.M., 2000. Common regions of the human frontal lobe recruited by diverse cognitive demands. *Trends Neurosci.* 23 (10), 475–483. [https://doi.org/10.1016/S0166-2236\(00\)01633-7](https://doi.org/10.1016/S0166-2236(00)01633-7).
- Eickhoff, S.B., Bzdok, D., Laird, A.R., Kurth, F., Fox, P.T., 2012. Activation likelihood estimation meta-analysis revisited. *NeuroImage* 59 (3), 2349–2361. <https://doi.org/10.1016/j.neuroimage.2011.09.017>.
- Eickhoff, S.B., Laird, A.R., Grefkes, C., Wang, L.E., Zilles, K., Fox, P.T., 2009. Coordinate-based activation likelihood estimation meta-analysis of neuroimaging data: a random-effects approach based on empirical estimates of spatial uncertainty. *Human. Brain Mapp.* 30 (9), 2907–2926. <https://doi.org/10.1002/hbm.20718>.
- Eickhoff, S.B., Nichols, T.E., Laird, A.R., Hoffstaedter, F., Amunts, K., et al., 2016. Behavior, sensitivity, and power of activation likelihood estimation characterized by massive empirical simulation. *NeuroImage* 137, 70–85. <https://doi.org/10.1016/j.neuroimage.2016.04.072>.
- Engel, T.A., Schölvinck, M.L., Lewis, C.M., 2021. The diversity and specificity of functional connectivity across spatial and temporal scales. *NeuroImage* 245, 118692. <https://doi.org/10.1016/j.neuroimage.2021.118692>.
- Escobar-Magariño, D., Turel, O., He, Q., 2022. Bilateral intraparietal activation for number tasks in studies using adaptation paradigm: a meta-analysis. *Neuroscience* 490, 296–308. <https://doi.org/10.1016/j.neuroscience.2022.02.024>.
- Fayol, M., Thevenot, C., 2012. The use of procedural knowledge in simple addition and subtraction problems. *Cognition* 123 (3), 392–403. <https://doi.org/10.1016/j.cognition.2012.02.008>.
- Fedorenko, E., 2021. The early origins and the growing popularity of the individual-subject analytic approach in human neuroscience. *Curr. Opin. Behav. Sci.* 40, 105–112. <https://doi.org/10.1016/j.cobeha.2021.02.023>.
- Fedorenko, E., Blank, I.A., 2020. Broca's area is not a natural kind. *Trends Cogn. Sci.* 24 (4), 270–284. <https://doi.org/10.1016/j.tics.2020.01.001>.
- Fedorenko, E., Ivanova, A.A., Regev, T.I., 2024. The language network as a natural kind within the broader landscape of the human brain. *Nat. Rev. Neurosci.* 25, 289–312. <https://doi.org/10.1038/s41583-024-00802-4>.
- Fedorenko, E., Nieto-Castañón, A., Kanwisher, N., 2012. Lexical and syntactic representations in the brain: an fMRI investigation with multi-voxel pattern analyses. *Neuropsychologia* 50 (4), 499–513. <https://doi.org/10.1016/j.neuropsychologia.2011.09.014>.
- Fehr, T., Code, C., Herrmann, M., 2007. Common brain regions underlying different arithmetic operations as revealed by conjunct fMRI-BOLD activation. *Brain Res.* 1172, 93–102. <https://doi.org/10.1016/j.brainres.2007.07.043>.
- Feng, S., Legault, J., Yang, L., Zhu, J., Shao, K., Yang, Y., 2015. Differences in grammatical processing strategies for active and passive sentences: an fMRI study. *J. Neurolinguist.* 33, 104–117. <https://doi.org/10.1016/j.jneuroling.2014.09.002>.
- Fengler, A., Meyer, L., Friederici, A.D., 2016. How the brain attunes to sentence processing: relating behavior, structure, and function. *NeuroImage* 129 (1), 268–278. <https://doi.org/10.1016/j.neuroimage.2016.01.012>.
- Fox, P.T., Laird, A.R., Eickhoff, S.B., Lancaster, J.L., Fox, M., et al., 2013. User manual for gingerALE 2.3. <https://www.brainmap.org/ale/manual.pdf>.
- Frahm, L., Cieslik, E.C., Hoffstaedter, F., Satterthwaite, T.D., Fox, P.T., Langner, R., Eickhoff, S.B., 2022. Evaluation of thresholding methods for activation likelihood estimation meta-analysis via large-scale simulations. *Human. Brain Mapp.* 43 (13), 3987–3997. <https://doi.org/10.1002/hbm.25898>.
- Friederici, A.D., 2004. Processing local transitions versus long-distance syntactic hierarchies. *Trends Cogn. Sci.* 8 (6), 245–247. <https://doi.org/10.1016/j.tics.2004.04.013>.
- Friederici, A.D., 2011. The brain basis of language processing: from structure to function. *Physiol. Rev.* 91 (4), 1357–1392. <https://doi.org/10.1152/physrev.00006.2011>.
- Friederici, A.D., 2012. Language development and the ontogeny of the dorsal pathway. *Front. Evolut. Neurosci.* 4, 1–7. <https://doi.org/10.3389/fnevo.2012.00003>.
- Friederici, A.D., 2019. Hierarchy processing in human neurobiology: how specific is it. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 375 (1789), 1–9. <https://doi.org/10.1098/rstb.2018.0391>. Article 20180391.
- Friederici, A.D., Bahlmann, J., Heim, S., Schubotz, R.I., Anwander, A., 2006. The brain differentiates human and non-human grammars: functional localization and structural connectivity. *Proc. Natl. Acad. Sci. USA* 103 (7), 2458–2463. <https://doi.org/10.1073/pnas.0509389103>.
- Friedrich, R., Friederici, A.D., 2009. Mathematical logic in the human brain: Syntax. *PLOS ONE* 4 (5), e5599. <https://doi.org/10.1371/journal.pone.0005599>.
- Gavazzi, G., et al., 2023. Cultural differences in inhibitory control: an ALE meta-analysis. *Brain Sci.* 13 (6), 907. <https://doi.org/10.3390/brainsci13060907>.
- Gazdar, G., Klein, E., Pullum, G., Sag, I., 1985. *Generalized phrase structure grammar*. Harvard University Press.
- Gonzalez, R., Rojas, M., Rosselli, M., Ardila, A., 2021. Acquired aphasia. *Arch. Clin. Neuropsychol. Off. J. Natl. Acad. Neuropsychol.* 36 (4), 455–464. <https://doi.org/10.1093/arclin/acaa072>.
- Gruber, O., Indefrey, P., Steinmetz, H., Kleinschmidt, A., 2001. Dissociating neural correlates of cognitive components in mental calculation. *Cereb. Cortex* 11 (4), 350–359. <https://doi.org/10.1093/cercor/11.4.350>.
- Hagoort, P., Indefrey, P., 2014. The neurobiology of language beyond single words. *Annu. Rev. Neurosci.* 37, 347–362. <https://doi.org/10.1146/annurev-neuro-071013-013847>.
- Halle, M., 1962. Phonology in generative grammar. *WORD* 18 (1-3), 54–72. <https://doi.org/10.1080/00437956.1962.11659765>.
- Hanakawa, T., Honda, M., Sawamoto, N., Okada, T., Yonekura, Y., Fukuyama, H., Shibasaki, H., 2002. The role of rostral Brodmann area 6 in mental-operation tasks: an integrative neuroimaging approach. *Cereb. Cortex* 12 (11), 1157–1170. <https://doi.org/10.1093/cercor/12.11.1157>.
- Hashimoto, R., Sakai, K.L., 2002. Specialization in the left prefrontal cortex for sentence comprehension. *Neuron* 35 (3), 589–597. [https://doi.org/10.1016/S0896-6273\(02\)00788-2](https://doi.org/10.1016/S0896-6273(02)00788-2).
- Hauser, M.D., Chomsky, N., Fitch, W.T., 2002. The faculty of language: what is it, who has it, and how did it evolve? *Science* 298 (5598), 1569–1579. <https://doi.org/10.1126/science.298.5598.1569>.
- Heard, M., Lee, Y.S., 2020. Shared neural resources of rhythm and syntax: an ALE meta-analysis. *Neuropsychologia* 137, 1–15. <https://doi.org/10.1016/j.neuropsychologia.2019.107284>.
- Heim, S., Opitz, B., Friederici, A.D., 2003. Distributed cortical networks for syntax processing: Broca's area as the common denominator. *Brain Lang.* 85 (3), 402–408. [https://doi.org/10.1016/S0093-934X\(03\)00068-3](https://doi.org/10.1016/S0093-934X(03)00068-3).
- Henderson, J.M., Choi, W., Lowder, M.W., Ferreira, F., 2016. Language structure in the brain: a fixation-related fMRI study of syntactic surprisal in reading. *NeuroImage* 132, 293–300. <https://doi.org/10.1016/j.neuroimage.2016.02.050>.
- Holloway, I.D., Battista, C., Vogel, S.E., Ansari, D., 2013. Semantic and perceptual processing of number symbols: evidence from a cross-linguistic fMRI adaptation study. *J. Cogn. Neurosci.* 25 (3), 388–400. https://doi.org/10.1162/jocn_a.00323.
- Holloway, I.D., Price, G.R., Ansari, D., 2010. Common and segregated neural pathways for the processing of symbolic and nonsymbolic numerical magnitude: an fMRI study. *NeuroImage* 49 (1), 1006–1017. <https://doi.org/10.1016/j.neuroimage.2009.07.071>.
- Holmberg, A., Roberts, I., 2013. The syntax-morphology relation. *Lingua* 130, 111–131. <https://doi.org/10.1016/j.lingua.2012.10.006>.
- Hornby, A.S., 2000. *Oxford advanced learner's dictionary of current English*, 6th ed. O.U. P., Oxford.
- Huber, S., Fischer, U., Moeller, K., Nuerk, H., 2013. On the interrelation of multiplication and division in secondary school children. *Front. Psychol.* 4. <https://doi.org/10.3389/fpsyg.2013.00740>.

- Humphreys, G.F., Jackson, R.L., Lambon Ralph, M.A., 2020. Overarching principles and dimensions of the functional organization in the inferior parietal cortex. *Cereb. Cortex* 30 (11), 5639–5653. <https://doi.org/10.1093/cercor/bhaa133>.
- Humphreys, G.F., Tibon, R., 2023. Dual-axes of functional organisation across lateral parietal cortex: the angular gyrus forms part of a multi-modal buffering system. *Brain Struct. Funct.* 228, 341–352. <https://doi.org/10.1007/s00429-022-02510-0>.
- Hunter, T., 2021. The Chomsky hierarchy 1. In: Allott, N., Lohndal, T., Rey, G. (Eds.), *A companion to Chomsky*. Wiley, pp. 74–95. <https://doi.org/10.1002/9781119598732.ch5>.
- Jeon, H.-A., 2014. Hierarchical processing in the prefrontal cortex in a variety of cognitive domains. *Front. Syst. Neurosci.* 8, 1–8. <https://doi.org/10.3389/fnsys.2014.00223>. Article 223.
- Johnson, M., 1998. PCFG models of linguistic tree representations. *Comput. Linguist.* 24 (4), 613–632.
- Jost, K., Khader, P., Burke, M., Bien, S., Rösler, F., 2009. Dissociating the solution processes of small, large, and zero multiplications by means of fMRI. *NeuroImage* 46 (1), 308–318. <https://doi.org/10.1016/j.neuroimage.2009.01.044>.
- Kleemans, T., Segers, E., Verhoeven, L., 2012. Naming speed as a clinical marker in predicting basic calculation skills in children with specific language impairment. *Res. Dev. Disabil.* 33 (3), 882–889. <https://doi.org/10.1016/j.ridd.2011.12.007>.
- Kleemans, T., Segers, E., Verhoeven, L., 2018. Individual differences in basic arithmetic skills in children with and without developmental language disorder: role of home numeracy experiences. *Early Child. Res. Q.* 43, 62–72. <https://doi.org/10.1016/j.ecresq.2018.01.005>.
- Klessinger, N., Szczerbinski, M., Varley, R., 2007. Algebra in a man with severe aphasia. *Neuropsychologia* 45 (8), 1642–1648. <https://doi.org/10.1016/j.neuropsychologia.2007.01.005>.
- Knops, A., 2017. Probing the neural correlates of number processing. *Neurosci. A Rev. J. Bringing Neurobiol. Neurol. Psychiatry* 23 (3), 264–274. <https://doi.org/10.1177/1073858416650153>.
- Koenigs, M., Barbey, A.K., Postle, B.R., Grafman, J., 2009. Superior parietal cortex is critical for the manipulation of information in working memory. *J. Neurosci.* 29 (47), 14980–14986.
- Kong, J., Wang, C., Kwong, K., Vangel, M., Chua, E., Gollub, R., 2005. The neural substrate of arithmetic operations and procedure complexity. *Brain Res. Cogn. Brain Res.* 22 (3), 397–405. <https://doi.org/10.1016/j.cogbrainres.2004.09.011>.
- Kumar, V., Croxson, P.L., Simonyan, K., 2016. Structural organization of the laryngeal motor cortical network and its implication for evolution of speech production. *J. Neurosci.* 36 (15), 4170–4181. <https://doi.org/10.1523/JNEUROSCI.3914-15.2016>.
- Lemaire, J.-J., Golby, A., Wells, W.M., Pujol, S., Tie, Y., et al., 2013. Extended Broca's area in the functional connectome of language in adults: combined cortical and subcortical single-subject analysis using fMRI and DTI tractography. *Brain Topogr.* 26 (3), 428–441. <https://doi.org/10.1007/s10548-012-0257-7>.
- Li, X., O'Sullivan, M.J., Mattingley, J.B., 2022. Delay activity during visual working memory: a meta-analysis of 30 fMRI experiments. *NeuroImage* 255, 1–19. <https://doi.org/10.1016/j.neuroimage.2022.119204>. Article 119204.
- Liakakis, G., Nickel, J., Seitz, R.J., 2011. Diversity of the inferior frontal gyrus - a meta-analysis of neuroimaging studies. *Behav. Brain Res.* 225, 341–347. <https://doi.org/10.1016/j.bbr.2011.06.022>.
- Makuuchi, M., Bahlmann, J., Friederici, A.D., 2012. An approach to separating the levels of hierarchical structure building in language and mathematics. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 367 (1598), 2033–2045. <https://doi.org/10.1098/rstb.2012.0095>.
- Malik-Moraleda, S., Ayyash, D., Gallée, J., Affourtit, J., Hoffmann, M., et al., 2022. An investigation across 45 languages and 12 language families reveals a universal language network. *Nat. Neurosci.* 25 (8), 1014–1019. <https://doi.org/10.1038/s41593-022-01114-5>.
- Marozzi, M., 2004. Some remarks about the number of permutations one should consider to perform a permutation test. *Statistica* 64 (1), 193–201. <https://doi.org/10.6092/issn.1973-2201/32>.
- Matejko, A.A., Ansari, D., 2019. The neural association between arithmetic and basic numerical processing depends on arithmetic problem size and not chronological age. *Dev. Cogn. Neurosci.* 37, 1–14. <https://doi.org/10.1016/j.dcn.2019.100653>. Article 100653.
- Mathieu, R., Gourjon, A., Couderc, A., Thevenot, C., Prado, J., 2016. Running the number line: Rapid shifts of attention in single-digit arithmetic. *Cognition* 146, 229–239.
- Matsumoto, D., Nakai, T., 2023. Syntactic theory of mathematical expressions. *Cogn. Psychol.* 146, 1–16. <https://doi.org/10.1016/j.cogpsych.2023.101606>.
- Matthews, P.H., 1991. *Morphology*, 2nd ed. Cambridge University Press. <https://doi.org/10.1017/CBO9781139166485>.
- Meibauer, J., Demske, U., Geilfuß-Wolfgang, J., Pafel, J., Ramers, K.H., et al. (2015). *Einführung in die germanistische Linguistik* (3. edition). J. B. Metzler. <https://ebookcentral.proquest.com/lib/kxp/detail.action?docID=2097052> <https://doi.org/10.1007/978-3-476-05424-1>.
- Menks, W.M., Ekerdt, C., Lemhöfer, K., Kidd, E., Fernández, G., et al., 2024. Developmental changes in brain activation during novel grammar learning in 8-25-year-olds. *Dev. Cogn. Neurosci.* 66 Article. 101347, 1–9. <https://doi.org/10.1016/j.dcn.2024.101347>.
- Menon, V., 2010. Developmental cognitive neuroscience of arithmetic: Implications for learning and education. *ZDM Int. J. Math. Educ.* 42 (6), 515–525. <https://doi.org/10.1007/s11858-010-0242-0>.
- Menon, V. (2024). Insular cortex: A hub for saliency, cognitive control, and interoceptive awareness. https://med.stanford.edu/content/dam/sm/scsnl/documents/insular_cortex_2024_menon.pdf.
- Menon, V., Rivera, S.M., White, C.D., Glover, G.H., Reiss, A.L., 2000. Dissociating prefrontal and parietal cortex activation during arithmetic processing. *NeuroImage* 12 (4), 357–365. <https://doi.org/10.1006/nimg.2000.0613>.
- Menon, V., Uddin, L.Q., 2010. Saliency, switching, attention and control: A network model of insula function. *Brain Struct. Funct.* 214 (5–6), 655–667. <https://doi.org/10.1007/s00429-010-0262-0>.
- Moro, A., Tettamanti, M., Perani, D., Donati, C., Cappa, S.F., Fazio, F., 2001. Syntax and the brain: disentangling grammar by selective anomalies. *NeuroImage* 13 (1), 110–118. <https://doi.org/10.1006/nimg.2000.0668>.
- Müller, V.I., et al., 2018. Ten simple rules for neuroimaging meta-analysis. *Neurosci. Biobehav. Rev.* 84, 151–161. <https://doi.org/10.1016/j.neubiorev.2017.11.012>.
- Nagel, E., Newman, J.R. (Eds.), 2001. Gödel's proof (Rev. ed.). New York University Press. <http://www.loc.gov/catdir/enhancements/fy0734/2001044481-b.html>.
- Nakai, T., Okanoya, K., 2018. Neural evidence of cross-domain structural interaction between language and arithmetic. *Sci. Rep.* 8 (1), 12873. <https://doi.org/10.1038/s41598-018-31279-8>.
- Nakai, T., Okanoya, K., 2020. Cortical collateralization induced by language and arithmetic in non-right-handers. *Cortex* 124, 154–166. <https://doi.org/10.1016/j.cortex.2019.11.009>.
- Nakai, T., Sakai, K.L., 2014. Neural mechanisms underlying the computation of hierarchical tree structures in mathematics. *PLOS ONE* 9 (11), e111439. <https://doi.org/10.1371/journal.pone.0111439>.
- Nee, D.E., Brown, J.W., Askren, M.K., Berman, M.G., Demiralp, E., et al., 2012. A meta-analysis of executive components of working memory. *Cereb. Cortex* 23 (2), 264–282. <https://doi.org/10.1093/cercor/bhs007>.
- Nieder, A., 2016. The neuronal code for number. *Nat. Rev. Neurosci.* 17 (6), 366–382. <https://doi.org/10.1038/nrn.2016.40>.
- Nieder, A., 2025. The calculating brain. *Physiol. Rev.* 105 (1), 267–314. <https://doi.org/10.1152/physrev.00014.2024>.
- Noferini, C., et al., 2026. Neural correlates of inhibitory control in impulsivity traits in non-ecological human-computer tasks: an ALE meta-analysis. *Brain Sci.* 16 (6), 609. <https://doi.org/10.3390/brainsci16060609>.
- Obleser, J., Meyer, L., Friederici, A.D., 2011. Dynamic assignment of neural resources in auditory comprehension of complex sentences. *NeuroImage* 56 (4), 2310–2320. <https://doi.org/10.1016/j.neuroimage.2011.03.035>.
- Page, M.J., McKenzie, J.E., Bossuyt, P.M., Boutron, I., Hoffmann, T.C., et al., 2021. The PRISMA 2020 statement: an updated guideline for reporting systematic reviews. *BMJ (Clin. Res. Ed.)* 372. <https://doi.org/10.1136/bmj.n71>.
- Park, J.-H., Nunes, T., 2001. The development of the concept of multiplication. *Cogn. Dev.* 16 (3), 763–773. [https://doi.org/10.1016/S0885-2014\(01\)00058-2](https://doi.org/10.1016/S0885-2014(01)00058-2).
- Patel, A.D., 2003. Language, music, syntax and the brain. *Nat. Neurosci.* 6 (7), 674–681. <https://doi.org/10.1038/nn1082>.
- Payne, T.E., 2012. *Exploring language structure: A student's guide*, 4th ed. Cambridge University Press.
- Peng, P., Fuchs, D., 2016. A meta-analysis of working memory deficits in children with learning difficulties: Is there a difference between verbal domain and numerical domain? *J. Learn. Disabil.* 49 (1), 3–20. <https://doi.org/10.1177/0022219414521667>.
- Peng, P., Lin, X., Ünal, Z.E., Lee, K., Namkung, J., et al., 2020. Examining the mutual relations between language and mathematics: a meta-analysis. *Psychol. Bull.* 146 (7), 595–634. <https://doi.org/10.1037/bul0000231>.
- Peters, L., de Smedt, B., 2018. Arithmetic in the developing brain: A review of brain imaging studies. *Dev. Cogn. Neurosci.* 30, 265–279. <https://doi.org/10.1016/j.dcn.2017.05.002>.
- 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 (2), 293–305. <https://doi.org/10.1016/j.neuron.2006.11.022>.
- Poeppel, D., Hickok, G., 2004. Towards a new functional anatomy of language. *Cognition* 92 (1–2), 1–12. <https://doi.org/10.1016/j.cognition.2003.11.001>.
- Pollack, C., Ashby, N.C., 2018. Where arithmetic and phonology meet: the meta-analytic convergence of arithmetic and phonological processing in the brain. *Dev. Cogn. Neurosci.* 30, 251–264. <https://doi.org/10.1016/j.dcn.2017.05.003>.
- Pozniak, C., Hemforth, B., Scheepers, C., 2018. Cross-domain priming from mathematics to relative-clause attachment: a visual-world study in French. *Front. Psychol.* 9 (2056), 1–20. <https://doi.org/10.3389/fpsyg.2018.02056>.
- Prado, J., 2018. The interplay between learning arithmetic and learning to read: Insights from developmental cognitive neuroscience. In: Henik, A., Fias, W. (Eds.), *Heterogeneity of function in numerical cognition*. Elsevier Academic Press, pp. 27–49. <https://doi.org/10.1016/B978-0-12-811529-9.00002-9>.
- Prado, J., Mutreja, R., Booth, J.R., 2014. Developmental dissociation in the neural responses to simple multiplication and subtraction problems. *Dev. Sci.* 17 (4), 537–552. <https://doi.org/10.1111/desc.12140>.
- Prado, J., Mutreja, R., Zhang, H., Mehta, R., Desroches, A.S., Minas, J.E., Booth, J.R., 2011. Distinct representations of subtraction and multiplication in the neural systems for numerosity and language. *Human. Brain Mapp.* 32 (11), 1–23. <https://doi.org/10.1002/hbm.21159>.
- Prado, J., Thevenot, C., 2026. Counting on automatization: the automatized counting theory of mental arithmetic. *Dev. Rev.* 79, 101252.
- Proios, H., Tsakpounidou, K., Karapanayiotides, T., Priftis, K., Semenza, C., 2021. Aphasia and math: deficits with basic number comprehension and in numerical activities of daily living. *J. Int. Neuropsychol. Soc.* 27 (9), 939–951. <https://doi.org/10.1017/S1355617720001368>.
- Purpura, D.J., Logan, J.A.R., 2015. The nonlinear relations of the approximate number system and mathematical language to early mathematics development. *Dev. Psychol.* 51 (12), 1717–1724. <https://doi.org/10.1037/dev0000055>.

- Purpura, D.J., Napoli, A.R., King, Y., 2019. Development of mathematical language in preschool and its role in learning numeracy skills. *Cognitive foundations for improving mathematical learning*. Elsevier, pp. 175–193. <https://doi.org/10.1016/B978-0-12-815952-1.00007-4>.
- Purpura, D.J., Reid, E.E., 2016. Mathematics and language: individual and group differences in mathematical language skills in young children. *Early Child. Res. Q.* 36, 259–268. <https://doi.org/10.1016/j.ecresq.2015.12.020>.
- Rasero, J., et al., 2024. Similarity in evoked responses does not imply similarity in macroscopic network states. *Netw. Neurosci.* 8 (1), 335–354. <https://doi.org/10.1162/netn.a.00354>.
- Rorden, C., Brett, M., 2000. Stereotaxic display of brain lesions. *Behav. Neurol.* 12 (4), 191–200. <https://doi.org/10.1155/2000/421719>.
- Rosenberg-Lee, M., Chang, T.T., Young, C.B., Wu, S., Menon, V., 2011. Functional dissociations between four basic arithmetic operations in the human posterior parietal cortex: a cytoarchitectonic mapping study. *Neuropsychologia* 49 (9), 2592–2608. <https://doi.org/10.1016/j.neuropsychologia.2011.04.035>.
- Rottschy, C., Langner, R., Dogan, I., Reetz, K., Laird, A.R., et al., 2012. Modelling neural correlates of working memory: a coordinate-based meta-analysis. *NeuroImage* 60 (1), 830–846. <https://doi.org/10.1016/j.neuroimage.2011.11.050>.
- Sakai, K.L., 2005. Language acquisition and brain development. *Science* 310 (5749), 815–819. <https://doi.org/10.1126/science.1113530>.
- Santi, A., Grodzinsky, Y., 2007. Working memory and syntax interact in Broca's area. *NeuroImage* 37 (1), 8–17. <https://doi.org/10.1016/j.neuroimage.2007.04.047>.
- Scheepers, C., Sturt, P., Martin, C.J., Myachikov, A., Teevan, K., Viskupova, I., 2011. Structural priming across cognitive domains: from simple arithmetic to relative-clause attachment. *Psychol. Sci.* 22 (10), 1319–1326. <https://doi.org/10.1177/0956797611416997>.
- Scheepers, C., Sturt, P., 2014. Bidirectional syntactic priming across cognitive domains: from arithmetic to language and back. *Q. J. Exp. Psychol.* 67 (8), 1643–1654. <https://doi.org/10.1080/17470218.2013.873815>.
- Shain, C., Kean, H., Casto, C., Lipkin, B., Affourtit, J., et al., 2024. Distributed sensitivity to syntax and semantics throughout the language network. *J. Cogn. Neurosci.* 36 (7), 1427–1471. <https://doi.org/10.1162/jocn.a.02164>.
- Shankweiler, D., Crain, S., Katz, L., Fowler, A.E., Liberman, A.M., et al., 1995. Cognitive profiles of reading-disabled children: comparison of language skills in phonology, morphology, and syntax. *Psychol. Sci.* 6 (3), 149–156. <https://doi.org/10.1111/j.1467-9280.1995.tb00324.x>.
- Siegler, R.S., 1988. Strategy choice procedures and the development of multiplication skill. *J. Exp. Psychol. Gen.* 117 (3), 258–275. <https://doi.org/10.1037/0096-3445.117.3.258>.
- Sioco, E.C., De Vera, D.P.V., 2018. Grammatical competence of junior high school students. *TESOL Int. J.* 13 (1), 82–94.
- 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. <https://doi.org/10.1016/j.neuroimage.2016.10.028>.
- Sophian, C., 2008. The origins of mathematical knowledge in childhood, 1st ed. Routledge. <https://doi.org/10.4324/9781315085654>.
- Spelke, E.S., 2017. Core knowledge, language, and number. *Lang. Learn. Dev.* 13 (2), 147–170. <https://doi.org/10.1080/15475441.2016.1263572>.
- Suárez-Pellicioni, M., Booth, J.R., 2022. Temporal cortex activation explains children's improvement in math attitudes from elementary to junior high school. *Child. Dev.* 93 (4), 1012–1029. <https://doi.org/10.1111/cdev.13749>.
- Tanaka, S., Honda, M., Sadato, N., 2005. Modality-specific cognitive function of medial and lateral human Brodmann area 6. *J. Neurosci. Off. J. Soc. Neurosci.* 25 (2), 496–501. <https://doi.org/10.1523/JNEUROSCI.4324-04.2005>.
- Tang, Y., Zhang, W., Chen, K., Feng, S., Ji, Y., et al., 2006. Arithmetic processing in the brain shaped by cultures. *Proc. Natl. Acad. Sci. USA* 103 (28), 10775–10780. <https://doi.org/10.1073/pnas.0604416103>.
- Tejaviubulya, L., et al., 2022. Large-scale differences in functional organization of left- and right-handed individuals using whole-brain, data-driven analysis of connectivity. *NeuroImage* 252, 119040. <https://doi.org/10.1016/j.neuroimage.2022.119040>.
- Tettamanti, M., Weniger, E.A., 2006. Broca's area: a supramodal hierarchical processor? *Cortex* 42 (4), 491–494. [https://doi.org/10.1016/S0010-9452\(08\)70384-8](https://doi.org/10.1016/S0010-9452(08)70384-8).
- Thornbury, S., 1999. How to teach grammar. Pearson Education Limited.
- Turkeltaub, P.E., Eickhoff, S.B., Laird, A.R., Fox, M., Wiener, M., Fox, P., 2012. Minimizing within-experiment and within-group effects in activation likelihood estimation meta-analyses. *Human. Brain Mapp.* 33 (1), 1–13. <https://doi.org/10.1002/hbm.21186>.
- Twain, M., 2013. Morphology: the words of language. Cengage Learn. 33–75. <https://www3.uji.es/~ruiz/0903/Lects/Fromkin-et-al13-Ch2-Morphology.pdf>.
- Tyler, L.K., Stamatakis, E.A., Post, B., Randall, B., Marslen-Wilson, W., 2005. Temporal and frontal systems in speech comprehension: an fMRI study of past tense processing. *Neuropsychologia* 43 (13), 1963–1974. <https://doi.org/10.1016/j.neuropsychologia.2005.03.008>.
- Uittenhove, K., Thevenot, C., Barrouillet, P., 2016. Fast automated counting procedures in addition problem solving: when are they used and why are they mistaken for retrieval? *Cognition* 146, 289–303.
- Ur, P., 1991. A course in language teaching: Practice and theory. Cambridge University Press.
- Varley, R.A., Klessinger, N.J.C., Romanowski, C.A.J., Siegal, M., 2005. Agrammatic but numerate. *Proc. Natl. Acad. Sci. USA* 102 (9), 3519–3524. <https://doi.org/10.1073/pnas.0407470102>.
- Verschaffel, L., De Corte, E., 1996. Chapter 3: Number and arithmetic. In: Bishop, A.J., Clements, K., Keitel, C., Kilpatrick, J., Laborde, C. (Eds.), *International Handbook of Mathematics Education: Vol. 1. International handbook of mathematics education*, 4th ed. Kluwer Academic Publishers, pp. 99–137.
- Viesel-Nordmeyer, N., Prado, J., 2023. Arithmetic skills are associated with left fronto-temporal gray matter volume in 536 children and adolescents. *NPJ Sci. Learn.* 8 (1), 1–9. <https://doi.org/10.1038/s41539-023-00201-x>. Article 56.
- Viesel-Nordmeyer, N., Reuber, J., Kuhn, J.-T., Moll, K., Holling, H., Dobel, C., 2023. The relation between cognitive profiles of children with isolated and comorbid learning difficulties in reading and math: a meta-analysis. *Educ. Res. Rev.* 35 (1). <https://doi.org/10.1007/s10648-023-09735-3>.
- Viesel-Nordmeyer, N., Ritterfeld, U., Bos, W., 2021. Acquisition of mathematical and linguistic skills in children with learning difficulties. *Front. Psychol.* 12, 1–12. <https://doi.org/10.3389/fpsyg.2021.793796>.
- Viesel-Nordmeyer, N., Röhm, A., Starke, A., Ritterfeld, U., 2022. How language skills and working memory capacities explain mathematical learning from preschool to primary school age: insights from a longitudinal study. *PLOS ONE* 17 (6), e0270427. <https://doi.org/10.1371/journal.pone.0270427>.
- Viesel-Nordmeyer, N., Schurig, M., Bos, W., Ritterfeld, U., 2019. Effects of pre-school mathematical disparities on the development of mathematical and verbal skills in primary school children. *Learn. Disabil. A Contemp. J.* 17 (2), 149–164.
- Vigneau, M., Beaucousin, V., Hervé, P.Y., Duffau, H., Crivello, F., et al., 2006. Meta-analyzing left hemisphere language areas: phonology, semantics, and sentence processing. *NeuroImage* 30 (4), 1414–1432. <https://doi.org/10.1016/j.neuroimage.2005.11.002>.
- Vogel, S.E., de Smedt, B., 2021. Developmental brain dynamics of numerical and arithmetic abilities. *NPJ Sci. Learn.* 6 (1), 22. <https://doi.org/10.1038/s41539-021-00099-3>.
- Wang, J., Lin, H., Cai, Q., 2023. How grammar conveys meaning: Language-specific spatial encoding patterns and cross-language commonality in higher-order neural space. *J. Neurosci. Off. J. Soc. Neurosci.* 43 (46), 7831–7841. <https://doi.org/10.1523/JNEUROSCI.0599-23.2023>.
- Wang, J., Wagley, N., Rice, M., Gaab, N., Booth, J.R., 2024. Syntactic and semantic specialization in 9- to 10-year-old children during auditory sentence processing. *Sci. Rep.* 14, 26965. <https://doi.org/10.1038/s41598-024-76907-8>.
- Westbury, C., Buchanan, L., Sanderson, M., Rhemtulla, M., Phillips, L., 2003. Using genetic programming to discover nonlinear variable interactions. *Behav. Res. Methods Instrum. Comput. A J. Psychon. Soc. Inc.* 35 (2), 202–216. <https://doi.org/10.3758/BF03202543>.
- Wilson, R.J., 2020. Number theory: A very short introduction. *Very short introductions*, 636. Oxford University Press.
- Wright, R., Ellemor-Collins, D., Tabor, P., 2012. Developing number knowledge: Assessment, teaching & intervention with 7–11-year-olds. SAGE Publications Ltd. <https://doi.org/10.4135/9781446250686>.
- Xu, F., Spelke, E.S., 2000. Large number discrimination in 6-month-old infants. *Cognition* 74 (1), B1–B11. [https://doi.org/10.1016/S0010-0277\(99\)00066-9](https://doi.org/10.1016/S0010-0277(99)00066-9).
- Yarkoni, T., Barch, D.M., Gray, J.R., Conturo, T.E., Braver, T.S., 2009. Bold correlates of trial-by-trial reaction time variability in gray and white matter: a multi-study fMRI analysis. *PLOS ONE* 4 (1), e4257. <https://doi.org/10.1371/journal.pone.0004257>.
- Yeung, A.W.K., Robertson, M., Uecker, A., Fox, P.T., Eickhoff, S.B., 2023. Trends in the sample size, statistics, and contributions to the BrainMap database of activation likelihood estimation meta-analyses: an empirical study of 10-year data. *Hum. Brain Mapp.* 44 (5), 1876–1887. <https://doi.org/10.1002/hbm.26177>.
- Yu, J., Pan, Y., Ang, K.K., Guan, C., Leamy, D.J., 2012. Prefrontal cortical activation during arithmetic processing differentiated by cultures: A preliminary fNIRS study. Annual international conference of the IEEE engineering in medicine and biology society (EMBC). IEEE. <http://ieeexplore.ieee.org/servlet/opac?punumber=6320834>.
- Zago, L., Pesenti, M., Mellet, E., Crivello, F., Mazoyer, B., Tzourio-Mazoyer, N., 2001. Neural correlates of simple and complex mental calculation. *NeuroImage* 13 (2), 314–327. <https://doi.org/10.1006/nimg.2000.0697>.
- Zamarian, L., Ischebeck, A., Delazer, M., 2009. Neuroscience of learning arithmetic-evidence from brain imaging studies. *Neurosci. Biobehav. Rev.* 33 (6), 909–925. <https://doi.org/10.1016/j.neubiorev.2009.03.005>.
- Zeige, L.E., 2015. Word forms, classification, and family trees of languages—why morphology is crucial for linguistics. *Zool. Anz.* 256, 42–53. <https://doi.org/10.1016/j.jcz.2015.02.003>.