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Neural indicators of numerical abilities in the infant human brain: A systematic review

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ABSTRACT

Infants are thought to possess an innate specific capacity to process numerical information. In this article, we review the past research that has focused on unveiling the timing and localization of the related brain mechanisms with the purpose of depicting a neurodevelopmental blueprint of this capacity from birth. A systematic search of studies published between 1998 and 2023 was conducted. A total of 21 studies with 732 participants (age rage: 30 weeks of gestation to 6 years) met the study selection criterion. EEG, fMRI and fNIRS studies consistently support the existence of brain responses (mainly in the right parietal, bilateral frontal and occipital cortex) that reflect sensitivity to numerical features even before birth. These enable the infant brain to code numerical information independently of other non-numerical magnitude dimensions. Small (<4) or large (>4) numerosities seem to diverge in dissociable brain responses from the second semester of life, suggesting a neurodevelopmental specialization. Variations in the brain's sensitivity to numerical information across participants and whether they can anticipate the individual's development of future numerical skills remains uncertain, due to the scarcity of longitudinal studies. Understanding how familial and other contextual factors shape these initial biological predispositions and give rise to typical and atypical trajectories requires further investigation.

Introduction

Efficiently dealing with numerical information is crucial in a modern society. Numbers are ubiquitous and required for many daily situations such as comparing the price of two products, calculating a discount, calculating arrival time or taking the correct bus. However, the notion of numbers is not exclusive to the literate adult. Foundational understanding of numbers and basic mathematical concepts can be observed even before formal education, in non-literate societies, in infancy and early childhood (Butterworth et al., 2018). These early abilities serve as the building blocks for more advanced math skills later in life (LeFevre et al., 2010). Identifying them may be crucial for advancing early markers of mathematical learning deficits and for providing valuable information that can guide educational and clinical practices.

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How early can the ability to extract numerical information be attested in children? Some scholars propose the existence of the so-called “number sense”, that is an evolutionarily relevant system that captures numerical properties from the surrounding environment, from birth (Brannon, 2002; Butterworth, 1999; Dehaene, 2011; Dehaene & Brannon, 2011; Feigenson et al., 2013; Mussolin et al., 2012; Wang et al., 2021). Empirical evidence shows, for instance, that newborns can already discriminate small (two vs three) sets of objects (Antell & Keating, 1983) and later on, at 9 months of age, develop additional skills for understanding basic operations such as additions and subtractions (Wynn, 1992; see also Christodoulou et al., 2017 for a *meta*-analysis on infants’ early arithmetic competence).

A clear consensus concerning the existence of the number sense, however, is yet to be reached. Some researchers propose that quantification in humans is initially based on the ability to extract continues magnitudes such as sizes and amounts (Gao et al., 2000; Henik et al., 2017) or non-numerical cues such area or contour length, which correlate with numerosities (Cantrell & Smith, 2013; Clearfield & Mix, 1999). Under this view, the ability to perceive numerosity in isolation would be a purely cultural construct. Young children would sort out the complex relations between magnitudes and the number of items throughout development (Leibovich et al., 2017; Mix et al., 2002; Núñez, 2017). This review, in accordance with the revised literature, will use the term “number sense” to refer to infants’ ability to process numerical information. The reader, however, should be aware that it remains open to debate whether sensitivity to numerical information really indicates a number-specific capacity.

The use of non-invasive brain imaging techniques to study the infant brain (Box 1) has contributed significantly to this debate, through studies exploring the availability of key brain responses linked to numerical abilities in infancy. The functional organization of these brain networks, the properties of the stimuli that trigger numerical encoding, as well as the unfolding of these processes in time is gradually emerging in the literature.

In this work we review the studies that focus on understanding the brain areas that support numerical representations in the first years of life and how these networks gradually change during development, throughout brain maturation. More specifically, in this systematic review we outline (1) which brain areas respond to numerical stimuli in infancy; (2) how the neural response is modulated by the numerical difference between numerosities; (3) whether the functional response is due to number-specific properties and (4) whether number-related brain activation varies across individuals and can anticipate successive mathematical abilities.

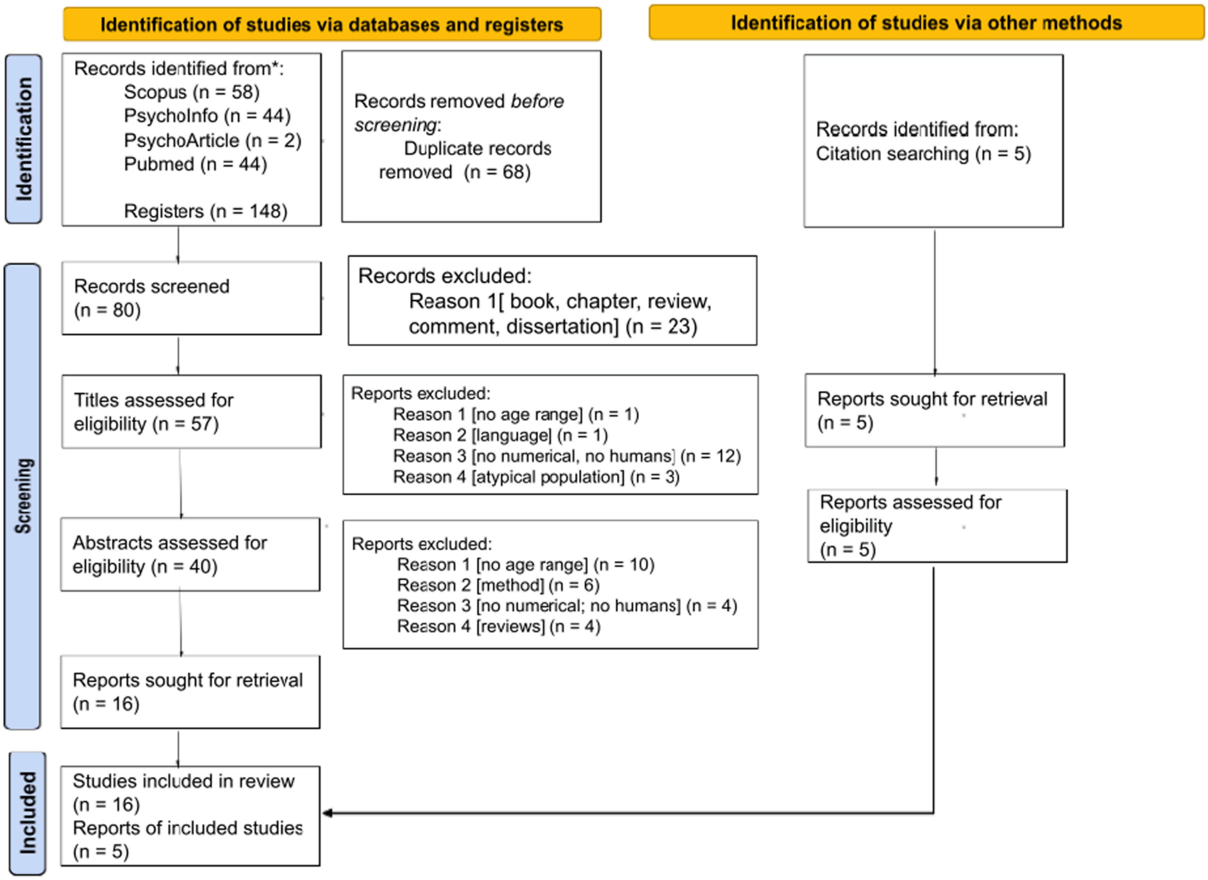


Fig. 1. Prisma Flow chart to summarize the study selection process.

Box 1

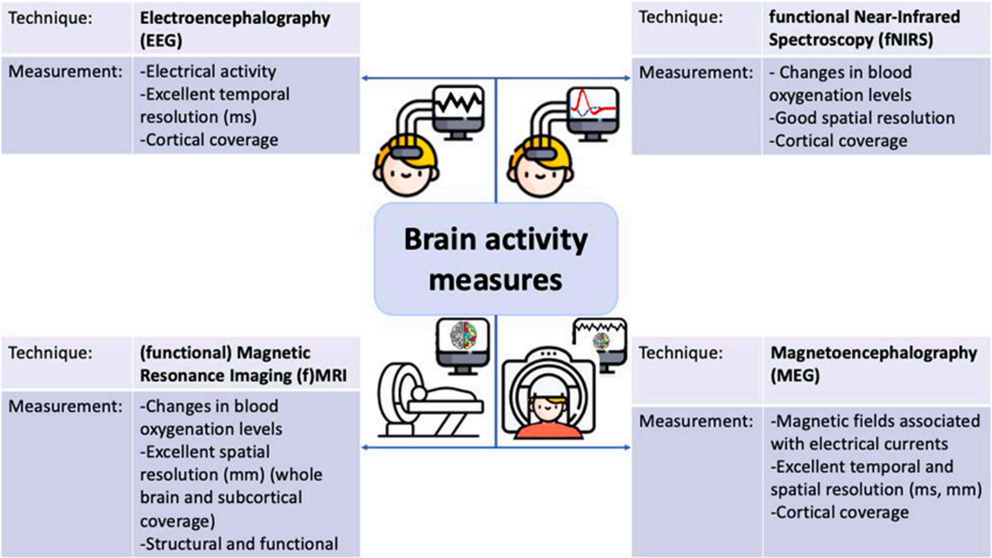
Techniques used to assess brain responses linked to numerical cognition in early childhood

The neural underpinnings of numerical cognition in the developmental population have been investigated during numerical cognitive tasks through several non-invasive brain measures (electroencephalography (EEG), magnetoencephalography (MEG), functional magnetic resonance imaging (fMRI), functional near-infrared spectroscopy (fNIRS)).

EEG: is a valuable technique for measuring the electrical activity associated with cognitive development in infants and children (Bell & Cuevas, 2012; Csibra et al., 2008). Although the spatial resolution is limited, *Event-Related Potentials* (ERPs; see Box 2 - Glossary), which are recorded using EEG, have a millisecond temporal resolution that allows electrical activity to be associated with a specific cognitive process or stimulus (Bell & Cuevas, 2012; Csibra et al., 2008; Kuhl & Rivera-Gaxiola, 2008).

MEG: The magnetic fields associated with electrical currents are measured by MEG, which provides an excellent temporal resolution (millisecond) and better spatial localization of neural sources compared to EEG (Chen et al., 2019; Kuhl & Rivera-Gaxiola, 2008).

Both **fMRI** and **fNIRS** measure changes in blood oxygenation in response to neuronal activity, so their temporal resolution is not in milliseconds but several seconds (Aslin & Mehler, 2005; Kuhl & Rivera-Gaxiola, 2008). Regarding spatial resolution, fMRI is excellent as it assesses deep cortical structural (MRI) and functional aspects (Aslin & Mehler, 2005; Gernsbacher & Kaschak, 2003; Minagawa-Kawai et al., 2008), whereas fNIRS does not evaluate deep cortical activity (Peng & Hou, 2021) but nevertheless provides better spatial resolution than EEG (Aslin & Mehler, 2005; Minagawa-Kawai et al., 2008; Wang et al., 2020). In practice, fMRI is more challenging as it is noisy and requires participants to be still (Chen et al., 2019; Copeland et al., 2021; Gervain et al., 2011, 2023; Hyde, 2021; Kuhl & Rivera-Gaxiola, 2008; Pfeifer et al., 2018), making fNIRS a better measure for developmental populations (Ferrari & Quaresima, 2012; Gervain et al., 2011, 2023), for example, by allowing some degree of movement (Gervain et al., 2011, 2023; Wilcox & Biondi, 2015). All of these measures are appropriate for younger populations as they can be carried out in combination with tasks that do not require any overt behavioral response or verbal instructions.



Technique:	Electroencephalography (EEG)
Measurement:	-Electrical activity -Excellent temporal resolution (ms) -Cortical coverage

Technique:	functional Near-Infrared Spectroscopy (fNIRS)
Measurement:	- Changes in blood oxygenation levels -Good spatial resolution -Cortical coverage

Technique:	(functional) Magnetic Resonance Imaging (f)MRI
Measurement:	-Changes in blood oxygenation levels -Excellent spatial resolution (mm) (whole brain and subcortical coverage) -Structural and functional

Technique:	Magnetoencephalography (MEG)
Measurement:	-Magnetic fields associated with electrical currents -Excellent temporal and spatial resolution (ms, mm) -Cortical coverage

Methods

This systematic review was conducted in accordance with the Preferred Reporting Items for Systematic Review and Meta-Analyses (PRISMA) guidelines (Cohen et al., 2021; Page et al., 2021).

Scopus, PUBMED, APAPsychoinfo and APAPSYCOARTICLE databases were searched until the 30th of May 2023. The keywords use to locate relevant studies were the following: (“numerical cognition” OR “numerosity” OR “number sense” OR “non-symbolic number”) AND (“neural” OR “brain-imaging” OR “electroencephalography” OR “EEG” OR “functional magnetic resonance imaging” OR “fMRI” OR “functional near-infrared spectroscopy” OR “fNIRS” OR “magnetoencephalography” OR “MEG”) AND (“infan*” OR “newborn*” OR “preschool”). Inclusion and exclusion criteria were applied. In addition, the reference lists of the included articles were checked for additional relevant articles.

Exclusion criteria

We excluded studies that (a) did not report results on children younger than 6 years old (age range), (b) provided only behavioral measures (method), (c) did not concern numerical abilities (no numerical), (d) were not carried out in humans (no humans), (e) did not include experimental and quantitative data and subsequent analysis of the results (book chapters, *meta*-analyses, reviews, comments, letters, and theoretical papers), (f) were not written in the English language (language) and (g) did concern an atypical population (atypical population).

Study selection and coding procedure

All identified citations were imported into the bibliographic manager software Zotero 5.0 (Corporation for Digital Scholarship, Vienna, VA, USA) (Fig. 1). First, duplicates were identified and removed. Secondly, we excluded reviews, chapters, commentaries and dissertations. Titles and abstracts were screened and assessed for eligibility (age, language, numerical topic, human subjects, typical population) (A.P. and E.V.).

The full texts of the eligible records were then obtained and screened for eligibility according to the exclusion criteria. Any doubts or conflicts were resolved by discussion between the three reviewers (S.B.V, A.P., and E.V.), to reach a consensus.

Two independent reviewers (A.P. and E.V.) systematically coded the relevant information of each study. The first author, year of publication, where it was conducted, participants' age, sample size, study design, paradigm, procedure, stimuli, neural measure, neural analysis and main results were extracted from each included study. Any discrepancies in the extracted data were resolved by a third reviewer (S.B.V.).

Included studies details

Descriptive information of the included studies (n = 21) are reported in Table 1. Studies have been published between 1998 and 2023 (mostly from 2006 to 2023). Most studies were conducted in the United States (n = 13) and other studies in France (n = 3), Israel (n = 3), Italy (n = 1) and Germany (n = 1). Data was available from a total number of 732 participants and the age range was from 30 weeks of gestation to 6 years. Attrition rate was on average 41 % and varied from 6 to 77 %. Analyzed sample size was N = 34 on average; range: 8–115 participants. All studies used a cross-sectional design except for two middle-term longitudinal studies (1.5 to 2 months from T1 to T2) where participants returned for a behavioral assessment at T2. The most commonly used paradigm was the visual *habituation task* (see Box 2 - Glossary) (n = 4). There were also numerical and magnitude comparison tasks (n = 3), passive viewing tasks (n = 3) and other tasks such as Wynn's arithmetical *violation of expectation task* (n = 2), number-alternation paradigm (n = 2), *auditory oddball* (n = 1), cueing (n = 1), Posner cueing paradigm (n = 1), Picture/Number Word task (n = 1), event-related adaptation paradigm (n = 1), numerical Stroop task (n = 1) and steady-state visual-presentation paradigm (n = 1). Brain activity was measured using EEG (n = 15), fMRI (n = 3), fNIRS (n = 2) and MEG (n = 1). In addition, Table 1 includes descriptive information of the numerical stimuli: the numerical quantities (numbers), how they were presented (type of stimuli), whether the non-symbolic stimuli were controlled for non-numerical variables (n = 16 out 19), and which variables were taken into consideration, if they included small or large numerosities (large numerosities n = 8; small numerosities n = 3; both n = 10) and ratio (n = 14).

Results and discussion

Brain areas and neural mechanisms supporting numerical representations in early infancy

Over the past decades, it has become clear that basic numerical competence is rooted in biological primitives that can be explored in very young infants. Early in life, children display behaviors which evidence their ability to detect changes in numerical information. This ability is observed behaviorally when both *small* (i.e. < 4 items; e.g., Antell & Keating, 1983; Benavides-Varela & Reoyo-Serrano, 2021; Jordan & Brannon, 2006; Starkey et al., 1983) *and large* (i.e. > 4 items; e.g., Coubart et al., 2014; Izard et al., 2009) *numerosity stimulus sets* (see Box 2 - Glossary) are presented, and independently of the input modality used e.g., visual or auditory (see review in Mix et al., 2002).

Neuroimaging and electrophysiological studies in infants and preschool children have not only contributed additional evidence showing that humans are equipped with the ability to hold basic numerical representations early in life but also provide insights into commonalities and differences between the primitive and the more mature numerical processing mechanisms. This enables a more complete developmental perspective of how mathematical cognition emerges and a better understanding of the role that both brain maturation and enculturation plays on it.

Electrophysiological studies

The primitive competence enabling basic numerical representations does not depend on language and education. However, later in development, the learning of symbolic numerical representations such as Arabic numbers, number words, etc. facilitates more precise and sophisticated mental tools for numerical understanding (Carey, 2009; Dehaene, 1997; Lipton & Spelke, 2005; Siegler & Opfer, 2003).

In the late 90′s, Temple and Posner (1998) recorded scalp electrical activity in both 5-year-olds and adults during a *number comparison task*. This study explored, for the first time, a possible continuity with respect to the neural mechanisms involved in the processing of non-symbolic and symbolic numerical representations across development. ERPs recorded in the inferior parietal cortex in both groups were highly similar in terms of both scalp localization and components of the waveform. This suggested notation-independency (symbolic and non-symbolic) of numerical representations at the neural level and also a clear interconnection of the underlying mechanisms across development (Temple & Posner, 1998). This pioneer report, however, did not clearly explain whether and how the non-numerical parameters such as size, density, and occupied area were controlled (see section 3.3 for additional details on number-specific responses). Moreover, the group of participants in this initial study was rather limited.

More recently, systematic controls for non-numerical features of the stimuli were implemented in two additional ERPs studies with a larger number of participants. Numerical changes were consistently found to have an effect over bilateral parieto-occipital electrodes in children starting at 3 years of age (Pinhas et al., 2023; 250 ms post stimulus onset). The study by Park (2018) further revealed a "visual sense of number", namely a selective neural sensitivity to numerical magnitude. This effect was explored by analyzing electrodes that were maximally tagged by the flickering of the dot arrays. The spectral magnitude was reported over right occipital

Table 1

Descriptive information of included studies: author and year of publication, where it was conducted, participants' age (mean and range), reported sample size, method (study design and paradigm) and neural technique. Studies have been listed in alphabetical order. The sample sizes match with what has been reported in the studies. [d = days; w = weeks; mos = months; y = years; r = range; M=mean; SD=standard deviation] [; = divide small and large numerosities] [NA=not applicable].

Study	Location	M_{age}	Age range	**Shared statistical approaches**Sample: Analyzed/(initial N); a priori calculated (YES, NO) ; % Attrition rate	Technique	Neural Measure	Numerical stimuli
Ben-Shalom et al., 2013	Israel	5.5y	5 – 6y	17/(not reported); No; Not reported	Study design: Cross-sectional Paradigm: Numerical Stroop task	EEG (128 electrodes)	Numbers: 1, 2, 3, 4; 6, 7, 8, Type of stimuli: Arabic digits Controlled for non-numerical variables: NA Numerosity: small and large Ratio: far (1– 6, 2–7, 3–8, 4–9), close (1–2, 3–4, 6–7, 8–9)
Berger et al., 2006	Israel	7.2mos	6 – 9mos	15/(57); No; 74 %	Study design: Cross-sectional Paradigm: Wynn's arithmetical violation of expectation (1992)	EEG (128 electrodes)	Numbers: 1, 2 Type of stimuli: puppets Controlled for non-numerical variables: No Numerosity: small
Berger, 2011	Israel	7.2 *m*	6 – 9mos	13/(15 from Berger et al., 2006); No; 77 % (sample from Berger et al, 2006)	Study design: Cross-sectional Paradigm: Wynn's arithmetical violation of expectation (1992)	EEG (128 electrodes)	Numbers: 1, 2 Type of stimuli: puppets Controlled for non-numerical variables: No Numerosity: small
Bettoni et al., 2021	Italy	285d (SE=2.70)	269 – 306d	19/(42); Yes; 55 %	Study design: Cross-sectional Paradigm: Posner cueing paradigm	EEG (128 electrodes)	Numbers: 2; 9 Controlled for non-numerical variables: cumulative area, total contour length, virtual square subtended by items Type of stimuli: lines Numerosity: small and large
Cantlon et al., 2006	USA	4.75y	4.25 – 4.95y	8/(17); No; 53 %	Study design: Cross-sectional Paradigm: Event-related Adaptation paradigm	fMRI (4T)	Numbers: 8, 16, 32, 64 Controlled for non-numerical variables: density, cumulative surface area, and element size Type of stimuli: dots Numerosity: large Ratio: 2:1; 1:2
Decarli et al., 2022	France	3mos 28d	3mos – 4mos 4d	19/(33); No; 42 %	Study design: Cross-sectional Paradigm: Cueing paradigm	EEG (128 electrodes)	Numbers: 4; 12 Controlled for non-numerical variables: 50 % individual size, 50 % total surface area Type of stimuli: shapes Numerosity: small and large
Edwards et al., 2016	USA	6.64mos (SD=0.62)	NA	13/(30); No; 57 %	Study design: Cross-sectional Paradigm: Number-alternation paradigm	fNIRS (24 channels)	Numbers: 8, 16 Controlled for non-numerical variables: 50 % individual dot size, 50 % density/total area Type of stimuli: dots

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Table 1 (*continued*)

Study	Location	M$_{age}$	Age range	**Shared statistical approaches**Sample: Analyzed/ (initial N); a priori calculated (YES, NO) ; % Attrition rate	Technique	Neural Measure	Numerical stimuli
							Numerosity: large Ratio: 1:1, 1:2
Gennari et al., 2023	France	13w 2d	12 – 14w	26/(49); No; 47 %	Study design: Cross-sectional Paradigm: Passive viewing (visual) and listening (auditory)	EEG (256 electrodes)	Numbers: 4; 12 Controlled for non-numerical variables: visual stimuli: 50 % total luminance and total occupied area; 50 % object surface size, average area; auditory stimuli: rate and duration Type of stimuli: tones or objects Numerosity: small and large Ratio: 1:3
Hyde & Spelke, 2011	USA	NA	6 – 7.5mos	32/(93); No; 66 %	Study design: Cross-sectional Paradigm: Number-alternation paradigm	EEG (128 electrodes)	Numbers: 1, 2, 3; 8, 16, 32 Controlled for non-numerical variables: 50 % item size and inter-item spacing, 50 % total occupied area and total luminance Type of stimuli: dots Numerosity: small and large Ratio: 1:1; 1:2; 1:3; 1:4; 2:3; 1:4
Hyde et al., 2010	USA	*NA*	5.5 – 6.5mos	36/(74); No; 51 %	Study design: Cross-sectional Paradigm: Visual habituation paradigm	fNIRS (4 channels)	Numbers: 8, 16, 32 Controlled for non-numerical variables: 50 % individual item size and inter-item spacing; 50 % total occupied area and total luminance Type of stimuli: shapes Numerosity: large Ratio: 1:2; 2:1
Hyde et al., 2017	USA	3y 10mos 22d (*SD*=52d)	3y 7mos 18d – 4y 3mos 16d	94/(100); Yes; 6 %	Study design: Cross-sectional Paradigm: Passive viewing paradigm	EEG (128 electrodes)	Numbers: 1, 2, 3, 4; 8, 16, 32 Controlled for non-numerical variables: 50 % individual item size, inter-item spacing; 50 % total occupied area, total luminance Type of stimuli: dots Numerosity: small and large Ratio: 1:1; 1:2; 1:4
Izard et al., 2008	France	103d	92 – 124d	36/(133); No; 73 %	Study design: Cross-sectional Paradigm: Visual habituation paradigm	EEG (65 electrodes)	Numbers: 2, 3, 4; 8, 12 Controlled for non-numerical variables: position of the objects, surface size, average area, total luminance, total occupied area Type of stimuli: objects Numerosity: small and large Ratio: 1:3; 1:2; 2:3

(*continued on next page*)

Table 1 (*continued*)

Study	Location	M_{age}	Age range	**Shared statistical approaches**Sample: Analyzed/(initial N); a priori calculated (YES, NO) ; % Attrition rate	Technique	Neural Measure	Numerical stimuli
Kersey & Cantlon, 2017	USA	5.45y	3.6 – 6.99y	35/(43); No; 19 %	Study design: Cross-sectional Paradigm: Visual habituationparadigm	fMRI (3 T)	Numbers: 8, 12, 16, 24, 32 Controlled for non-numerical variables: dot area, number of dots, color, cumulative area Type of stimuli: dots Numerosity: large Ratio: 1:2; 2:3
Libertus et al., 2009	USA	7mos 3d	6mos 10d – 7mos 27d	50/(74); No; 32 %	Study design: Cross-sectional Paradigm: Visual familiarization task	EEG (19 electrodes)	Numbers: 8, 12, 16, 18, 24, 36 Controlled for non-numerical variables: 100 % average cumulative surface area; moreover 50 % of trials controlled for individual element size, 50 % of trials cumulative perimeter Type of stimuli: dots Numerosity: large Ratio: 1:1; 1:2; 1:3
Libertus et al., 2011	USA	7mos 5d (*SD*=17)	*NA*	28/(35), Longitudinal n = 19; No; 20 %	Study design: Middle-term longitudinal (2 mos later) Paradigm: Steady-state visual-presentation paradigm	EEG (19 electrodes)	Numbers: 6, 8, 9, 12, 18, 24 Controlled for non-numerical variables: 25 % cumulative surface area, 25 % cumulative perimeter, 25 % individual element size, 25 % random Type of stimuli: dots Numerosity: large Ratio: 1:2; 1:3; 2:3
Park, 2018	USA	NA	3 – 11y	47(only 6 children $3 \leq$ age < 5)/(52); No; 10 %	Study design: Middle-term longitudinal ($M_{days} = 48$ days later) Cross-sectional Paradigm: Passive viewing paradigm	EEG (64 electrodes)	Numbers: 8, 11, 16, 23, 32 Controlled for non-numerical variables: individual area, total area, field area, and sparsity (logarithmic scaling construction of two orthogonal dimensions to numerosity: size and spacing) Type of stimuli: dots Numerosity: large
Park et al., 2014	USA	5.55y	4.82 – 6.59	21/(41); No; 49 %	Study design: Cross-sectional Paradigm: Magnitude comparison task	fMRI (3T)	Numbers: symbolic task (1, 2, 3, 4; 5, 6, 7, 8, 9); non-symbolic (4——18) Controlled for non-numerical variables: 50 % average dot size, 50 % total surface area Type of stimuli: Arabic digits and dots Numerosity: small and large Ratio: dots: 1:3; 2:3; digits: far (1–5, 2–7, 3–7, 4–9, 5–9, 2–8), close (1–3, 2–4, 3–5, 5–7, 6–8, 7–9)
Pinhas et al., 2014	USA	3.98y	3.11 – 5.57y	115/(150); No; 23 %	Study design: Cross-sectional Paradigm: Picture/Number Word task	EEG (32 electrodes)	Numbers: 1, 2, 3; 6 Controlled for non-numerical variables: NA Type of stimuli: objects and spoken words

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Table 1 (*continued*)

Study	Location	M_{age}	Age range	**Shared statistical approaches**Sample: Analyzed/(initial N); a priori calculated (YES, NO); % Attrition rate	Technique	Neural Measure	Numerical stimuli
							Numerosity: small and large Ratio: 1:2; 1:3; 1:6; 2:3
Pinhas et al., 2023	USA	5.07y	4.4 – 5.5	56/(75); No; 25 %	Study design: Cross-sectional Paradigm: Numerical comparison task	EEG (32 electrodes)	Numbers: 6, 8, 9, 12, 16, 18, 21, 24, 32, 48 Controlled for non-numerical variables: cumulative surface area, dot diameter Type of stimuli: dots Numerosity: large Ratio: 1:2; 3:4
Schleger et al., 2014	Germany	Fetuses: 34.9w (*SD*=2.8w) Neonates:37.3d (*SD*=15.5d)	Fetuses: 30 – 39w Neonates: 14 – 67d	23/(30) fetuses, 16 (30) neonates; No; fetuses: 23 %, neonates: 47 %	Study design: Cross-sectional Paradigm: Auditory Oddball paradigm	MEG (156 magnetic sensors)	Numbers: 2, 4 Controlled for non-numerical variables: frequency, intensity, duration Type of stimuli: tones Numerosity: small
Temple & Posner, 1998	USA	5y 5.4mos	*NA*	13/(16); No; 19 %	Study design: Cross-sectional Paradigm: Numerical comparison task	EEG (128 electrodes)	Numbers: 1, 4; 6, 9 Controlled for non-numerical variables: No Type of stimuli: Digits and dots Numerosity: small and large

electrodes and increased across ages in children from 3 to 11 years old. Notably, no neural sensitivity to other non-numerical magnitudes was found across ages. This finding suggests that numerosity might be coded from the visual stream before actually involving the parietal cortex (see Fornaciai et al., 2017; Park et al., 2016 for converging evidence in adults). However, the study reported comprehensive data of 6 participants under the age of 5 years and 41 school age children between 5 and 11 years. This suggests that the findings gave stronger weight to older participants and left it unclear whether the same neural substrates of the visual sense of number can be observed in younger children and infants.

Other studies with younger participants – who have received little exposure to the external world – provided additional insights regarding the emergence of this brain network. Izard et al. (2008) recruited infants as young as 3 months of age for an event-related potential (ERP) study. Although ERPs have low spatial resolution, they can provide coarse information about brain localization. Indeed, using a source localization algorithm and implementing several stimuli and statistical controls, the authors revealed a brain response to numerical changes originating at around 800 ms over right parieto-frontal regions of the dorsal pathway, including the right inferior parietal and right inferior frontal region. Nevertheless, the ratio of change was not included as a factor in this study, this left unresolved the question of whether both large and small numerosities were processed using the same representational system (see section 3.2).

Subsequent investigations provided converging evidence that the right fronto-parietal cortex may constitute the neural substrate of infants' initial numerical competence. Studies with slightly older infants confirmed the results of Izard et al. (2008) namely that electrodes located in occipito-parietal (Hyde & Spelke, 2011) and frontal areas (Libertus et al., 2009) were sensitive to habituation and numerical change detection. Noticeably, however, the brain responses in 6 to 7-months-old infants occurred overall earlier (400 ms to 500 ms post-stimulus) compared to those observed in the younger 3-month-olds, possibly due to maturational factors leading to faster and more efficient communication between neurons. In addition, dissociable neural signatures for both large and small numerosities were reported in the 6-month-olds. Specifically, while small numbers evoked a response at around 400 ms (*P400*; see Box 2 - Glossary) over occipital-temporal sites, large numbers evoked a later response at around 500 ms (*P500*) over posterior parietal sites (Hyde & Spelke, 2011). Although the actual time windows and electrode sites of interest were chosen by visual inspection in this study, the overall pattern of results seems to fit with adult studies and subsequent investigations in children using data driven approaches and with considerably larger sample sizes. Indeed, two separate neural signatures associated with numerosity changes in small (1 to 3) and large (4+) sets were also found in 3- to 4-year-old children (Hyde et al., 2017). As in infants, responses for small numerosities emerged earlier (N1) than responses to large numerosities (P2p). However, in children these ERPs were observed about 100 ms earlier than in infants, but 200 ms later than adults (Hyde & Spelke, 2009). At any rate, the ERP components persisting through adulthood (N1 and P2p; Hyde & Spelke, 2009), suggest developmental continuity of neural signatures in parietal regions of the brain (Hyde & Spelke, 2011). Taken together, Izard's and Hyde's studies show a relevant developmental phenomenon that will be further analyzed in section 3.3. For the time being we note that, while common brain response is observed to both (small and large) numerosities at 3 months of age, two different electrophysiological responses were identified starting at 6 months of age.

Neural measures not only reveal the presence and timing of brain responses to number-deviant stimuli, but can be applied for other purposes, including understanding infants'' reactions to correct or incorrect arithmetic operations. In the original behavioral violation-of-expectation paradigm assessing 5-month-olds infants' early arithmetic abilities, Wynn (1992) interpreted increased looking time at the impossible operation (e.g., $1 + 1 = 1$) as a preference for it, thus showing their ability to perform simple addition and subtraction of small numerosities. However, Wynn's (1992) conclusions were solely made from looking-time measures. To support the correctness of this interpretation, Berger et al. (2006) combined Wynn's (1992) violation-of-expectation paradigm with EEG recording. The authors showed that increased looking time was associated with a neural response in 6- to 9-month-old infants. ERPs differed between the two solutions: when incorrect solutions were presented (e.g., $1 + 1 = 1$), ERPs over midline frontal and central scalp electrodes showed an increased negative-polarity amplitude (between 330 and 530 ms) compared to correct solutions (e.g., $1 + 1 = 2$) and power in the *theta and alpha frequency bands* (see Box 2 - Glossary) was greater over fronto-central scalp sites. However, this error-detection neural mechanism probably indexed a general process of violation detection (reflected in the infants' behavioral response to such implausible events), rather than arithmetic specific reactions. In a subsequent analysis of the same dataset, Berger (2011) showed that the infant's frontal response to incorrect solutions was preceded by right parietal activity where the amplitude between the processing of two quantities (one and two) differed. This was taken as an indication that at 6 months of age infants' brains differentiates small quantities over the right parietal area initially, then this response feeds forward to a frontal error detection mechanism associated with arithmetic violations (Berger, 2011; Tzur et al., 2010). Generally speaking, this study is an example of how neural measures complement behavioral hypotheses. Nevertheless, because real objects i.e. puppets were used, no rigorous controls over the non-numerical properties of the stimuli were implemented. The studies of Berger (2011) also included only a small sample of participants. Thus, these results should be viewed cautiously until subsequent studies can confirm and extend them.

The EEG studies reviewed above show that the timing of the responses to numerical information changes with age and may occur a few milliseconds apart depending on the numerical range of the processed stimuli. EEG studies also reveal number-specific brain responses in electrodes located in occipito-parieto-frontal sites of the scalp (Fig. 2B). Importantly, however, ERPs lack spatial resolution and may not be particularly accurate in identifying the neural locus and neural circuits underlying numerical processing. Results obtained with other techniques, such as fMRI and fNIRS, which will be discussed below, have been informative in this respect.

fMRI and fNIRS studies

The study by Cantlon et al. (2006) was the first to compare the neural areas responsible for processing large non-symbolic numerosity in 4-year-old children and adults using fMRI. With a habituation paradigm, this study revealed a significant activity evoked by non-symbolic numerical changes in the right IPS and right superior parietal lobule (SPL) in both age groups, but with greater responses in the adult group. In addition, in accordance with previous studies (Dehaene et al., 1993; see Sokolowski et al., 2017 for review), adults showed a significant bilateral IPS activity. By contrast, children had decreased activity in the left IPS and a more bilateral activity in the SPL region. Therefore, this study suggests that in preschool children the involvement of the IPS is lateralized to the right hemisphere, whereas SPL regions are more bilateral compared to adults. Of note, as the first of its kind, this study used an adult spatially normalized brain template also for assessing children, which might have produced slight shifts of relevant loci. Moreover, as in many other studies in young children, there was a high attrition rate, with more than 45 % of the participants excluded due to movement artifacts in the scanner. This implies a noticeably limited final sample size (N=8) for a fMRI study. Still, the results of this groundbreaking study are in accordance with the results of the EEG studies reported in the previous section, and with the

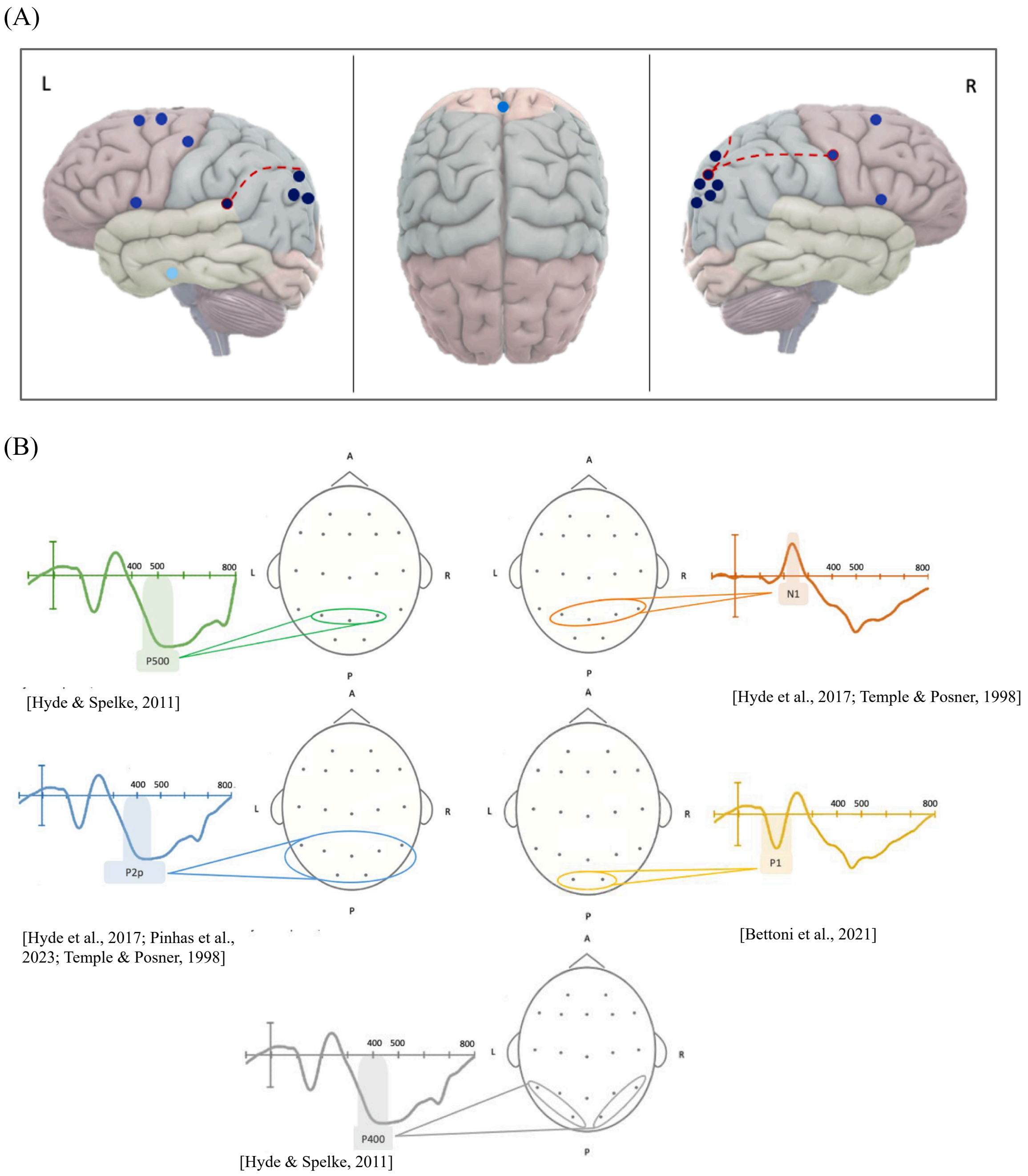

Fig. 2. Neural localization of numerical abilities in infancy and preschool. In the first figure (A) each dot indicates a single study that localized a region (labeled by color) for numerical abilities using fMRI and NIRS. The dashed line indicates areas where effective connectivity was found. In the second figure (B), we refer to the localization and timing of known evoked potentials using EEG. The localization of scalp electrodes does not imply that the underlying areas are the ones necessarily involved (source localization was carried out only in Izard et al., 2008 EEG study).

conclusions of a recent review on the lateralization of math functions throughout development (Salillas et al., 2023).

Indeed, these issues were overcome in subsequent studies of the same group, which confirmed the trend observed in the first study. Developmental continuity of numerosity representations in the right IPS was also demonstrated by Kersey and Cantlon (2017) with thirty-five 3 to 6-year-olds. By combining fMRI with a habituation paradigm, they showed that this region is neurally tuned to numerosity at an individual level. In contrast to adults who showed *neural tuning* (see Box 2 - Glossary) curves to numerosity bilaterally in the IPS (Piazza et al., 2004), children's curves were sharper in the right IPS compared to the left. These findings confirm that numerical representations follow different trajectories in the right and left hemispheres across development (Kersey & Cantlon, 2017).

Using fMRI for testing infants is challenging as participants have to remain still and the machine is noisy. By contrast, fNIRS is more child-friendly and less sensitive to motion artifacts (Bahnmueller et al., 2014), thus facilitating the testing in the young population (see Box 1). fNIRS studies have also revealed increased oxygenated hemoglobin in the right IPS when 6-month-old infants were presented with non-symbolic numerical changes during habituation paradigms (Edwards et al., 2016; Hyde et al., 2010). This extends and confirms previous EEG findings on infants (Berger, 2011; Izard et al., 2008) and fMRI results on preschoolers (Cantlon et al., 2006; Kersey & Cantlon, 2017).

Symbol to number mappings

Evaluating the knowledge of Arabic digits may be relevant when investigating the development of numerical cognition in 3- to 6-year-old children. Starting in the third or fourth year of life, children begin to learn words for numbers (Dehaene-Lambertz & Spelke, 2015) and by the age of four or five, most children in industrialized countries have mastered the mechanics of counting and the exact meanings of many number words (Carey, 2009; Davidson et al., 2012; Dehaene-Lambertz & Spelke, 2015; Lipton & Spelke, 2005). Thus, investigating the neural basis of symbolic number processing in children who are actively establishing symbol-to-number mapping provides a unique way to understand important developmental stepping stones.

Pinhas et al. (2014) investigated the mechanisms of learning the first number words by assessing 3–5-year-old children in a passive picture-word task during EEG recording. Participants were first divided into three number-knower level groups according to the number of words they knew during a behavioral task: 1–2 knowers, 3–5 knowers and cardinal principle knowers (CP-knowers who comprehended the cardinal meaning of number words above 5; Sarnecka & Carey, 2008). Visually presented pictures of sets of objects (non-symbolic) were paired with incongruent or congruent auditory numerical words (symbolic). The results revealed an early centroparietal ERP (Ninc; 200 ms), differentiating congruent and incongruent trials in 3–5 knowers and in CP-knowers. The results on 3–5 knowers are particularly intriguing, as they suggest that number words are being mapped onto numerical representations before children have their ability to master the cardinality principle, i.e. the meaning of the number words within their count list. However, differences between sub-set knowers (1–2-knowers vs 3–5 knowers) were not expected or hypothesized *a priori*. Thus, the separate analysis on the EEG data for these groups was possibly based on data-driven observations. The reasons behind the observed differences remain unclear as well as whether the same findings can be generalized to other datasets.

In parallel, Park et al. (2014) investigated the connectivity of neural regions underpinning number processing in 4- to 6-year-old children using fMRI. The study implemented a number comparison task with both numerical (symbolic and non-symbolic) and non-numerical magnitudes (lines). In agreement with previous studies, Park et al. (2014) identified a core area for number processing, namely the right parietal region, which was specifically responding to the numerical magnitudes in 4- to 6-year-old children. More sophisticated analyses revealed effective connections between this region, the left supramarginal gyrus (left SMG) and the right precentral gyrus (right PreC), which are crucially involved in symbolic numerical processing (e.g., the PreC: Kaufmann et al., 2006; SMG: Roux et al., 2008). Moreover, the degree of the effective connectivity to the left SMG was correlated with age. Because the SMG is implicated in phonological storage (Henson et al., 2000; Paulesu et al., 1993), its connections to the right parietal cortex were interpreted as an indicator that children progressively solidify the mapping between the newly acquired numerical symbols and their underlying magnitudes. Other brain regions, such as the left angular gyrus and the prefrontal regions, were also expected to show progressive functional connections with the right parietal cortex as they are usually interlinked in the adult brain. However, no such connections were observed. Thus, understanding how these regions and also the homologous left parietal cortex become more associated with the right parietal cortex throughout development is an important avenue for future research.

In summary, neuroimaging and electrophysiological evidence in infants and preschool children provides direct evidence of specific brain processes underpinning early numerical capacities (Fig. 2; Table 2). Infants from the first months of life are endowed with a neural substrate for numerical processing that appears to be right lateralized specially in the posterior parietal cortex (Edwards et al., 2016; Hyde et al., 2010; Izard et al., 2008). These studies extend adult and older children's data by providing evidence of the continuity of cerebral number specialization in the parietal cortex in infants, arising before sophisticated estimation and symbolic numerical abilities (Cantlon et al., 2006; Edwards et al., 2016; Hyde et al., 2010; Kersey & Cantlon, 2017; Park et al., 2014). This contrasts with the more balanced, bilateral IPS activation pattern and with the involvement of more extended networks (e.g., the medial temporal regions, Kutter et al., 2023) observed when healthy older children or adults, and patients engage in numerical tasks of varying complexity (e.g., Ansari & Dhital, 2006; Arcara et al., 2021; Benavides-Varela et al., 2016; Cantlon et al., 2006; Dehaene et al., 2003; Emerson & Cantlon, 2015; Piazza et al., 2004; Rivera et al., 2005).

Importantly, these set of studies also show that besides the right parietal cortex, occipital (Hyde & Spelke, 2011; Park, 2018; Pinhas et al., 2023) and frontal areas (Cantlon et al., 2006; Izard et al., 2008; Libertus et al., 2009; Park et al., 2014) seem to be recruited when processing numerical information early in life. Understanding the conditions or developmental stepping-stones that favor the involvement of each of these regions (see Table 2) and the interactions between them might be an important direction in future studies.

Table 2
Numerical function for each area.

Area	Functions revealed in infancy
Parietal lobe	- Small and large numerical change detection [Cantlon et al., 2006; Edwards et al., 2016; Hyde et al., 2010; Hyde et al., 2017; Hyde & Spelke, 2011; Izard et al., 2008; Kersey & Cantlon, 2017; Park et al., 2014; Temple & Posner, 1998] - Sensitivity to the distance between numerical quantities [Hyde et al., 2017; Kersey & Cantlon, 2017; Libertus et al., 2009; Libertus et al., 2011; Pinhas et al., 2014; Pinhas et al., 2023; Temple & Posner, 1998] - Error detection of numerical operations or proto-arithmetic [Berger, 2011] - Varying functional patterns reveal individual differences [Cantlon et al., 2006] - Its neural entrainment predicts behavioral number discrimination abilities [Libertus et al., 2011] - Congruent and incongruent numerical picture-word pairings [Pinhas et al., 2014]
Frontal lobe	- Small and large numerical change detection [Cantlon et al., 2006; Izard et al., 2008; Libertus et al., 2009] - Sensitivity to the distance between numerical quantities [Park et al., 2014] - Congruent and incongruent number-action pairings [Decarli et al., 2022] - Error detection of numerical operations or proto-arithmetic [Berger et al., 2006] - Its *effective connectivity* correlates with performance in math tests [Park et al., 2014] (see Box 2 - Glossary)
Occipital lobe	- Detection of large non-symbolic numerical changes [Kersey & Cantlon, 2017; Park, 2018] - Congruent and incongruent space-number pairings [Bettoni et al., 2021]
Parietal-occipital areas	- Sensitivity to the distance between numerical quantities [Ben-Shalom et al., 2013] - Comparison of large numbers [Pinhas et al., 2023] - Congruent and incongruent number-action pairings [Decarli et al., 2022]
Temporal lobe	- Detection of large non-symbolic numerical changes [Kersey & Cantlon, 2017]
Occipital-temporal area	- Small number processing [Hyde & Spelke, 2011]

Numerical abilities in fetuses

Many studies have supported the existence of an innate number sense, namely a biologically determined ability to represent and manipulate numerical quantities (Butterworth, 1999; Dehaene, 1997; Dehaene et al., 2004; Nieder & Miller, 2004); for reviews in childhood see Dehaene et al., 1998; Dehaene & Cohen, 1997; Gallistel & Gelman, 1992; in animals see Butterworth, 2022; Dehaene, 2011; Lyon, 2003; Matsuzawa, 1985; McComb et al., 1994; Roitman & Brannon, 2003; Rugani et al., 2009, 2014). Conclusions on the innate nature of a dedicated numerical processing system in humans requires the involvement of a population that has not been exposed or has been exposed minimally to the external world. Using fetal magnetoencephalography (fMEG, Preissl et al., 2004), Schleger et al. (2014) attained such a test by assessing women during the last trimester of pregnancy and, more specifically, their fetuses' magnetic field response during an auditory oddball paradigm. Mismatch responses during auditory sequences with deviant numerosities suggested that auditory numerical discrimination is already present before birth. It's worth noting, however, that the deviant stimuli had a longer total sequence duration and a greater amount of auditory stimulation, and it is possible that the responses were also linked to these changes. Therefore, these results are compatible both with the notion that number processing foundations are innate and do not require any significant exposure or experience with the external world and also with theories postulating general magnitude systems (e.g., Walsh, 2003). If future studies were conceived in this field, it would be worthwhile to explore whether other deviants that vary in aspects such as sound duration elicit similar brain responses. This should contribute to distinguishing between these two different theoretical approaches.

Signatures of number sense in the young human brain

The Number Sense, namely the ability to understand numbers and their relationships without formal mathematical procedures, is a foundational skill and plays a crucial role in early mathematical learning (Butterworth, 1999; Dehaene et al., 1998; Gallistel & Gelman, 2000; Hauser & Spelke, 2004). The *Approximate Number System (ANS)* (see Box 2 - Glossary) *and the Object Tracking System (OTS)* are often considered candidate "Core Systems" supporting the Number Sense (Agrillo et al., 2012; Atkinson et al., 1976; Carey, 2000; Feigenson et al., 2004; Halberda & Feigenson, 2008; Spelke & Kinzler, 2007; Xu, 2003). One key characteristic of the ANS is its similarity to some perceptual representations, where the performance is determined by the *ratio* of the stimuli's intensity, following Weber's law (Cantlon et al., 2009; Moyer & Landauer, 1967; Walsh, 2003). The ratio-based performance of the ANS is supported by one critical phenomenon, namely the *Distance Effect (DE),* meaning that the greater the distance between two numbers, the easier it is to discriminate them (Moyer & Landauer, 1967). Consequently, in the literature, the presence of DE is considered indicative of ANS. Another frequently reported phenomenon, which results from the logarithmic nature of the ANS, is the *Size Effect (SE)*, that is, the larger the numbers to be compared, the more difficult the task is.

The OTS, instead, is based on the visual-spatial perception and decoding of discrete small objects. Originally, it was described as the mechanism allowing for object-specific integration of information (Kahneman et al., 1992), and it is held to consent the parallel representation of small number of individual objects (i.e. 3–4 elements; Le Corre & Carey, 2007)[2]. Moreover, it is often assumed to support 'subitizing' – the accurate reporting of the numerosity of small sets without serial counting (e.g., Le Corre & Carey, 2007; Piazza, 2010; Pylyshyn & Storm, 1988; Trick & Pylyshyn, 1994). A difference between the ANS and OTS systems is that the latter refers only to small numerosities (1–4) (Feigenson et al., 2004; Feigenson & Carey, 2003, 2005; Geary & Moore, 2016; Moore & Ashcraft, 2015; Piazza, 2010) and enables fast and accurate numerosity processing. In contrast, the ANS, the second basic numerical processing mechanism, allows to make an approximate estimation of large numerosities (>4) without counting (Dehaene, 2011; Halberda & Odic, 2015; Izard et al., 2009; Piazza et al., 2004; Xu et al., 2005; Xu & Spelke, 2000).

In the previous sections, we concluded that specific brain regions and neural responses are observed in the infant brain when it is exposed to varying numerosities. This section aims to understand how these neural responses are modulated in the large (by DE and SE) and in the small numerosity ranges and thus potentially reflecting ANS and OTS neural signatures (see Table 1 for descriptive information of the stimuli included in the studies). Ratio-dependent signal modulation can further contribute to identifying number-selective regions and, most importantly, understanding their early functioning. Neural measures could potentially clarify whether a processing boundary exists between small and large number ranges, an issue that continues to be under discussion in behavioral research.

Some neuroimaging and electrophysiological data in adults and older children found ratio-dependent changes in brain activation and revealed a ratio-dependent region in the horizontal segment of the IPS associated with the ANS (e.g., Ansari & Dhital, 2006; Cantlon et al., 2006; Dehaene, 1996; Piazza et al., 2004; Pinel et al., 2001). The study by Temple and Posner (1998) cited in the section 3.1 also investigated the DE (far and close) concurrently at a behavioral and electrophysiological level using both dots and digits. ERPs in parietal scalp sites (***N1***and ***P2p,*** a neural proxy of large numerosities; Hyde & Spelke, 2009; Temple & Posner, 1998; see Box 2 - Glossary) associated with the DE were found for both symbolic (digits) and nonsymbolic (dot arrays) stimuli at a similar timing in both adults and in 5-year-old children, suggesting developmental continuity of the mechanisms involved in number comparison starting at preschool. Later on, the DE was replicated by Ben-Shalom et al. (2013) which showed, in a numerical Stroop task, that electrophysiological responses varied with numerical distance in occipito-parietal areas.

Subsequently, Hyde et al. (2017) presented 3- to 4-year-old participants with two passive viewing tasks; an approximate number change task with large numerosities and an individual object processing task with small numerosities. First, they extracted the locations of the small and large numerosity signatures, through a data driven approach (N1 in response to small numerosities over right temporo-parietal areas and P2p in response to large numerosities over right-lateralized posterior area). Then, participants were divided into developing and proficient counters based on their understanding of symbolic number words. In the small numerosity task, the temporo-parietal N1 ERP increased in amplitude as the items increased (from 1 to 4) for proficient counters while it increased only up until 2 for the developing counters. This showed that the amplitude did not linearly increase for developing counters which were not familiar with higher numerical values (3 and 4) and that the N1 amplitude varied as a function of the absolute value (number of items presented). In the large numerosity task, with increasing distance (from 1:2 to 1:4), the P2p ERP linearly decreased for the developing counters and increased the proficient group. An increase in the P2p amplitude with larger distance is in agreement with Temple & Posner (1998) study that found a DE in the P2p component. These findings suggest that the modulation of P2p as a function of ratio can be observed in young children, and that the direction of the modulation is related to the children's level of counting proficiency.

More recently, the P2p component was also found to be modulated by the ratio in 4–5-year-old children with a high ANS acuity (Pinhas et al., 2023). More specifically, the P2p amplitude in this group was more pronounced for easier ratios (i.e., 1:2 ratio) than for harder ones (i.e., 3:4 ratio). Interestingly, the amplitude of the P2p was not modulated by the ratio in a low ANS acuity group of the same age, suggesting that a higher ANS acuity is directly linked to a more sophisticated numerical discriminatory ability that can be tracked at the neural level. Thus, contrary to Hyde et al. (2017) which reported that P2p responds differently to large changes in both developing and proficient groups, Pinhas et al. (2023) found it in the high proficiency group only. The source of the difference might arise from the nature of the task used to separate the groups based on proficiency. Indeed, while in Pinhas et al., 2023, the task was based on approximate capacities, Hyde et al. (2017), relied on children's exact representational abilities.

Besides investigating the links between the modulation of specific EEG components and the developing exact or approximate abilities in children, studies in the field have also explored other neural signatures of number sense using different methodologies or analytic approaches which might be also suitable for younger children.

Ratio-dependent electrophysiological correlates may also be reflected by frequency bands (Libertus et al., 2009). An EEG study found parametric variations in neural oscillations as a function of numerical ratio in 7-month-old infants. Specifically Alpha-band (6–8 Hz) oscillations over midline and right posterior scalp sites were modulated by the ratio between familiar and novel numerosities (Libertus et al., 2009). More specifically, the authors found a decrease in the alpha power associated with numerical novelty detection, consistent with previous research in adults (Sauseng et al., 2005). Although the study implemented stimulus controls to rule out the contribution of perceptual variables such as cumulative area or element size, they do not necessarily represent neural correlates

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[2] Whether OTS can represent numerosities is debated. According to (Gelman & Butterworth, 2005) the nature of the OTS mechanism which operates by keeping track of specific objects in the space, stands in contradiction with the ability to extract abstract properties (e.g., twoness) which can be applied to any set of objects.

specific to number processing in infants. See section 3.3 for further considerations on this topic.

Subsequently, Libertus et al. (2011) compared EEG data of 7-month-old infants and adults while implementing a rapid steady-state visual-presentation paradigm (RSVP), an innovative design that allowed the repeated presentation of the same numerosity with rapid flickering images. Neural entrainment was observed over occipital and parietal channels for adults and in the corresponding electrodes in infants, following a large switch (1:3 ratio). Moreover, in both age groups, numerical switches were modulated by the ratio. By comparing infant and adult data, this study provided further evidence of ANS neural signature continuity from infancy to adulthood. Remarkably, however, the repetition of the same numerosity in this study yielded an increment – rather than the expected decrement – in the stimulus-locked neural entrainment in both groups. Because no other study has further implemented the same paradigm, it remains an open question whether attentional, perceptual or exclusively numerical factors are causing this increment.

Kersey and Cantlon (2017) used fMRI to show how the IPS tuned to numerical variations in 3–6-year-old children. During the habituation paradigm, the right IPS adapted to a constant numerosity and then responded to the deviant number varying with the distance between the two numerical quantities, as in adults (Piazza et al., 2004). When comparing the behavioral and right IPS neural tuning curves, they found the same inverted Gaussian shape that followed Weber's Law features. By contrast, the left IPS was only weakly tuned to numerosity and the behavioral responses. This study demonstrates that the right IPS is modulated by the numerical distance between familiar and novel numerosities in children starting at 3 years of age.

In conclusion, these studies confirm and extent behavioral findings by indicating the existence of specific electrophysiological and hemodynamic responses dependent on the ratio or on the absolute cardinal value for both large and small numerical ranges before formal schooling (Hyde et al., 2017; Kersey & Cantlon, 2017; Park et al., 2014; Pinhas et al., 2023; Temple & Posner, 1998), from infancy (Hyde & Spelke, 2011; Libertus et al., 2009, 2011) and similar to the adult population (e.g., Dehaene, 1996; Piazza et al., 2004).

The similarities across age groups provide neural evidence of ontogenetically continuous neural responses both for small and large quantities. Importantly, not all studies have found DE modulations in the parietal cortex. For example, Park et al. (2014) found DE related activation in inferior frontal regions when including both dots and Arabic digits in 4- to 6-year-old children, but absent or small neural DE in the parietal areas (see Holloway & Ansari, 2010; Kaufmann et al., 2006 for similar results in older children and adults). This suggests that, under certain circumstances, number-selective responses might not be confined to parietal regions. The reasons for the different activations have not been yet clarified in the studies with infants or children.

Number-specificity of neural responses

In everyday life, we do not recognize numerical quantities as an isolated piece of information, but rather perceive them within a context. For example, besides detecting changes in numerosity, we may perceive that objects vary in their shape, size, color, identity, etc. One critical question regards whether neural responses in the first period of life depend on numerosity per-se i.e., are number-specific, or whether the non-numerical dimensions of the presented stimuli determine the outcome. Studies including dimensions and features other than numerical ones have shed light on whether numerical properties are more salient or spontaneously recognized compared to other stimulus properties (see Table S3 in Appendix A for descriptive information of the non-numerical features controlled in the studies).

To explore the existence of number-specific responses in infancy, previous studies have contrasted them with brain responses that code for other features of the stimuli. For example, by manipulating both number and object (color and shape) simultaneously, Izard et al. (2008) were able to show a double dissociation for numbers vs objects; changes in number but not in identity elicited differences in ERPs over right parieto-frontal regions (dorsal pathway) at 800 ms whereas changes in identity but not in number elicited differences over occipito-temporal areas (ventral pathway) areas at around 400 ms to 800–1,000 ms.

Also, Hyde et al. (2010) assessed whether brain regions that show an increased hemodynamic response to number changes also respond to shape change (squares and triangles) in 6-month-old infants. Like in Izard and colleagues' investigation, this study found that number-deviant stimuli elicited an increased hemodynamic response in the right parietal area while shape-deviant ones elicited an increase in the right occipital one. Differently from Izard et al. (2008) the stimulus changed in shape but not in color and the changes in shape and numerosity did not occur simultaneously. However, both studies agree that, before the first year of life, the response to number and shape occurs in two distinct areas of the brain: numerical change is encoded in parietal regions and shape change in the occipital one. Interestingly, Hyde et al. (2010) showed that number and shape changes were both lateralized to the right hemisphere at different timings: the parietal response to number change occurred 2 and 5 s after the stimulus onset, whereas shape-deviant responses were found in the right occipital region after 5 and 8 s post stimulus onset. They propose that the response to number change occurs earlier on compared to shape-changes, although in a more anterior region (parietal areas compared to occipital ones).

In yet another study with 4-year-olds, number-specific activations were found in the IPS while shape-specific activations were found in the left lateral occipital-temporal region and the right fusiform gyrus (Cantlon et al., 2006). A shape-specific response in the occipital cortex (Hyde et al., 2010; Izard et al., 2008) and a number-specific response to number change in the parietal cortex is in line with previous studies carried out with infants (Edwards et al., 2016; Hyde et al., 2010; Izard et al., 2008), thus showing continuity from infancy to preschool years.

In addition to considering shape to study numerical specificity, the study by Kersey and Cantlon (2017) cited above, further confirmed that the right IPS in 3–6-year-old children was neurally tuned to numerical changes and not to color or area. Interestingly, these authors showed that the anterior IPS is tuned to numerosity and not to color whereas the posterior IPS to color and not numerosity. This pattern of localization aligns with previous findings in adults (Pinel et al., 2001) and contributes at unveiling the extent to which the brain displays number-specific responses early in life.

Besides distinguishing numerosity from other object-features, it is highly debated whether neural responses specifically follow numerosity or rather rely on low-level visual features that often co-vary with numerosity, such as surface area, convex hull, perimeter, etc. Park (2018) evaluated early sensitivity exclusively to numerical quantities by varying the frequency of presentation during a steady-state visual evoked potential (SSVEP; see Box 2 - Glossary) technique in 3- to 10-year-old children and adults. Medial (Oz) and right (PO8′) occipital electrodes in adults and the right occipital (O2′) electrode in children were selectively sensitive to numerosity and not to other non-numerical variables (size and spacing), presented at 1 Hz. With the use of EEG, Park (2018) suggested that in children as young as 3 years old, occipital areas are number-specific in the early visual processing stage. This finding reveals an area that may be responsible for the visual early perception of the numerosity dimension.

More recently, Gennari et al. (2023) pushed the boundaries as to the presence of an abstract number sense in sleeping 3-months-old infants. This ability, the authors show, enables infants to code numbers independently of other non-numerical magnitudes dimensions, but also sensory modalities and vigilance states. The conclusion was achieved using increased scalp EEG coverage (256 electrodes) and more sophisticated techniques (Multi-voxel pattern analysis (MVPA) and representation similarity analysis (RSA)). The authors hypothesized that, if number is a primary sensory property that infants encode, then the decoder must discern between numbers regardless of the physical variations of the stimuli and presentation format (visual or auditory). It was thus tested whether the same numerical code was retrieved even if varying several parameters (i.e., auditory sequences varied in duration, tone rate, musical instrument and pitch; visual displays in object size, density, identity and color). Furthermore, spontaneous numerical encoding was assessed minimizing the emphasis on the numerical dimension, unlike other tasks such as numerical change detection paradigms or numerical comparisons. Results showed preliminary tracking of each additional item during and before the end of the sequence (105–280 ms) and significant number decoding at the end of the numerical sequences (400–800 ms). In other words, non-overlapping patterns were observed between stimulus presentation frequency and number decoding. This suggests the presence of a mechanism that successfully discriminates and classifies numerical from non-numerical information.

Studies have also demonstrated that brain responses to numerosity in 6-month-old infants can be dissociated from other related cognitive processes. Edwards et al. (2016) specifically investigated whether neural responses to novel numerosities can be distinguished from responses due to a general increase in visual attention when novel “interesting” stimuli are presented. For this purpose, they used measured hemodynamic responses with fNIRS to compare colored audio-visual stimuli (increasing visual attention) with numerical silent conditions with white and gray images. Using a cluster correction for multiple comparisons approach, they found that only one channel of the right parietal region showed a greater response to numerical changes compared to “attentional” changes. By contrast, a greater subset of channels in the central occipital and mid-parietal region showed a greater response to “attentional” changes compared to numerical ones. Although the sample size of the study was somewhat limited, these findings converge with others in that right parietal regions may be number selective from infancy. Moreover, this study contributes to dissociating these number-specific responses from mere attentional responses.

The interaction of numbers with other dimensions

Studies in developmental populations have considered numerical information in interaction with other dimensions of the world (e.g., spatial, action, time). For example, it has been observed that human adults organize numerical information according to a specific left (small numerosities) to right (large numerosities) spatial orientation (space to number association or SNA; Dehaene et al., 1993). Traditionally, this association was thought to be a product of culture, mainly influenced by writing and reading habits (Shaki et al., 2009) but recent studies demonstrated it in young children and even newborns (de Hevia et al., 2017; Di Giorgio et al., 2019; West & McCrink, 2021), as well as in macaques (Drucker & Brannon, 2014), chimpanzees (Adachi, 2014), chicks (Rugani et al., 2015) and insects (Giurfa et al., 2022). This suggests that the origins of this interaction might also be evolutionarily relevant. Investigating the relationship between numerical information and other dimensions in infants can shed light on the importance of developing numerical cognition to successfully interact with the external environment.

In their research Bettoni and colleagues (2021) investigated the neural correlates underpinning the attentional shifts induced by large and small non-symbolic numerical cues in an a priori defined sample of 8- to 9-months-old infants using EEG. An enhancement of the early occipital P1 component was found when targets appearing on the right were cued by a large number and targets appearing on the left were cued by a small number (valid condition), compared to the reverse (invalid condition). This was the first neural evidence showing a neural mechanism underlying SNAs in infancy.

Furthermore, Decarli et al. (2022) aimed to shed light on the neural mechanisms underlying numerical-action association (NAA) in 3- to 4-month-old infants to clarify whether the link between numerosity processing and hand actions (Ranzini et al., 2011, 2022), is already functional in infancy. ERP amplitudes located over frontal and parietal-occipital areas differed when observing congruent (e.g., small numerosity paired with a small hand opening) or incongruent (e.g., large numerosity paired with a small hand opening) pairings. It thus seems that infants can spontaneously integrate these two types of magnitudes and create an expectation of their congruency (Decarli, Veggiotti, et al., 2022). As the authors suggest, future research could investigate the developmental trajectory of neural NAA to provide evidence of the continuity of the neural substrate that supports this association and to investigate NAA in young children with a developmental coordination disorder, who have been found to have mathematical difficulties (Gomez et al., 2015).

In conclusion, these findings reveal that from infancy, parietal areas specifically process numerical information over non-numerical variables (color, shape; Cantlon et al., 2006; Hyde et al., 2010; Izard et al., 2008; Kersey & Cantlon, 2017; area: Kersey & Cantlon, 2017; lines: Park et al., 2014) or other cognitive processes (attention; Edwards et al., 2016). The right occipital cortex may instead respond to the early numerical perceptual information which correlates with numerical information (size and spacing; Park, 2018). Although these neural signals are specific to numbers, neural evidence suggests that numerical cognition from infancy may not be processed independently as it shares a common system with the motor output (action; Decarli, Rämä, et al., 2022) and with other magnitude dimensions (space; Bettoni et al., 2021) to interact with the external environment.

Individual differences in brain activation and early numerical abilities

Behavioral assessments have provided evidence that children's basic numerical abilities are related to their future mathematical performance (Piazza et al., 2010; Rousselle & Noël, 2007) and can contribute at identifying deficits in children with developmental dyscalculia (Landerl et al., 2004). Recent studies have attempted to extend these findings by exploring early neural markers that could potentially explain individual differences in math performance. The studies are limited in number, but provide foundational evidence that early brain responses can be associated with concurrent or subsequent behavioral outcomes in the same sample of participants. Of note, none of these studies attempted to extend their results to out-of-sample individuals.

First evidence of concurrent brain-behavior correlations was reported in the fMRI study by Kersey and Cantlon (2017). As summarized in the above sections, the study showed how the right IPS responses tuned to numerical variations in 3–6-year-old children, specifically following Weber's Law. Crucially, they also provided initial evidence of a correlation between the Weber fractions calculated over the signal in the right IPS and those calculated over behavioral responses. The attempt to explore correlations is laudable as it constitutes a breakthrough in the field and a significant progress in combining different approaches to better understand numerical development. However, it should be noted that brain-behavior correlations could be fragile with somewhat reduced sample sizes (Marek et al., 2022), in this case N=35. Future studies should consider larger sample sizes when investigating brain-behavior correlations.

In parallel, Hyde et al. (2017) explored possible correlations between individual ERPs and early counting abilities in a larger sample of 3 to 4-year-old children. Results evidenced significant correlations between N1 (a neural marker of small numerosities, Hyde & Spelke, 2009) and counting abilities even after controlling for general non-numerical cognitive abilities (i.e., executive functions and linguistic abilities). By contrast, associations between behavioral performance and P2p (a neural proxy of large numerosities; Hyde & Spelke, 2009; Temple & Posner, 1998) did not hold after controlling for cognitive and linguistic abilities. These results indicate that neural signatures of the small numerosities play a role in early symbolic numerical cognition. Moreover, they suggest that other general cognitive aspects might explain the association between large numerosities and symbolic numerical abilities. The correlation found between individual differences in counting ability and in neural signatures associated with the small numerosities, may prompt future research to investigate whether these early ERPs can predict future numerical difficulties.

Another study regarding individual differences that is worth mentioning is the one by Park et al. (2014) which used fMRI to investigate the neural substrates of symbolic number acquisition in children between 4 and 6-years of age. The results indicated that the process of symbol-to-number mapping is supported by effective neural connectivity between the right parietal cortex, the left SMG and right PreC. Interestingly, the degree of connectivity to the right PreC predicted individual scores in a standardized test of mathematical achievement (TEMA-3) about a month and a half later. These correlations indicate that progressive connectivity between foundational areas underlying numerical abilities supports subsequent individual performance in numerical tasks. At the current state of the research, it is an open question whether early connectivity patterns can be also linked to longer term mathematical or numerical outcomes.

Another middle-term longitudinal study was conducted by Libertus et al. (2011), who found that neural entrainment to number repetition, as measured by EEG at 7 months, significantly predicted number discrimination abilities two months later. The authors demonstrated that this paradigm can be applied to participants at different age ranges. Thus, this neural response may potentially constitute a measure to track the developmental progression of early numerical abilities. These results are highly promising, however, like in the majority of studies in the field, replications of the effect are scarce or lacking. The concrete clinical or educational applications might be still pending further and follow up studies of this kind.

Other research has also reported individual neural responses that could be informative as to the progression of numerical abilities in infants, but did not specifically assess the relation between the neural patterns and behavioral performance in the tasks. For example, Cantlon et al. (2006) noted individual differences in hemispheric lateralization in 4-years-old children: while the majority of children exhibited greater number-related activity in the right IPS, some showed greater activity in the left IPS instead. Longitudinally tracking individual differences could contribute to understanding whether the pattern of hemispheric lateralization during early stages is related to later mathematical abilities (see also, Bugden et al., 2012; Emerson & Cantlon, 2015; Price et al., 2016). A similar approach has already provided promising insights in older children enrolled in formal schooling (e.g., Emerson & Cantlon, 2015; Rivera et al., 2005).

In summary, information on the neural processes that accompany the behavioral outcomes of numerical skills is beginning to be explored. From the current body of literature it seems difficult to understand the determining predictors of mathematical learning, as the vast majority of the studies available implemented a cross-sectional design. Therefore, it may be worth considering how longitudinal studies beginning in early childhood can potentially predict math performance and identify children at risk of mathematical learning difficulties. Neuroscientific methods, in combination with behavioral ones, can be indicative of mathematical abilities and may constitute a valuable integration for current diagnosis and treatment programs (e.g., Benavides-Varela et al., 2020, 2023). Similar approaches in older children have been successful in identifying, for example, developmental trajectories of gray and white matter in children with dyscalculia (Ranpura et al., 2013). Likewise, additional studies on connectivity might be a fertile area of research, useful to understanding developmental milestones and predicting mathematical performance. This is supported by recent fNIRS findings in adults, showing that pre-training resting-state connectivity patterns can predict the effectiveness of arithmetic learning in adults (Zhao et al., 2019).

Limitations and directions for future research

Although brain measures have enriched knowledge in the field of numerical cognition, many questions remain open. This review encountered some limitations in the literature and suggests a few points that might be considered in future studies to better define the neurodevelopment of numerical skills in infants and preschool children.

First, an important factor that should be taken into consideration when interpreting these findings is the enormous variation in the experimental approaches across the studies reviewed. Although overall there seems to be a great level of consistency in the conclusions achieved, relevant differences for example in the paradigms used, sample sizes, the nature and extent of the non-numerical controls, statistical and analytical approaches to define time windows or regions of interest (i.e. data-driven versus theory-driven approaches), etc. should be considered when evaluating the strength of the evidence and generalizability of each individual study. It would be appropriate in the future, when more primary studies become available, to further investigate the relative role of these variables as moderators of the general results and the size of the effects observed. Major caution should be exercised when evaluating the statistical evidence provided by studies addressing brain-behavior correlations (section 3.4). According to recent proposals, ensuring the reproducibility of this type of analysis requires samples with thousands of individuals (e.g., Marek et al., 2022). This is a standard that can barely be achieved in a single study with special populations. Indeed, high attrition rates are often obtained in neuroimaging studies with infants and young children (e.g., 41 % on average in the studies reviewed here). This is due to numerous factors, including frequent movement artifacts, fuzziness, not sufficient number of trials collected, etc.

It should also be noted that this outcome is based on the 21 neuroimaging studies which met the criteria for this review. However, all the studies were concentrated in a few countries from the Global North which belong to the so-called WEIRD (Western, Educated, Industrialized, Rich, Democratic) populations. It remains an open question if they can be extended to other countries/ethnicities. From a developmental perspective, it is also relevant to understand how contextual factors (e.g., parental socioeconomic status, Demir et al., 2015; home environment, Susperreguy et al., 2020), or deficits in other cognitive abilities (e.g., language, attention, spatial or temporal abilities) affect the numerical abilities during this relevant period of brain development (Ackerman, 1992; Greenough et al., 1987).

Collaborative or multi-lab research efforts might contribute, in the near future, larger and more diverse sample sizes, thus enhancing statistical power and generalizability of the findings.

Another limitation has to do with the scarcity of studies at some specific age ranges. This is the case for newborns (before 3 months) and toddlers (1–3-year-olds). Including these age ranges in future studies could open up other several questions, such as the changes in neural networks over time (e.g., how and when the left parietal cortex becomes associated with numerical symbols) due to maturation and or to the acquisition of more complex numerical concepts (see Decarli et al., 2023 for a behavioral longitudinal study) or the neural correlates underpinning the transition from non-symbolic to symbolic numerical learning between two and five years of age.

Relatedly, the majority of the studies reviewed here implemented a cross-sectional design. These are informative in regard to the numerical abilities and brain processes expected at a given age but remain short at revealing how numerical processing changes over time at both group and individual levels. Longitudinal studies might thus constitute an exciting arena for future research. Longitudinal data could also contribute to understanding atypical functional and structural abnormalities and how different educational experiences and social contexts can affect brain function (e.g., Peters & De Smedt, 2018). Moreover, neural techniques could be coupled to obtain both a temporally and a spatially accurate measure of brain activity. The presence of various measures within a study could serve to corroborate, extend and complement one with the other (see also Matejko & Ansari, 2018).

The development of ANS acuity and whether it predicts future mathematical abilities has only been investigated using behavioral measures (e.g., Halberda et al., 2008). Since neural measures appear to detect finer ANS acuity than behavioral ones (e.g., up to 2:3 ratio in 3-months-old, Izard et al., 2008) versus 1:2 ratio in 6-months-old, Xu & Spelke, 2000), they could serve as an early indicator of future mathematical skills. However, this evidence was only found in one study and for one ratio (Izard et al., 2008), possibly due to the fact that ratios chosen for neural studies are limited to those reported in behavioral ones. Future research could verify this possibility in basic and/or applied research designs.

Lastly, open practices such as pre-registration, open access, open data, and pre-prints are a relatively recent requirement in the scientific community. These practices improve transparency and the reproducibility of the research, and reduce the likelihood of publication. bias, among other advantages. The field is just transitioning to adopt these practices. Indeed, none of the studies were pre-registered or reported *a priori* power analysis calculation (Bettoni et al., 2021; Hyde et al., 2017) while only three most recent studies made their data (Decarli, Rämä, et al., 2022; Pinhas et al., 2023) or their code (Gennari et al., 2023) publicly available. Thus, continuously adhering to these scientific standards seems reasonable and advisable for future research in the field.

Conclusions

This review aimed to provide a comprehensive and systematic overview of the brain mechanisms that support the development of numerical abilities before formal education, with the intent of delineating early neurodevelopmental trajectories (see Fig. 3) and of understanding to what extent they can possibly anticipate future mathematical outcomes. Several conclusions can be derived from this summative report.

Firstly, evidence from neuroimaging and electrophysiological techniques points to the existence of an early non-verbal system for the representation of numerical magnitude. The system represents numerical information independent of the input modality (auditory or visual; Gennari et al., 2023). The neural network dedicated to this non-verbal numerical representations mainly involves the right parietal cortex (Edwards et al., 2016; Hyde et al., 2010; Izard et al., 2008), as well as the occipital (Hyde & Spelke, 2011; Park, 2018; Pinhas et al., 2023) and frontal areas from infancy (Cantlon et al., 2006; Izard et al., 2008; Libertus et al., 2009; Park et al., 2014). The right parietal responses also appear to support primitive proto-arithmetic skills in young infants (Berger, 2011). Altogether the studies suggest a predominant role of the right IPS over the left IPS in supporting early numerical abilities (see also Salillas et al., 2023 for a similar conclusion). However, the biological meaning of this asymmetry is not particularly well understood. As summarized by Bisiacchi and Cainelli (2022), in young infants there is a predominance of right-lateralized functions in several other domains outside number, including those focusing on memory (Benavides-Varela et al., 2012, 2017) non-speech auditory stimulation (Telkemeyer et al., 2009) rhythmic visual stimuli (Crowell. et al., 1973), and taste (Fox & Davidson, 1986). The dominance of the right hemisphere for many early-life functions is in line with theories stating that it develops earlier than the left hemisphere and that its development is less subject to external influences because it sustains functions necessary to survive (Geschwind et al., 2002; Geschwind & Galaburda, 1985). The right-hemisphere dominance in numerical processing might be resulting from this biologically determined neurodevelopmental pattern. Alternatively, the right-lateralization pattern might be considered a specific yet undetermined condition that supports typical numerical development from the start. Cantlon et al. (2006) observed differences in parietal-hemispheric lateralization at the individual level, suggesting that it may not be straightforward to conclude that number-related activity is right-lateralized in all children. The effects of these differences need to be clarified in future studies longitudinally assessing children with different lateralization patterns at birth and their mathematical outcomes at different points in development.

Secondly, responses in number-selective regions are modulated by the relationship between the presented numerosities. Specifically, findings in infants (Hyde & Spelke, 2011; Libertus et al., 2009, 2011) and young children (Hyde et al., 2017; Kersey & Cantlon, 2017; Park et al., 2014; Pinhas et al., 2023; Temple & Posner, 1998) point to the existence of ERPs and hemodynamic responses for numerical quantities dependent on the ratio of large numerical quantities or on the absolute value of small ones. Specifically, a distance effect was found in the parietal region, particularly in the right IPS of children as early as 3 years of age (fMRI: Kersey & Cantlon, 2017; EEG: Hyde et al., 2017; Pinhas et al., 2023; Temple & Posner, 1998). By contrast, Park et al. (2014) found this effect exclusively in inferior frontal regions. Small numerosity signatures were found in the temporo-parietal area, namely ERPs varied as a function of the absolute value only if the participants were familiar with the numerical values. Interestingly, Izard et al. (2008) found a response for both numerical ranges in the right parietal cortex in 3-month-old infants while Hyde and Spelke (2011) revealed a dissociable response in 6-month-old infants: responses to small numerosities were found over the left and right occipital-temporal sites whereas the responses to large numerosities were observed in the expected posterior parietal sites. This possibly reflects a neural mechanism underlying a developmental specialization occurring in the first year of life.

Thirdly, the literature suggests that the functional response in specific brain areas is due to number-specific properties. From brain activity measures it emerges that parietal areas may be specifically recruited to process numerical information above and beyond other non-numerical features (color, shape; Cantlon et al., 2006; Hyde et al., 2010; Izard et al., 2008; Kersey & Cantlon, 2017), non-numerical variables (e.g., Gennari et al., 2023; Kersey & Cantlon, 2017) or visual attentional processes (Edwards et al., 2016). The right occipital cortex may, on the other hand, respond to early numerical perceptual information (size and spacing; Park, 2018). These findings suggest that number is one of the primary sensory properties we use to make sense of the external world from infancy. Together with other non-numerical dimensions (e.g., motor output, Decarli, Rämä, et al., 2022; space, Bettoni et al., 2021) it allows the child to efficiently interact with the surrounding environment.

Fourthly, tracking individual differences and anticipating the development of future numerical skills is of broad and current interest. Yet, up to now, the majority of studies have focused on exploring individual differences in cross-sectional designs (Cantlon et al., 2006; Hyde et al., 2017; Kersey & Cantlon, 2017), or on assessing performance in behavioral tasks 1.5 to 2 months after the neuroimaging data was collected, but no study looked at how early neural responses can predict future and more complex mathematical abilities. This prompts future research to investigate how neural responses of numerical cognition can constitute a potential measure to track the developmental progression of numerical abilities throughout the lifespan.

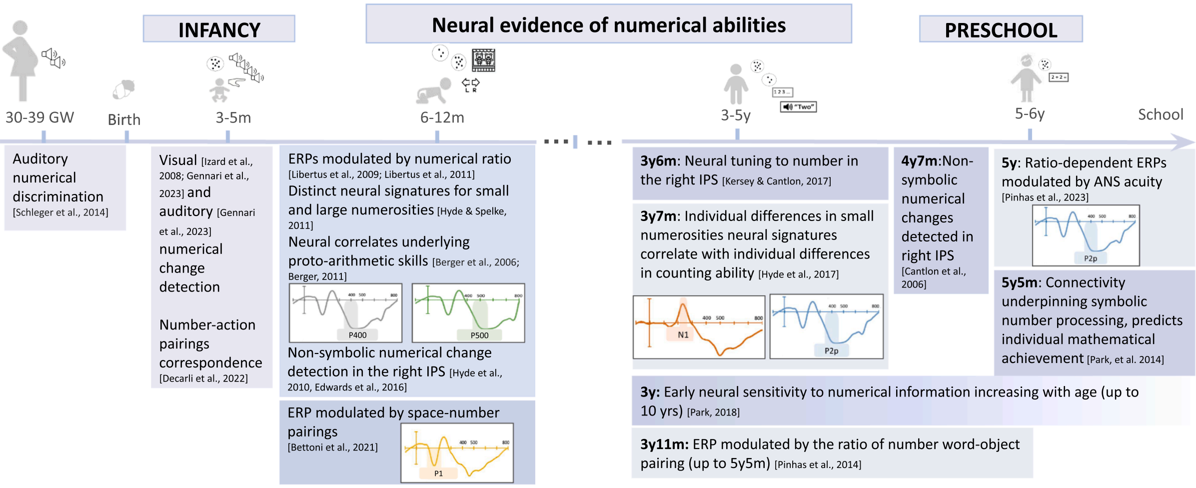

Fig. 3. Early neurodevelopmental trajectory for numerical abilities.

To conclude, the findings in the infant population suggest that number processing foundations are innate, abstract, and do not require any significant exposure or experience with the external world. Moreover, brain measures have been instrumental for complementing and extending behavioral data, for addressing several outstanding questions, and for informing crucial debates in the field of numerical cognition that go beyond the nature vs nurture long standing one e.g. the extent to which number processing is independent of other non-numerical features, whether OTS or ANS are parallel processes or prevail one over the other early in infancy, the degree to which number processing might be affected by other cognitive abilities such as executive functions, general intelligence, etc. Tracing a full neurodevelopmental trajectory of numerical skills from birth will eventually provide a more comprehensive overview of how typical and atypical numerical capacities evolve and offer additional tools to understanding the neurobiology of numerical learning at different levels of analysis (e.g., Visibelli et al., 2024). We anticipate that forthcoming research within only a few years will yield additional insights regarding early individual differences and possible biomarkers linked to brain structure and function. Neuroimaging studies could, in that sense, contribute to early detection in at-risk populations and inform the development of personalized intervention strategies tailored to the specific needs of each child. This prediction may constitute a pragmatic contribution of developmental cognitive neuroscience to society and other fields, but this contribution will require the continued application of rigorous scientific and ethical considerations.

Box 2
Glossary

Number-related terms	
Object Tracking System (OTS)/small numerosity sets	Preverbal cognitive system for accurately representing distinct small sets of objects (three or four items) without counting, referred to as small numerosities (1-4).
Approximate Number System (ANS)/large numerosity set	Preverbal cognitive system for approximately representing and manipulating large sets of objects without counting, referred to as large numerosities (>4).
Ratio	The relationship between two quantities is obtained by dividing their values (i.e., the ratio in a habituation paradigm is found by dividing (A:B) the familiar number (A) by the novel one (B)).
Distance and Size Effects	Distance effect (DE): Numerical discrimination acuity increases as the distance between two numerosities increases. Size effect (SE): Numerical discrimination acuity increases as the numbers decrease in size.
Effective connectivity	The causal influence between the neural activities of different brain regions.
Paradigms	
Habituation task	The habituation paradigm consists in repeatedly presenting the same numerosity (habituation) and then a novel number of items (dishabituation). To investigate numerical discrimination abilities, this paradigm may be used in behavioral studies by observing the looking time or in combination with neural measures.
Violation-of-expectation task	The task consists in hiding or removing objects one by one behind and from the screen. When revealing the number of objects behind it, the number could be consistent or inconsistent with the events (e.g., two puppets are hidden behind the screen and only one is revealed or two puppets are hidden behind the screen and two are revealed). In this case, they combined Wynn's (2002) behavioral task with electrophysiological recording.
Auditory Oddball task	The task consists in interrupting the repetitive presentation of the same numerical stimulus with a deviant one. The reaction to this "oddball" (deviant) stimulus is recorded.
Neural correlates	
Neural tuning	Neurons in a specific region are selectively tuned to numerical information: firstly, a habituation to constant numerosity and then a tuning curve in response to a neural preference for numerosity changes.
Theta and alpha frequency bands	EEG data can be described in terms of frequency bands categorized as delta (δ) (1–4 Hz), theta (θ) (4–8 Hz), alpha (α) (8–13 Hz) and beta (β) (12-35 Hz).
Event-Related Potentials (ERPs)	Electrophysiological response in the brain, measured with EEG, to a specific event (e.g., a stimulus).
Steady-state visual evoked potential (SSVEP) technique	Technique used to quantify early visual neural sensitivity to numerical magnitudes of dot arrays presented in a specific temporal frequency.
Event-Related Potentials (ERPs)	
Negative polarity incongruency response (N_{inc})	A negative ERP component (N450) elicited from about 200-500 ms.
N1	First (1) negative (N) ERP component.
P2p	Positive (P) posterior (p) ERP component peaking at around 200–250 ms (2).
P400	Positive (P) ERP component peaking at 400ms.
P500	Positive (P) ERP component peaking at 500ms.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.dr.2024.101150.

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