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The Neuroscience of Mathematical Cognition and Learning

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THE NEUROSCIENCE OF MATHEMATICAL COGNITION AND LEARNING

OECD Education Working Paper No. 136

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This working paper has been authorised by Andreas Schleicher, Director of the Directorate for Education and Skills, OECD.

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ABSTRACT

The synergistic potential of cognitive neuroscience and education for efficient learning has attracted considerable interest from the general public, teachers, parents, academics and policymakers alike. This review is aimed at providing 1) an accessible and general overview of the research progress made in cognitive neuroscience research in understanding mathematical learning and cognition, and 2) understanding whether there is sufficient evidence to suggest that neuroscience can inform mathematics education at this point. We also highlight outstanding questions with implications for education that remain to be explored in cognitive neuroscience. The field of cognitive neuroscience is growing rapidly. The findings that we are describing in this review should be evaluated critically to guide research communities, governments and funding bodies to optimise resources and address questions that will provide practical directions for short- and long-term impact on the education of future generations.

RÉSUMÉ

Le potentiel synergétique des neurosciences cognitives et de l'éducation pour l'efficacité de l'apprentissage suscite un vif intérêt de la part du grand public, des enseignants, des parents, des universitaires et des décideurs. Cet examen entend : 1) offrir un aperçu général accessible des progrès réalisés par la recherche en neurosciences cognitives dans la compréhension des processus d'apprentissage et de cognition en mathématiques ; et 2) déterminer s'il existe des données suffisantes pour étayer la possibilité, à ce stade, d'une contribution des neurosciences à l'enseignement des mathématiques. Nous mettons également en lumière certaines questions en suspens ayant des implications en termes d'éducation et restant à explorer dans les neurosciences cognitives, domaine connaissant un essor rapide. Les résultats que nous présentons dans cet examen doivent faire l'objet d'une évaluation critique afin de guider les communautés de chercheurs, les pouvoirs publics et les organismes de financement dans leurs efforts pour optimiser les ressources et répondre aux questions qui orienteront l'incidence à court et long termes sur l'éducation des générations futures.

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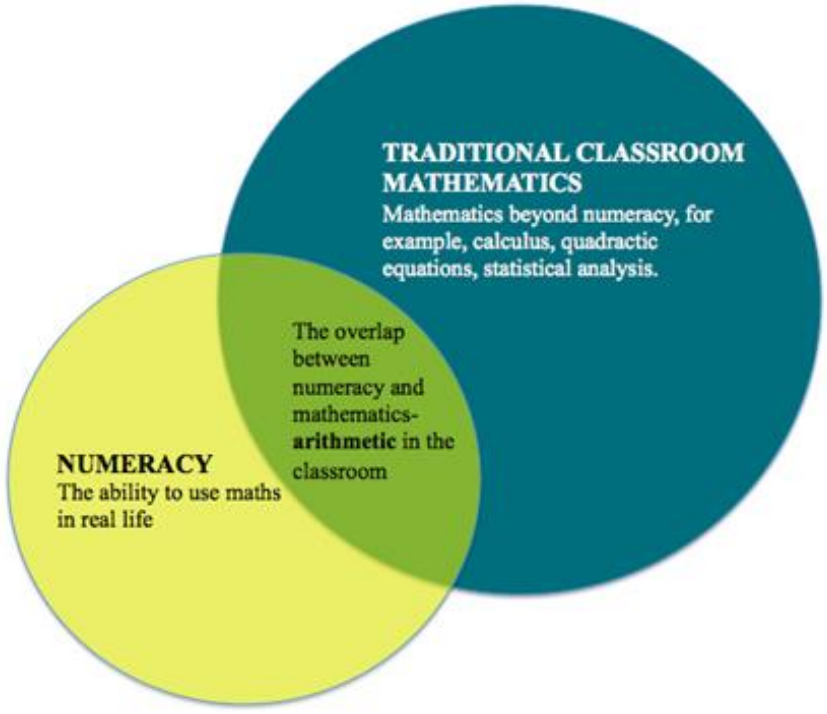
THE NEUROSCIENCE OF MATHEMATICAL COGNITION AND LEARNING

Introduction

The aim of this review is to provide an overview of the progress in the field of cognitive neuroscience of mathematical cognition and learning. However, before undertaking with this ambitious aim, we would like to start by defining the key concepts in this review.

In the field of cognitive neuroscience of mathematical learning, the terms "mathematics", "arithmetic" and "numeracy" are often used interchangeably. **Mathematics (or maths)** refers to the abstract science of number, quantity and space, **arithmetic** is the branch of mathematics that deals with the logical properties and manipulation of numbers, whereas **numeracy** is the ability to understand and work with numbers in everyday life. Arithmetic belongs to the intersection between numeracy and mathematics in the classroom (see Figure 1). Mathematics is important not only for academic achievement, but also predicts many aspects of an individual's other life achievements (Parsons and Bynner, 2005). At a societal level, the standard of numeracy greatly affects science and technological progress, which is crucial for national economic outcomes (Gross, Hudson, and Price, 2009).

Figure 1. The relationship between mathematics in the classroom, arithmetic and numeracy



Source: Adapted from www.nationalnumeracy.org.uk.

In referring to the term **education,** we include *formal education*, referring to organised, intentional, structured modes of education with learning objectives, such as degree programmes at universities, *informal education*, cited as education that is not organised, with no set objectives and is not intentional, for example self-learning at home, and *non-formal education*, which encompasses a wide variety of approaches, is rather organised, and can have learning objectives, such as workshops, seminars, and short courses (OECD, 1996).

Cognitive neuroscience is the scientific study of the biological substrates underlying cognition, specifically the neural basis of mental processes. It is an interdisciplinary field involving disciplines such as molecular neuroscience, cognitive and experimental psychology, physiology, computer science, and psychiatry, to name a few. It employs a wide range of methods from basic neuropsychological measures, to psychophysics, neuroimaging, electrophysiology, and more recently, behavioural and cognitive genomics to explore the relationship between neural processes, cognition and human behaviour. As the field of cognitive neuroscience expands rapidly, it has become evident that knowledge of the brain and its functions could be applied to improve learning. The outlook for combining the expertise, theories and methods of cognitive neuroscience to enhance learning and education is promising. With global policies, together these could transform education and human learning as a whole.

Before we begin reviewing the contribution of cognitive neuroscience to mathematical cognition and learning, we would like to briefly highlight a theory of learning at the neuronal network level.

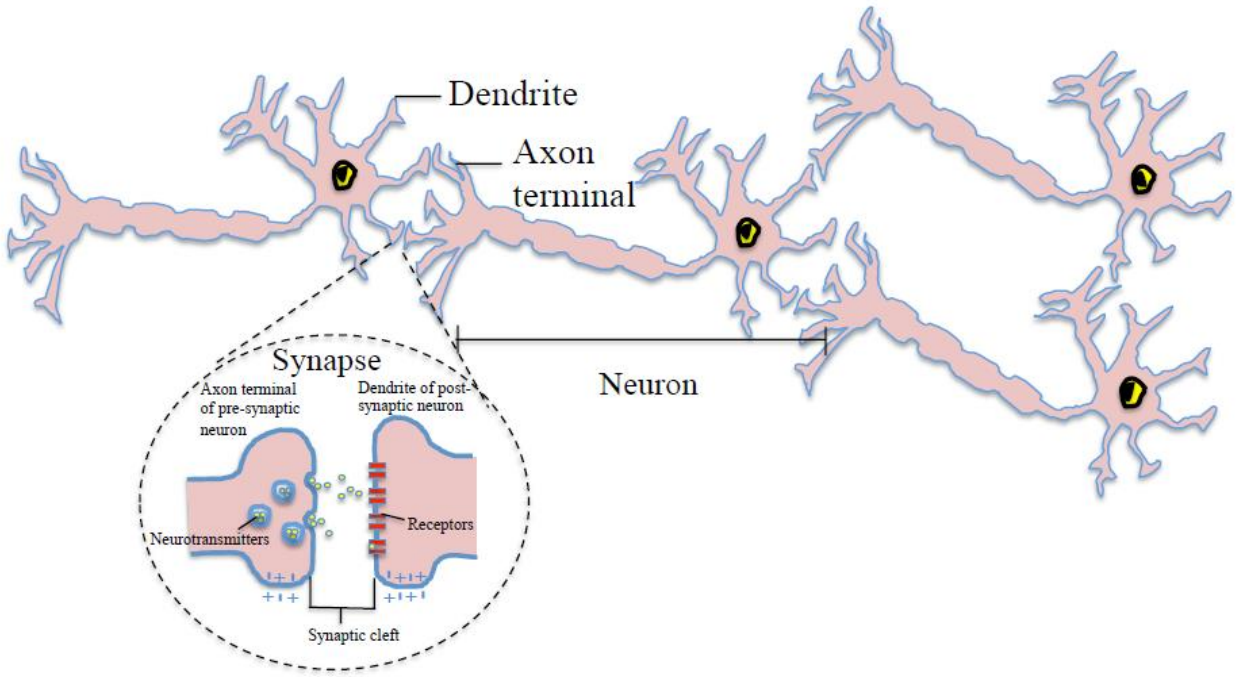
Hebbian Learning

In 1949 a learning model was proposed by Donald Hebb to account for "associative learning" (1949) at the brain level through neuroplasticity, which is a term referring to changes in neural pathways and synapses due to changes in environment and behaviour. Before we attempt to understand this theory, we would first like to describe the basic workings of the brain. A neuron is a single nerve cell within the central nervous system (CNS), which is connected to other neurons by dendrites (incoming connections) and axons (outgoing, fast connections). A connection between two neurons is called a synapse, and communication between neurons occurs via the transfer of neurotransmitters from the axon of one neuron to the dendrite of another.

Neuronal activity can be expressed in both electrical and chemical processes. The neuron's membrane is semi-permeable, which means that the neuron allows for free access for some molecules but not others. Information travels through neurons via the exchange of such molecules with different electrical charges (i.e. some are positively charged while some are negatively charged) between the inside and outside of the neuron in one direction. If sufficient activity, i.e. inside-outside exchange along the dendrites, reaches the cell body, an action potential is generated at the root of the axon, which sends fast-traveling electrical signals to the axon terminal end.

Activity reaching the axon terminal stimulates the release of neurotransmitters into the gap between the two neurons. If the subsequent neuron has received sufficient amounts of specific neurotransmitter(s) on its relevant receptors, it forwards the activity to its own cell body. This way, information cascades through a network of neurons that work together to achieve a certain task, for instance, numerical processing (Nieder and Miller, 2004). Once the information transfer has been completed, the neuron has a brief refractory period, during which time it cannot be active. The resting equilibrium between the electrical charges on the outside and the inside of the neuron can only be changed by new incoming signals.

Figure 2. Learning at the neuronal level



Note: When an action potential in the pre-synaptic neuron arrives at the synapse, it triggers the release of neurotransmitters. This release will influence the post-synaptic neuron and might cause it to fire too. If the post-synaptic neuron fires when the pre-synaptic neuron releases neurotransmitters, then the synaptic efficiency will be increased. The synaptic efficiency refers to the probability of being stimulated into further firing or, in other words, the strength of connection between neurons.

Hebb's model postulates that learning is mediated by the modification of the efficiency between synapses in the brain. A synapse grows in efficiency when the postsynaptic neuron reliably fires following the repeated and persistent release of neurotransmitters by the presynaptic neuron, or in other words "neurons that fire together, wire together." The more often the postsynaptic neuron is activated by presynaptic release, the stronger the synaptic connection becomes. Such increased synaptic strength is termed synaptic efficiency. In psychology and in education, the use of strategies such as repetition of learning material, reward or punishment to reinforce behaviour (termed conditioning), and environmental/material priming (e.g. Anderson, 2000) are in line with this idea to reinforce associative learning. This model is highly popular in cognitive neuroscience, and is supported by a large body of evidence from both animal (e.g. Black, 1990) and human studies (e.g. Zatorre, Fields and Johansen-Berg, 2012) showing how experiences can shape the brain at the neural level.

Having reviewed the progression of theoretical frameworks of learning in general, we can now evaluate the contribution of neuroscience specifically in the context of mathematical cognition and learning. For a more holistic view of mathematics learning, literature concerning this subject ranging from psychology to genetics will be reviewed.

The Meaning of Numbers

Before we delve into the details of numerical cognition, we would like to briefly explain the meaning of numbers. A licence plate number is a number or numerical label, but it is does not represent a quantity. In other words, the licence plate number "7743" is not somehow smaller or "less" than the licence plate number "9823". The meaning of numbers has been interchangeably referred to as magnitude and

numerosity (Wiese, 2003), but there is a subtle difference between the two: "numerosity" refers to exact quantities that are potentially countable, whereas "magnitude" denotes continuous dimensions that are not necessarily countable (for a dissociation between these abilities at the neural level see Castelli, Glaser, and Butterworth, 2006). With magnitude, comparing between two numbers can be similar to comparing two lengths or two weights and results in an approximate quantification.

The meaning of numbers is abstract. It is the "Threeness" that associates three animals, three oranges and three events together. It is also generally conceived that number meaning is independent of the format that represents it (e.g. 3, III, "three", "trois" or three fingers). However, it has been recently proposed that the representation of numerosities in the brain is primarily non-abstract, and this has been supported by neuroimaging evidence that showed differences in brain activation depending on the format of stimuli, e.g. symbolic digits vs. non-symbolic dot arrays (R. Cohen Kadosh and Walsh, 2009).

Integers or whole numbers are properties of a collection of items. Two collections can be combined to produce a single collection represented by a different number. Similarly, each collection or each integer consists of smaller collections added together. Counting is the action of putting each item in the collection in one-to-one correspondences with a number or some other internal/external tally ("one, two, three, four, five- there are five apples!") (Gelman and C.R., 1978). Most fractions can be explained in terms of collections. In other words, 4/9 refers to 4 parts of 9. Other types of number (e.g., zero, infinity, negative numbers, complex numbers) are harder to grasp and are learned later in formal educational if at all. Although basic concepts of numbers and numerosity seem to be self-evident to the typically developing individual, some special populations find them difficult to grasp and relate to (see section on Developmental Dyscalculia).

The Triple-Code Model

One of the most popular cognitive models of numerical processing is the triple-code model proposed by Dehaene and colleagues (Dehaene and Cohen, 1995; Dehaene et al., 2003; for other models, see Campbell and Epp, 2004; McCloskey, 1992). According to this theoretical model, three distinct codes of representations might be recruited in mathematical cognition depending on the task to be solved.

The first system, the quantity system, commonly referred to as the "number sense" in cognitive neuroscience, employs a non-verbal semantic representation of size and distance associations between numbers on a number line. It facilitates in magnitude comparisons (e.g. more vs. less), and approximation (i.e. estimation) tasks, and recruits both the right and left sides of the intraparietal sulcus, a brain structure that has previously been associated with the processing of numerical information amongst other cognitive functions (see sections on Representation of Numbers in the Brain and Parietal Cortex).

The second system, the verbal system, represents numbers in a verbal format (i.e. lexically, phonologically, and syntactically). This system is engaged when familiarised, arithmetic facts learned through rote learning such as addition and multiplication tables are retrieved. This system is thought to rely on the left angular gyrus (see sections on Temporo-Parietal Junction, Angular Gyrus, and Left Superior Temporal Gyri).

The visual system has been proposed to be involved in the representation and spatial manipulation of numbers in symbolic format (e.g. Arabic numerals). It is recruited in tasks that demand orientation of spatial attention, such as in number comparison, approximation, subtraction and counting. The posterior superior parietal lobe is thought to support this system (see section on Parietal Cortex).

This model has been most frequently referred to in order to test hypotheses on arithmetic learning and to speculate about neural networks that support numerical cognition. It has also inspired the design of

intervention programmes to remediate mathematical learning difficulties and to promote numerical development (see section on Intervention for Academic Improvement).

We will now begin the review with a step-by-step introduction to the literature on numbers, numerical cognition and learning, interventions, and the synergy of research and practice for better learning.

Universality of Numbers

Numbers are the building blocks of mathematics, and they are omnipresent; they appear on the clock, price tags, calendar, and bank notes, to name a few. In order to become competent in mathematics, one is required to learn and associate initially arbitrary notations and their meaning (e.g. 2, 7, +, -, x and >), and but also to understand the use of specific arithmetic principles, such as the different operations. However, even before the acquisition of such knowledge, humans as well as other species, appear to possess a fundamental set of numerical abilities that allow them to estimate quantity and execute basic calculations. At this more fundamental level, numeracy can be said to be universal or shared across species, and to some degree in humans, can exist before formal education takes place.

For instance, human babies of just one day old can distinguish between small quantities of objects (Antell, 1983) and they can judge whether quantities are equal even when they are presented to two different senses (e.g. sight and hearing). For example, in one experiment, the majority of infants preferred looking at a 2-object display followed by sequence of 2 drum beats compared to a 3-object display accompanied by 2 drumbeats (Starkey, Spelke, and Gelman, 1983; see section on Infants). This illustrates that infants at this age are able to discriminate between the different quantities of 2 and 3, and prefer to look at quantities that are matched across different perceptual modalities (i.e. different senses). Human infants can discriminate between, as well as represent and remember, small numbers of items. This suggests that some number abilities, such as non-verbal counting and precursors of verbal counting might have been present during infancy (Simon, 1995). For example, infants as young as a few hours are sensitive to small numerosity arrays (McCrink and Wynn, 2007). In one study, infants looked over stimulus cards with smaller numbers for longer than those with larger numbers, suggesting that they can recognise differences in quantities (Geary, Frensch, and Wiley, 2000; Wynn, 1992). By the age of six months, infants have shown the capacity to discriminate up to three or four physical objects (Lemaire and Siegler, 1995) and determine numerical similarity between sets of numbers across perceptual modalities (Izard, Dehaene-Lambertz, and Dehaene, 2008; Starkey et al., 1983).

Further research has shown that even illiterate cultures have developed counting and trading systems. For example, people from indigenous Amazonian groups who lack cultural transmission of number symbols, and thus cannot count (e.g. cannot represent exact quantities exceeding two or three items), can still quantify objects (e.g. estimate quantities or breaking larger number of items into smaller, manageable chunks) (Gordon, 2004), carry out arithmetic operations in an approximate manner (Pica et al., 2004), and possess intuition of Euclidean geometry (Izard et al., 2011). Archaeological evidence suggests that European Early Modern Humans (EEMH) or "Cro-Magnon" around 30 000 years ago made collections of marks on bones to keep track of phases of the moon (Marshack, 1991).

Research on animals provides another line of support for the universality of numbers. It has been shown that primates such as monkeys have the ability to perform simple arithmetic operations such as "1+1" and "2-1" (Hauser, MacNeilage, and Ware, 1996; see also Wynn, 1992 for similar evidence in babies, and Berger, Tzur, and Posner, 2006 for the neural correlates), and that they could generalise skills gained from training on a specific set of quantities and apply them to a new situation that also involves quantities with little training (Brannon and Terrace, 1998). Such crude ability to calculate provides animals such as lions the ability to decide between "fight or flight" based on the size of their group in comparison to their rivals' (McComb, Packer and Pusey, 1994).

These examples provide an illustration of the universality of numbers that varies from basic comparison abilities to rudimentary arithmetic, and even geometry. In the next section, we will discuss the issue of number semantics.

Extraction of Numerosity

To represent numerosity or the non-symbolic quantity of things, the physical properties of the elements in a set need to be ignored (e.g. three apples and three watermelons must have the same numerosity even though they differ in size). Similarly, in order to judge the numerical amount of a collection of objects or events, a similar process that will ignore non-numerical physical magnitude properties such as size, density, and luminance, is required (Durgin, 2008; Gebuis and Reynvoet, 2012).

Researchers have proposed a computer simulation model of how the brain may extract non-symbolic quantity for a visual set of objects (Dehaene and Changeux, 1993). This model suggests that, first, the locations of each separate item are coded by separate neurons. Then, these neurons relay their information to a system that is tuned into a specific numerosity (e.g. the number 7).

Both animals and human studies have supported the model above. Single-cell recordings in the lateral intraparietal area of the macaque monkey (Roitman, Brannon and Platt, 2007) have supported the evidence for a numerosity summation coding system (see also Nieder and Miller, 2004). A number-selective neuron system has also been identified within and near the intraparietal cortex of the macaque monkey (Nieder, Freedman and Miller, 2002; Nieder and Miller, 2004; Sawamura, Shima and Tanji, 2002). In humans, two similar types of cerebral pathways have been described for symbolic and non-symbolic numerosities (see Santens et al., 2010).

Automaticity of Number Processing

A large body of evidence suggests that the meaning of a number (i.e. 7 is a collection larger than 6 and smaller than 8) is automatically retrieved when one perceives it. Through number Stroop tasks (see Table 2), it has been shown that there is interference, for example exhibited through longer reaction times, when the numerical size of digits or their meaning is incompatible with the physical size of the font (Girelli, Lucangeli, and Butterworth, 2000; Henik and Tzelgov, 1982; Rubinsten et al., 2002). Notably, the emergence of numerical automaticity seems to depend on formal education for symbolic numbers (i.e. numerals or words) (Girelli et al., 2000; Henik and Tzelgov, 1982; Rubinsten et al., 2002), and seems to be less-dependent on formal education for non-symbolic numbers or numerosities, for example, represented as clusters of dots (Gebuis et al., 2009).

People who suffer from developmental dyscalculia, a learning disorder characterised by specific and persistent poor achievement in mathematics learning (R. Cohen Kadosh and Walsh, 2007), show impairment in automatic processing of symbolic numbers (Rousselle and Noel, 2007; Rubinsten and Henik, 2005). The intact ability to automatically process symbolic numbers has been examined using functional magnetic resonance imaging (fMRI)-guided transcranial magnetic stimulation (TMS). R. Cohen Kadosh et al. (2007) showed that the right intraparietal sulcus (IPS) is central for automatic magnitude processing. Only disruption of the right, but not the left, IPS activity induced dyscalculia-like performance in automatic accessing of numerical magnitude. That is, when participants without dyscalculia received stimulation to their right IPS, their performance became similar to those with developmental dyscalculia. The evidence from automaticity also points to the dissociation of automatic processing as a function of format; while symbolic processing is impaired in individuals with dyscalculia, non-symbolic automatic processing seems to be intact (Rousselle and Noel, 2007).

We will now refer to experimental data that support the view that numerical processing is subserved by a non-unitary system.

Basic Numerical Skills

Humans are thought to have basic numerical abilities that are sustained by two different systems: an approximate number system shared with non-human animals, which is also present in infants, that enables them to discriminate and approximately represent visual and auditory numerosities without verbal counting, and an exact representation system that allows the precise representation of small numerosities (Feigenson, Dehaene and Spelke, 2004). There is a general view that higher mathematical abilities, which are usually acquired years later compared to basic number processing, depend on the proficiency in early numerical activities such as counting and numerical estimation (e.g. Libertus, Feigenson and Halberda, 2013). Therefore, exploring the relationship between basic skills and higher mathematical abilities could inform us of the degree to which higher mathematical abilities are linked to basic numerical skills. The following sections are aimed at providing a general overview of such basic skills explored in the context of cognitive neuroscience.

Non-Symbolic Quantities

Approximate Number System (ANS)

According to Piazza and colleagues (Piazza et al., 2004), numerosities are represented in an increasingly imprecise manner, with larger numerosities represented less precisely than smaller ones at both the behavioural and neuronal level. It is an intuitive process, as it is fast, automatic, and inaccessible to introspection (Dehaene, 2009). Two behavioural effects that have been replicated consistently in different languages and numerical notations (Buckley, 1974; Dehaene, 1996) reflect this representational system:

a. The *distance effect*: Performance, as measured by reaction times and error rates, in numerical comparison tasks (e.g. which of two Arabic numerals or sets of dots is larger in magnitude?) increase as the numerical distance between the two numbers decreases. That is, e.g. comparing "2 vs. 8" yields faster and more accurate responses than "2 vs. 3". Note that the distance effect could be reversed when symbolic numbers are properly ordered in an increasing or decreasing count-list (Lyons and Beilock, 2013). This finding suggests that ordinality could be an important property for understanding the representation of numbers symbolically.

b. The *size effect*: In the same comparison task, reaction times and error rates increase as the absolute size or numerical magnitude of the two numbers increases, while the numerical distance between the two numbers is held constant. For instance, individuals are faster when comparing "2 vs. 3" than "7 vs. 8" (Moyer and Landauer, 1967; Restle, 1970).

These characteristics of the ANS have been observed across the human lifespan (e.g. Halberda et al., 2012; Halberda, Mazzocco and Feigenson, 2008; Libertus and Brannon, 2010) and across a range of non-human animal species (e.g. Cantlon and Brannon, 2006; see also Libertus et al., 2013). The acuity of the ANS in humans has been shown to increase until about 30 years of age (Halberda and Feigenson, 2008; Halberda et al., 2012; Lipton and Spelke, 2003), although baseline acuity varies considerably among individuals (e.g. Halberda et al., 2008; Piazza et al., 2010). Such individual differences in ANS acuity have been shown to correlate with concurrently measured individual differences in mathematics ability in preschool children (Libertus, Feigenson and Halberda, 2011), and this association extends to secondary school (Halberda et al., 2008), college (Libertus, Odic and Halberda, 2012) and beyond (Halberda

et al., 2012). More recently, it has also been found that early ANS acuity predicted mathematical ability six months later, when individual differences in age, expressive vocabulary, and baseline mathematical ability at the initial testing were controlled (Libertus et al., 2013). However, performance in this task might be affected by the level of inhibition, as there is a need to suppress non-numerical cues that co-vary with numerical information (Fuhs and McNeil, 2013).

On the other hand, many studies have not found correlations between ANS acuity and mathematical ability. For example, Lyons et al. (2014) examined the relationship between eight basic numerical skills and early arithmetic ability in over a thousand children across grades 1-6 (7-12.3 years old) and did not find that ANS could predict arithmetic ability at any grade. Sasanguie et al. (2013a) also did not find such correlations in 6-8 year-old children. In another study, Gilmore et al. (2013) found that inhibition skills, rather than the precision of ANS, accounted for the relationship between ANS and mathematics achievement.

Price et al. (2012) suggested that the mixed findings on the relationship between ANS acuity and math achievement might be due to differences between studies, such as sample size, age groups, type of arithmetic test, and the measures used to assess ANS. Overall, it remains unclear how acuity in ANS might cause improvements in formal mathematical ability, the directionality of the relation between ANS and mathematics ability over time, how domain-general functions such as inhibition skills interact with acuity in ANS, and how the frequency of using number symbols might increase ANS acuity (for a full review see Libertus et al., 2013).

Subitising

It has been widely documented that pre-verbal infants, children and adults can automatically estimate the size of a collection of up to approximately four items in an array without serial and attention-demanding counting processes. However, beyond this amount, the duration of estimation times increases as a function of the number of additional items, based on serial counting (Chi, 1975; Kaufman, 1949; Mandler, 1982). This quick and accurate subitising process, around 40-100 msec/item, has been found not only for visual (e.g. Chi, 1975), but also auditory (Camos, 2008) and tactile presentation (Riggs, 2006). Beyond the 4-item range, counting involves a slower, more effortful and error-prone process, around 250-350 msec/item (Trick, 1994). It has been suggested that children with low numerical competence, such as those with dyscalculia, show atypical subitising ability (Koontz and Berch, 1996; Reeve et al., 2012), underscoring its potential importance as a foundation for number learning.

At the neural level, a study using Positron Emission Tomography (PET) has shown that subitising and counting may share a common network involving the bilateral middle occipital and parietal areas, challenging the common perception that both processes are based on two separate networks. The intensity and spatial extent of activation in these areas increase with the number of dots and are dependent on their spatial arrangement (random>canonically arranged items); it was shown that activation reached a maximum peak and extent when counting larger numerosities that were randomly arranged (Piazza et al., 2002). To summarise, it seems that humans share with animals the ability to approximate numbers of objects in the real world.

However, everyday maths needs to be exact, and requires the understanding of quantity based on symbolic understanding. In the next section, we will refer to studies that have focused on the processing of symbolic numbers.

Symbolic Quantities

Exact Number System (ENS)

The ability to represent numbers using symbols is thought to enable the mapping between symbolic number codes and the ANS. Such acquisition has been shown to involve profound changes in the cerebral network responsible for numerical processing, through a progressive shift from predominance of the right IPS to bilateral IPS for both symbolic and non-symbolic processing (Ansari, Dhital and Siong, 2006; Cantlon et al., 2006; Izard et al., 2008; Piazza et al., 2007), as well as an activation in and around the left IPS, which increases with age for arithmetic processing (Rivera et al., 2005).

These changes are thought to reflect a fine-tuning of the ANS into a second, symbolic, number system for exact number representation and processing, termed the exact number system (ENS). A body of evidence from behavioural studies supports the idea that the ENS is a refinement of the ANS upon the acquisition of symbolic numerical knowledge (see Castronovo, 2012). For instance, Ashcraft and Moore showed that children (mean age between 6.75 and 10.71 years old) and college students (mean age 23 years old) showed an increasingly linear pattern of number line estimation with age (Ashcraft and Moore, 2012). They also found that the strength of linear estimation correlated significantly with children's maths achievement, suggesting that education and the acquisition of symbolic number knowledge might be crucial for the development of the ENS from the ANS (e.g. Siegler and Booth, 2004).

This shift from ANS to ENS as a function of development and mathematical abilities has been found in several studies. One of the indications is that the representation of numbers shifts with age from logarithmic to a mixture of logarithmic and linear, and finally to a primarily linear representation (Ashcraft and Moore, 2012; Dehaene, 1997; Siegler and Booth, 2004; Siegler and Opfer, 2003). More specifically, children tend to represent numbers in an unevenly spaced logarithmic or "compressed" mental number line, in which the smaller values are represented further apart than they should be and larger values are compressed closer together (see Moeller et al., 2009). As children develop, it has been shown that at the average age of 6.9 years old, their representation of numbers shifts towards a more linear one-to-one representation (Siegler and Booth, 2004). However, the logarithmic representation continues to be exhibited by children with mathematical learning difficulties (Geary et al., 2008).

More recently, it has been suggested that the left IPS is critical for the mapping between ENS and ANS. Sasanguie, Göbel and Reynvoet (2013b) showed that the disruption of activity in the left, but not the right IPS using repetitive TMS impaired the processes that are crucial for priming between symbolic and non-symbolic number representations (Sasanguie et al., 2013b). This result is in line with previous studies indicating that acquisition of ENS relies on the left IPS, rather than the right IPS (Rivera et al., 2005).

Accurate numerical understanding can also be achieved without using symbols, and before symbolic acquisition. It has been suggested that the ability to represent numbers in an exact fashion has been accomplished using counting (Carey, 2004).We will now discuss the phenomenon of counting, an ability that is paramount for intact mathematical development.

Counting with Fingers, Body Parts, and Bases

In order to count beyond a small collection of items, humans have developed various aids to keep track of their counting such as the tally system (e.g. tally marks found on artefacts), symbols such as written numerals and number names, the abacus, and most recently, the calculator. Despite large cultural diversity, two common ways of counting are employed: the use of body parts and base systems.

Fingers and other body parts are typically used to keep record of the number of items counted. It is not surprising that the word "digit" is used to refer not only to numbers, but also to fingers and toes.

Anthropological evidence can provide support for this reference; in Papua New Guinea for example, the Yupno have no specialised names for numbers. They use the names of body parts to count and represent numbers. For example, "one" is the left little finger (Lancy, 1978). For the people of Kilenge in Papua New Guinea, body parts are combined and used as bases. For instance, 5 is represented by one "hand", 10 is "two hands", and 20 is "man". These terms can be combined, to represent quantity i.e. 30 is a "man and two hands" (Lancy, 1978; Wassmann, 1994).

When body parts are exhausted to represent larger quantities, bases are used. Bases are derived from a core property of numbers that is culturally independent. Any given number except 1 or 0 can be decomposed into a collection of collections. For example, in base-10 system, the number "45" refers to 4 collections of 10 and 5 collections of 1. Base-10 system is not the only base system, cultures such as the Maya uses base 20 with subunits of 5. Traces of a base-20 system can be heard in some European languages such as in French (e.g. "quatre-vingt-dix-sept", literally "four twenties and seventeen"). The ancient Babylonians used a base-60 system with subdivisions of 10 units that has been retained in our measurement of angles and time (Hodgkin, 2005).

The tendency to use body parts for counting might have a close evolutionary relationship with numerical cognition (Butterworth, 1999). For example, in Gerstmann syndrome (Mayer et al., 1999), damage to the left parietal cortex produces not only the inability to perform arithmetic, termed acalculial; but also finger agnosia, classified as impairment in identifying fingers by touch; agraphia, which means the inability to write; and left-right disorientation (see section on Gerstmann Syndrome). In this respect, a number of studies have suggested that use of numbers has emerged from other "older" evolutionary cognitive functions (R. Cohen Kadosh, Lammertyn and Izard, 2008; Dehaene and Cohen, 2007). For example, representations of space, along with those of number, are subserved by the parietal lobes in partially overlapping structures (Walsh, 2003).

Numbers and Space

One of the general functions of the parietal lobes is the representation of space, time, and quantity (Walsh, 2003). Numbers can be represented as ordinal, when rank is based on a sequential order, e.g., first, second, third; cardinal, as in the size of sets or quantities; and nominal, when the numerals are used for identification only and do not represent quantity, rank, or other measurement, information. There is a body of evidence that suggests that the representation of numbers has a strong spatial element (van Dijck et al., in press).

The most consistently replicated finding that supports the spatial feature of number representation is the Spatial Numerical Association of Response Codes (SNARC) effect. This effect is demonstrated in tasks that require individuals to make judgments about numbers (e.g. odd/even judgments). It refers to the consistent finding that Western (i.e. left-to-right reading) participants respond more quickly to small numbers with the left hand, and to large numbers with the right hand. Recently, it has been reported that the directionality of writing contributes to the directionality of the SNARC effect; Arabic monoliterates who use only the right-left writing system showed a right-to-left bias, whereas Arabic-English biliterates showed weaken right-to-left bias, and illiterate Arabic speakers showed no SNARC effects (Zebbian, 2005). Furthermore, this effect is based on the side of the response and not the responding hand. Therefore, if the hands are crossed, larger numbers will be processed with a faster response on the right side of space even though it is made with the left hand, and vice versa (Dehaene, Bossini and Giraux, 1993). This supports the idea that numbers may be represented through a "spatial number line" (Restle, 1970) that extends from left to right.

Numbers can even affect the orientation of visuospatial attention. For example, Fisher et al. (2003) showed that, when presented in the centre of the screen, small numbers such as 1 and 2 direct attention to

the left, while larger numbers such as 8 and 9 direct attention to the right. The influence of visuospatial attention on number ability is further supported by studies with patients with visuospatial neglect, that is, patients with right parietal lesions that cause them to ignore the left hemisphere of space. When these patients, who are neither dyscalculic nor acalculic, are asked to bisect a line, they show spatial-numerical biases similar to their visuospatial biases (e.g. when asked what number is midway between 11 and 19, they might provide the answer "17") (Zorzi, Priftis and Umilta, 2002).

The representation of numbers from the left to right in the form of a spatial "mental number line" might be associated with two different possible properties of numbers: (i) their numerical cardinality or quantity; or (ii) their ordinality—that is, numbers are an ordered set and the fact that they represent quantities is irrelevant. In the latter case, similar effects should be found with stimuli such as alphabets or months of the year, which form an ordered set but do not represent quantity. Current data support the latter possibility. For example, Gevers, Reynvoet, and Fias (2003) found that the SNARC effect also applies for stimuli such as months. For instance, a faster left-sided response was given for "January", and a faster right-sided response for "December".

More recently, empirical evidence has also illuminated the sensory and bodily aspect of numerical cognition, termed embodied numerosity (see Moeller et al., 2012). Some examples of this concept include finger counting and finger-based representations. It has been proposed that embodied representations of number (magnitude) influence number processing in a systematic and functional way, and that it can be trained to increase the efficiency of numerical learning (Moeller et al., 2012). A spatial-numerical training by Fischer et al. (2011) was shown to be more effective than performance on a non-spatial control training in enhancing children's performance on a number line estimation task and a subtest of a standardised mathematical achievement battery. The improvements were driven by enhanced mental number line representation and not by attention or motivation factors, suggesting the benefits of spatial-numerical connections. More recently, it has also been reported that embodied training, involving bodily movement, is more effective than non-kinesthetic training in improving number line estimation performance, and is especially beneficial to children with low cognitive abilities. These embodied training improvements also transferred to performance in solving addition problems (Link et al., 2013).

Therefore, it seems that the link between space and numbers is widely supported, and may be rooted at the ordinal level. We will now discuss the issue of numerical representation at the neural level, with most of the studies examining numerical magnitude.

Representation of Numbers in the Brain

Research has led to a convincing body of evidence that suggests the presence of specialised neural networks for numerical cognition (R. Cohen Kadosh et al., 2008; Dehaene, 2009; Zamarian, Ischebeck and Delazer, 2009). These networks appear mainly in the parietal and prefrontal cortices, but also involve other brain regions including occipital cortex, subcortical regions, and the cingulate cortex.

Parietal Cortex

When humans engage in quantity processing and calculation, the parietal lobe is systematically and bilaterally activated (for reviews see Arsalidou and Taylor, 2011; R. Cohen Kadosh et al., 2008; Kaufmann et al., 2011; Menon, in press). The IPS, in particular, has been consistently associated with numerical representation in the brain (R. Cohen Kadosh et al., 2008). For example, it is activated when participants decide whether a given quantity is smaller or larger than a standard and even during subliminal presentation of numbers [presentation of numbers below the threshold of conscious perception, without participant's being aware of it, e.g. during a priming task (see Table 2, Appendix)] (Naccache and

Dehaene, 2001). The latter finding lends further support to previous studies that have suggested that quantity information is automatically accessed by the perception of symbolic numbers.

Further studies have supported the role of the IPS in numerical representation (Piazza et al., 2004). For example, fMRI studies have demonstrated that IPS activity is sensitive to quantity information by using a neural adaptation paradigm. They show that IPS activity adapts, or slowly decreases, in response to repetition of the same numerical stimulus, and that it increases again in response to other, or deviant, quantities (Cantlon et al., 2006; R. Cohen Kadosh et al., 2011; Piazza et al., 2007). Further research has shown that stimulating the IPS using TMS can also modulate numerical representation of specific numbers, therefore supporting the view that neurons in the human brain are more sensitive to specific numbers than other numbers; for example, some neurons are more optimally tuned to a given number, such as 4 and less to a closer number, like 3 and 5, and even less to, for example, 7 (R. Cohen Kadosh et al., 2010a), similar to monkeys' brains (Nieder and Miller, 2004). It has been suggested that the right IPS is recruited for numerical processing early in life (Cantlon et al., 2006; Izard et al., 2008), remains fundamentally unaltered by education, and is mainly influenced by genetic factors (Pinel and Dehaene, 2013). Meanwhile, activation in the left IPS during a number comparison task has been found to correlate with children's arithmetic performance at school (Bugden et al., 2012).

As we mentioned previously, it is important to acknowledge that the specificity of IPS activation for numerical processing has been questioned, as the IPS is also activated during activities such as grasping, pointing, eye movements, orientation of attention, general attention or response-selection mechanisms (Shuman and Kanwisher, 2004), and during tasks involving other physical dimensions such as size, location, angle and luminance (R. Cohen Kadosh and Henik, 2006; R. Cohen Kadosh et al., 2005; Fias et al., 2003; Kaufmann et al., 2005; Pinel, Piazza, Le Bihan, and Dehaene, 2004; Zago et al., 2008); for a review and meta-analysis see R. Cohen Kadosh et al., 2008. This has led to two interpretations: i) there is a sub-system in the IPS that subserves numerical processing that is only partially independent of, and is intertwined with, other specific magnitude systems (R. Cohen Kadosh et al., 2008); or ii) the IPS is the headquarters of a general system committed to the assessment of magnitude of time, space and numbers (Walsh, 2003), and such a magnitude system supports the primary role of the parietal lobes in visuomotor abilities (R. Cohen Kadosh et al., 2011).

Although there is a general emphasis on the role of the IPS in magnitude processing, some researchers have stressed its role in the processing of order. The anterior part of the IPS is activated by both numerical and non-numerical order such as letters and months (Fias et al., 2007), supporting the proposed role of IPS in working memory for information involving order (Marshuetz et al., 2006a; Marshuetz et al., 2006b). However, dissociation between numerical and non-numerical order has been found in the IPS, suggesting that while this general area may have a role in processing both types of order, their processing may be largely separate (Zorzi, Di Bono and Fias, 2011).

Temporo-Parietal Junction

Following the finding that the left angular gyrus is involved in language processing (Dehaene et al., 2003; C. J. Price, 2000), researchers have proposed that this area might be involved in the retrieval of verbally stored arithmetic facts, such as multiplication facts, from long-term memory. The left angular gyrus has been reported to display greater activation during exact compared to approximate addition (Dehaene et al., 1999), during processing of relatively smaller problems compared to larger ones (Stanescu-Cosson et al., 2000), when solving multiplication compared to subtraction problems (Lee, 2000), and after training on arithmetic facts (Delazer et al., 2003). Based on brain imaging data and self-reports of strategy use, (Grabner et al., 2009) suggested that the left angular gyrus mediates the retrieval of arithmetic facts when individuals solve addition, multiplication, subtraction, and division.

It has been proposed that the angular gyrus and the left superior temporal gyri are strongly implicated in the representation of symbolic arithmetic, as both regions are more activated for symbolic (i.e. numerals and words) compared to non-symbolic (i.e. clusters of dots) numerical magnitude judgements (Holloway and Ansari, 2009). However, all these results can be explained by automatisation, which is greater in the case of symbolic numbers, and by fact retrieval (Zamarian and Delazer, in press).

Prefrontal Cortex

The prefrontal cortex, in the anterior region of the frontal lobes, is known to be involved in orchestrating a range of core domain-general processes, such as executive functions, which include inhibitory control, working memory, cognitive flexibility, and higher-order functioning such as reasoning, problem solving, and planning (e.g. Lehto, 2003; Miyake, 2000; Collins, 2012; Diamond, 2013).

It has been consistently reported that parietal and prefrontal cortices are activated simultaneously when individuals perform arithmetic tasks (Grabner et al., 2009; Pesenti et al., 2000; Rivera et al., 2005; for meta-analysis see Arsalidou and Taylor, 2011). Menon et al. (2000b) was the first to show that such co-activation could be dissociated quantitatively; the main effect of arithmetic complexity was reported in the left and right IPS, whereas the main effect of domain-general task difficulty was found in the left ventrolateral prefrontal cortex. Menon et al. (2002) further highlighted the role of the prefrontal cortex in detecting incorrect arithmetic expressions and incongruity between internally computed and externally presented incorrect answers.

Other studies have also reported the role of prefrontal regions in numerical magnitude processing. For example, it has been shown that there is a negative correlation between the strength of the numerical distance effect and the level of activation in the prefrontal and precentral regions (Ansari et al., 2005; Pinel et al., 2001). These areas were modulated to a significantly larger extent in children compared to adults, possibly due to involvement of other cognitive functions such as attention, and executive functions.

Visual Streams

It has been reported that ventral visual stream areas such as the lateral occipital cortex and the fusiform gyrus are commonly activated together with the IPS, and their responses have been observed to increase as a function of arithmetic complexity, when other processing demands are controlled (e.g. Keller and Menon, 2009; Rickard et al., 2000). Rosenberg-Lee (2011b) has reported functional dissociations across different arithmetic operations in the inferior temporal cortex, areas thought to be crucial in recognition and discrimination of number-letter strings (Allison, 1999; Milner, 2008). It was proposed that deconstruction of arithmetic problems, especially those with unfamiliar problem format and involving less automatised procedures, are likely to demand dynamic interactions between dorsal and ventral visual areas (Rosenberg-Lee et al., 2011; see Menon, in press).

Arithmetic Task-Specific Functional Dissociations

When referring to arithmetic, it is easy to give the false impression that it is a unitary process. As the following examples will illustrate, this is clearly not the case (see section on Arithmetic Ability is not Unitary). Distinct functional dissociations between different areas of the brain have been reported for specific arithmetic operations such as number comparison, addition, subtraction, and multiplication.

For example, a study by Chochon and colleagues (1999) showed that, compared to digit naming only (which does not involve intentional quantity processing), number comparison activated the bilateral parieto-fronto-cingular network. When the authors analysed differential activations among the tasks of naming, comparison, multiplication, and subtraction, they found that each task in this list, respectively, added a specific area of activation to the immediately preceding task. Compared to digit naming, number

comparison activated the depth of the right postcentral sulcus; meanwhile, multiplication added a strong additional left intraparietal activation compared to number comparison, and subtraction resulted in a greater right postcentral and bilateral prefrontal activation relative to multiplication (Chochon et al., 1999). However, this type of result might stem from differences in task difficulty, as more difficult tasks are more metabolically demanding.

In another example, Rosenberg-Lee et al. (2011b) found that compared to a number identification control task, all arithmetic operations apart from addition yielded a consistent activation of the left posterior IPS and deactivation in the right posterior angular gyrus. Contrary to the common view that the left angular gyrus differentially facilitates retrieval during multiplication, that is to say via verbal processing instead of quantity processing, as proposed by the "triple-code" model (Dehaene and Cohen, 1997; Dehaene et al., 2003), the same study found that multiplication and subtraction evoked significantly different activity in the right, but not in the left angular gyrus. The authors also found that even though addition and multiplication both depend on retrieval processes, multiplication elicited a greater activation in the right posterior IPS, prefrontal cortex, lingual and fusiform gyri. Such subtle differences have been proposed to account for different retrieval processes employed for both operations.

Overall, these findings suggest that the various arithmetic operations evoke different levels and areas of activation in parietal cortex, but that neural responses associated with these different numerical operations cannot be distinctively and directly mapped to specific posterior parietal cortex regions. It is important to note that with the current resolution of neuroimaging tools, there remains uncertainty and debate about the extent and nature of the associations and dissociations between specific functions and specific brain regions. Nevertheless, these findings suggest that arithmetic ability is not a single entity but rather a composite of related but distinct components (Dowker, in press-a).

Involvement of Other Cognitive Domains

Numbers are not a cognitive module. That is, the successful implementation of basic numerical tasks and complex maths relies on a plethora of cognitive abilities. Domain-general cognitive processes such as executive functions (Baddeley, 1996), inhibitory control, shifting of attention, updating, and working memory are all critical for numerical cognition. These functions have been suggested to provide the framework for the development of more efficient strategies during the early stages of arithmetic skill acquisition (Bull, Espy and Wiebe, 2008).

Working memory, the limited capacity to control, regulate and actively maintain information during goal-driven cognitive tasks, has been regarded as an important contributor to mathematical outcomes even when other cognitive and academic factors are controlled for (K. M. Wilson and Swanson, 2001; for a review see Raghubar, Barnes and Hecht, 2010). For example, working memory uniquely predicted solution accuracy on word problems in both children with and without significant mathematics difficulties (Swanson, 2004), while verbal working memory predicted end of year performance on mathematics curriculum tests (Fuchs, 2005). It is likely that further research on the contribution of working memory to maths learning and performance will have implications for interventions for mathematical learning difficulties. Meanwhile, executive functions have been connected to age-related improvements in children's skills in maths problem solving strategy choice. Specifically, the extent of inhibitory control and cognitive flexibility correlated with strategy selection and age-related differences in strategy selection (Lemaire and Lecacheur, 2011).

Development of Human Numerical Cognition

Infants

Human infants can discriminate between, as well as represent and remember, small numbers of items. This suggests that some number abilities, such as pre-verbal counting and precursors of verbal counting, might have been present during infancy (Starkey and Cooper, 1980). For example, infants as young as a few hours (Izard et al., 2009) are sensitive to small numerosity arrays, such as 2 to 3, but not to larger sets like 4 to 6 (Antell, 1983; Starkey, Spelke and Gelman, 1990). By the age of 6 months, infants have shown the capacity to enumerate or count a small (e.g. 2 or 3) series of discrete actions (Sharon, 1998; Wynn, 1996) and by age 18 months, they can enumerate up to 3 or 4 physical objects (Starkey, 1992) and determine numerical correspondences between sets of entities across perceptual modalities (Starkey et al, 1983; 1990; Izard et al., 2009). These findings suggest that infants can discriminate, see the relationships between numerosity and objects, and represent small quantities before they are formally educated on numeracy.

Five-month-old infants have demonstrated sensitivity to simple arithmetic such as addition and subtraction operations on small sets of physical objects (Wynn, 1992); replicated by Simon, 1995). They seem to have already developed the expectation of a decrease in quantity when one item is removed from a set of 2 items and an increase in quantity when one item is added to another item. More recently, it has also been documented that infants at the age of 9 months can successfully perform large-number addition and subtraction (McCrink and Wynn, 2007), suggesting that they already have a magnitude-based estimation system for the representation of numerosities at an early age.

Children

Pre-School

Preschool children's understanding of quantity relationships, such as "more than" and "less than", develops as they mature, along with their ability to add and subtract. Starkey (1992) showed that infants' understanding of addition and subtraction expands gradually to include set sizes of up to 4 items by the age of 4, and larger sets from then on (see also Geary et al., 2000).

Later, the preverbal number system becomes integrated with children's emerging language abilities through the use of number words (e.g. "one," "two," etc.) and verbal counting to solve basic addition and subtraction problems (e.g. to solve 2+3, counting "one, two, three, four, five") although the system can also operate without language (Geary et al., 2000).

By the end of pre-school years, most children have a good understanding of counting concepts (see Table 3). They can use these counting skills to compute relatively large sets of items and to support adding and subtracting items from these sets. Additionally, they have a basic understanding of ordinality (e.g. $1<2<3<4$) and cardinality (i.e. that the last number word in a counting sequence defines the number of items in a set). Importantly, they can use these skills in practical ways, such as for measurements (Geary, Frensch and Wiley, 1994).

Primary and Secondary School

At this level, most of the quantitative skills that children and adolescents are expected to learn are culturally determined, and can be classified as secondary abilities (see Table 4) that are built from more universal primary systems (Geary et al., 2000). A distinction between the two systems is important because the developmental trajectory of the secondary abilities can vary between generations and cultures, depending on the educational practices.

Between six to eight years old, numerical representation seems to shift gradually from a logarithmic to a primarily linear format, thereby reflecting a more exact numerical understanding. A strong correlation has been found between individual differences in numerical representation, as indicated by the performance in a number-line estimation task, and mathematics achievement test scores (Siegler and Booth, 2004). That is, increased maths performance is associated with increased linearity in estimation. It has been suggested that exposure to relevant experiences (e.g. with the formal number system in counting, arithmetic and other numerical contexts) tends to support improvement on estimation accuracy (Siegler and Booth, 2004).

While most developmental number cognition studies have focused on basic numerical skills, some have shed light on the developmental changes in arithmetic strategy use. For example, compared to younger children who tend to rely on time-consuming step-by-step procedures (e.g. counting from 1 for each sum), children receiving formal education show an increasing degree of optimisation in their strategies, such as the use of "min strategy", i.e. counting from the larger addend (Groen, 1977), "tie-strategy", e.g. 2+2, 3+3, 4+4 (Barrouillet and Fayol, 1998; Lemaire and Siegler, 1995), and eventually direct retrieval of arithmetic facts from memory. Unsurprisingly, older children are also quicker and more accurate than younger children when solving mathematical problems (Imbo, 2007), and show a decrease in the problem size effect, a well-replicated observation of increasing reaction time with problems involving large numbers (e.g. Roussel, Fayol and Barrouillet, 2002).

Siegler and Shrager (1984) have shown that even children at an early kindergarten age already possess a variety of strategies to solve addition problems, including min-procedure, retrieval, tie-strategy, and more. The majority of studies suggest that for an individual type of problem, individuals progress over time from counting to using other strategies (e.g. min-, tie-strategies), to direct retrieval (see Imbo, 2007). Children's initial associative network of problem-answer associations strengthens into a more automatically activated long-term memory knowledge as they develop (Campbell and Graham, 1985). This idea is supported by studies that have shown increased frequency of interference between different problem-answer associations, such as for different types of arithmetic operations, as children develop (e.g. LeFevre, 1991; Lemaire, Barrett, Fayol, and Abdi, 1994).

Table 1. Biologically Primary Quantitative Abilities

Numerosity The ability to determine accurately the quantity of small sets of items, or events, without counting. In humans, accurate numerosity judgments are typically limited to sets of four or fewer items, from infancy to old age.
Ordinality A basic understanding of more than and less than and, later, an understanding of specific ordinal relationships. For example, understanding that 4 > 3; 3 > 2; and 2 > 1. For human infants, the early limits (i.e. before learning number words) of this system are not known, but appear to be limited to quantities of < 5.
Counting Early in development there appears to be a preverbal counting system that can be used for the enumeration of sets up to 3, perhaps 4, items. With the advent of language and the learning of number words, there appears to be a pan-cultural understanding that serial-ordered number words can be used for counting, measurement, and simple arithmetic.
Simple Arithmetic Early in development there appears to be sensitivity to increases (addition) and decreases (subtraction) in the quantity of small sets. In infancy, this system appears to be limited to the addition or subtraction of items within sets of 2, and gradually improves to include larger sets, although the limits of this system are not currently known.

Source: Geary, D.C., Frensch, P.A., and Wiley, J.G. (2000), "From infancy to adulthood: The development of numerical abilities", *European child and adolescent psychiatry*, Vol. 9/2, S11-S16, https://web.missouri.edu/~gearyd/ECAPsychiatry.pdf .

Table 2. Biologically Secondary Number, Counting, and Arithmetic Competencies

Number and Counting In most, if not all, industrialised nations, primary school children are expected to master the counting system (e.g. learning the associated number words), gain an understanding of the base-10 system, and learn to translate, or transcode, numbers from one representation to another (e.g. verbal – "two hundred ten" – to Arabic – "210"). In the early grades, counting errors are common for teen values (e.g. forgetting the number word) and for decade transitions (e.g. 29 to 30, often misstated as "twenty nine, twenty ten"). Number transcoding errors (e.g. transcoding "two hundred ten" as "20010") are common in primary school children, especially in the first few grades. Learning the base-10 system appears to be the most difficult counting and number concept that primary school children are expected to learn, and many of these children never gain a full understanding of the system.
Arithmetic: Computations In most industrialised nations, primary school children are expected to learn the basic arithmetic facts and learn computational procedures for solving complex arithmetic problems (e.g. 472+928). With sufficient practice, nearly all academically normal children will memorise most basic arithmetic facts; in some countries, however, the level of practice is not sufficient to result in the memorisation of these facts, which, in turn, results in retrieval errors and prolonged use of counting strategies. The ability to solve complex arithmetic problems is facilitated by the memorisation of basic facts, the memorisation of the associated procedures, and an understanding of the base-10 system. The latter is especially important for problems that involve borrowing or carrying (e.g. 457+769) from one column to the next.
Arithmetic: Word Problems In most, if not all, industrialised nations, primary school children begin to solve simple word problems in kindergarten and first grade, although the complexity of the problems they are expected to solve in later grades varies greatly from one nation to the next. The primary source of difficulty in solving these problems is identifying problem type (e.g. comparing two quantities vs. changing the value of one quantity) and translating and integrating the verbal representations into mathematical representations. In secondary school, the complexity of these problems increases greatly and typically involves multi-step problems, whereby two or more verbal representations must be translated and integrated. Without sufficient practice, the translation and integration phases of solving word problems remain a common source of errors, even for college students.

Source: Geary, D.C., Frensch, P.A., and Wiley, J.G. (2000), "From infancy to adulthood: The development of numerical abilities", *European child and adolescent psychiatry*, Vol. 9/2, S11-S16, https://web.missouri.edu/~gearyd/ECAPsychiatry.pdf .

Adults

In comparison to children and adolescents, basic quantitative skills in adults have not been studied as extensively (see Geary et al., 2000). It has been proposed that adults' competence in quantitative abilities is best predicted by the extent to which these skills were mastered in primary and secondary schools (Bahrick HP, 1991). For example, the frequency and distribution of practice on algebraic skills during secondary school were found to be the best predictors of algebraic skills in middle- and old-age even when individual differences in basic maths skills were controlled (Bahrick HP, 1991).

In terms of strategy use, although it is generally expected that adults are able to compute arithmetic problems automatically, they continue to use retrieval and a variety of non-retrieval strategies (Campbell and Epp, 2004; Campbell and Timm, 2000; Campbell and Xue, 2001; Geary, Frensch and Wiley, 1993; Kirk and Ashcraft, 2001; Siegler and Shrager, 1984), including implicit activation of their fingers, which might indicate finger counting (Sato, 2007). The rate of retrieval, compared to other calculation strategies, varies depending on the operations involved (Campbell and Alberts, 2009). For example, for multiplication and small addition problems, retrieval is the most commonly used strategy, while it is common that adults rely on other strategies, such as counting, when solving subtraction and division (see section on Strategy Use). With training, adults take less time to solve arithmetic problems, and provide more accurate answers (see Mathematics Learning), suggesting that performance can be further improved even at ages beyond formal education.

The Developmental Shift in Activation Pattern

During tasks involving numerical symbols such as digits, children rely more on prefrontal areas compared to adults (Ansari, 2008; Kaufmann et al., 2006; Kucian et al., 2008). As children grow older, distinct parietal networks begin to form in the bilateral IPS and the left temporo-parietal cortex for numerical processing; an increase in brain activation as a function of age in the left supramarginal gyrus and anterior IPS and the left lateral temporo-occipital cortex has been reported in children and adolescents asked to verify simple addition (e.g. 4+2=6?) and subtraction (e.g. 4-2=3?) equations (Kawashima et al., 2004). This localised increase was accompanied by a decrease in activation in the frontal brain regions, subcortical structures such as the basal ganglia and thalamus, brainstem, and the left medial temporal lobe, which suggests that the arithmetic procedures might have become more automatised.

Similarly, in a cross-sectional study of subjects aged 8-19, Rivera et al. (2005) reported age-related changes in activation of many of these same brain regions during calculation tasks. This included increases in the recruitment of the left inferior parietal cortex (left supramarginal gyrus), anterior IPS, and left lateral temporo-occipital cortex, along with decreases in activation in the bilateral regions of the frontal cortex, hippocampus and the basal ganglia (Rivera et al., 2005). The decrease in the reliance on frontal regions has been suggested to reflect automatisation, a change characterised by reduced reliance on processes of cognitive control, attention and working memory with development. On the other hand, the decrease in reliance on the hippocampus might be the result of increased consolidation of arithmetic facts into long-term memory (Rivera et al., 2005; see also Menon, in press).

This fronto-parietal-shift has also been viewed as a more general development of learning processes, shifting from a main reliance on controlled executive processing to more task-specific processes (see section on Mathematics Learning). For example, Delazer et al. (2005) trained adults to perform two new types of arithmetic operations. One was learnt via rote learning, the drill condition, and the other through the use of strategy. After the initial learning phase, participants in the drill condition showed a strong activation in the angular gyrus, while those in the strategy condition demonstrated larger network activation including bilateral occipito-parietal area including the precuneus, which is the medial area of the superior parietal cortex.

It is important to note that the reduced activation in general cognitive areas and more focal activation in number-relevant areas are very similar to development in other domains such as in cognitive control (e.g. S. Durston et al., 2006; Schlaggar et al., 2002), or face processing (K. Cohen Kadosh and Johnson, 2007). This suggests that cognitive development is achieved through fine-tuning of relevant neural systems (for discussion, see S. Durston and Casey, 2006).

The developmental shift from frontal to parietal activations has also been observed during basic numerical tasks, such as symbolic and non-symbolic comparison tasks (Ansari and Dhital, 2006), and in an fMRI adaptation task with numerosities, where deviant numerosities activated bilateral IPS in adults, but only the right IPS in 4-year-old children (Cantlon et al., 2006). This suggests that children at that age have yet developed a more refined neural representation of quantities. Overall, the development and refinement of the IPS activation from childhood to adulthood suggests that there is an increasing functional specialisation for numerical processing over the course of development.

Elderly

Compared to young adults, older individuals have been reported to employ different strategies, and use them in different ways, when solving complex arithmetic problems (Lemaire and Arnaud, 2008). Elderly individuals show reduced flexibility in using strategies and tend to rely on the same strategy for different problems. Brain activity also differs between elderly and younger populations; an electroencephalography (EEG) study has shown that both right and left hemispheres in elderly brains work more symmetrically than young adults' brains when engaged in complex arithmetic (El Yagoubi, Lemaire and Besson, 2003).

One possible reason for these age-related changes in strategy use, and their resultant poorer performance, might be age-related declines in memory-retrieval and processing speed, along with other higher-level cognitive functions (Sasson, 2012). Elderly individuals have shown the capacity to learn associations between problems and solutions, but show slower acquisition compared to younger adults. These older individuals are slower in acquiring strategies based on memory retrieval and show low confidence in their memory (Touron, 2004). Therefore, they might be less likely to use retrieval-based strategies. Declines in other cognitive functions may also be to blame for poorer performance; these include working memory, associative learning that involves visual, but not verbal, task material, and greater difficulty in learning new materials (Jenkins, 2000). Neurological evidence supports the behavioural evidence of drop in cognitive functions; for instance, memory-related brain areas such as frontal and temporal brain regions undergo ageing-related decline (Sasson, 2012). In addition, lower capacity to learn amongst the elderly might also be due to reduced efficiency of white matter connections between brain areas, which could result in slower information processing and response (Kerchner, 2012). However, it is unclear if such anatomical and functional changes are the results of cognitive decline, or the causal factors themselves.

Mathematics Learning

In the current section, we review studies under the umbrella term "mathematics", with a focus on arithmetic, as it is the most widely researched area in the context of learning. We chose to not review studies on geometrical and algebraic reasoning as, while important, they are sadly limited in number and inconsistent in their research methods.

Studies have shown that with the gain of arithmetic expertise, there is a shift from slow, effortful, and error-prone procedures to skilled, fast, direct memory retrieval (e.g. J. R. Anderson, Fincham and Douglass, 1999; Logan, 1988; Rickard, 2004). These studies have explored the learning of both simple (e.g. Núñez-Peña, 2006; Pauli et al., 1994) and complex arithmetic (e.g. Delazer et al., 2003;

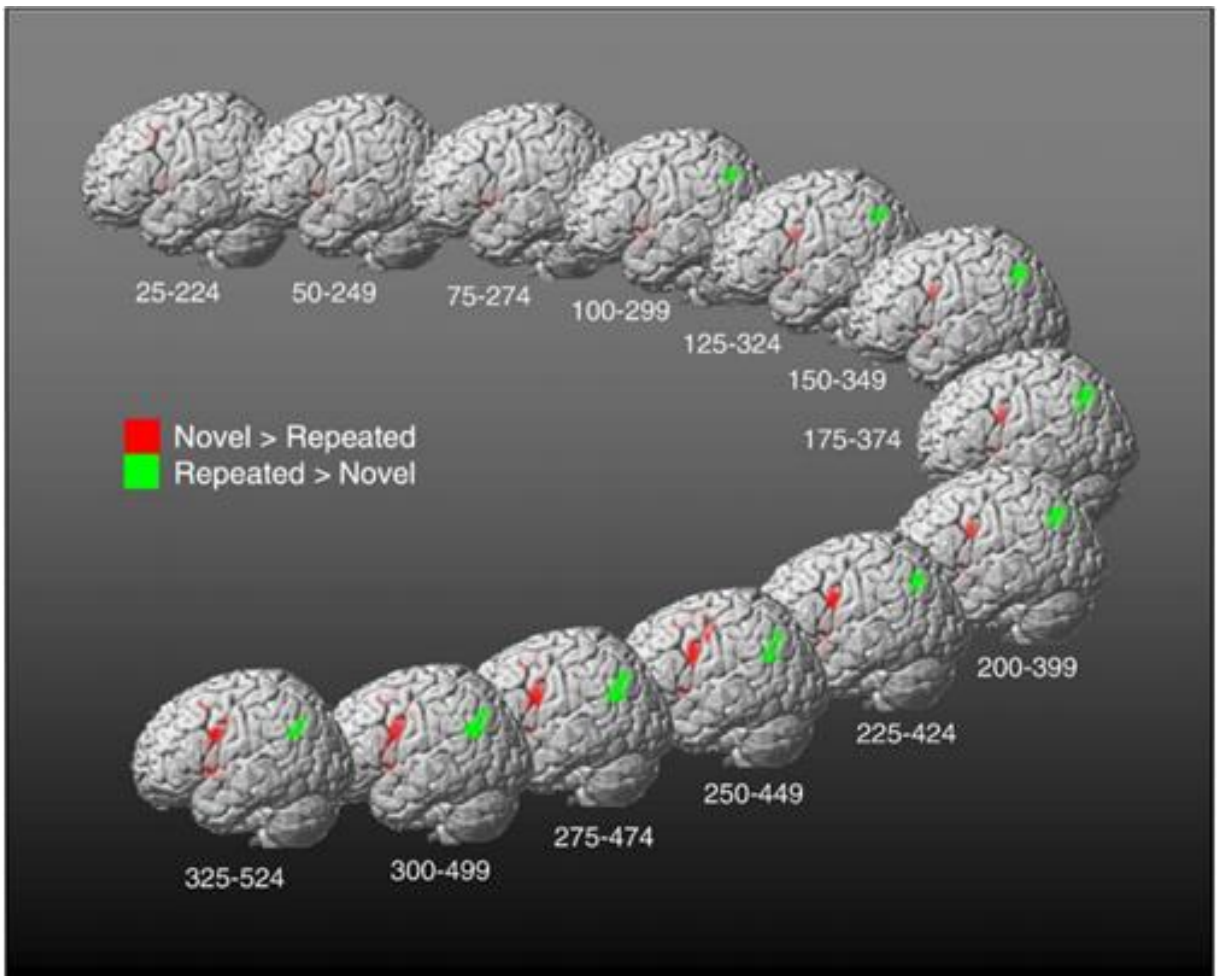
Grabner et al., 2009) and have shown that intensive arithmetic training can lead to significant changes at the brain level (Delazer et al., 2003; Grabner et al., 2009; Ischebeck, Schocke and Delazer, 2009; Ischebeck et al., 2007; Ischebeck et al., 2006; Pauli et al., 1994). For example, Delazer et al. (2003) showed that young adults trained over five days on complex multiplication problems (e.g. 23 x 8 =?) showed higher proficiency post-training on trained problems than novel problems. Compared to the trained problems, solving untrained problems significantly activated the left IPS, inferior parietal lobule, and the inferior frontal gyrus, brain regions that are involved in calculation algorithm and manipulation of quantity, rather than rote retrieval (Delazer et al., 2003). In contrast, solving trained problems resulted in stronger activation within the left angular gyrus, an area that is involved in rote retrieval. Similar results emerged in other studies (Delazer et al., 2005; Ischebeck et al., 2007; Pauli et al., 1994), suggesting that the repetition of problems strengthened retrieval of the correct solution, which reduced quantity-based processing, and hence the demands on working memory, monitoring and attention sustained by the frontal regions. This view is in line with Poldrack (2000), who observed that learning tends to progress from general purpose processes to task-specific processes.

The effects of learning have also been studied with respect to different learning methods, different content, time course of learning, and transfer between related operations (Zamarian and Delazer, in press). Studies on different learning methods have shown that both drill, referring to emphasis on the rote memorisation, such as arithmetic facts and procedures (Cowan, 2003) and strategy, referring to focusing on understanding basic concepts and arithmetic relationships, approaches to learning led to skilled performance and automatisation of memory retrieval when solving arithmetic problems (Zamarian and Delazer, in press). Delazer et al. (2005) showed that differences between these methods are reflected in the pattern of brain activation; compared to strategy-trained problems, drill-trained problems evoked a relatively greater activation of the left angular gyrus, supporting the idea that retrieval methods are more predominantly used during drill learning than strategy learning (Delazer et al., 2005).

With regard to differences in training effects based on the content of learning, Ischebeck et al. (2006) showed that comparable training on two different arithmetic procedures, complex multiplication and complex subtraction, did not lead to similar effects at the brain level. After training on multiplication problems, there was a stronger left AG activation compared to untrained multiplication problems. However, there were no significant differences in the activation of the left angular gyrus between trained and untrained subtraction problems. These differences between operations suggest that when problems are frequently encountered, complex multiplication might be solved most efficiently via direct memory retrieval, whereas even in familiarised subtraction problems, rapid and basic processing might continue to be employed.

Studies have reported that the effects of learning can be observed through brain activation patterns during early training. For instance, Ischebeck et al. (2007) showed that after only eight problem repetitions, there was already a significant decrease in fronto-parietal activation and increase in temporo-parietal activation, including the left angular gyrus. These effects were stable throughout the course of the scanning duration, and were comparable to the pattern observed by previous studies that have involved longer training periods (Delazer et al., 2003; Delazer et al., 2005; Ischebeck et al., 2006).

Figure 3. Brain activation pattern reflecting changes due to practice over the duration of training



Notes: The effects of training (green: repeated>novel; red: novel>repeated) became significant beginning the time window from 100-299 scans (permission to be obtained). There was an increased recruitment of the angular gyrus (shown in green) for the repeated problems compared to novel problems. The activation of the area in the left middle frontal gryus (shown in red) increased in response to novel compared with repeated problems as a function of training. These results suggest that the neural correlates of mental arithmetic undergo changes at the early stages of learning.

Source: Ischebeck et al. (2007), "Imaging early practice effects in arithmetic", *NeuroImage,* Vol. 47, http://dx.doi.org./10.1016/j.neuroimage.2007.03.051 .

Meanwhile, the transferability of acquired knowledge between related operations has also been studied. For example, Ischebeck et al. (2009) showed that after intensive training on multiplication problems, greater activation in the left angular gyrus was associated with division problems that were related to previously trained multiplication problems. This activation pattern was also positively correlated with the degree of transfer effects observed in their behavioural findings. These data suggest that acquired multiplication knowledge through initial training was applied when solving untrained related division problems.

More recently, mathematics learning has also been studied using non-invasive brain stimulation techniques such as transcranial electrical stimulation. A recent finding by Snowball et al. (2013) has shown that depending on the learning regime, brain stimulation can induce long-lasting enhancement of cognitive and brain functions (see section on Transcranial Electrical Stimulation). In this study, tRNS during calculations, i.e. strategy or deep learning, but not during drill learning or shallow learning, showed

long-lasting improvement behaviourally and physiologically for at least six months and generalisation to new, untrained materials.

Special Populations

So far, we have reviewed findings mainly based on healthy populations. In this section, we will now describe the cognitive characteristics of various populations with atypical development and cognition.

Acalculia

Acalculia is an acquired impairment in the ability to perform mathematical tasks. It is a heterogeneous disorder and can manifest in different forms, i.e. patients might exhibit impairments in number processing or calculation or both. It differs from developmental dyscalculia (see section below), as acalculia is usually a result of cerebral damage (e.g. Carlomagno, 1999; Girelli et al., 1999) from neurological conditions such as stroke or neurodegenerative disease, whereas developmental dyscalculia is a specific developmental condition.

The prevalence of acalculia in patients with left hemispheric injury is estimated between 16% and 33%, and about 90% amongst those with early stage Alzheimer's disease (Carlomagno, 1999; Girelli et al., 1999; Humphreys et al., 2012; Mantovan et al., 1999). Findings from lesion studies showed that (a) damage to the parietal lobes, the central hub of numerical cognition, does not necessarily result in number impairments. Most patients with right parietal lesions demonstrated preserved comprehension of core numerical concepts (e.g. Cappelletti and Cipolotti, 2006; Cohen et al., 2007), possibly maintained by compensatory mechanisms from other brain regions (e.g. Cappelletti, Freeman and Cipolotti, 2009a); (b) damage to other brain regions could also lead to number impairments. For example, (i) damage to the frontal and temporal lobes has been reported to result in impaired calculation skills (e.g. Basso, 2009) and sometimes to impairments in processing quantity (e.g. Delazer and Butterworth, 1997); (ii) damage to subcortical areas can cause impaired quantity processing, arithmetic fact retrieval and conceptual knowledge (e.g. Delazer and Benke, 1997; Delazer et al., 2004), and (iii) lesions to posterior regions, the areas usually recruited in numerical symbolic and word recognition (Dehaene and Cohen, 1997), have shown more subtle number impairments, for example a patient with severe impaired written word recognition who could make accurate, albeit slow, semantic decisions on visually presented numbers (Cappelletti, Muggleton and Walsh, 2009b).

Studies on acalculic patients have revealed the independence and multi-componential nature of number and calculation processing, through the existence of selective impairment in various particular abilities: the comprehension of written arithmetical symbols (e.g. Ferro, 1980; Laiacona, 1997), arithmetic fact retrieval (e.g. Dehaene and Cohen, 1991), calculation procedures (e.g. Ardila and Rosselli, 1994), or arithmetic conceptual knowledge (e.g. Warrington, 1982). These findings also emphasise the fact that there is no one-to-one correspondence between a specific number ability and a specific brain area (see Cappelletti, in press) as lesions to different areas can cause similar impairments, or lesions to the same area can cause different outcomes.

Developmental Dyscalculia

Developmental dyscalculia (DD) is a condition characterised by a specific difficulty in learning or understanding arithmetic in otherwise typically-developing individuals. This condition affects about 3.5-6.5% of the population (von Aster and Shalev, 2007). Although DD is not as well-known as dyslexia, some have suggested that the lack of competence in numeracy has a more severe impact on an individual's life achievements compared to functional illiteracy (S. Parsons and Bynner, 2005).

Individuals with DD usually struggle to subitise small numbers of objects, exhibit poor sense of number magnitude, employ immature strategies in solving arithmetic problems and demonstrate difficulty in retrieving arithmetic facts (Landerl, Bevan and Butterworth, 2004; Rousselle and Noel, 2007). It is common that despite producing a correct solution to an arithmetic problem, individuals with DD might have done so mechanically and without confidence (DFES, 2001).

Despite the consistent finding of deficits in elementary numerical processing in DD, the cause underlying this condition is not fully understood. Two major problems challenge the classification and definition of DD: the co-morbidity with other conditions such as attention-deficit hyperactivity disorder (ADHD) and dyslexia, which usually manifest differently in each individual, and myriad potential confounding factors which may occur at different and/or multiple levels, i.e. biological, such as atypical neural connectivity, cognitive, for example working memory, and psychological, like anxiety.

Two main hypotheses have been proposed to account for the behaviours observed in individuals with DD: the defective number module hypothesis (Butterworth, 2005) and the access deficit hypothesis (Rousselle and Noel, 2007). According to the defective number module hypothesis, individuals with DD have a highly specific and innate deficit in understanding and processing numerical magnitude in general. In contrast, the access deficit hypothesis, as the name implies, suggests that individuals with DD have impairments in accessing numerical meaning, such as quantity via symbols.

More recently however, brain-imaging studies have shown that there are deficient fibre projections in the brains of children with DD, and these include the connectivity between parietal, temporal, and frontal areas, suggesting a new hypothesis that DD might be a result of a disconnection syndrome (K. Kucian et al., 2013; Rykhlevskaia et al., 2009). Considering the functions of these regions, these findings highlight the importance of considering domain-general functions, for example, executive functions, inhibitory control, shifting of attention, updating, and working memory (see section on Involvement of Other Cognitive Domains) in the diagnosis and intervention of dyscalculia.

Gerstmann Syndrome

As described previously in this review, Gerstmann Syndrome is an enigmatic condition characterised by a tetrad of symptoms including finger agnosia, acalculia, left-right confusion and agraphia, which is the loss of the ability to write (Gerstmann, 1940). Over the years, claims that this is a unitary syndrome have been criticised and questioned (see Rusconi et al., 2010). The rarity of "pure" Gerstmann syndrome patients and the difficulties in characterising the constellation of symptoms challenge the definition, theoretical value, clinical prevalence and diagnostic relevance of this condition (Benton, 1991).

Initially, this condition was thought to be the outcome of damage to the left angular gyrus, a region, which was presumed to subserve a single, speculative cognitive function that would link the four observed impairments (see Rusconi et al., 2010). It is now generally thought that this condition is related to damage of the inferior parietal lobe/superior temporal regions in the dominant hemisphere. It has also been proposed that the condition could arise from damage to some other common functional denominator (see Kleinschmidt, 2011).

In addition to the conceptual inconsistencies, there remains a lack of neurofunctional evidence of this condition. Recently however, using functional and fibre tracking, Kleinshmidt and Rusconi (2011) identified a focal lesion in the left parietal white matter that could account for the specific symptoms associated with the condition. Such a lesion was proposed to affect not just a single fibre tract but also crossing or overlapping of different fibre tracts, resulting in disconnections in cortical networks and hence behavioural deficits. This finding suggests that Gerstmann syndrome could be considered as a disconnection syndrome (see also Mayer et al., 1999). Further investigating these clues into the

neurological basis of Gerstmann syndrome could potentially shed light on its component symptom of acalculia, and through this, the connections that are vital for normal numerical cognition.

Finger Agnosia

Finger agnosia is the impairment of the ability to distinguish, name, or recognise one's own fingers, fingers of others, or drawings and other representation of fingers (Ardila, Concha and Rosselli, 2000). Individuals with finger agnosia usually have difficulty with selectively moving their fingers, whether it is voluntary or by imitation. It occurs as one of the four symptoms of Gerstmann syndrome, but can also exist on its own without the presence of other disorders (Sala, 1994). Lesions to the left angular gyrus and posterior parietal areas can lead to this condition (Ardila et al., 2000; Sala, 1994).

As one of the strategies for counting involves using one's own fingers, it has been suggested that mathematical difficulties might be associated with finger agnosia (see Seron, 2012). Repetitive TMS in healthy adults on the intraparietal sulcus, supramarginal gyrus, bilateral angular gyrus, and posterior parietal areas can induce "virtual" finger agnosia, which is characterised by impairment in naming, recognising and distinguishing fingers (Rusconi, Walsh and Butterworth, 2005). Such virtual impairment was associated with acalculic behaviour when the parietal lobes were stimulated. The authors concluded that the brain regions underlying finger agnosia and acalculia are within close proximity but distinct.

Maths Anxiety

Competence in maths relies not only on cognitive abilities, but also on emotional factors and attitudes (Dowker, Bennett and Smith, 2012; Maloney and Beilock, 2012). Studies have shown that emotional factors greatly affect mathematical performance, and those with mathematics anxiety are particularly affected (Baloglu, 2006; Miller, 2004).

Typically, individuals with maths anxiety panic when they are confronted with a problem involving numerical information. It is not limited to questions in maths textbooks, but also daily activities such as paying for a bill and/or telling the time. Such type of activities causes worries about the situation and its consequences. Therefore, it is unsurprising that those with mathematics anxiety tend to avoid maths-related activities, which in turn contribute towards reduced practice and therefore, poor performance (Ashcraft, 2002). The lack of self-confidence and the worries regarding performance in maths-related situations introduce stress and thereby compromise cognitive resources such as working memory (Beilock, 2010). It is also possible that maths anxiety might arise from an individual's repeated failures and poor basic numerical and spatial competence, which is the ability to represent and reason about distance, shape, order, and relations involving two- and three- dimensional space, and the communication of such information.

On the other hand, it has been suggested that the development of maths anxiety could stem from social factors such as exposure to teachers who themselves experience maths anxiety. In these cases, those with initial difficulties in understanding maths are more likely to be affected by such negative social influence about maths (Maloney and Beilock, 2012). Additionally, social identity has an influence; previous research has shown that only the female students of highly math anxious female teachers who adopt the stereotypical perception of "boys are good at math, girls at reading" show such bias and perception (Beilock et al., 2010). Together, these findings highlight the contribution and importance of affect in the learning of mathematics.

Blindness

Over the last few years, a new line of research has emerged on blindness and numerical cognition. Contrary to the common belief that vision is critical for the acquisition of numerical representation and skills (Burr and Ross, 2008; Ross, 2010), findings concerning blindness and numerical cognition indicate that vision is not necessary (e.g. Cattaneo, 2011b; Szűcs, 2005).

Szucs and Csepe (2005) found that at the behavioural level, congenitally blind individuals exhibit distance and size effects comparable to sighted individuals. At the neural level, the same authors used EEG and showed that numerical representation and neural circuits involved in numerical comparison in blind individuals are similar to those of their sighted counterparts. The only difference between the two groups was the topography of the distance effect detected at the initial phase of numerical comparison process. The later stage involving parietal effects was similar between the two groups. It was suggested that the deprivation of vision involves the development of a "partially normal number processing network". It has been suggested that blind individuals might rely on compensatory mechanisms that employ high-level cognitive resources such as working memory and/or attention when performing on numerical tasks (Salillas, 2009; Szűcs, 2005).

Cattaneo et al. (2011) replicated Szucs and Csepe's (2005) behavioural findings, and further showed that blind and sighted individuals demonstrate similar leftward bias in bisecting numerical intervals in a numerical bisection task. These findings suggest the existence of semantic numerical representation with similar spatial properties to those typically found in sighted individuals, i.e. a "mental number line" which extends from left to right.

In contrast to these studies, Crollen et al. (2011a) found that although early visual deprivation does not prevent the development of numerical representation with similar properties as in sighted individuals, the ability to refer to space based on an individual's body positioning is crucial when mapping numbers into space; early-blind participants showed reversed SNARC effect contrary to blind and sighted participants in the crossed-hand comparison task. This finding supports the hypothesis that the SNARC effect derives from reading habits (Dehaene et al., 1993; but see Shaki and Fischer, 2008).

More recent research on blindness also suggests that, surprisingly, early visual deprivation might have a positive impact on numerical skills. Early blindness seems to involve the development of compensatory mechanisms which engage high-level cognitive resources such as attention (Collignon, 2006) and working memory (Crollen et al., 2011b; Salillas, 2009), which in combination with numerical mapping abilities, contribute to greater numerical skills in blind compared to sighted people.

Low-Birth Weight and Pre-Term Children

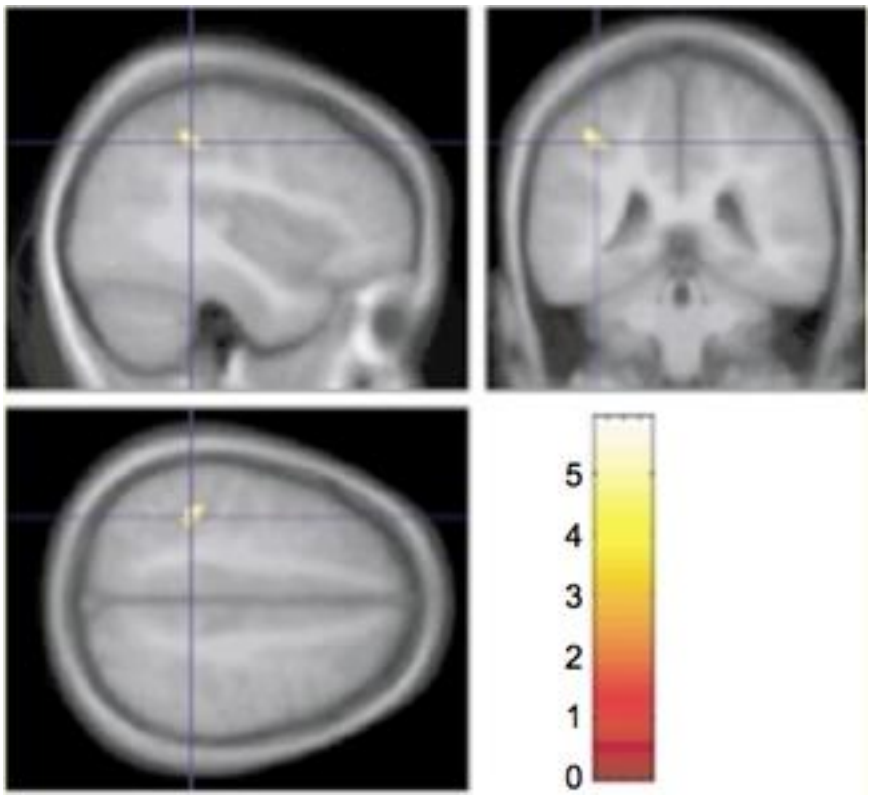
Advances in neonatal intensive care over the last decades have resulted in increased rate of survival of children born very pre-term, which refers to children born at less than 32 weeks gestational age, and/or with very low birth weight (<1500 g). These children have shown more and higher rates of difficulties in learning mathematics (e.g. Grunau, Whitfield and Davis, 2002; Taylor et al., 1995), are consistently reported to have scored poorly on mathematics tests, and receive lower teacher ratings in classroom performance in mathematics (Anderson and Doyle, 2003; Botting, 1998; Hagen, 2006; Klebanov, 1994).

It has been suggested that the degree of low birth weight is associated with the extent of mathematical difficulties. For instance, Taylor et al. (1995) found that children born with <750 g birth weight had a higher rate of learning difficulty in applied problems than children with 750-1499 g birth weight. Johnson and Breslau (2000) found a similar pattern in which the rate of mathematics learning difficulties increased with lower birth weight throughout the ≤2500 g range.

Neonatal complications and postnatal neurological abnormalities have also been identified as contributing factors to difficulties in mathematics learning (Taylor et al, 1998). For example, the severity of intraventricular haemorrhage, chronic lung disease, treatment with postnatal steroids, necrotising enterocolities, such as infection and inflammation of the intestines, and longer neonatal hospitalisation have all been linked with poorer mathematics performance (Sherlock, 2005; Short, 2007; Taylor, Espy and Anderson, 2009; Taylor et al., 2006; B.R. Vohr et al., 2003).

Isaacs et al. (2000) used magnetic resonance imaging (MRI) and found that adolescents who were born prematurely with low birth weight showed selective impairment in mathematics processing, accompanied by a reduction of bilateral hippocampal volumes. There were no group differences in total intracranial volume, suggesting that structural differences in the hippocampus might have given rise to the observed difficulties in mathematics learning, although such abnormalities might be due to behaviour, rather than the cause of it. In another study, Isaacs and colleagues (2001) discovered a reduced parietal grey matter density in children born prematurely, and found that such a reduction is linked with lower maths performance at the age of 15 years old, despite controlling for other variables such as gestational age and birth weight.

Figure 4. Reduced grey matter in the left inferior parietal lobe of children with low birth weight



Note: Imaging data showing a region of grey matter in the left inferior parietal lobe that is significantly reduced in size in children with very low birth weight. These children also show calculation difficulties

Source: Isaacs et al. (2001), "Calculation difficulties in children of very low birth weight: A neural correlate", *Brain*, Vol. 124, http://dx.doi.org/10.1093/brain/124.9.1701.

To date, there is no consistent finding on whether there is a sex difference in the prevalence of mathematical difficulties in children born with low birth weight or prematurely. In two studies, O'Callaghan et al. (1996) and Johnson and Breslau (2000) found that the frequency is higher amongst

males than females, while others (e.g. Grunau, Whitfield and Fay, 2004; Saigal, 2000; Taylor et al., 2000) did not find significant differences between males and females.

Changes in arithmetic skills with age have also been documented by two longitudinal studies of low birth weight children. Saigal et al. (2000) found that when compared to typical controls, there was a greater decline in standard scores on the Arithmetic subtest of the WRAT-R from ages eight years to adolescence (12-16 years) amongst a cohort who were born with <750 g birth weight. There was a stable mathematical difficulty across age according to the study by Breslau et al. (2004) who followed a sample of children with other outcomes (Aylward, 2005).

It is important to note that due to subtle differences in perinatal and neonatal management practices, the consequences of children born prematurely and with very low birth weight could differ across eras, cohorts and sites (Pinto-Martin, 2004; B. R. Vohr et al., 2004). To ensure comparable samples, the matching of control groups should ideally include factors such as background, socioeconomic status, histories of educational interventions, genetic background, parenting characteristics, prenatal drug and alcohol exposures (Taylor et al., 2009). This is important as it has been shown, for example, that home environment and early learning experiences affect subsequent mathematics achievement at the age of 10 years (Melhuish, 2008). Moreover, such factors might help to explain why and how some children, even those with extreme degrees of low birth weight and/or premature birth, perform well academically despite high-risk birth (Anderson and Doyle, 2003) Contribution of both biological and environmental factors such as individual differences in the degree of plasticity, or effectiveness of academic instruction, might shed light on ways to optimise the development of mathematics skills (Taylor et al., 2009).

From these summaries of research on mathematical abilities in special populations, it is clear that a wide variety of factors can affect mathematical cognition. While much of the extant literature on differences in mathematical ability has focused mostly on the comparison of atypical vs. typical populations, more recent studies have emphasised the issue of inter- and intra-individual differences. Such lines of research have important implications for psychology and education. We will discuss this in the next section.

Inter- and Intra-Individual Differences

In the following sections, we refer to inter-individual differences as the factors that account for the variation between individuals, and intra-individual differences as the factors that account for the differences within the same individual.

Inter-Variability

Language and Culture

One profound way in which culture can affect numerical cognition is through language. Although the use of Arabic numbers in mathematics is universal across most cultures, including English and Chinese, a functional distinction in the brain networks involved in arithmetic tasks has been found between native speakers of those two languages. Native English speakers showed reliance on the left perisylvian cortices for mental calculation during simple addition tasks, suggesting the use of language-related processes, while native Chinese speakers engaged a visuo-premotor association network for the same task (Tang et al., 2006), possibly indicating a reliance on visuospatial abilities. The authors suggested that this differential biological encoding of numbers, which cannot be accounted for solely by language differences, may arise partly from visual reading experiences throughout language acquisition, as well as from other factors such as mathematics learning strategies and education systems. Cultural effects on functional brain organisation are not limited to mathematics, but have also been reported for other cognitive domains such

as object processing (e.g. Goh et al., 2007; Kobayashi, 2007; Paulesu et al., 2000), thus underscoring the effects of culture on psychology and biology.

Mathematics Abilities

Inter- individual differences in the mathematical brain arise not only cross-culturally, but also vary widely based on individual mathematical competence. Neuroimaging studies have revealed the neural correlates of some such individual differences. For example, a study by Menon et al. (2000b) showed that individuals who performed at ceiling level, termed perfect performers, displayed less activation and variability in the left angular gyrus during an arithmetic verification task, but not in other brain regions compared to non-perfect performers. This was interpreted as higher functional optimisation in the left angular gyrus of perfect performers, who also showed relatively shorter reaction times on the same task compared to non-perfect performers, possibly due to long-term practice effects and skill mastery in the former group. In another study however, Wu et al. (2009) found the opposite when using the same verification task but presenting two different formats, i.e. Arabic vs. Romans numerals. They found that better performance was associated with stronger activation within bilateral AG, and greater deactivation, classified as neural activity below baseline level, was linked to poorer performance. In the more familiar format, the Arabic numerals, there was a greater response in both AG due to less deactivation compared to the less automated format, the Roman numerals (Wu et al., 2009). Together, these findings suggest that differences in individual automaticity in relation to the type of task, performance level and competence can influence numerical processing at the neural level.

Similarly, Grabner et al. (2007) reported that high-achieving individuals demonstrated greater activation within the angular gyrus, middle temporal gyrus, supplementary motor area and medial superior frontal gyrus (all left-lateralised) compared to low-achieving individuals when verifying the correctness of single-digit and multi-digit multiplication problems. The reverse comparison did not yield any significant network of activation present in low- but not high-performers. The activation of the angular gyrus and individual level of mathematical competence were positively correlated; individuals with higher mathematical competence were supported by a network engaging the left angular gyrus to a higher degree than their less competent counterparts. In another study, Grabner et al. (2009) replicated and extended their previous findings by showing that after training, there were no group differences in the activation of the angular gyrus. This suggests that activation in the left angular gyrus during mathematical tasks may be related to the intensive training required in gaining mathematical expertise.

In another study, Aydin et al. (2007) found structural differences between academic mathematicians and non-mathematicians in brain regions implicated in numerical processing. They found higher grey matter density (GMD) in the bilateral inferior parietal lobule and left inferior frontal gyrus in mathematicians compared to non-mathematicians. They also revealed a positive correlation between time spent as a mathematician and the relative increase in GMD in the parietal lobule, suggesting that persistent training in mathematics can result in structural modifications in brain regions that subserve numerical computation, arithmetic calculation and visual-spatial processing. More recently, another study reported that mathematicians have lower GMD in the right IPS, but higher GMD 2 cm anterior, that is, at the right superior parietal lobule, compared to non-mathematicians (Sader et al., submitted). This finding contradicts previous findings by Molko et al. (2003) that linked poor numerical performance and lower GMD in the right IPS, but instead suggested an inverted U-shape relationship between GMD in the right IPS and mathematical skills. It seems that exceptional abilities in mathematics were reflected in either increased or decreased GMD, depending on the specific brain areas.

Fehr et al. (2010) later compared a calculation prodigy against typical controls and found that there were no significant differences in brain activation patterns during average calculation tasks. Interestingly, however, during exceptionally difficult tasks, the prodigy showed activation patterns in areas close to those

observed during normal calculation. It was proposed that with intensive practice, skill enhancement leading to exceptional performance is achieved through neuroplastic modifications in brain regions initially employed for normal calculation, where the initial strategy is increasingly used more efficiently.

Pesenti et al. (2001) on the other hand, showed that exceptional mathematical abilities might be achieved by recruiting different strategies and relying on additional brain areas compared to the average-performing individual. Using PET, they showed that a calculation expert relied on not only the common brain regions implicated in mathematics processing (bilateral activation with left side predominance in the supramarginal gyrus, IPS, inferior occipital and middle occipital gyrus, occipito-temporal junction and frontal areas), but also activation in the left paracentral lobule, right medial frontal gyrus, parahippocampal gyrus, anterior cingulate gyrus and middle occipito-temporal junction, areas associated with visuo-spatial working memory, visual imagery, episodic memory and numerical processing.

When Hanakawa et al. (2003) compared qualified Japanese abacus masters to non-expert controls during mental calculation, they found that activation patterns in the cerebellum, fusiform gyrus, superior pre-central sulcus and posterior parietal cortex were bilaterally symmetrical for the experts but left-lateralised for the non-experts. It was speculated that the experts' greater reliance on these brain areas that underlie visuo-spatial and visuo-motor processing might reflect their main strategy employed during mental calculation (Hanakawa, 2003).

Finally, through a PET study, Wu et al. (2009), found that Chinese abacus experts might have relied on the same procedures when solving simple and complex addition, with almost no increased workload on the complex addition, while non-experts showed dissociable brain activations between simple versus complex calculation. The latter group showed activation in areas implicated in language, such as the inferior frontal cortex, and visuo-spatial processing, the left fronto-parietal network, during simple additions, and stronger activation in regions associated with visuo-spatial processing during complex addition problems.

In sum, both quantitative and qualitative differences have been reported in the neural profiles of individuals with differing levels of mathematical competence, with different extent of practice, or with reliance on different strategies (see Zamarian and Delazer, in press). Mapping of the trajectory for acquisition of mathematical expertise might shed light on the neuroplasticity-related changes that underlie the processes of building such high competence. Additionally, such research could help uncover the extent to which training would be able to promote changes at both behavioural and neural levels to maximise an individual's potential for mastering mathematics.

Arithmetic Ability is Not Unitary

According to Dowker, there is no unitary measure of individual differences in arithmetic. Instead, arithmetical ability is composed of a range of components from counting to understanding arithmetical principles. This view is supported by the following findings:

- Patients who become acalculic from brain damage can show selective impairments in knowledge of arithmetical facts, in understanding arithmetical concepts, or in understanding and comparing the relative magnitude of numbers. Some might show impairments in one of these components but show little or no impairment in others (Dehaene and Cohen, 1997; Delazer et al., 2003; Demeyere, 2010).

- Some patients with Alzheimer's disease and other degenerative brain disorders have also demonstrated selective impairment of arithmetic components. For example, some early stage

Alzheimer's disease patients have shown a range of dissociations between arithmetic facts and procedures and the ability to understand and compare numbers (Kaufmann et al., 2002). It has been suggested that no component is a necessary prerequisite for other components (Dowker, in press-b).

- Neuroimaging studies have also shown that components of arithmetic, and of number representation, can engage different brain areas and networks (e.g., Cappelletti et al., 2010; Castelli et al., 2006; Chochon et al., 1999; see section on Arithmetic Task-Specific Functional Dissociations).

- In typical adults, individual differences in arithmetic performance was observed even in tasks that were expected to result in ceiling effects, such as written and oral counting, transcoding between digits and written and spoken number words (Deloche, 1994).

- Cross-cultural studies have shown that the different components of arithmetic are influenced by age and educational background to different degrees. For instance, Dellatolas et al. (2000) showed that both factors strongly predicted ability in number comparisons, mental calculation, word problem solving, and reading and writing numerals, but had very little influence on counting dots, counting backwards, and estimations. In a similar vein, Carraher et al. (1985) showed that individuals with little or no schooling might perform poorly at formal written arithmetic but extremely well at practical mental arithmetic in the workplace.

- Some specific language features have also been shown to selectively affect certain components of arithmetic. For example, Welsh children studying the same mathematic curriculum as English children outperform their English counterparts in reading and comparing two digit-numbers (Dowker, Bala and Lloyd, 2008). This advantage was attributed to the relatively more transparent counting system in Welsh (which resembles counting in languages such as Chinese and Japanese) as compared to English.

- In studies of children with typical and atypical arithmetical development, numerous studies have highlighted specific deficits in various aspects of arithmetic ability and emphasised that "pure" dyscalculia rarely occurs (e.g. Desoete, 2004; Gifford, 2012; Jordan, 2003; O. Rubinsten and Henik, A., 2009).

Based on the view that arithmetic consists of different components, some of which are interrelated, Catch Up™ Numeracy programme (see Dowker, 2009, pp. 29-30) has been developed and used in schools amongst children with mathematical learning difficulties by targeting components that they underperform in. Overall, evidence suggests that the mathematical performance is influenced by individual differences and is dependent on the task assessed. These are important points to consider when designing both learning and intervention materials. It has been suggested individual variability in arithmetic in both typical and atypically developing populations might be affected by genetic and environmental factors.

Genetic and Environmental Contributions to Arithmetic Variability

Understanding individual differences is also one of the main focuses of genetic studies of learning abilities and disabilities. In terms of maths ability, familial studies on developmental dyscalculia have revealed a high prevalence of this developmental condition amongst siblings (Alarcon, et al., 1997; Shalev et al., 2001), and quantitative genetic studies have suggested concordances (the probability that one twin will be affected if the other is affected) of about 70% for monozygotic (MZ) or identical twins, and 50% for dizygotic (DZ) or fraternal twins (Oliver, 2004). Such twin studies are valuable source of information because considering that twins share many aspects of their environment such as parental upbringing style

and education, and "identical" or monozygotic twins share almost 100% of their genes, most of the differences between them are likely to be due to experiences that affects one but not the other. Meanwhile, "fraternal" or dizygotic twins share only about 50% of their genes and this allows us to study the effects of genetic differences and its interaction with environmental effects. A review of twin studies by Plomin and Kovas (2005) reported that the average phenotypic variance that is attributed to genetics is about 0.63 for mathematics learning abilities and 0.61 for mathematics disabilities. In another study, Kovas et al. (2007) found a genetic correlation of 0.67 between reading and mathematics disability, indicating that these conditions are likely to be influenced by the same genetic factors. Such results might explain the high prevalence of co-morbidities of DD with, for example, dyslexia. A genome-wide association analysis further identified ten genetic polymorphisms that might partially account for variation in individual mathematics achievement (Docherty et al., 2010). These findings suggest that genetics contributes substantially towards explaining differences in both learning difficulties and abilities (Plomin, Kovas and Haworth, 2007).

More recently, a study by Pinel and Dehaene (2013) directly explored the localisation of the cerebral regions underlying this genetic contribution. By comparing the functional correlation in the brain activation in MZ and DZ twins during a subtraction task, they found that there is a strong genetic contribution to the activation of both a superior fronto-parietal set of regions and the left angular gyrus, supporting previous studies that have highlighted the high degree of heritability in aspects of anatomical structures of this area (e.g. Schmitt et al., 2008; Thompson, 2001). They also found that shared environment contributed to the functional lateralisation of the IPS, and that the level of deactivation of the left IPS is positively correlated with an individual's calculation score; those with higher arithmetic score showed less deactivation of the left angular gyrus, consistent with previous findings by Grabner et al. (2007) and Wu et al. (2009). Future longitudinal studies (similar to Kovas et al., 2007) should explore how an individual's cerebral profile might modulate the acquisition of mathematics knowledge and skills throughout education, ideally in children. Such findings will have important implications for the diagnosis, treatment and prevention of mathematical difficulties. For example, identifying genes for dyscalculia and other, less severe, mathematical deficits will contribute towards new diagnostic classifications that are founded upon aetiology rather than symptomatology (Plomin et al., 2007).

Intra-Individual Variability

Strategy use

Performance does not only differ between individuals, but also within the same individual across different contexts. Within the context of strategy use for example, factors such as problem features (e.g. problem size, type of operation), and individual cognitive capacities (e.g., executive functions) have been shown to affect an individual's strategy choice and, hence, performance. Campbell and Xue (2001) reported that retrieval strategy is mostly used in multiplication (98%), followed by addition (88%), subtraction (72%) and division (69%). As for the size of problems, Campbell and Xue (2001) found three main strategy-related resources of problem size effects in adults: (1) lower frequency of retrieval strategy use for large compared to small problems; (2) lower retrieval efficiency for large relative to small problems and (3) lower procedural efficiency for large when compared with small problems (Campbell and Xue, 2001).

Lemaire and Lecacheur (2011) reported that increased efficiency in executive functions contributed significantly to age-related improvements in children's skills in strategy choice. In particular, inhibition processes and cognitive flexibility were associated with strategy selection and age-related differences in strategy choice. In terms of working memory, it has been reported that individuals with higher working memory capacity tend to use retrieval strategies more and procedural strategies less (e.g. Barrouillet and

Lépine, 2005; Noël, 2004). In children with high working memory spans, memory retrieval was faster than their low-span counterparts.

The examples provided above constitute only the "tip of the iceberg" when it comes to intra-individual differences in performance. Other factors such as an individual's competence in various components of arithmetic should also be taken into account (Dowker, 2005).

After discussing the variation in mathematical abilities between different populations and within populations, we will now discuss how intervention is targeted in order to improve cognitive functions, with focus on maths.

Interventions and Cognitive Enhancement

Interventions for Academic Improvement

A number of mathematics intervention programmes have been designed to be used as supplementary mathematics learning material to children in small groups or individually. However, very few of these programmes have been either validated through the use of empirical, peer-reviewed research or informed by neuroscience research in their development. Five mathematics intervention programmes that have demonstrated support from empirical, peer-reviewed research according to (Kroeger, 2012) are:

- *Accelerated Math (AM)*: A computerised mathematical assessment and instructional tool for the purposes of monitoring practice and progress for students in Grade 1-2. This programme does not claim that it was developed based on the neuroscience literature, but it involves elements that are included in the triple-code model of numerical processing (see section on The Triple-Code Model). For instance, lessons include magnitude comparison and estimation tasks, using the quantity system, linking maths facts with their correct answers, which uses the verbal system, and practice on multi-digit computation problems, which requires the visual system. AM also targets changes in declarative memory and working memory. A large body of research by independent research bodies and internal research by the developers has reported statistically significant results from using this programme in a range of populations (e.g. Bolt, 2010; Burns, 2010). It was reported in these studies that students who have achieved significant academic improvements were generally those whose classroom teachers used AM consistently.

- *Corrective Mathematics (CM)*: A remedial programme for children from Grade 3-12 to be used in small- or large-group teaching. Similar to AM, it also has links to the triple-code model, e.g. lessons on place value (quantity system), emphasis on fact retrieval (verbal system), and teaching of strategies to solve multi-digit arithmetic problems (visual system). CM targets improvements in working memory and executive function. So far, the efficacy of this programme has been supported by positive results based on independent research studies using CM with a student who suffered from brain injury (Glang, 1992), with at-risk secondary school students (Sommers, 1991), and as part of peer-tutoring programme with secondary school students (J. L. Parsons, Martella, Martella, and Waldron-Soler, 2004). In sum, these studies have explored the effectiveness of CM in students of different characteristics across various settings and it is difficult to establish a clear causal relationship between this programme and students' performance.

- *Fluency and Automaticity through Systematic Teaching (FAST Math)*: A computerised software for children in 2^{nd}-12^{th} grades designed to facilitate and improve children's access to the mathematics curriculum via training on fact fluency. This research-based programme focuses on several facets of mathematical learning: automaticity, relationship between numerical symbols

and their associated verbal representations, which are consistent with the triple-code-model, representation of knowledge, and working memory. Although one independent research study has reported positive training effects of FAST, it lacks statistical evidence and details concerning the groups trained (Kroeger, 2012).

- *Number Worlds*: An instructional programme for pre-kindergarten to sixth grade to acquire central cognitive understanding of mathematics via training on skills from number sense through to algebra. This interactive programme includes the use of computerised, hands-on and paper-and-pencil activities to teach mathematical concepts. It claims to have consulted neuroscience literature in the development of the programme, although the specific research is not described. The components of this programme are also consistent with the triple-code model; they include understanding the meaning behind quantities (quantity system) and computation proficiency with emphasis on accuracy and efficiency (verbal system). The programme also supports changes in working memory and executive functions by teaching strategy use. Research by the developers showed that NW successfully increases the conceptual understanding of number in children with socioeconomic disadvantage (Griffin, 2007).

- *The Number Race (NR)*: An adaptive software for promoting number sense amongst typically developing kindergarteners, and for preventing and remediating dyscalculia in young children between 4-8 years old (A. J. Wilson et al., 2006). This programme was developed by Wilson and Dehaene, and incorporates elements of the triple-code model: number sense and numerical comparison (quantity system), counting numbers (verbal system) and reading Arabic digits (visual system). NR targets improvements in working memory by adapting the response window and the complexity of response options. The only evident improvement in pre-schoolers who played the NR was in number comparison (Kroeger, 2012) and research on its effectiveness has been conducted by the developers and their collaborators (Räsänen et al., 2009).

Other intervention programmes that incorporate neuroscience research include:

- Siegler and Ramani (2008) designed linear numerical board games based on the concept of the number line to promote the numerical development of low-income children. The game involves moving a token along a horizontal line, for example in the number version with Arabic digits between 1-10, a child will have to move the token on the squares labelled 1-10 based on the number indicated on the spinner. By playing this simple linear board game for four 15-minute sessions within 2 weeks, 4-year-old children showed significantly more linear representation of numbers, comparable to their peers from upper-middle-income backgrounds. The gains were reported to still be evident nine weeks later.

- *Rescue Calcularis*: Kucian et al. (2011) developed a computer game for training the mental number line representation in order to facilitate formation of—and automated access to—spatial representation of numbers. After completing 15 minutes per day of training for 5 weeks, groups of children aged 8-10 years old, either with or without developmental dyscalculia, both showed improved spatial representation of numbers and increase in the number of correctly solved arithmetic problems. The authors also examined the neuroplastic effects of training, using fMRI. Children showed reduced recruitment of areas involved in number processing, namely, frontal areas, bilateral intraparietal sulci, and the left fusiform gyrus, suggesting increased automatisation of cognitive processes critical for mathematical reasoning (Ischebeck et al., 2007; Ischebeck et al., 2006; Pauli et al., 1994). This study also reported an increased activation in bilateral parietal regions including the IPS in a follow-up assessment five weeks later, suggesting that time for consolidation is required post-training to establish number representation.

Although quite a number of intervention programmes have been developed, more research is warranted to establish their efficacy, cost-benefit ratio, and how other factors such as individual differences in initial mathematical competence or cognitive abilities might influence the success of these interventions (see also R. Cohen Kadosh et al., in press). It seems that most of the existing, commercialised interventions are not informed by neuroscience, and the usefulness of neuroscientific knowledge in the education field remains to be explored. It is critical that schools, parents and teachers appreciate the challenges involved in translating neuroscience research to directly influence classroom learning (Goswami, 2006) and seek evidence before investing time, effort and money in marketed interventions.

Rehabilitation of Arithmetic Skills in Patients

Acquired acalculia due to brain lesion or injury compromises an individual's autonomy. However, targeted programmes for rehabilitation are rare (Girelli and Seron, 2001; Lochy, Domahs and Delazer, 2005). The majority of studies on the rehabilitation of simple calculation skills have adopted a drill-based approach, i.e. repetition of problems that are followed by immediate feedback (for discussion, see Girelli and Seron, 2001; Lochy et al., 2005). Conceptual approaches have also been used (Domahs, 2003; Girelli, Bartha and Delazer, 2002). An increased activation in the right angular gyrus on trained compared to untrained problems was observed in a patient with left-hemispheric brain lesion after training on multiplication facts (Zaunmuller et al., 2009). The area of increased activation is on the right, which suggests increasing recruitment of the hemisphere contralateral to both the lesion and similar to typical activation reported for individuals for arithmetic fact retrieval after rehabilitation. However, as this is a single case study, this finding should be interpreted with caution as patients typically differ in their lesion location, aetiology, functional deficits and so forth (Zamarian et al., 2009). Moreover, there are considerable inter-individual differences in the arithmetic performance of healthy adults (e.g. Grabner et al., 2007), including factors such as general intelligence (e.g. Kelly, 2006) and level of education, on the effects of practice on the brain.

Enhancement

Cognitive Training

Neuroimaging studies have shown that experiences can contribute towards anatomical and functional changes in the human brain, even during adulthood (e.g. Zatorre et al., 2012). However, the majority of such studies on brain plasticity are based on sensorimotor research. To our knowledge, only one study has shown changes in brain correlates of children with DD after training on a neuroscience-inspired computer-based maths game (Kucian et al., 2011). They identified changes in brain activation after training that might indicate more automatic mathematical reasoning, and found that further consolidation of acquired knowledge from training takes longer to be expressed at the neural level in DD children (see section on Interventions for Academic Improvement). Some other training programmes that target maths and other cognitive functions such as working memory have also claimed to contribute towards behavioural improvements, but very few are supported by empirical findings (see section on Interventions for Academic Improvement).

As mentioned earlier, academic mathematicians who have undergone extensive and persistent training in mathematical thinking for years were found to have significant differences in their brain anatomical structures (Aydin et al., 2007). It has been shown that they possess higher grey matter densities than non-mathematicians in areas supporting numerical processing, calculation and visuospatial processing. As the period of time spent as a mathematician was significantly correlated with the relative grey matter density increase, this might suggest that long-term, intense practice could result in anatomical changes. However, as mathematicians and non-mathematicians were not compared in other cognitive abilities such as IQ and working memory, this result should be interpreted with caution.

Transcranial Electrical Stimulation

Transcranial electrical stimulation (tES) is a painless, relatively cheap, and increasingly promising tool to be used in combination with cognitive training or learning regimes in healthy populations, especially when the use of other interventions have not been successful (Krause and R. Cohen Kadosh, in press). tES methods involve the application of a weak electrical current on the scalp above the brain region of interest, and are thought to work by modulating the endogenous electrical activity of neuronal assemblies in the targeted area (Nitsche and Paulus, 2000).

It has been shown that one type of tES, transcranial direct current stimulation (tDCS), could selectively improve brain functions, including numerical processing (R. Cohen Kadosh et al., 2010; Iuculano and R. Cohen Kadosh, 2013; Snowball et al., 2013). Depending on the type of stimulation, i.e., anodal or cathodal stimulation, tDCS could enhance or inhibit neuronal functions respectively. Using this method, it has been shown that six days of training on artificial numerical symbols while receiving anodal tDCS to the right parietal lobe and cathodal tDCS to the left parietal lobe resulted in enhanced performance in automatic number processing and number mapping onto space; meanwhile, the reverse polarity resulted in underperformance in both tasks. The enhancement effects remained after six months (R. Cohen Kadosh et al., 2010b). However, this proof-of-concept study was carried out on a relatively low number of subjects (five in each group), and only the group that showed enhancement was examined after 6 months. Another study has shown that simultaneous stimulation of bilateral parietal cortex resulted in improved ability to compare numerosities quickly, while stimulation of the left and inhibition of the right parietal cortex improved performance on subtraction problems within a single session (T. U. Hauser et al., 2013). Together with R. Cohen Kadosh et al. (2010b), the current results support the view that different mathematical abilities are subserved by a non-unitary mechanism.

With respect to arithmetic learning, Snowball et al. (2013) showed that an innovative non-invasive brain stimulation technique, transcranial random noise stimulation (tRNS), applied to bilateral DLPFC during arithmetic training resulted in short- and long- term improvements, at 6 months, in trained and untrained calculation material. Hemodynamic responses measured online by near-infrared spectroscopy (NIRS), an optical brain imaging technique, suggested increased neurovascular coupling efficiency within the left DLPFC, supporting the observed enhanced behavioural performance.

Based on the current findings, tES offers a potential intervention tool that can be modulated to produce specific and long-lasting effects. However, a recent study revealed that stimulation of the parietal cortex while individuals receive training on artificial numerical symbols resulted in faster acquisition of these numerical symbols but impaired automaticity of the associations that have already been acquired. In contrast, stimulation of the DLPFC resulted in impaired learning of new associations, but increased automaticity in the use of acquired associations (Iuculano and R. Cohen Kadosh, 2013). This double dissociation indicates that cognitive enhancement might be associated with mental costs, and calls for greater attention to monitor psychological side effects as well as further initiatives to optimise stimulation and training parameters to avoid such a cost (Logan, 1988).

Synergy for a Future of Better Learning: Cognitive Neuroscience and Mathematics Learning

This section is aimed at summarising the current review and highlighting the most relevant and promising outcomes from the synergy between cognitive neuroscience research and mathematics learning in the classroom. It is important to note that the potential outcomes highlighted below are illustrative, and not exhaustive or prescriptive.

Research in Practice

The rapidly growing literature on mathematical learning from the cognitive neuroscience perspective is at a stage where it could benefit significantly from collaborations between neuroscientists, experimental psychologists, and educators. The collaboration between schools, teachers and neuroscientists would enable an inter-disciplinary approach to view and understand how issues in education and learning can be evaluated and addressed at multiple levels, such as behavioural, cognitive, and physiological. The understanding of how behaviour is an outcome of multiple factors, for example individual differences in cognition and interaction with different environments, can raise the awareness amongst parents and teachers as well as learners that there is no single factor that "causes" a condition, but instead a variety of aspects contribute to a certain outcome (Brown, 1998).

By sharing expertise and skills from different disciplines, it would be possible to assess more rigorously the effectiveness of current practice, identify limitations and opportunities to maximise the practical applications in the classroom, advance research ideas, and bridge the relevant fields for closer collaboration towards improving not only mathematics learning, but human learning as a whole.

Teaching and Assessment

Through further research, additional layers of insight from cognitive neuroscience could potentially contribute towards identifying and designing developmentally appropriate content and assessments within mathematics curriculum. It addition, further understanding of individual differences in the various aspects of mathematics learning could eventually guide the design of mathematics assessments that takes individual differences into account. Accurate and detailed assessments are not only vital for monitoring self-progress and targeting outcomes, but could also be used to identify flexible individual learning tactics. For instance, high performance in certain cognitive domains, for example working memory, might be helpful to improve performance in others, such as arithmetic. It is likely that mathematics learning will be more effective if teaching is informed by individual differences (Dowker, 2005). Developments in learning mediums such as educational games could be an economical and fun way to achieve individualised learning (Howard-Jones et al., 2011).

With further research and collaboration between schools and researchers, future findings might contribute towards classroom planning and identification of teaching and learning methods that might be more effective depending on students' learning profiles and the content to be learned. As reflected in this brief section, although research within the area of cognitive neuroscience seems to promise exciting contributions to mathematics education, there are currently very few implications for mathematics teaching at this stage of research.

Diagnosis and Intervention

Research into the componential skills of mathematics, and how these skills predict children's global learning and performance in mathematics might be useful for (i) predicting outcomes and (ii) the early detection of special needs/attention for intervention. However, there are not many research-based interventions in the field of maths (see section on Interventions for Academic Improvement). As a consequence, little is known about how parameters such as individual differences and age may interact with different training regimes, and how the type of material focused on in the intervention modulates the outcome of training. Different individuals might benefit from bottom-up (e.g. focusing on componential improvements to improve global performance in mathematics) or top-bottom approach (e.g. improving on complex mathematics task while indirectly sharpening basic skills).

The research for reliable biomarkers, e.g. neurochemical concentrations, neural connections, morphology, as well as the design of reliable, sensitive and cost-effective biofeedback technology could be useful in future for diagnosis, and for monitoring response to intervention (e.g. Dahlin et al., 2008). Such research would in turn contribute molecular insights into treatment mechanisms. For example, in the study of McNab et al. (2009), it was found that cognitive training in healthy participants was linked to changes in the density of cortical dopamine D1 receptors using PET scan, and such findings could shed light on the mechanisms accompanying the results of cognitive training of children with ADHD (Klingberg, 2005).

Enhancement

The potential of incorporating adaptive cognitive training software including fun mathematics games into classroom and after school learning for children might help to increase motivation and inject a sense of fun into the process and experience of learning mathematics. This might be particularly useful to those with mathematics anxiety, or mathematics learning difficulties as performance in games might help them to feel that they can perform and improve, to see that the subject that they fear can be fun and relevant in other contexts, and that their performance is within their control.

The use of non-pharmacological form of cognitive enhancement via non-invasive brain stimulation might provide an adjuvant or alternative form of intervention for those with mathematics learning difficulties. In respect to tES, more research is warranted in the future to establish the optimal parameters to achieve desired learning outcomes including stimulation sites, frequency and intensity of stimulation, the type of training material, and how age and individual differences might affect the efficacy of tES. Methods of enhancements, such as tES, that could reduce the cognitive disparity due to gaps in biological (e.g. reduced grey matter) or environmental (e.g. socio-economic) backgrounds would allow more equal opportunities for effective learning.

Challenges and Future Directions

Cognitive neuroscience research on mathematics learning is continually growing and expanding our understanding of mathematics learning. However, consistent with the current state of the emerging field of neuroscience and education, there have been very few applications in the classroom (Bruer, 1997; Howard-Jones, 2013; The Royal Society, 2011; The Wellcome Trust, 2014; Varma, McCandliss and Schwartz, 2008), although some potential contributions to education in general, have been proposed.

Why is this the case? First of all, despite the exciting prospects of applying cognitive neuroscience findings to mathematics learning, or learning in general, few studies have shown ecological validity and direct relevance to the mathematics curriculum. Secondly, there is a lack of collaboration between mathematics educators and cognitive neuroscientists, which also applies to the general field of neuroscience and education, possibly due to a lack of understanding of the goals and roles of each field in such efforts (Hook and Farah, 2013; Willingham, 2009). This can negatively affect participant recruitment, compromising research sample size, and arguably, the generalisability of findings. The first and second points could be a vicious loop, as schools are less likely to collaborate when there is a lack of evidence (The Wellcome Trust, 2014) and in turn, there will be a lack of research if there is little collaboration. Thirdly, the process of translating and integrating cognitive neuroscience and mathematics education share similar challenges of the umbrella field of "neuroscience and education", including disciplinary differences in goals, practices, analyses and expectations of the two fields (see Willingham, 2009).

So, what would need to happen for this to change? We have a few suggestions. Firstly, there need to be more cognitive neuroscience studies with clear, practical implications for the mathematics curriculum without sacrificing basic research at the same time. Funding bodies and governments should encourage and support more integrated research efforts between cognitive neuroscientists and mathematics educators. In

the UK, this step has been recently achieved by the joint effort of the Wellcome Trust and Education Endowment Foundation. Such efforts could begin by encouraging policy makers, representatives of researchers, teachers, and parents to discuss this research in workshops, and gather information via reports and surveys to assess the appetite, areas, and challenges for integrating knowledge and practice of cognitive neuroscience and mathematics education. Greater understanding of the goals and roles of professionals in these fields might foster future collaborations that benefit both fields. Finally, with further collaborations and research, such research developments could be integrated into teacher training. This could be useful as one current survey suggests that more than 90% of teachers think that their understanding of neuroscience influences their practice, teachers tend to learn about interventions from schools and other teachers instead of scientific and academic sources, and that 77% of teachers would like neuroscience to be integrated into their training (The Wellcome Trust, 2014). Similarly, researchers in the field of cognitive neuroscience should also gain some practical experience of how mathematics learning occurs in the classroom to refine the targets of their research ideas for more direct classroom implications. Both cognitive neuroscientists and mathematics teachers should have open conversations through joint workshops and training to foster a more integrative view of mathematics learning and research.

Every burgeoning field has its own strengths and challenges. Constructive collaborations between professionals from different fields are crucial to ensure that the potential of cognitive neuroscience to improve mathematics education can be realised and that the challenges can provide impetus for further improvements in mathematics research and education.

Conclusions

Research in cognitive neuroscience has allowed the possibility of exploring the neural basis of complex and sophisticated cognitive processes such as numerical cognition. Using an expanding range of tools from single-cell recording to brain stimulation, progress is being made in not only localising brain regions involved in specific functions, but also mapping the complexity of networks engaged in mathematical learning. Overall, advances in cognitive neuroscience research is beginning to shed light on the ontogeny of mathematical cognition, how cognition and behavioural performance can be modulated based on the knowledge on neuroplasticity, and how such findings can be used as a model to understand the workings of the brain as a whole. Collaborations between scientists and educators and professionals relevant to the field of mathematics learning promises further advances in the understanding of not only mathematical cognition, but also learning in general, with long-term implications to enrich the mental wealth of mankind.

APPENDEX A: INTRODUCTION TO BASIC BRAIN ANATOMY AND REGIONS INVOLVED IN NUMERICAL COGNITION

Brain Structures

Term	Description
Gyrus (plural, *Gyri*)	A ridge on the cerebral cortex
Sulcus (plural, *Sulci*)	A "furrow", depression or fissure in the cortex

Anatomical Directional Terminology of the Brain

Term	Description
Rostral/ Anterior	Head/ Front end
Caudal/ Posterior	Tail/ Hind end
Dorsal/ Superior	Back/ Top side
Ventral/Inferior	Belly/ Bottom side
Lateral	Away from the midline
Medial	Toward the midline
Proximal	Closer
Distal	Farther away
Contralateral	The opposite hemisphere
Bilateral	Both hemispheres

Figure A.1. Anatomical directional terms of the brain

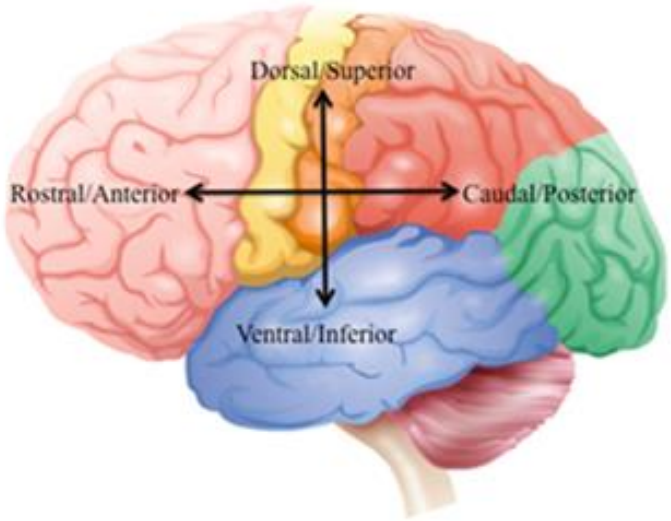
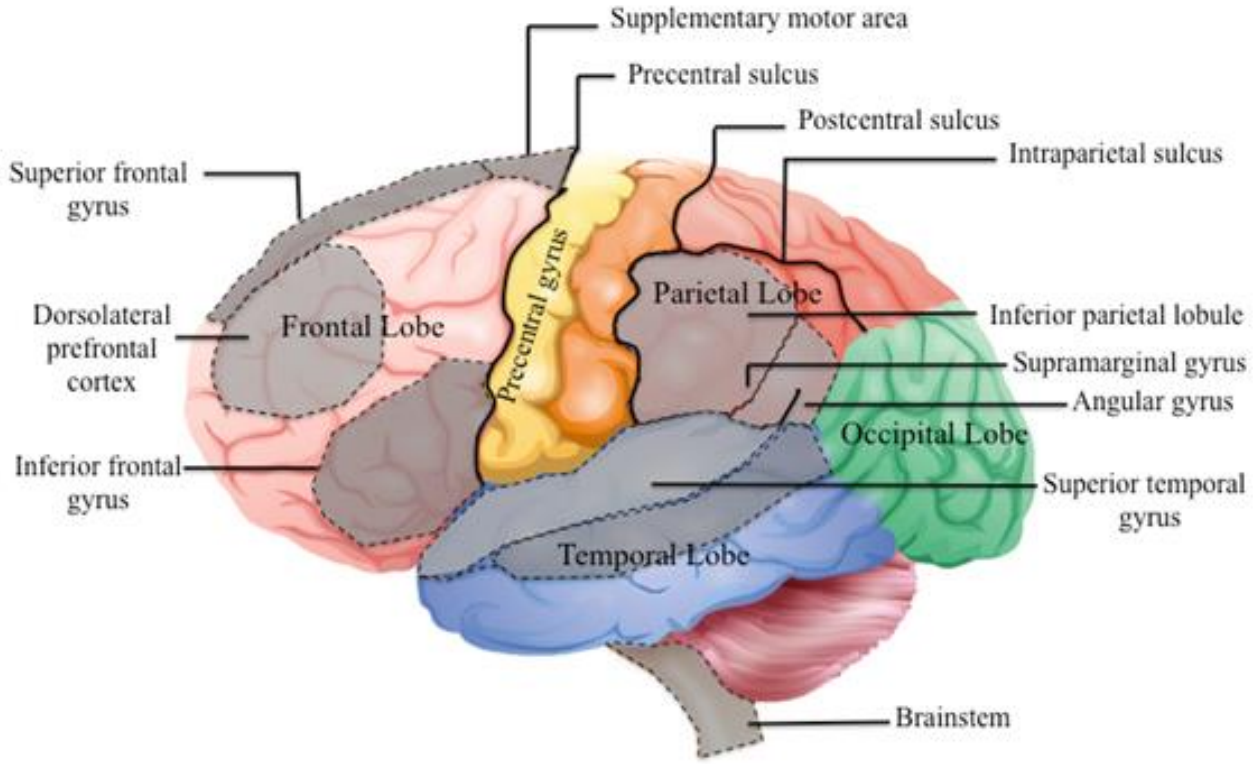


Figure A.2. Brain regions involved in numerical cognition



APPENDIX B: BASIC TECHNIQUES AND PARADIGMS OF NEUROSCIENCE AND PSYCHOLOGY

Important insights into brain function, cognition and behaviour have been derived from the fields of neuroscience and psychology: notably, the traditional case studies of patients with brain lesions (see section on *Acalculia)*. Advances in the field of neuroimaging, in particular, have allowed researchers to study the living brain using non-invasive tools.

We would first like to introduce the different neuroscientific methods that have been used to examine brain response to mathematical processing and learning, and the typical behavioural paradigms that are used in this field of research. The different techniques and behavioural paradigms are presented in Table 1 and Table 2 (respectively), together with a short description.

Table A.1. Neuroscientific Techniques

Technique	Description
Single-cell/unit recording	An invasive method to measure the response of a single neuron using a microelectrode. A microelectrode is placed within or closely to the cell to record the rate of change in voltage (following the current generated by a firing neuron) over time within or outside the cell). This method is used in animals.
Positron Emission Tomography (PET)	An imaging technique that relies on radiation (nuclear magnetic imaging) to generate 3-dimensional coloured images of functional processes within the human body. It can capture chemical and physiological changes related to metabolism instead of just anatomy and structure. It functions by detecting signals emitted indirectly by a radioactive tracer injected into the body.
Magnetic Resonance Spectroscopy (MRS)	This method is used to study changes in energy usage in the brain. It uses signals from protons to determine the relative concentrations of substances that are produced during chemical processes in the brain.
Electroencephalography (EEG)	This is used to record the brain's electrical activity using electrodes on the scalp. One of the derivatives of this technique is a method called event-related potentials (ERPs), the averaged EEG responses that are time-locked to the presentation of a stimulus.
Functional Magnetic Resonance Imaging (fMRI)	A non-invasive procedure that measures brain activity. As brain activity requires oxygen, it is based on the change between oxygen-rich and oxygen-poor blood, and blood flow, which is termed the blood-oxygen-level-dependent (BOLD) contrast.
Diffusion Tensor Imaging (DTI)	A technique used to reveal microscopic details of tissue architecture through mapping the diffusion process of molecules, mainly water in biological tissues.
Near-Infrared Spectroscopy (NIRS)	An optical brain imaging technique used to assess brain activation by transmitting near-infrared light through the scalp and measuring how it passes through the cortex. It registers online changes in biological processes (e.g. blood flow and blood oxygenation) triggered by neural activity.
1. Non-invasive brain stimulation (NIBS) **2. Transcranial Magnetic Stimulation (TMS)** **3. Transcranial Direct Current Stimulation (tDCS)** **4. Transcranial Random Noise Stimulation (tRNS)**	1. This method uses an alternating current to create magnetic field pulses, which transiently induce or suppress activity in particular brain regions with relatively minimal discomfort in order to study brain functions. 2. A form of brain stimulation that involves the delivery of constant, low electric current (e.g., 1-2mA) to the scalp over the brain region of interest via small electrodes (e.g., 25 cm^2) to alter spontaneous cortical activity during behavioural tasks. It can enhance (anodal tDCS) or reduce

5. Transcranial Alternating Current Stimulation (tACS)	(cathodal tDCS) the ease of neuronal firing, in some cases with long-lasting effects. 3. This is a relatively new technique similar to tDCS, but using a random electrical oscillation spectrum rather than a constant current. In contrast to tDCS, this type of stimulation is mainly used to enhance brain activity. 4. This type of stimulation involves the application of alternating electric currents at specific frequencies on the scalp to modulate on-going rhythmic brain activity.

Table A.2. Behavioural Paradigms and Tasks Used to Examine Mathematical Cognition and their Description

Paradigm/Task	Description
Violation of expectation	This is the main method for studying infants' knowledge of their physical world. This paradigm is based on the assumption that infants will show increased attention toward events that violate their physical understanding of the world. This increased attention is measured by the extent of their "eye gaze"; infants tend to look at a particular object for longer if it violates their expectation (e.g. if a ball seems to defy gravity).
Habituation	This is one of the methods typically used in infant studies to study perception or cognitive abilities. Habituation occurs when a stimulus (e.g., image, sound or smell) is repeatedly presented until the infant "gets used to it" and stops responding to the stimulus (e.g., reduced looking behaviour) as a result of familiarisation. When changes are made to the accustomed stimulus, the infant resumes normal looking behaviour (this is called "dishabituation".)
Verification	This task typically requires a subject to verify, i.e., answer "Yes" or "No" to a statement or a sum. The response can be made verbally or manually (usually by button pressing on a keyboard, e.g. "Z" button for "Yes", and "/" button for "No") and is measured in terms of accuracy and time taken to respond ("reaction time").
Number line estimation/bisection	This task is used to investigate an individual's representation of magnitude. Usually, a horizontal line is presented with fixed anchors on either ends such as 0 and 10 or 0 and 100, and subjects are asked to map a specific number, e.g., 39 on this line. The accuracy of response (i.e., deviation from the correct position) is usually measured and the responses can be plotted to determine the subject's internal representation of numbers and magnitude.
Number judgments	Depending on the task instructions, this could involve judging 1) whether one number in a pair is larger or smaller in magnitude than the other, 2) whether a given number is larger or smaller in magnitude than a remembered reference number (e.g., 5), or 3) whether a given number is odd or even. Answers are typically given by button-press (e.g., using designated keys on a keyboard), and reaction times and accuracy are measured. These tasks are usually used to investigate an internal numerical representation.
Number Stroop task/Size congruity	Stroop tasks are used to investigate how one aspect of a stimulus (e.g. its size) can interfere with other aspects (e.g. its meaning). A participant will see various stimuli for which those 2 aspects are either congruent (e.g. physically larger numeral is also larger magnitude), incongruent, or neutral. For example in a number Stroop task, when asked to judge which number is bigger in magnitude, the response to 8 vs. 5 is usually slower than 8 vs. 5 because the *physical* size of the numbers interferes with the processing of their *numerical* size.
Priming	This task is based on the finding that priming, i.e. seeing or hearing a particular stimulus (the "cue"), will make future responses to that stimulus easier and faster. Conversely, responses to stimuli that are incongruent, or very different to the cue (e.g. small versus large numbers), will become slower and more difficult.

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