The role of the angular gyrus in arithmetic processing: A literature review

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Abstract

Since the pioneering work of the early 20th century neuropsychologists, the angular gyrus (AG), particularly in the left hemisphere, has been associated with numerical and mathematical processing. The association between the AG and numerical and mathematical processing has been substantiated by neuroimaging research. In the present review article, we will examine what is currently known about the role of the AG in numerical and mathematical processing with a particular focus on arithmetic. Specifically, we will examine the role of the AG in the retrieval of arithmetic facts in both typically developing children and adults. The review article will consider alternative accounts that posit that the involvement of the AG is not specific to arithmetic processing and will consider how numerical and mathematical processing and their association with the AG overlap with other neurocognitive processes. The review closes with a discussion of future directions to further characterize the relationship between the angular gyrus and arithmetic processing.

Key Words: Arithmetic, Strategy, Expertise, Neuroimaging, Numerical Thinking, Mathematical Thinking

Introduction

The angular gyrus (AG) has been implicated as a key brain region supporting function across a wide range of cognitive domains, including mathematical thinking (For a review see: Seghier 2013). The first associations between the AG and mathematical cognition were revealed through the study of brain-damaged patients by neurologists and began over 100 years ago (Henschen 1919). In 1919, Henschen reported that individuals with damage to the left parietal cortex exhibited deficits in arithmetic abilities. Nearly twenty years later, in 1940, Gerstmann revealed that damage to the left AG is associated with a constellation of symptoms that include deficits in calculation, finger agnosia, and left–right disorientation, known today as Gerstmann syndrome (Gerstmann 1940). With the invention of brain imaging methodologies (e.g., positron emission tomography; PET, functional magnetic resonance imaging; fMRI), pioneering empirical neuroimaging research revealed that the AG is associated with calculation in healthy adults (Dehaene et al. 1996; Gruber et al. 2001; Rickard et al. 2000; Rueckert et al. 1996). Since then, many empirical studies have explored the precise role of the AG in a range of mathematical competencies including the processing of number symbols (Holloway et al. 2010; Rusconi et al. 2005; Sokolowski et al. 2021), the mental number line (Göbel et al. 2001) numerical and sensorimotor associations (Krause et al. 2014), arithmetic (Zamarian et al. 2009), and higher-level mathematical reasoning (Liu et al. 2019). While the AG has been implicated in a range of basic and advanced skills within the domain of mathematical cognition, the association between the AG and arithmetic problem-solving (i.e., mental arithmetic) is the only association with consistent, replicable, and well-documented evidence.

In the current review, we provide a summary and evaluation of theories on AG function in mathematical cognition, with a particular focus on arithmetic. We first review what has been learnt from non-invasive functional neuroimaging methods (particularly fMRI) about the association between the AG and mathematical thinking. Following this, we review several theories explaining the role of the AG in arithmetic and present empirical evidence supporting these distinct theories. Finally, we outline what potential cognitive mechanisms may be underpinned by the AG and discuss debates regarding the relationship between the AG and mathematical thinking.

Functional neuroimaging of arithmetic

While early neuropsychological studies revealed that calculation, and particularly simple calculation, was associated with a set of brain regions, including the AG (for review see: Delazer et al. 2003), it was the development of neuroimaging techniques that led to the precise identification of the brain regions that underpin the uniquely human capacity for mental arithmetic. Early brain imaging studies revealed that there is an association between the AG, particularly the left AG, and calculation in healthy adults (Zamarian et al. 2009) An early functional imaging study using the Xe intra-carotid injection method (an early method developed to measure regional cerebral blood flow) was the first to reveal that a subtraction task is related to activation in the bilateral AG, over and above other cognitive tasks, including a jingle task where participants internally jumped every second word of a nine-word jingle, and a route-finding tasks where participants imagined walking through their house (Roland and Friberg 1985). Based on these findings, the authors speculate that activation in the AG, especially in the left hemisphere, reflects the retrieval of numerical information from memory.

Cognitive models postulated that arithmetic ability is supported by at least two representational formats: a language-based format used to store tables of exact arithmetic knowledge, and a language-independent magnitude representation that is used for quantity manipulation and approximation (Dehaene and Cohen 1995). Building on early findings revealing that the bilateral AG supports arithmetic processing, Dehaene et al. (1999) sought to identify whether overlapping or distinct brain regions support linguistic compared to magnitude aspects of arithmetic processing. To do this, the authors examined differences in the brain regions that support exact arithmetic (i.e., an arithmetic task that required participants to select the correct answer) and approximate arithmetic (i.e., an arithmetic task that required participants to select the most plausible answer), guided by the prediction that the exact arithmetic task relies on relatively more linguistic processes than the approximate arithmetic task. Findings revealed that exact arithmetic, compared to approximate, correlated with greater activation in bilateral parietal and temporal regions, including the bilateral AG (Dehaene et al. 1999).

Another approach to understanding nuances in the brain regions that support arithmetic is to examine the neural correlates of the problem size effect; an effect highlighting that participants are faster and more accurate at solving problems with relatively smaller numerical operands and answers, compared to problems with larger operands and answers (Stanescu-Cosson et al. 2000). It has long been suggested that the problem size effect is a consequence of small problems being solved using retrieval strategies (i.e., recalling the answer from memory) and large problems being solved using computational strategies (i.e., solving the problem by counting or decomposing it into smaller parts) (Campbell 1994). Early imaging research probing the neural correlates of the problem size effect revealed that the bilateral AG also shows greater activation in response to arithmetic problems with a relatively small compared to large problem size (Stanescu-Cosson et al. 2000). While these early brain imaging findings point to an association between arithmetic and the AG, these findings do not preclude the possibility that these brain regions also support the processing of non-arithmetic operations. Indeed, the brain regions associated with arithmetic, including the AG, have long been linked to attention, working memory, and linguistic processes (For a review see: Seghier 2013).

The first evidence for a specific role for the AG in arithmetic computation, independent of other processing demands, emerged when Menon et al. (2000) modulated arithmetic task difficulty by varying either the number of operands (i.e., arithmetic complexity) or the rate of stimulus presentation (i.e., task difficulty). In this task, the participant was presented with a set of addition or subtraction problems and had to indicate whether the resultant was correct or incorrect. For arithmetic complexity, easy blocks consisted of two-operand problems and difficult blocks consisted of three-operand problems. For task difficulty, easy blocks consisted of problems for which the participant was given 6 s to solve and hard blocks consisted of problems for which the participant was given 3 s to solve. Manipulating arithmetic complexity allowed the authors to identify the specific effect of calculation while manipulating the rate of presentation. This allowed them to increase task difficulty in a way that was independent of calculation. Results revealed that arithmetic complexity was associated with activity in bilateral AG. In contrast, the rate of stimulus presentation (i.e., task difficulty) was associated with activation in the left insular/orbitofrontal cortex. This suggests that it is arithmetic complexity that specifically relates to activation in the bilateral AG, rather than AG activation being a consequence of general task difficulty (Menon et al. 2000).

While these early neuroimaging studies provide compelling, evidence that the AG supports arithmetic processing, these methods cannot identify the precise role the AG plays during arithmetic processing. Nonetheless, this early work contributed to the emergence of a highly influential model that posits that three parietal circuits support number processing (Dehaene et al. 2003). These circuits include the bilateral intraparietal sulci (IPS) thought to support domain-specific number processing, a posterior superior parietal system that supports attentional orientation to numerical information, and the left AG which supports the manipulation of numbers in a verbal form in connection with other left-hemispheric perisylvian areas (Dehaene et al. 2003). More specifically, with respect to the AG, Dehaene and colleagues (2003) proposed that activation in the left AG during simple arithmetic might reflect the retrieval of arithmetic facts stored in verbal memory.

Since these early studies, a large and growing number of empirical studies have canvased the brain to understand the brain regions that support arithmetic and test the notion that the AG supports verbal fact-retrieval (for a review see: Arsalidou and Taylor 2011). Meta-analytic syntheses of this literature reveal that arithmetic processing is supported by a large fronto-parietal network, which includes the AG (Arsalidou and Taylor 2011; Hawes et al. 2019). While these meta-analyses reveal convergent evidence across empirical studies that the AG is indeed implicated in arithmetic processing, they cannot reveal the specific role of the AG in arithmetic computations. Therefore, it is important to qualitatively synthesize specific empirical manipulations that uncover the precise role of the AG in arithmetic processing. In what follows, we review three key hypotheses regarding the role of the AG in mathematical thinking: (1) linguistic fact-retrieval, (2) symbol-referent mapping, and (3) attention allocation. We present relevant supporting evidence for these hypotheses from learning paradigms, interference effects, individual differences approaches, non-invasive brain stimulation, and developmental studies.

Linguistic fact-retrieval

Early neuroimaging research, reviewed above, indicates that activation in the AG during arithmetic problem-solving reflects retrieval of arithmetic facts stored in verbal memory (Dehaene et al. 2003). This hypothesis is supported by data from a range of research methods including learning studies, individual differences approaches, non-invasive brain stimulation and developmental studies.

Evidence from learning studies

Learning studies are a powerful way to better understand the functioning of brain regions in a given process. When participants are trained in solving a particular set of arithmetic problems, the degree to which they can retrieve solutions from memory will increase as a function of the training. Therefore, training studies can be used to better understand the brain regions involved in arithmetic fact-retrieval. Learning studies have used drill training (i.e., a technique intended to aid memorization through systematic repetition of practice problems) of arithmetic problems to explore the neural correlates of arithmetic fact acquisition. More specifically, these training studies compared brain activation associated with trained arithmetic problems that had been extensively practiced with untrained problems that participants had not been exposed to during the training (for a review see: Zamarian et al. 2009).

In the first of these training studies, adults were trained on complex multiplication problems (e.g., 24×9) over the course of five days (Delazer et al. 2003). Behavioral results revealed that after the five days of training, participants answered the trained problems faster and more accurately than untrained problems that were equated on difficulty. At the neural level, trained problems had greater activation in the left AG compared to untrained problems, which was thought to reflect a training-driven shift from calculation to retrieval-based strategies. These findings have also been replicated across different operation types (Delazer et al. 2005; Ischebeck et al. 2006). Additionally, an innovative design where participants were trained on problems within the scanner revealed that participants exhibited training-related activation decreases in fronto-parietal regions, and increases in temporo-parietal regions including the left AG over the duration of the fMRI scan (Ischebeck et al. 2007). Together, findings showing that activation in the AG is associated with trained arithmetic problems have been taken to suggest that the AG is related to the retrieval of arithmetic facts. One caveat to this conclusion is that most learning studies have examined the effects of arithmetic training in adults. Indeed, a recent study in children failed to show AG activation for trained compared to untrained complex multiplication problems (Declercq et al. 2022). These findings may suggest that the role of the AG in learning arithmetic facts may differ in children and adults (for a more detailed discussion, see the unresolved questions section below).

Evidence from individual differences

The evidence from learning studies, which revealed an association between trained problems and activation in the AG, relies on the inference that training leads to retrieval and therefore lacks direct empirical support for the idea that activation in the AG is associated with the use of a retrieval strategy. To more directly probe the association between the AG and fact-retrieval, researchers began using an individual differences approach to directly assess whether participant's strategy use related to activation in the AG. In the first of these studies, following the completion of an arithmetic task while in an fMRI scanner, participants were shown the problems they completed and were asked to report the strategy they used to solve each problem on a trial-by-trial basis. Results revealed that the left AG exhibited greater activation when participants were solving arithmetic problems for which they reported using fact-retrieval rather than computational strategies (Grabner et al. 2009). The important role of the AG for retrieval has also been confirmed in more recent research using individual strategy reports in both adults (Tschentscher and Hauk 2014) and children (Polspoel et al. 2017). Other studies using an individual differences approach also lend support to the conclusion that the AG supports arithmetic fact-retrieval. For instance, a correlational study revealed that individuals with higher mathematical competence also exhibited higher activation in the left AG during arithmetic problem-solving, suggesting that more mathematically competent individuals rely more strongly on automatic, language-mediated processes when performing arithmetic (Ansari et al. 2011).

Together, individual differences studies corroborate those from the learning literature to suggest that activation of the left AG during arithmetic processing correlates with the use of fact-retrieval strategies. Yet, it is important to acknowledge that many of these studies have relied on participants' retrospective strategy assessments, which may not provide the most reliable and valid measure of strategy use (for a greater discussion on strategy reports and brain activity, see Tenison et al. (2014)). As a result, these findings need to be corroborated with alternative methods that can provide more direct causal evidence.

Evidence from non-invasive brain stimulation

Unlike previously described correlational studies, non-invasive brain stimulation can provide essential insights into the causal role of specific brain regions during mathematical processes (For a review see Garcia-Sanz et al. 2022). More specifically, this research primarily consists of studies that apply transcranial magnetic stimulation (TMS), a non-invasive brain stimulation method with high spatial specificity, to regions associated with mathematical thinking while participants compute arithmetic problems, to uncover the causal role of these regions during arithmetic thinking (Göbell et al. 2006; Maurer et al. 2016; Montefinese et al. 2017). A subset of these studies assessed the causal role of the AG during mathematical thinking. The first of these studies revealed that stimulation of the bilateral AG had a greater effect on addition compared to subtraction, providing additional evidence that the AG may be central to retrieval-based arithmetic

(Montefinese et al. 2017). With respect to lateralization, another study found that stimulation of the right AG had a greater effect on subtraction problems, whereas stimulation of the left AG had a greater effect on multiplication problems, suggesting that arithmetic fact-retrieval might be supported primarily by the left AG (Maurer et al. 2016). A related experimental study showed that disruption of the left AG using transcranial magnetic stimulation (rTMS) selectively disrupted individuals' ability to solve arithmetic problems that they reported using retrieval strategies to solve, compared to problems where participants reported that they relied on calculation strategies (Fresnoza et al. 2020). These non-invasive brain stimulation studies converge to support the idea that the left AG might support verbal fact-retrieval of simple arithmetic problems. However, this approach has not been used to assess the symbol-referent mapping and attention allocation hypotheses of the AG in arithmetic (discussed below). Therefore, future research using non-invasive brain stimulation is needed to test distinct hypotheses regarding the causal relationship between the AG and mathematical thinking.

Evidence from development

Children initially use computational strategies for most arithmetic problems and then switch to using retrieval strategies with age and experience (Ashcraft 1982). Therefore, examining how the neural correlates of arithmetic change with age can provide important insights into the role of the AG and retrieval use. Neural changes during arithmetic processing tasks across ages are thought to be due to an increasing reliance on fact-retrieval. Therefore, developmental research provides support for the idea the AG relates to fact-retrieval. The first examination of age-related activation during arithmetic examined the development of arithmetic processing across a wide age range (8–19 years) (Rivera et al. 2005). In this study, participants verified whether the solution to an arithmetic problem was correct or incorrect while in an fMRI scanner. The activation during arithmetic problem-solving was then correlated with chronological age. Results revealed age-related increases in activity in the left supra-marginal gyrus (anterior to the left angular gyrus), during arithmetic problem-solving, suggesting that the left parietal cortex becomes specialized across developmental time (Rivera et al. 2005). Additionally, this study revealed that chronological age negatively correlated with activations in the prefrontal cortex, and superior and inferior parietal lobules during arithmetic processing. This might reflect decreasing involvement of non-retrieval (e.g., computational/procedural) strategies during arithmetic problem-solving as a function of chronological age. Together, these findings provide developmental support for the idea that the age-related shift from a fronto-parietal network to the angular gyrus during arithmetic problem-solving is due to an increasing reliance on fact-retrieval.

A study examining the neural correlates of arithmetic problem-solving over a narrow age range (grades 2 and 3) revealed that arithmetic complexity was associated with regions implicated in cognitive control (i.e., the inferior frontal sulcus and anterior insula) and with regions associated with numerical thinking (i.e., the left

IPS and SPL). Critically, compared to second graders, third graders exhibited larger activation differences in the right AG, as well as in other regions of the parietal cortex, occipital cortex, and para-hippocampal cortex (Rosenberg-Lee et al. 2011a). Additionally, third graders, compared to second graders, also showed greater functional connectivity between the left dorsolateral prefrontal cortex and the right AG and the superior parietal lobule, as well as between the left dorsolateral prefrontal cortex and ventral stream visual areas and para-hippocampal gyrus. Interestingly, the authors found greater age differences in connectivity between the dorsolateral prefrontal cortex and posterior parietal areas compared to connectivity with the ventral visual and para-hippocampal regions. These findings suggest that there are changes in the degree to which the AG supports arithmetic problem-solving, even within a narrow one-year interval. However, additional developmental studies report that regions other than the AG, most notably the hippocampus, also correlate with age-related changes in arithmetic for particular problem types (For a review, see: Peters and De Smedt (2018)).

While the evidence reviewed above suggests that the AG specifically relates to the retrieval of arithmetic facts during arithmetic problem-solving, some data contradict this notion. For instance, Rosenberg-Lee and colleagues (2011b) examined brain responses in cyto-architectonically defined subdivisions of the parietal lobes (i.e., the AG, IPS and superior parietal lobule) during arithmetic problem-solving. They compared brain activity for each of the four arithmetic operations (addition, subtraction, multiplication, division) to a control number identification task where participants were asked to identify whether the number 5 was present in a string of stimuli (e.g., 3 o 4 @ 5). Critically, each of these four operations tend to be solved using different strategies, with participants using retrieval strategies most often on multiplication and addition problems, and computation strategies on subtraction and division (Campbell and Xue 2001). These authors discovered that all operations except addition exhibited less activation (i.e., deactivation) in the right AG compared to the number identification control task. Additionally, multiplication had greater activation than subtraction in the right, but not left AG (Rosenberg-Lee et al. 2011b). This finding is inconsistent with the notion that the left AG is especially sensitive to the retrieval of arithmetic facts, and suggests there is some ambiguity about the role of the left versus right AG. Together, these results led the authors to argue that there is heterogeneity in the way the parietal cortex, including the AG, represents arithmetic operations and that the relationship between the AG and arithmetic is more complex than simply a linguistic fact-retrieval module.

Symbol-referent mapping

While the idea that the AG supports the retrieval of arithmetic facts is compelling in its simplicity, empirical data have revealed that the learning and individual differences effects reviewed above are not specific to arithmetic. Accordingly, an alternative symbol-referent mapping hypothesis was proposed (Ansari 2008). The symbol-referent hypothesis suggests that the AG might support the link between a symbol and the concept to which the symbol refers (i.e., referent). Evidence from learning studies, individual difference studies, and the phonological processing literature (e.g., Schlaggar and McCandliss 2007) lend support to the alternative symbol-referent mapping hypothesis.

Evidence from learning studies

Studies that employ learning paradigms can enhance our understanding of whether the AG is specific to the processing of numerical information, rather than general symbol-referent mapping. In such a learning paradigm, participants are trained using both numerical and non-numerical stimuli. Grabner et al. (2009) used this approach and trained participants on arithmetic facts as well as a figural–spatial problem where a participant is shown a three-dimensional object and asked to determine the number of faces on a given object. The results from this study indicated that the bilateral AG also exhibits increased activation following training on both arithmetic, but also non-arithmetic (i.e., figural–spatial) problem-solving (Grabner et al. (2009)). Thus, the training-related activation associated with the AG is not specific to arithmetic fact learning. Accordingly, it was proposed that the AG might be involved in symbol-referent mapping more generally, including mapping between arithmetic problems and their solutions, but also between other symbol-referent pairs, such as numerical symbols and corresponding magnitudes, and letter-sound correspondences (Ansari 2008). This hypothesis is consistent with the arithmetic findings, but also with findings that the AG responds to the processing of symbolic digits, without arithmetic demands (Holloway et al. 2010; Price and Ansari 2011), though note that findings from Price and Ansari (2011) did not replicate (Merkley et al. 2019). Together, evidence from learning studies suggests that increased activation in the AG during learning is observed in non-arithmetic problem-solving tasks, indicating that this AG activation may not be not specific to arithmetic.

Evidence from individual differences studies

An individual differences approach is needed to directly test whether the association between the AG and mathematical thinking is specific to arithmetic retrieval. Grabner et al. (2011) examined brain responses to arithmetic problem-solving, as well as to extracting numerical information from different representation formats including equations, tables, and diagrams in individuals with different levels of mathematical competence (i.e., higher vs. lower mathematical competence). Results revealed that individuals with higher, relative to lower, mathematical competence exhibit stronger activation in the left AG across all numerical representation task conditions, and this effect was not moderated by the presence of arithmetic demand. These findings align with the evidence from learning studies to suggest that activation in the AG may not be constrained to individuals using more retrieval strategies during arithmetic problem-solving. Instead, the authors conclude that the greater activation in the left AG observed in individuals with more mathematical competence may be a consequence of individuals with higher mathematical thinking having a higher proficiency in processing mathematical symbols, thus supporting the symbol-referent hypothesis.

Evidence from phonological processing

Research on phonological processing (the ability to understand and manipulate the sounds of language) also provides support for the symbol-referent hypothesis. Phonological processing studies reveal that the left AG is associated with phoneme discrimination, which is the ability to distinguish between speech sounds (Turkeltaub and Coslett 2010). Critically, the left AG is thought to be important in mapping between letters and sounds (i.e., grapheme to phoneme correspondences) (Schlaggar and McCandliss 2007). One study found that the left inferior parietal cortex (including the AG) was especially engaged when participants had to integrate phonological and orthographic information (determining if auditory words were spelled the same or if two visual words rhyme), suggesting that the AG plays a role in mapping across representations in spoken and written language (Booth et al. 2002). Adults also tend to engage the left AG more than children when integrating phonological and orthographic information (Booth et al. 2004), potentially indicating that greater activation of the AG may be associated with stronger or more mature links between spoken and written language. This finding converges with evidence showing that individuals with stronger cross-modal integration skills (phonological-orthographic mapping) have greater activation in the left AG (Booth et al. 2003). Finally, a study using a training paradigm to teach adults new letter-sound correspondences found training-related changes in the parieto-occipital cortex near the AG, demonstrating that this brain region is important when learning grapheme–phoneme associations (Hashimoto and Sakai 2004). Considering that the left AG has not only been implicated in mapping between spoken and written language (discussed above), but also between visual words and semantics (Sliwinskia et al. 2015), the left AG may play a broader role in binding information.

This body of evidence suggests that the AG may play an important role in symbol-referent mapping within the domain of language and that it may undergo similar age- and experience-related increases to those observed in arithmetic. Moreover, a recent neuroimaging meta-analysis directly examined which brain regions were consistently activated by both retrieval-based arithmetic and phonological processing and found the left AG was engaged during both types of tasks (Pollack and Ashby 2018). The authors of this meta-analysis speculate that this overlapping activation might reflect a similar connection of symbols (i.e., letters, and arithmetic facts) to their associated verbal representations, though they note that the notion that left AG acts as a hub for cross-modal integration is also a parsimonious explanation for their findings (Seghier 2013). Together, this evidence suggests that the AG may play an important role in symbol-referent mapping across multiple domains.

Attention allocation

While the hypotheses that the AG supports (1) arithmetic fact-retrieval or (2) symbol-referent mapping are compatible with imaging findings, both hypotheses are challenged by the fact that the AG is a core region of the default mode network (DMN), a large-scale brain network that exhibits greater activity when the brain is not engaged in a specific mental task and shows stronger deactivations during more difficult tasks (Buckner et al. 2009; Buckner and Carroll 2007; Grabner et al. 2013; Sestieri et al. 2011). During mental arithmetic, the left AG is deactivated for complex compared to simple arithmetic, thus behaving similarly to how it acts as a node within the DMN (e.g., Ischebeck et al. 2006. Relatedly, while there is compelling evidence suggesting that the AG is associated with verbal fact-retrieval, a process engaged during symbol-referent mapping (for review see Seghier 2013), a distinct body of work has shown that the AG mediates bottom-up attentional processes during direct memory retrieval (Cabeza et al. 2012). This has been taken to suggest that activation in the AG during arithmetic processing reflects general effects of task difficulty (Wu et al. 2009) or perhaps is a general attentional resource (Cabeza et al. 2012). Here we will discuss evidence that has used confusion and interference effects to probe whether or not attention allocation may drive AG activation during arithmetic. We also discuss evidence from recent training studies that provide additional insights into the role of the AG in arithmetic from an attentional allocation perspective.

Evidence from confusion and interference effects

The first study to directly probe whether AG activation is a consequence of deactivation due to task difficulty used the associative confusion effect (Grabner et al. 2013). The associative confusion effect is the phenomenon where individuals exhibit poorer performance while verifying addition and multiplication problems when an incorrect solution to the problem is the correct solution to the other operation (e.g., confusion equations: $3 \times 4 = 7$ or $3 + 4 = 12$). Results revealed that the left AG exhibits greater activation during confusion equations compared to equations where the solution was not related to the solution of the other operator, which is inconsistent with the notion that AG activation during arithmetic merely reflects modulations of the DMN in response to task difficulty. Instead, the results suggest that the AG is highly sensitive to arithmetic facts even when those correspond to an arithmetic operation other than the one presented.

A similar pattern of results emerged from the multiplication interference effect, namely an effect that reflects interference of some multiplication problems that have shared digits with other previously learned multiplication facts (De Visscher and Noël 2014). More specifically, the multiplication interference account posits that problems that share many features with other problems are more interfering and thus more difficult to retrieve than problems with rare associations of digits (which are therefore more distinctive problems). For example, the occurrence of two 2's in multiplication problems is rare (i.e., only two problems include two 2 s: 2 × 2 = 4 and 2 × 6 = 12), making problems with two 2's relatively distinct and therefore low interfering problems. In contrast, many problems include both a 2 and an 8 (e.g., 2 × 8 = 16, 2 × 9 = 18, 8 × 3 = 24, 7 × 4 = 28, 4 × 8 = 32, and 8 × 9 = 72), which means that these problems have relatively more interference than problems with two 2's. An empirical study using this multiplication interference effect revealed that the AG exhibits greater activation for multiplication problems that have low interference, compared to high interference, even when controlling for problem size (De Visscher et al. 2015). The authors interpreted this finding as indicating that AG activation during arithmetic processing reflects an automatic mapping between the arithmetic problem and its solution that has been stored in long-term memory.

Evidence from training studies

While the majority of training literature converged to suggest that the AG has a specific role in arithmetic processing relating to fact-retrieval or symbol-referent mapping, the neural correlates of processing trained versus untrained problems were only compared after training. Bloechle and colleagues (2016) examined brain activation during an established learning paradigm in which they extensively trained multiplication problems. They then compared brain activation following training to the same problems during the pre-training session to evaluate neural correlates of arithmetic fact acquisition more specifically. When comparing brain responses for trained vs. untrained problems in the post-training session, the authors report higher AG activation for trained problems, thereby replicating previous research. However, when contrasting activation associated with trained problems with activation for the same problems in the pre-training session, the authors report that no signal change in the left AG was observed (Bloechle et al. 2016). Instead, the authors identify training-based responses in the hippocampal, para-hippocampal, and retro-splenial structures, suggesting that these regions, rather than the AG, may be critical for arithmetic fact-retrieval. Based on these findings, the authors propose that the AG might respond to differences in top-down vs. bottom-up attentional processes associated with trained and untrained problems, rather than actual retrieval of arithmetic facts or symbol-referent mapping. More specifically, Bloechle et al. (2016) make the compelling proposal that during arithmetic processing, the left AG acts as a "circuit breaker" that adjusts the allocation of attentional resources to neural networks involved in fact-retrieval and magnitude processing.

Evidence from a recent training study also probed the specific role of the AG from an attention allocation perspective. Specifically, these authors hypothesized that the left AG might be an attentional node within a specific learning network (Fias et al., 2021). Indeed, an fMRI study presented participants with a set of alphabet arithmetic problems (e.g., a + 2 = c) and tracked behavioral performance and neural activity across repeated trials. Results revealed two neural networks with opposed learning-related changes: (1) a network consisting of the basal ganglia and fronto-parietal regions that decreased with learning and (2) a network consisting of the left AG and hippocampus that increased with learning. Notably, connectivity analyses revealed that these two networks are functionally connected, despite their opposing trajectories, and that connectivity increases with learning. These findings indicate that arithmetic learning is sub-served by a procedural calculation system that decreases in activation during learning, and a retrieval system (composed of the AG and hippocampus) that increases in activation during learning. Together, this body of research suggests that the AG does support arithmetic processing but within the context of its functional role within known neural networks (e.g., the default mode network; specialized learning network).

Hippocampal engagement during arithmetic

While the AG has been highlighted as critical for arithmetic retrieval, the emergence of network neuroscience has revealed that cognition is supported by a network of regions, rather than individual modules (Cole et al. 2014). As a result, it is crucial to understand the function of the AG in the context of other connected brain regions, such as the hippocampus. The hippocampus is a complex brain structure located in the medial temporal lobe that is known to have a major role in learning and memory. Based on the long-understood notion that the hippocampus is a key brain region associated with the encoding and retrieval of both semantic and episodic memories, it has been suggested that within the context of arithmetic the hippocampus might be critical for the encoding and storage of arithmetic facts (e.g., Qin et al. 2014). Findings of hippocampal engagement during arithmetic processing have been reported prior to the alphabet arithmetic study (i.e., Fias et al. 2021), especially in children. Indeed, De Smedt et al. (2011) reasoned that comparing neural activation during small compared to large problems and addition compared to subtraction problems in children would reveal brain networks that supported fact-retrieval, with the prediction that the AG would be a key neural substrate that emerged from these contrasts. While they did find that the bilateral AG responded to small > large problem types, this was not the case for addition versus subtraction. Instead, it was the medial temporal lobe, and specifically, the left hippocampus (HC), that had greater activation for small versus large problems and for addition versus subtraction problems. This indicates that the left HC is crucial for computations of problems expected to rely on fact-retrieval strategies in children (De Smedt et al. 2011).

This discovery that the HC might be important for the formation of long-term memory for arithmetic facts in children has been replicated across a range of developmental studies (For a review see: Menon 2014; Peters and De Smedt 2018). For example, children who were categorized as “retrievers” rather than “counters” (i.e., children who used retrieval strategies on more than 60% of arithmetic trials) exhibited relatively more activity in the bilateral hippocampus (Cho et al. 2011). Additionally, differences in multivariate activation patterns between retrievers and counters were present in the bilateral medial temporal lobe including the hippocampus, frontal and pre-motor regions, and parietal regions, including the right AG. Relatedly, functional connectivity between the hippocampus and neocortical regions, especially the prefrontal cortex, may play an important role in the development of arithmetic problem-solving (Qin et al. 2014). This same study reveals that stable inter-problem representations in the hippocampus relate to retrieval strategy use in adolescents and adults.

The role of the AG in semantic memory

An alternative explanation for activation in the AG during fact-retrieval emerges from human functional imaging studies that implicate this region as essential for representational aspects of semantic memory (Binder and Desai 2011). Indeed, research into the role of the AG in semantic memory reveals that the AG responds to real words more strongly than to matched pseudo-words (Binder et al. 2009). Convergent evidence of this view comes from research highlighting that the AG responds more to high-frequency words compared to low-frequency words, concrete words compared to abstract words and sentences with more meaning compared to sentences that are relatively more meaningless (Binder et al. 2005; Graves et al.2010; Humphries et al. 2007). In view of these findings, it has been suggested that AG activation relates to the degree to which semantic information can be successfully retrieved. This view of the AG also aligns with recent evidence showing that judgments involving higher-order mathematical thinking (math tasks involving logic and mathematical principles) engaged the left AG more than arithmetic computation (Liu et al. 2019). These findings indicate that the AG may be particularly important for mathematical processing that requires semantic knowledge. The semantic memory account of the AG could also explain findings related to arithmetic processing, as the problems for which adults have a greater degree of semantic knowledge of the solution correspond to greater activation.

Unresolved questions

While we have made significant advances in our understanding of the AG in arithmetic, there remain several unresolved questions that need to be addressed in future research to form a more complete model of AG function in mathematical cognition.

How does the AG interact with other systems?

It remains unclear precisely how the AG interacts with other systems during arithmetic, including those involved in language processing, semantic memory, spatial thinking, magnitude processing, and attention. Some of the recent evidence discussed above has pointed to the left AG and hippocampus working in tandem when adults learn to do alphabet arithmetic and that this network becomes more integrated with procedural networks (fronto-parietal and basal ganglia) with learning (Fias et al. 2021). The AG has a distributed connectivity network with prefrontal, subcortical, and medial temporal regions (including the hippocampus) (Uddin et al. 2010). Therefore, understanding the dynamic relationships between the AG and other neural systems during mathematical problem-solving could provide further insights into the AG's role (e.g., see Price et al. 2018), and can help determine whether the AG has a similar function regardless of the network it is functioning within.

Does the role of the AG change over development?

How the function of the AG changes with development remains elusive, especially since arithmetic training studies in children have failed to show AG activation in trained compared to untrained arithmetic problems (Declercq et al. 2022). This might suggest that the neural underpinnings of learning arithmetic facts may differ in children. Longitudinal studies in children could provide more insights into how the AG is involved in calculation skills as children learn arithmetic facts over the first years of schooling.

Do the left and right AG have distinct functions?

Another unresolved question about AG function during arithmetic is the distinction between the left and right AG during mathematical problem-solving. Specifically, many studies report left-lateralized activation for arithmetic fact-retrieval (Delazer et al. 2003; Grabner et al. 2009; Ischebeck et al. 2007), whereas others report bilateral activation in the AG (De Smedt et al. 2011; Polspoel et al. 2017; Stanescu-Cosson et al. 2000). Further, one of the only rTMS studies to simultaneously examine both the left and right AG found that disruption of the AG in both hemispheres affected addition performance to a similar degree (Montefinese et al. 2017). Therefore, existing literature on the function of the left and right AG is mixed. It remains unclear whether the left and right AG play similar or distinct roles, and whether their function might differ depending on how they interact with other networks (e.g., left-lateralized language networks). Future research will need to more systematically test how processes in the left and right AG may differ in mathematical cognition.

Does the AG play a similar role across different cognitive domains?

We have discussed evidence that the AG may have similar functions across cognitive domains (e.g., associations between written and spoken language). However, we do not know whether these processes occur in the exact same way, and this is an assumption based on independent studies that observe similar activation within the AG. Therefore, it is necessary to understand whether the processes carried out by the AG are indeed similar across multiple contexts.

Does AG activation during arithmetic processing reflect processes beyond deactivation of the default mode network?

As discussed above, it has repeatedly been demonstrated that the involvement of the AG in arithmetic processing is driven by relative differences in deactivation rather than activation. For example, when examining which areas are involved in arithmetic calculation versus retrieval, the AG exhibits greater deactivation for problems that are calculated rather than retrieved (e.g., Grabner et al. 2009). This raises questions about the specificity of the AG for mental arithmetic. More specifically, does the AG respond to arithmetic retrieval or is AG activation during retrieval compared to procedural problems a consequence of the DMN becoming deactivated during complex problems? While some studies have provided evidence against the explanation that activation during arithmetic in the AG reflects relative degrees of the involvement of the default mode network and/or reflects differences in relative task difficulty that are not specific to arithmetic, the question of what the relative levels of deactivation reflect remain unresolved.

Do current methods blur the individual anatomical boundaries of the AG?

Most neuroimaging methods, including fMRI, have limits to their anatomical resolution. A recent study used intracranial recording to more precisely test whether the AG is activated during arithmetic (Pinheiro-Chagas et al. 2022). This technique overcomes several limitations of fMRI, namely, it can directly measure neural activity and precisely target the anatomical source. This study revealed that the AG is deactivated during arithmetic processing and that those AG recording sites that exhibited activation were close to other parietal areas, such as the SMG and IPS (Pinheiro-Chagas et al. 2022). The authors posit that previous non-invasive neuroimaging studies that claimed to have found engagement of the AG in arithmetic processing may have blurred across different regions within the inferior parietal lobe, giving rise to the false impression that the AG is activated during arithmetic processing. Future non-invasive neuroimaging studies, such as those using fMRI, must pay greater attention to individual differences in neuroanatomy and more precisely, perhaps using high-field imaging, map the exact locations within the parietal cortex that are activated during arithmetic processing.

Conclusion

The AG has been known to have an important role in numerical and mathematical processing from very early neuropsychological studies in patients. The advent of neuroimaging has helped refine our understanding of the AG's specific role in arithmetic. In this review, we outlined three leading theories that provide a framework for how the AG might underpin arithmetic problem-solving: (1) linguistic fact-retrieval, (2) symbol-referent mapping, and (3) attention allocation. Evidence suggesting that the AG is specifically involved in verbal fact-retrieval (linguistic fact-retrieval) is challenged by the notion that this brain area serves a similar function across different cognitive domains, such as language (symbol-referent mapping). Therefore, the AG likely plays a role in binding information between symbols and concepts that are not specific to arithmetic. While evidence suggesting that the AG is involved in attention allocation is somewhat more mixed, these findings indicate that the AG might play a pivotal role in bottom-up attention required when an arithmetic solution is recalled from long-term memory. Importantly, these three theories of AG function in arithmetic are not necessarily incompatible with each other, in fact, the AG may be engaged during fact-retrieval due to the AG's broader computational role in binding information between symbols and their meanings (symbol-referent theory), and due to its role in attention allocation within the context of arithmetic. These theories together provide a more nuanced account of the AG's function during arithmetic. In sum, the initial proposal by Dehaene and colleagues (2003) that the AG is involved in retrieving arithmetic facts stored in verbal memory does not account for other evidence from symbol-referent and attention allocation theories that suggest that the AG's role in arithmetic needs to be conceptualized more broadly. Future empirical work in this area should aim to directly address the various theories that have been put forward and reviewed in this paper.

Data availability

Since this is a narrative review, there are no data associated with this manuscript and thus none is available.

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