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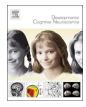
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Arithmetic in the developing brain: A review of brain imaging studies

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ABSTRACT

Brain imaging studies on academic achievement offer an exciting window on experience-dependent cortical plasticity, as they allow us to understand how developing brains change when children acquire culturally transmitted skills. This contribution focuses on the learning of arithmetic, which is quintessential to mathematical development. The nascent body of brain imaging studies reveals that arithmetic recruits a large set of interconnected areas, including prefrontal, posterior parietal, occipito-temporal and hippocampal areas. This network undergoes developmental changes in its function, connectivity and structure, which are not yet fully understood. This network only partially overlaps with what has been found in adults, and clear differences are observed in the recruitment of the hippocampus, which are related to the development of arithmetic fact retrieval. Despite these emerging trends, the literature remains scattered, particularly in the context of atypical development. Acknowledging the distributed nature of the arithmetic network, future studies should focus on connectivity and analytic approaches that investigate patterns of brain activity, coupled with a careful design of the arithmetic tasks and assessments of arithmetic strategies. Such studies will produce a more comprehensive understanding of how the arithmetical brain unfolds, how it changes over time, and how it is impaired in atypical development.

1. Introduction

Brain imaging studies on academic achievement offer an exciting window on experience-dependent cortical plasticity, as they allow us to understand how developing brains change when children acquire culturally transmitted skills, such as reading or arithmetic (Dehaene and Cohen, 2007). This contribution focuses on the learning of arithmetic, i.e. the ability to add, subtract, multiply and divide symbolic whole numbers. This skill constitutes a major element of the mathematics curriculum in primary school (National Mathematics Advisory Panel, 2008) and has a quintessential role in mathematical development (Kilpatrick et al., 2001) for children around the globe. There are large individual differences at the behavioral (Dowker, 2005; Vanbinst and De Smedt, 2016, for a review) and neural levels in this basic competence, even in adulthood (Grabner et al., 2007). On the other hand, persistent deficits in learning arithmetic constitute the hallmark of dyscalculia, a specific neurodevelopmental learning disorder that is characterized by life-long difficulties in calculation that are not merely explained by intellectual disabilities, uncorrected sensory problems, mental or neurological disorders or inadequate instruction (American Psychiatric Association, 2013).

This contribution starts with a succinct discussion of children's arithmetic development and its supporting cognitive competencies, as well as a brief summary of brain imaging studies in adults. These two sections are short and only provide a lens through which we subsequently discuss the available neural data in children. We systematically review functional brain imaging studies in typically and atypically developing populations and provide an overview of connectivity studies. We also discuss structural brain imaging data that have correlated variability in arithmetic performance with individual differences in white and grey matter properties. This review ends with challenges and outstanding issues that should be considered in future studies.

2. Arithmetic development is characterized by strategy change

Decades of cognitive developmental research have investigated the acquisition of arithmetic and this development involves a change in the mix of strategies that are used to calculate the answer to a particular problem (Geary, 2011; Jordan et al., 2003; Siegler, 1996; for reviews). Already before the start of formal schooling, children use counting to solve simple sums. These counting strategies are initially executed with additional support, such as manipulatives or fingers, yet progressively, children execute these strategies without external aids (verbal counting). The efficiency of these counting strategies increases rapidly with grade, where children move from counting all sets in their entirety to

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counting from the first (counting-on) or larger (counting-on-larger) number (Geary et al., 1992). The repeated use of these counting routines allows children to develop associations between problems and their answers, arithmetic facts, which are stored in long-term memory. The acquisition of these facts is important because fact retrieval is more efficient and it consumes less working memory than the more cognitively demanding and error-prone procedures, such as counting. The availability of arithmetic facts also allows children to use these facts to decompose problems into smaller problems, such as 7 + 8 =, 7 + 3 = 10, 10 + 5 = 15. These decomposition strategies usually occur in problems with larger numbers (typically when they cross 10) and, evidently, in multi-digit calculations. They are used more often during addition and subtraction - albeit more frequently in subtraction than in addition (Barrouillet et al., 2008) - but they are much less used in multiplication, in which fact retrieval is the most dominant strategy from an early point on in development, i.e. second grade (Imbo and Vandierendonck, 2007; Lemaire and Siegler, 1995). This is because multiplications are typically learned by extensive (rote) training of the multiplication tables rather than by decomposing the problem in its smaller sub-parts, as is often the case in subtraction. On the other hand, multiplication and addition are commutative operations (e.g. $6 \times 4 = 4 \times 6$), in contrast to division and subtraction. This commutativity might facilitate the formation of problem-answer associations in long-term memory for multiplication and addition, for which reason they are more often solved via fact retrieval. Surprisingly little is known about the development of division, but the available evidence suggests that its strategies follow a somewhat different developmental trajectory (Robinson et al., 2006). Because, to the best of our knowledge, there are no developmental brain imaging studies on division, this operation is not considered further.

The development of these strategies is not an abrupt shift from one strategy to the other but rather a change in the frequency distributions of strategies children use, the so-called overlapping waves theory (Siegler, 1996). This theory posits that strategies remain available over development, even in adulthood (LeFevre et al., 1996), but that the frequency in their use changes at different time points, with the more efficient strategies, such as fact retrieval, becoming more dominant. This change is also accompanied by changes in brain activity, as we will review below. Interestingly, similar strategy shifts have been documented in the learning of other academic domains (Siegler, 1996). For example, in word reading, children move towards an increased reliance on efficient orthographic direct recognition coupled with a decreased reliance on phonological decoding (Schlagger and McCandliss, 2007) and the changes in brain structure and function that accompany this (a) typical development have been described (Eden et al., 2016 for a review).

The acquisition of these strategies is supported by additional cognitive competencies that can be characterized as domain-specific, i.e. specifically relevant for learning arithmetic but not for other academic skills, or domain-general, i.e. relevant to learning other academic skills, such as reading, or to learning in general, such as working memory (e.g., Geary and Moore, 2016; Vanbinst and De Smedt, 2016 for a review). A detailed review of these factors is beyond the scope of this paper, but we briefly highlight some of them to frame the subsequent brain imaging data.

One domain-specific factor that has received a lot of attention in studies on individual differences in arithmetic is the ability to process numerical magnitudes (De Smedt et al., 2013; Schneider et al., 2017, for a *meta*-analysis). It turns out that specifically the ability to process symbolic numerical magnitudes is uniquely related, cross-sectionally (Vanbinst et al., 2012) and predictively (Vanbinst et al., 2016; Vanbinst et al., 2015a; Vanbinst et al., 2015b), to children's arithmetic strategy use and their increasing reliance on fact retrieval. These associations are not limited to addition and subtraction, but are also observed in multiplication (De Visscher and Noël, 2016; Schleepen et al., 2016).

arithmetic development has been connected to the observation that the intraparietal sulcus (IPS) is consistently active whenever people calculate. Indeed, increases in IPS-activity during calculation have been frequently interpreted to reflect the processing of numerical magnitude (e.g., Ansari, 2008; Menon, 2015). On the other hand, atypical IPS structure (e.g., Isaacs et al., 2001) or function (e.g., Price et al., 2007) has been suggested to represent the neural origin of dyscalculia, and these are assumed to reflect poor numerical magnitude processing, which is seen as the core deficit in dyscalculia that cascades into impairments in arithmetic (e.g., De Smedt et al., 2013; Rubinsten and Henik, 2006). This recent emphasis on particularly symbolic numerical magnitude processing has somewhat mistakenly narrowed down the attention to the IPS in studying brain activity during arithmetic (see Fias et al., 2013; Menon, 2015; for critical analyses). Indeed, arithmetic tasks typically recruit a large set of bilateral regions including the dorsolateral (DLPFC) and ventrolateral prefrontal cortex (VLPFC), anterior cingulate (ACC), temporo-parietal cortex (angular (AG) and supramarginal gyri (SMG)), the occipito-ventral cortex (including fusiform gyrus (FG)) and the medial temporal lobe (Arsalidou and Taylor, 2011; Menon, 2016). This suggests the involvement of domain-general processes as well, and behavioral studies have already confirmed that working memory (Peng et al., 2016), executive functions (Bull and Lee, 2014), interference control (De Visscher et al., 2015), phonological processing (De Smedt et al., 2010; Hecht et al., 2001) and retrieval from long-term memory (Garnett and Fleischner, 1983) are uniquely related to individual differences in arithmetic. In all, these data suggest that both domain-specific and domain-general factors should be considered when studying brain activity during arithmetic and that such analysis should not be restricted to the parietal cortex.

We end this section with a brief discussion on how arithmetic strategies are measured (De Smedt, 2016, for a more elaborate discussion). In behavioral research, this mix of strategies has typically been measured through verbal report data (e.g., Campbell and Xue, 2001; Imbo and Vandierendonck, 2007; Siegler, 1996) in which children have to verbally indicate on a trial-by-trial basis which strategy they used to solve the problem. Responses can be reliably and validly classified into categories (Siegler and Stern, 1998), such as retrieval (the child immediately knew the answer with no overt signs of calculations) or procedures (the child counted or decomposed the problem into smaller problems). The collection of verbal report data is quite difficult in brain imaging studies. Some adult studies have analyzed brain activity as a function of verbally reported strategy (Grabner et al., 2009; Grabner and De Smedt, 2011; Tschentscher and Hauk, 2014), but such trial-by-trial strategy data have not been reported in children. For this reason, brain imaging studies have typically used designs in which they compared brain responses of sets of problems on which the use of a particularly strategy was expected on the basis of specific characteristics of the problem, i.e. its size (De Smedt et al., 2011), complexity (Ashkenazi et al., 2012) or operation (Prado et al., 2014). This approach has been criticized (De Smedt, 2016; Siegler, 1987): Not all problems of a given type are solved by the same strategy and aggregating across problem types leads to misleading conclusions (Siegler, 1987). This is especially true for developmental research and studies in atypical populations: Children will differ in their mix of strategies for a given problem type or operation, depending on their age, education or ability level (typical vs. atypical). Therefore, verbal report data may be the most optimal way to study brain activity during arithmetic in developing populations. On a related note, electrophysiological data in adults (Grabner and De Smedt, 2011) have shown that such verbal report data correlate with differences in brain activity, which are not revealed when focusing on problem size or operation alone.

3. Adult brain imaging data

The fact that symbolic numerical magnitude processing is key to

The vast majority of research on the neural correlates of arithmetic

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