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Number cognition

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From our very early school years we start to realize that numbers govern much of our life. A glance at the headlines will tell us a crucial parliamentary bill was defeated by 149 votes, that inflation is steady at .9%, that the GNP has declined by 1% and so on. A flick of our telephone gives us the time (in digits) and date, the telephone numbers of our friends, with apps to furnish our bank balance, and how many steps we have made today. However, these symbolic representations of quantity, usually by Arabic numerals, capture only a small fragment of our daily experience with numerable quantities, and how these quantities guide our behaviour, and the ways we exploit our inner ability to "sense" the numerosity of these quantities.

By showing that birds can perform both simultaneous visuo-spatial and temporal-sequential coding of the numerosity of simple visual items (clouds of dots), the German zoologist Otto Koehler (1941; 1950) was among the first to suggest that the symbolic mathematical competence that characterises much human activity might be grounded in phylogenetically older systems that allow approximate, but behaviourally adaptive, estimates of numerosity. During biological evolution these rudimentary mathematical abilities might have been crucial for survival and adaptation by allowing, for example, the recognition and memorization of environments with more or fewer food items, or by favouring rapid "fight or flight" decisions dependent on the relative numerosities of conspecific allies and opponents.

Over the past 25 years the study of the neural bases and the functional mechanisms that regulate mathematical cognition in animals and humans has proliferated. In this special issue, we offer an overview of some promising lines of ongoing research on number processing in the brain. The various contributions cover different aspects of mathematical cognition, including studies of the basic neural and functional mechanisms that underlie the sense of numerosity, the interaction between number and the representation of space or time (a field pioneered by Galton's (1880 a,b) description of mental number lines and revitalised by the discovery of the Spatial-Number Association of Response Codes, i.e., the SNARC effect, by Dehaene et al., 1993), the neural regulation of mathematical operations and the correlates of normal or abnormal development of mathematical competence.

1. Numbers: interaction with space and time processing

Numerosity and numbers convey, more or less inherently, an idea of quantity and magnitude: 5 is greater than 2. Magnitude is shared with other dimensions, such as space – is it larger, longer? – and time – did it last longer? A number of studies reported in this issue clarify how magnitude estimates of numerosities overlap or interact with magnitude estimates in other domains. Tsouli, Dumoulin, te Pas, and van der Smagt (2019) used an adaptation technique, exposing subjects to large and small numerosities, and to long and short durations; they reported partial cross-talk between the two dimensions, pointing to partially overlapping neural mechanisms.

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Borghesani et al. (2019) adopted a different approach, recording by fMRI BOLD responses from parietal cortex while participants made length or numerosity judgements. Decoding the responses showed magnitude-dependency to both numerosity and length in much of parietal and occipital cortices, but no cross-talk between the two. Thus while length and numerosity may share neural resources, their representations seem not to active a common neural code. Sahan, Majerus, Andres, and Fias (2019) present an fMRI imaging study that attempts to distinguish parietal areas representing number-related information for magnitude processing from working memory. They generated an internal numerical landmark task to be used in a fragmented trial event-related fMRI design, which solves the often-discussed problem of separating encoding from decision processes. This approach allowed them to separate number magnitude encoding subserved by the right anterior intraparietal sulcus from working memory and internal spatial orienting processes involved during number processing, the latter relying on more posterior partly bilateral parietal regions.

2. Basic neural and functional mechanisms of numerosity and numerical processing

Investigating the neural foundations of numerical competence has both theoretical and empirical implications. The role played by a parietal-frontal network that includes the intraparietal sulcus and the prefrontal cortex in the representation of number magnitudes is now well established. De Wind, Park, Woldorff, and Brannon (2019) report an fMRI study showing that number is also encoded in occipital cortex, in areas V1, V2 and V3, with careful controls to ensure that the response is not driven by covarying factors such as density. This suggests that number is encoded rapidly and directly very early in the visual processing stream, and that output from this early elaboration probably feeds parietal and prefrontal number areas.

In recent years there has been debate on whether the visual number sense depends on the activity of a functionally independent system dedicated to numerosity extraction, or whether the visual number sense is essentially non-numerical and depends on weighted integration of continuous magnitude features that covary with numerosity. Using TMS, Karolis et al. (2019) provide evidence that superior parietal areas play a role in weighting stimulus features, whereas the intraparietal region contains an abstract ‘read-out’ of numerosity. Using an original approach, Fornaciai, Farrel, and Park (2019) show that the effect of the size of simple circular visual items on the perception of numerosity depends on whether the items are interpreted as apples or human faces, showing that numerosity perception can be influenced by the semantic interpretation of a non-numerical visual feature as size. Matejko, Hutchison, and Ansari (2019) investigate hemispheric specialization in the activity of the intraparietal sulcus in humans: they provide evidence for developmental trends in the left hemispheric specialization for numerical ordering of symbolic magnitudes. Are inter-individual differences in mathematical performance reflected in differences in the activity and anatomo-functional organization of the parietal-frontal number network? The paper by Lasne, Piazza, Dehaene, Kleinschmidt, and Eger (2019) suggests that they are: the accuracy decoding of number from the BOLD response of right parietal cortex correlated well with precision in discriminating numerosities. Subjects with higher precision for discrimination of numerosities also showed better decoding accuracy of numerosity in this region.

The cultural invention of symbols to indicate empty sets (“0”) has provided crucial support for the development of positional number systems. Ramirez-Cardenas and Nieder (2019) report the results of a single cell recording study in the monkey that help clarify how empty sets, as a precursor of 0, are represented in working memory. The study shows that activity in the prefrontal cortex (PFC) best correlates with behavioural performance with empty sets. Moreover, while during the retention interval the tuning curves of PFC remain stable, neurons in the ventral parietal cortex progressively bias their tuning preference towards empty sets, thus producing a corresponding overrepresentation of zero.

3. Operating on numbers

Establishing the organization of brain networks that underpin number processing can furnish focused insights into the anatomical correlates of normal or defective mathematical competence, and the neural changes that match improvements of mathematical competence due to education and training. In the normal brain, white matter pathways support the integrated function of cortical networks. Some neuropsychological syndromes, such as neglect and aphasia, can result from white matter lesion disrupting anatomical and functional connectivity. Using DTI, Klein, Willmes, Bieck, Bloechle, and Moeller (2019) provide evidence that intensive multiplication training increases the structural connectivity of the left hippocampus, a structure that, together with the parietal cortex of the angular gyrus, is implicated in the retrieval of arithmetic facts. The authors conclude that while the hippocampus might subserve fact-encoding and retrieval, the angular gyrus could be in charge of choosing whether to employ arithmetic knowledge as a function of the mathematical context and task at hand. In a study related to this special issue, Zhao et al. (2019) used functional near-infrared spectroscopy to investigate changes in resting state functional connectivity following learning of new subtraction and multiplication problems. Learning produced a shift from left parietal-right frontal resting state connectivity to right parietal-left frontal connectivity. Interesting inter-individual differences were also highlighted in this study, as participants with stronger right parietal – left frontal connectivity showed better subtraction learning, while those with poor left parietal-right frontal connectivity learned multiplication better. Together with other evidence (see for example investigations with functional intraoperative neurosurgical mapping; Della Puppa et al., 2013), this type of investigations is starting to shed new light on the neural dynamics that underpin different mathematical operations. Along this line of inquiry, Pinheiro-Chagas, Piazza, and Dehaene (2019) used a multivariate pattern analysis approach to characterise the temporal development of MEG signals during the solving of simple additions and subtractions of Arabic numerals presented sequentially in central fixation. The authors could decode, at the single-trial level, the specific brain topographies associated with the visual and numerical-magnitude features of the two operands. Most importantly, they were able to decode topographies that were specifically associated with the on-going operation. These results importantly expand on previous investigations that have investigated the brain correlates of mathematical computations with conventional univariate ERP techniques.

Popescu et al. (2019) looked at another aspect of mathematical competence by undertaking one of the first few comprehensive cross-sectional comparisons of professional mathematicians and non-mathematicians with regard to functional cognitive and grey and white matter structural characteristics related to experience-dependent plasticity. Not only did they find mathematical expertise to be associated with better performance in domain-specific and also domain-general aspects, but also specific grey matter density level differences and brain region specific correlations of performance with grey matter density. No structural differences were apparent for white matter tracts. The authors also stress that longitudinal research designs combined with training studies would be required to disentangle mutual dependencies between structural brain changes and experience, which themselves are seen as dynamic across the lifespan. Dotan and Friedmann (2019) report neuropsychological dissociations to inquire whether number-reading and word-reading rely on the same cognitive and neural mechanisms. They summarise an in-depth study of two cases with selective deficits in number reading, the specific locus of their number reading deficits being impaired parsing Arabic digit strings into triplets. The authors employed their own recent cognitive model for number reading, to show that even specific homologous subprocesses of number as compared to word reading can be selectively impaired, leading them to conclude that word and number reading pathways are almost entirely separate.

4. Developmental issues

The functional correlates of normal or abnormal mathematical competence in children have an important place in the field of mathematical cognition. Using a novel task, Cicchini, Anobile, and Burr (2019) measured the reproduction of dot arrays that varied simultaneously in numerosity, area and density, in normal and dyscalculic pre-adolescents. In participants with normal mathematical abilities, errors in the reproduction of area and density were negatively correlated, a finding that suggests numerosity-based performance. In contrast, dyscalculic participants showed significantly enhanced reliance on area during reproduction. These findings are in line with studies pointing at the existence of a "dedicated" numerosity sense that does not depend on covarying visual attributes of numerosity as area or density.

A few years ago, Doricchi, Merola, Aiello, Guariglia, Bruschini, Gevers, Gasaparini and Tomaiuolo (2009) highlighted that healthy adults show typical error biases during the mental bisection of number intervals: for intervals positioned at the beginning of tens the subjective interval midpoint is shifted toward values that are higher than those of the true midpoint, whereas for intervals at the end of tens the direction of the error bias is reversed toward values lower than the true midpoint. In this issue, Rotondaro, Ponticorvo, Gigliotta, Gazzellini, Dolce, Pinto, Miglino and Doricchi (2019) demonstrate that the same error biases are present in preschoolers and remain unchanged in first-, second-, third- and fifth-grade school children. Through a biologically plausible computational model, they propose that these biases reflect the modifications produced by the use of the decimal system on the Gaussian representations of numerosity in parietal and prefrontal number neurons.

5. Conclusions

One of the most fascinating aspects of science is "what to expect next". As our intuition of the significance of the data and observations that we keep collecting is often incomplete, we look for future investigations for fuller insight into the interpretation of our efforts. This special issue demonstrates how the field of math cognition is becoming differentiated and polymorphous. The results provided by such a wide variety of lines of inquiry, ranging from the perception of numerosity to the performance of different types of mathematical operations with Arabic numbers and the use of mathematical symbols and operands, renew and advance the understanding of math tools that biological and cultural evolution have jointly forged in our brains. These improvements will positively impact math education and re-education, and plausibly optimise the interaction of humans and machines. So we conclude by expressing our gratitude to our colleagues who contributed to this Special issue, and hope that their joint efforts will set solid bases for improving our "reasoned" intuition of numbers.

REFERENCES

Borghesani, V., de Hevia, M. D., Viarouge, A., Pinheiro-Chagas, P., Eger, E., & Piazza, M. (2019). Processing number and length in the parietal cortex: Sharing resources, not a common code. *Cortex, 114*, 17–27.

Cicchini, G. M., Anobile, G., & Burr, D. C. (2019). Spontaneous representation of numerosity in typical and dyscalculic development. *Cortex, 114*, 151–163.

De Wind, N. K., Park, J., Woldorff, M. G., & Brannon, E. M. (2019). Numerical encoding in early visual cortex. *Cortex, 114*, 76–89.

Dehaene, S., Bossini, S., & Giraux, P. (1993). The mental representation of parity and number magnitude. *Journal of Experimental Psychology: General, 122*(3), 371–396.

Della Puppa, A., De Pellegrin, S., d'Avella, E., Gioffrè, G., Munari, M., Saladini, M., & Semenza, C. (2013). Right parietal cortex and calculation processing: Intraoperative functional mapping of multiplication and addition in patients affected by a brain tumor. *Journal of Neurosurgery, 119*(5), 1107–1111.

Doricchi, F., Merola, S., Aiello, M., Guariglia, P., Bruschini, M., Gevers, W., et al. (2009). Spatial orienting biases in the decimal numeral system. *Current Biology, 19*(8), 682–687.

Dotan, D., & Friedmann, N. (2019). Separate mechanisms for number reading and word reading: Evidence from selective impairments. *Cortex, 114*, 176–192.

Fornaciai, M., Farrell, A., & Park, J. (2019). Looking for more food or more people? Task context influences basic numerosity perception. *Cortex, 114*, 67–75.

Galton, F. (1880a). Visualized numerals. *Nature, 21*, 252–256, 1880.

Galton, F. (1880b). Visualized numerals. *Nature, 21*, 494–495.

Karolis, V. R., Grinyaev, M., Epure, A., Tsoy, V., Du Rietz, E., Banissy, M. J., et al. (2019). Probing the architecture of visual number sense with parietal tRNS. *Cortex, 114*, 54–66.

Klein, E., Willmes, K., Bieck, S. M., Bloechle, J., & Moeller, K. (2019). White matter neuro-plasticity in mental arithmetic: Changes in hippocampal connectivity following arithmetic drill training. *Cortex, 114*, 115–123.

Koehler, O. (1941). Vom Erlernen unbenannter Anzahlen bei Vögeln. In *Die Naturwissenschaften* (pp. 201–218). Berlin, Heidelberg: Springer.

Koehler, O. (1950). The ability of birds to count. *Bulletin of Animal Behaviour, 9*, 41–45.

Lasne, G., Piazza, M., Dehaene, S., Kleinschmidt, A., & Eger, E. (2019). Discriminability of numerosity-evoked fMRI activity patterns in human intra-parietal cortex reflects behavioral numerical acuity. *Cortex, 114*, 90–101.

Matejko, A. A., Hutchison, J., & Ansari, D. (2019). Developmental specialization of the left intraparietal sulcus for symbolic ordinal processing. *Cortex, 114*, 41–53.

Pinheiro-Chagas, P., Piazza, M., & Dehaene, S. (2019). Decoding the processing stages of mental arithmetic with magnetoencephalography. *Cortex, 114*, 124–139.

Popescu, T., Sader, E., Schaer, M., Thomas, A., Terhune, D. B., Dowker, A., et al. (2019). The brain-structural correlates of mathematical expertise. *Cortex, 114*, 140–150.

Ramirez-Cardenas, A., & Nieder, A. (2019). Working memory representation of empty sets in the primate parietal and prefrontal cortices. *Cortex, 114*, 102–114.

Rotondaro, F., Ponticorvo, M., Gigliotta, O., Pinto, M., Pellegrino, M., Gazzellini, S., & Doricchi, F. (2019). The number interval position effect (NIPE) in the mental bisection of numerical intervals might reflect the influence of the decimal-number system on the Gaussian representations of numerosities: A combined developmental and computational-modeling study. *Cortex, 114*, 164–175.

Sahan, M. I., Majerus, S., Andres, M., & Fias, W. (2019). Functionally distinct contributions of parietal cortex to a numerical landmark task: An fMRI study. *Cortex, 114*, 28–40.

Tsouli, A., Dumoulin, S. O., te Pas, S. F., & van der Smagt, M. J. (2019). Adaptation reveals unbalanced interaction between numerosity and time. *Cortex, 114*, 5–16.

Zhao, H., Li, X., Karolis, V., Feng, Y., Niu, H., & Butterworth, B. (2019). Arithmetic learning modifies the functional connectivity of the fronto-parietal network. *Cortex, 111*, 51–62.