Neurocognitive evidence for cultural recycling of cortical maps in numerical cognition

Kumulative Habilitationsschrift
Zur Erlangung der Lehrbefähigung für das Fach Psychologie

Vorgelegt dem Rat der Mathematisch-Naturwissenschaftlichen Fakultät II der Humboldt-Universität zu Berlin

von

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Berlin, den 20.03.2014

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Verteidigung der Habilitation am:

05.01.2015

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Acknowledgments

I would like to express my sincere gratitude to the following persons who inspired my work and helped me improving it in many ways.

Before all I would like to thank Klaus Willmes for bringing me to the field of numerical cognition and his continued and precious support throughout the years. My utmost gratitude goes to Stanislas Dehaene who represents a never-ending source of inspiration and motivation. I cannot overestimate the advice, encouragement and support I received from Ed Hubbard, Bertrand Thirion, Jan Willem Koten, and Hans-Christoph Nürk. I still consider myself lucky to have shared some precious time working on common ideas and projects with Jan Lonnemann, Guilherme Wood, and Elise Klein. Last but certainly not least, I would like to thank Elke van der Meer for providing me with an efficient and friendly work environment at the Humboldt Universität.

My stay in Paris was undoubtedly the most important experience in my life because it allowed me meeting Laurianne, the woman I love and with whom I look forward to seeing our beloved daughter grow up.

2. Submitted manuscripts

Sorted alphabetically.

1. Huckauf, A., **Knops, A.**, Nuerk, H.-C., & Willmes, K. (2008). Semantic processing of crowded stimuli? *Psychological Research*, *72*(6): 648 – 656.
2. Klein, E., Nuerk, H.-C., Wood, G., **Knops, A.** & Willmes, K. (2009). The exact vs. approximate distinction in numerical cognition is not exact, but only approximate: How different processes work together in multi-digit addition, *Brain and Cognition, 69*, 369 – 381.
3. **Knops, A.,** Dehaene, S., Bertelletti, I., Zorzi, M. (in Druck). Can Approximate Mental Calculation Account for Operational Momentum in Addition and Subtraction? *The Quarterly Journal of Experimental Psychology.*
4. **Knops, A.,** Thirion, B., Hubbard, E.M., Michel, V. & Dehaene, S. (2009). Recruitment of an area involved in eye movements during mental arithmetic. *Science*, 324(5934):1583-5.
5. **Knops, A.**, Viarouge A., & Dehaene, S. (2009). Dynamic representations underlying symbolic and non-symbolic calculation: Evidence from the operational momentum effect. *Attention, Perception & Psychophysics*, 71(4), 803-821.
6. **Knops, A.** & Willmes, K. (2014). Linking ordinality and cardinality - evidence for a network of right parietal and right inferior frontal areas, *Neuroimage*. [doi: http://dx.doi.org/10.1016/j.neuroimage.2013.09.037]
7. **Knops, A.**, Zitzmann, S. & McCrink, K. (2013). Examining the presence and determinants of operational momentum in childhood. *Frontiers in Psychology, 4:325*. [doi: 10.3389/fpsyg.2013.00325]
8. Koten, J.W.*, Lonnemann, J., Willmes, K., & **Knops, A.*** (2011) Micro and macro pattern analyses of fMRI data support both early and late interaction of numerical and spatial information. *Frontiers in Human Neuroscience*. 5:115. [doi:10.3389/fnhum.2011.00115]
9. Lonnemann, J., Krinzinger, H., **Knops, A.**, & Willmes, K. (2008). Spatial representations of numbers in children and their connection with calculation abilities. *Cortex, 44*(4), 420-428.

* equal contributions

3. Introduction & Overview

Recent years have brought forward a plethora of evidence supporting the idea of a core system in the human brain that enables us to approximately perceive and process numerical information, the *approximate number system (ANS)*. Humans share this system with various species, pointing to an early evolutionary offspring and high evolutionary significance. One may wonder, though, what particular evolutionary advantage this system provides. Due to the ubiquitous nature of numerical information in the environment, being sensitive to the numerical ratios offers an enormous advantage that can be crucial for survival. For example, the ANS allows for comparing the respective approximate numbers of individuals in two groups during a hostile group encounter and choosing appropriate behaviour based on the numerical relation between groups ("fight or flight"). Equally importantly, choosing the more abundant of two food supplies (e.g. berries on bush) is of obvious evolutionary advantage.

Although modern post-industrial societies require more sophisticated behaviour and decision going beyond mere choices between fight of flight, numerical capabilities still are of outstanding importance both to everyday life and professional career prospects. A good mastery of numerical and arithmetic skills affects virtually all aspects of life – from grocery shopping to risk evaluation of medical interventions. Low mathematical understanding "distorts perceptions of risks and benefits of screening, reduces medication compliance, impedes access to treatments, impairs risk communication (limiting prevention efforts among the most vulnerable), and, based on the scant research conducted on outcomes, appears to adversely affect medical outcomes" (Reyna, Nelson, Han, & Dieckmann, 2009). Deficient numeracy – an overarching concept including all facets of numerical cognition, from basic numerical skills to highly abstract procedural knowledge in the mathematical domain - has been associated with elevated health risks, lowered willingness to participate in health prevention programs and lowered adherence. Finally, developmental dyscalculia (DD), the deficient development of appropriate numeracy in early childhood has been associated with increased risk of unemployment, lowered average income, and increased risk of coming into conflict with the law (Butterworth, Varma, & Laurillard, 2011). Indeed, it has been estimated that low numeracy in the United Kingdom produces annual costs of about £2.4 billion (Gross, Hudson, & Price, 2009). Together, this makes it very clear that a comprehensive understanding of the cognitive and cortical mechanisms underlying numerical and arithmetic processes is of high significance to society.

Here, I will argue that abstract mathematical competencies are tightly linked to the aforementioned ANS. I will argue that abstract arithmetic competencies are grounded in the ANS. Both, the ANS and arithmetic processes rely on overlapping brain circuits (Arsalidou & Taylor, 2011). Parietal cortex (PC) appears to be of particular importance. I will demonstrate that this notion goes beyond the report of mere overlap between activations in functional imaging studies. Instead, the spatial pattern of activation that is elicited by different tasks in parietal and prefrontal areas manifests a high degree of ordered similarity and possesses predictive value across cognitive domains. Low-level perceptual processes such as saccades lead to spatial patterns of activation in posterior superior parietal lobe (PSPL) that are predictive of patterns during abstract approximate calculation processes (Knops, Thirion, Hubbard, Michel, & Dehaene, 2009). This is interpreted in terms of cultural recycling of cortical maps for cognitive purposes that go well beyond the evolutionary scope of a given region. The proposal is that human mathematics builds from foundational concepts (space, time, and number) by progressively co-opting cortical areas whose prior organization fits with the cultural need. I will build upon behavioral and neuroimaging results from experiments with adults and children to support this idea and demonstrate its implications.

How can we identify the involvement of a particular neural system ***X*** and its original associated process ***x*** in a given process ***y***? The following criteria have been formulated with respect to the idea of neuronal recycling (Dehaene & Cohen, 2007, p. 385):

1. "Variability in the cerebral representation of a cultural invention should be limited.
2. Cultural variability should also be limited.
3. The speed and ease of cultural acquisition in children should be predictable based on the complexity of the cortical remapping required.
4. Although acculturation often leads to massive cognitive gains, it might be possible to identify small losses in perceptual and cognitive abilities due to competition of the new cultural ability with the evolutionarily older function in relevant cortical regions."

Applying these criteria Dehaene and Cohen identified arithmetic as one candidate domain for the concept of cultural recycling. They demonstrated that numbers activate circumscribed areas in the horizontal aspect of the intraparietal sulcus (hIPS), irrespective of format, modality or cultural background of the participants. Additionally, evolutionary precursors in putative homologue areas in the monkey have been described (criteria 1 & 2). Progressive change in anatomical structure and functional scope of hIPS has been demonstrated during the acquisition of numerosity in children (criterion 3).

Here, I will further operationalize the above criteria by defining predictions at the behavioral and neural level. If a given area ***X*** underlies process ***x*** and is 'recycled' to also serve process ***y***,

P1. the functional signature of area ***X*** should be reflected in processes ***x*** and ***y***. That is, the behavioral characteristics in terms of cognitive biases and effects in the co-opting domain (***y***) should reflect behavioral characteristics of the processes initially associated with area ***X***. The involvement of ***X*** in ***y*** might lead to particular cognitive biases.

P2. we should be able to identify, at a neural level, similar contributions of area ***X*** in both processes, ***x*** and ***y***. This entails
   a. common, overlapping activity and
   b. similar spatial pattern of activation in both contexts ***x*** and ***y***.

   Going beyond previous research this stipulates that cortical circuits exhibit sufficiently stable activation patterns across tasks and domains.

P3. area ***X*** should carry information from both processes when triggered at the same time. In particular, any interference between ***x*** and ***y*** should be reflected in region ***X***. This notion is a direct consequence from criterion 4. But rather than looking for altered or impaired functioning in domain ***x***, I argue that interference between ***x*** and ***y*** may be attributed to the shared recruitment of area ***X*** if criteria 1 and 2 are fulfilled. The interference should lead to identifiable activation patterns and behavioral signatures.

This thesis is divided into four parts. In part one (Study 1 to 4) I will use the operational momentum effect to demonstrate that (a) symbolic and non-symbolic approximate calculation partly rely on a common cognitive magnitude system, and that (b) mental arithmetic co-opts evolutionarily older cortical systems. In part 2 (Study 5 to 7) I will demonstrate the consequences and expenses that follow from the representational overlap, which in turn follows from the co-option of relevant brain circuits. I will show that the parietal implementation of numerical magnitude information leads to an automatic activation of numerical information even under a crowding regime (Study 5). I will argue that the interference between spatial and numerical information can be interpreted as a consequence of a representational overlap (Studies 6 & 7). Part three (Study 8) elucidates the grounding of mental arithmetic abilities in the ANS and argues for a mediation of the association between ANS and symbolic arithmetic via numerical ordering abilities, which in turn rely on neural circuits in right-hemispheric prefrontal cortex. Finally, part four will address some technical issues in the examination of approximate and exact calculation. In particular, I will argue that the involvement of approximate calculation in high-level symbolic calculation remains elusive due to a number of technical issues with stimulus-inherent numerical features (Study 9).

I will conclude this synopsis with a brief outlook how the current results can inform future research and help elucidating the functional architecture underlying numerical cognition.

4. Operational Momentum in symbolic and non-symbolic approximate calculation implies common underlying processes

- **Study 1 - Knops, A.**, Viarouge A., & Dehaene, S. (2009). Dynamic representations underlying symbolic and non-symbolic calculation: Evidence from the operational momentum effect. *Attention, Perception & Psychophysics, 71(4),* 803-821.
- **Study 2 - Knops, A.**, Dehaene, S., Bertelletti, I., Zorzi, M. (in press). Can Approximate Mental Calculation Account for Operational Momentum in Addition and Subtraction? *The Quarterly Journal of Experimental Psychology*.
- **Study 3 - Knops, A.**, Zitzmann, S., McCrink, K. (2013). Examining the presence and determinants of operational momentum in childhood. Frontiers in Psychology, 4:325. [doi: 10.3389/fpsyg.2013.00325]
- **Study 4 - Knops, A.,** Thirion, B., Hubbard, E.M., Michel, V. & Dehaene, S. (2009). Recruitment of an area involved in eye movements during mental arithmetic. *Science, 324(5934)*:1583-5.

According to the influential and widely accepted triple-code model (Arsalidou & Taylor, 2011) numerical information is internally represented by three separate but interacting codes: A *verbal representation* of numbers is activated in linguistically mediated operations like number naming, counting and retrieval of arithmetic facts (e.g., addition results < 10; multiplication table facts) which are stored in a verbal code in long term memory. The verbal code is associated with left perisylvian language areas and left angular gyrus (AG). A *visual number form representation* allows for recognizing Arabic digits and multi-digit numbers. It is associated to bilateral fusiform and lingual regions of the ventral visual stream, involved in object recognition. Most centrally to the following work, an *analog magnitude representation* is supposed to represent numerical quantity information (Dehaene, Spelke, Pinel, Stanescu, & Tsivkin, 1999; Molko et al., 2003; Rickard et al., 2000) in an approximate manner. The analog magnitude representation corresponds to the above mentioned approximate number system (ANS). The ANS follows Weber's law: In number estimation tasks increasing numerical magnitude leads to increasingly variable estimates. The increase in variability is proportional to the mean, resulting in a constant coefficient of variation. ANS acuity can be measured via the Weber fraction, that is the ratio at which two sets of objects (e.g. dot clouds) can be differentiated with a given accuracy (e.g. 75%). The Weber fraction correlates with mathematical performance, both retrospectively and cross-sectionally (Halberda, Ly, Wilmer, Naiman, & Germine, 2012). Higher precision (i.e. lower Weber fraction) goes along with better curricular mathematical performance. During childhood the ANS precision increases, peaking in adulthood (around 30 years), and decreasing again thereafter (Halberda et al., 2012). Importantly, training the ANS using non-symbolic (i.e. using dot patterns) addition and subtraction problems improves symbolic (i.e. using Arabic digits) math proficiency (Park & Brannon, 2013). It has been argued that the ANS provides humans with the 'start-up' tools for the acquisition of more advanced symbolic mathematical skills (Piazza, 2010).

Two hall-mark effects in numerical cognition have been interpreted as support for a spatially organized mental magnitude representation. First, in numerical magnitude comparison tasks using both symbolic and non-symbolic numerosities, performance is inversely related to numerical distance. The *distance effect* describes increasing reaction times and error rates with decreasing numerical distance of the to-be-compared stimuli. With increasing overall numerical magnitude of the stimulus pair, numerical distance must increase proportionally to guarantee constant performance. This is referred to as the *size effect*. Both effects can be explained assuming a linear arrangement of numerical magnitude with overlapping activation distributions centered on the presented numerosities. With increasing numerical magnitude overlap increases, either due to compression of the underlying scale in combination with constant width of activation (logarithmic model; Dehaene, 2003) or due to increasing variability and linearly spaced underlying scale (linear model; Gallistel & Gelman, 1992). In particular, the mental representation of numerical information is often hypothesized as a mental number line (MNL) with smaller number being located left from larger numbers, at least in left-to-right reading cultures. Recent findings of topographic representation of numerical magnitude information in parietal cortex provide a neural instantiation of the concept of a MNL (Harvey, Klein, Petridou, & Dumoulin, 2013).

Surprisingly little is known about how humans combine mental magnitudes in the course of mental arithmetic. In 2007 McCrink and colleagues (McCrink, Dehaene, & Dehaene-Lambertz, 2007) investigated if adult participants would be able to solve non-symbolic addition and subtraction problems. In their task participants were presented with non-symbolic addition and subtraction problems using clouds of dots. They showed that for additions and subtractions, both the mean number chosen by the participants and the variability of these chosen numbers increased with the correct outcome. However, the values chosen by the participants were not centered on the correct result, but were influenced by the arithmetic operation. In addition problems the estimated outcome was larger than the actual outcome, while it was smaller than the actual outcome in subtraction problems. McCrink and colleagues (McCrink et al., 2007) argued that this bias showed similarity to a perceptual phenomenon called “representational momentum” (Freyd & Finke, 1984). When they watch a moving object suddenly disappear, participants tend to misjudge its final position and report a position displaced in the direction of the movement (Halpern & Kelly, 1993; T. L. Hubbard, 2005; Kerzel, 2003). Analogously, McCrink and colleagues described their finding as an “operational momentum” (OM) since the misjudgment was related to the arithmetic operation carried out and suggested that subjects were moving “too far” on the number line.

A crucial theoretical stance following from the idea that the ANS is foundational for abstract arithmetic capabilities predicts that symbolic and non-symbolic numerical operations should be characterized by comparable behavioral performance patterns. While this has been extensively shown in the context of symbolic and non-symbolic magnitude perception and comparison (Burr & Ross, 2008; Fias, Lammertyn, Reynvoet, Dupont, & Orban, 2003; Piazza, Pinel, Le Bihan, & Dehaene, 2007; but see also Roggeman, Verguts, & Fias, 2007) for a different view) and in children (Barth, Beckmann, & Spelke, 2008) less evidence exists for the arithmetic domain with adults (Barth et al., 2006). Demonstrating that symbolic and non-symbolic numerical operations are guided by crucial psychophysical characteristics of the underlying ANS and exhibit similar cognitive biases puts prediction P1 to a test.

Study 1 tested this idea in a series of behavioral experiments using non-symbolic and symbolic quantities. The paradigm is depicted in Figure 1. Participants were instructed to indicate which numerosity was numerically closest to the actual result by clicking on the respective image.

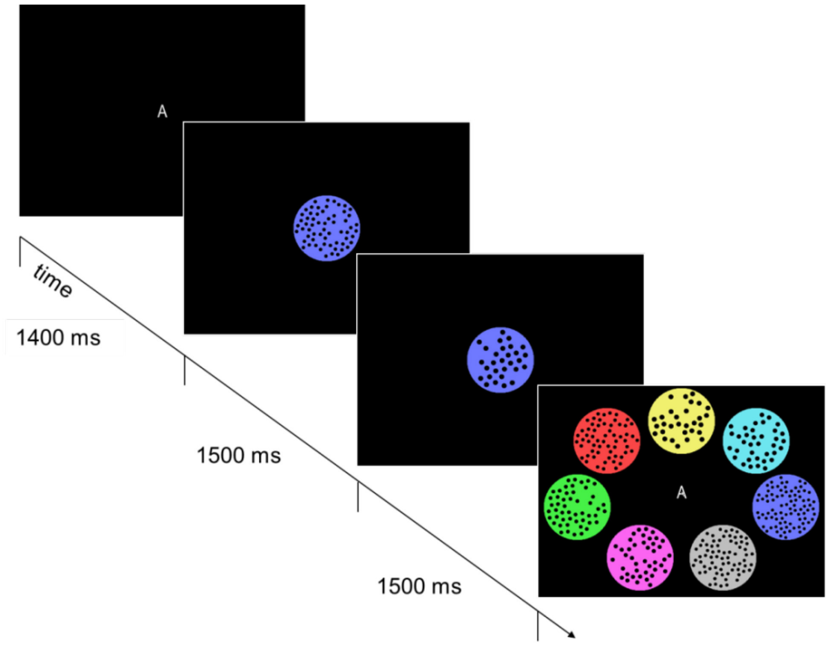

Figure 1: Graphical illustration of the paradigm. After an initial appearance of the letters "A" or "S", indicating addition and subtraction, respectively, the first and second operand successively appeared in the center of the screen. For trials in symbolic notation the sequence of events was identical. Dots were replaced by Arabic numbers. Figure 1 corresponds to Figure 1 in Study 1.

The results of experiment 1 from Study 1 (see Figure 2) can be summarized as follows. First, participants were able to solve both symbolic and non-symbolic addition and subtraction problems as indicated by the increasing mean response with increasing correct response. Second, variability of the responses increased proportionally with the mean chosen values, yielding a constant coefficient of variation, as stipulated by Weber's law. Again, this was observed in both notations with an overall higher accuracy in the symbolic notation. Most crucially, however, we observed an operational momentum effect in both non-symbolic and symbolic problems. Addition led to significantly larger responses than subtraction, even though this effect was larger in the non-symbolic notation. Finally, a Space-Operation Association of Responses (SOAR) was observed. Participants preferentially selected values presented at the upper left position with non-symbolic subtraction and values presented at the upper right position with non-symbolic addition. A similar left-ward bias was found in symbolic subtraction.

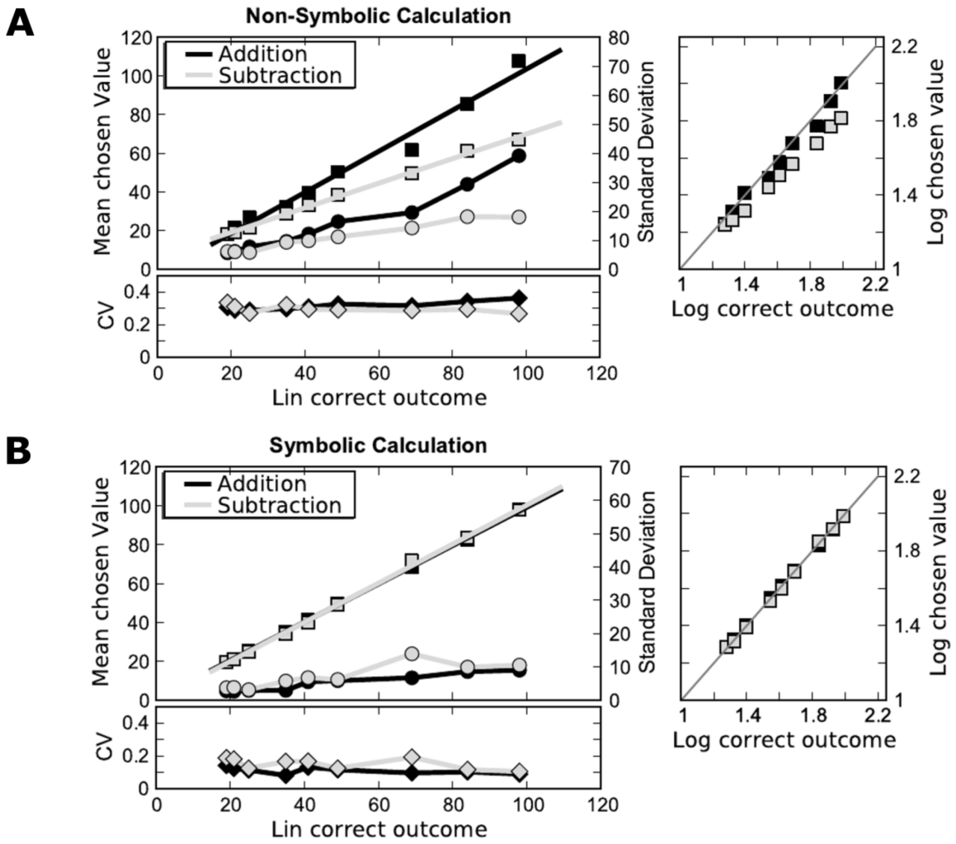

Figure 2: Left: Participants' average responses (chosen values, squares) and average standard deviation (circles) of their responses plotted against the correct outcome for both non-symbolic (A) and symbolic (B) addition (black) and subtraction (grey). The lower parts of Figure 2A and Figure 2B depict the coefficient of variation (CV), i.e. the ratio between standard deviation and mean chosen value. Right: The logarithm if the correct outcome plotted against the logarithm of the mean value chosen for non-symbolic (top) and symbolic (bottom) notation. The grey line indicates a ratio of 1, i.e. perfect performance. Figure 2 corresponds to Figure 3 in Study 1.

These results imply both partially different and shared subprocesses in the course of solving symbolic and non-symbolic approximate calculation problems. First, the overall higher accuracy in symbolic notation may reflect verbally mediated exact calculation, involving recall of verbal representations and retrieval of arithmetic facts from long-term memory. More interestingly, the observed similarity of biases (OM & SOAR) implies shared subprocesses, in line with prediction P1. In particular, these findings are consistent with the idea that mental arithmetic is mediated by attentional shifts along the MNL. According to this view, the OM results from attentional shifts to the left for subtraction and to the right for addition. These results also demonstrate that symbolic approximate arithmetic is characterized by central features of the underlying numerical magnitude representation (see prediction P1). Finding a constant CV in both notations strengthens the hypothesis that approximate arithmetic, even when the operands are presented as Arabic numerals, relies on magnitude representations and arithmetic procedures that are partially similar to those used for non-symbolic calculation. In sum, these results may be interpreted as evidence for partly shared cognitive systems and procedures in symbolic and non-symbolic approximate calculation and provide additional support for the grounding of mental arithmetic in the ANS.

Study 2 investigates in more detail how mental arithmetic is grounded in the ANS. By combining basic psychophysical parameters capturing the core properties of the ANS, we sought to predict participants' performance in simple mental arithmetic tasks and specify how the OM relates to the ANS. In detail, we reasoned that the overall underestimation in previous studies on the operational momentum (see Figure 1) might be the consequence of an overall miscalibration in estimating (i.e. underestimation) the number of items in a visual set. According to the logarithmic model of magnitude scale (see above), the OM effect might be linked with the overall acuity of the ANS. The idea is that in the course of mental arithmetic the cognitive system 'undoes' the compression, operating on uncompressed magnitudes. This process of uncompression may be subject to a systematic bias which results in a slightly compressed magnitude code during calculation. Consequently, higher overall acuity of the ANS may lead to less OM due to more efficient and more accurate compression/decompression mechanisms.

The task was similar to the paradigm from Study 1, but operands and response alternatives were not always in the same notation. For example, the operands (Op) of a given addition problem were presented in non-symbolic notation and the response alternatives (RA) in symbolic notation. Except for the purely symbolic combination of operands and response alternatives all Op-RA combinations were presented. Based on supplemental experiments we additionally computed the Weber fraction and the overall numerical estimation bias (miscalibration) for each participant and combined these values in a simple psychophysical model to predict performance in the arithmetic tasks.

The values predicted by the psychophysical model lined up nicely with the chosen values (see Figure 3). The majority of predicted values fell close to the diagonal which indicates an adequate fit between model predictions and observed data. Hence, the overall miscalibration in cross-notational mental calculation tasks can by and large be explained by the individual response bias in numerosity estimation in combination with the individual accuracy of the ANS. However, the psychophysical model did not capture the operation-specific over- and underestimation pattern, i.e. the OM effect that we observed in all notations. We found virtually no explanatory value of the proposed model: relative to the correct outcome, contrary to what was observed, the model predicted negative values for subtraction and positive values for addition, taking the form of a full cross-over effect for cross-notational conditions. Furthermore, inter-individual variance in non-symbolic number processing did not correlate with the amount of operational-momentum effect. These results suggest that the observed OM bias in approximate mental arithmetic is due to factors outside the ANS and not captured in the current model.

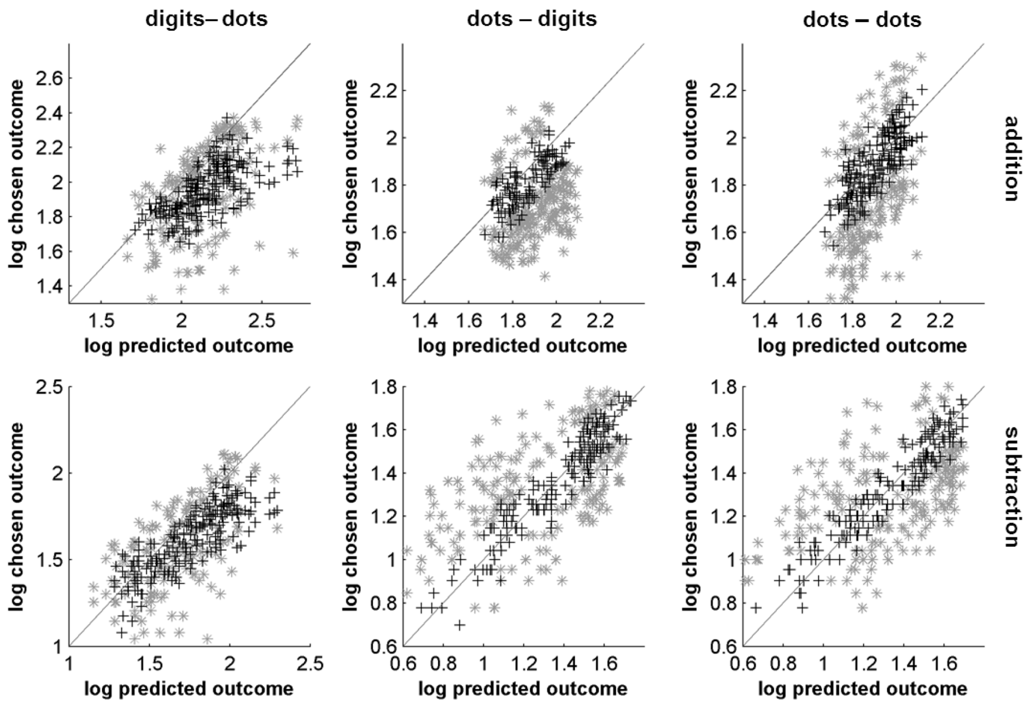

Figure 3: Predicted values of the model (x-axis) against the chosen values (y-axis) for all participants in different notations and operations. Left column: addition; right column: subtraction; first row: dots – dots; second row: dots – digits; third row: digits – dots. Values within the predicted range are shown as black crosses and values outside the predicted range are shown as grey asterisks. Each data point represents one trial. Note that data points may be superimposed if identical. The light grey diagonal indicates perfect correspondence between model prediction and observed performance. Figure 3 corresponds to Figure 2 in Study 2.

In particular, the results of Study 2 are not in line with the idea that the OM effect results from flawed compression-uncompression mechanisms. This interpretation is further corroborated by the results of Study 3 which tested OM in 6-and 7-year-old children and adult controls (see Figure 4). In a child-friendly adaptation of the above paradigm children and adult controls were presented with non-symbolic addition and subtraction problems. Additionally, reading abilities and spatial attention parameters were tested. Reading abilities were assessed via the reading time for a standardized text. Two components of spatial attention, orienting benefit and re-orienting costs, were assessed in an adaptation of the Posner paradigm.

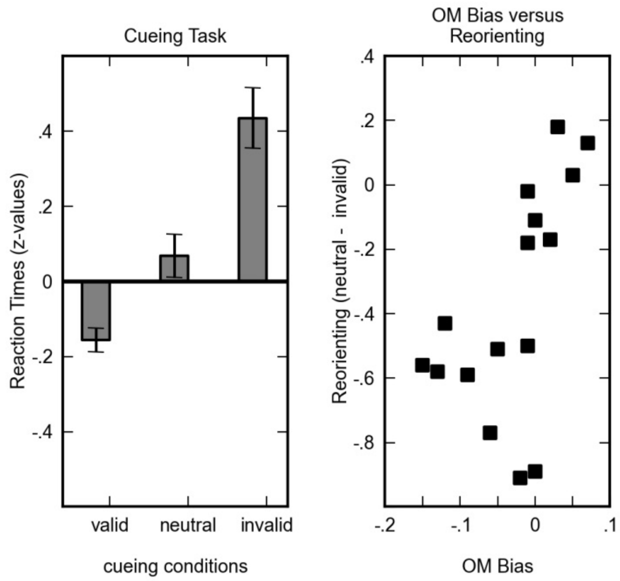

Figure 4: Left column: Z-standardized mean reaction times for valid, neutral and invalid conditions of the attention paradigm. Error bars indicate standard error of the mean. Right column: The reorienting effect (difference between neutral and invalid trials) plotted against the operational momentum bias. For reorienting better performance is indicated by numerically larger (i.e. less negative) values. A regular operational momentum effect corresponds to positive values, an inverse operational momentum effect corresponds to negative values. The correlation between reorienting and operational momentum signifies that the less children suffer from invalid cueing the more they are prone to exhibit a regular operational momentum effect. Figure 4 corresponds to Figure 6 in Study 3.

In line with previous research children were able to solve the non-symbolic problems, albeit with lower accuracy compared to adults. Most importantly, we observed an overall reversed OM effect in children, with addition leading to overall smaller responses than subtraction. This was in stark contrast to the regular OM effect in adult controls using the identical paradigm and is hard to reconcile with the compression approach, which predicts a regular OM effect in children. Due to the overall stronger compression of the MNL in children, one may even expect a stronger OM in children compared to adults.

The attentional shift account explains OM as the result of shifts of spatial attention along the MNL that lead participants to prefer outcomes in the “direction” of the arithmetic operation (Knops et al., 2009). According to this hypothesis we expected (a) a response distribution in children similar to the pattern observed in adults and (b) a relationship between attentional indices and the strength and/or presence of OM in children. In contrast, children showed a reverse OM bias under a Bayesian approach. The OM bias was positively correlated with the reorienting effect (r = .59, p = .017). With decreasing reorientation effect the tendency to exhibit a regular OM bias increased across children. Reorientation captures the ability to switch attention from invalidly-cued locations to the uncued location at which the actual stimulus appears (Carrasco, 2011). Children who are more proficient in this process tend to show a more adult-like OM bias. The size of the reorienting effect might be interpreted as an index for the integrity of the described attentional systems, and/or the extent to which the attentional system is connected to executive control functions in prefrontal cortex. Together with a functional attentional selection system - as evidenced by the significant benefit from valid cues - this implies a key role for a functional and mature attentional system for the OM to arise in the context of non-symbolic calculation tasks. Since OM effect did not significantly correlate with orienting, the observed pattern of results is not fully compatible with the attentional shift hypothesis. The results of Study 3 nevertheless imply a link of the OM to the attentional system.

Study 4 explicitly tested the hypothesis first put forward by Hubbard and colleagues (Hubbard, Piazza, Pinel, & Dehaene, 2005) that mental calculation involves shifts of the locus of activation along a MNL which relies on neural circuitry in posterior superior parietal lobule (PSPL) shared with those involved in updating spatial information during saccadic eye movements. Specifically, we tested prediction P2 stipulating that cultural recycling should lead to a stable pattern of activation in a given area in the context of a given cognitive process that can be identified in the context of a different process.

The fMRI study involved a saccade task and a symbolic and non-symbolic calculation paradigm. We employed a multivariate classifier to activation data from PSPL to distinguish between leftward and rightward saccades. Without further training this classifier then successfully differentiated between addition and subtraction trials from the calculation task. This generalization was observed with numbers presented either as Arabic symbols or as non-symbolic sets of dots, which implies shared cognitive processes between both notations. Results are depicted in Figure 5.

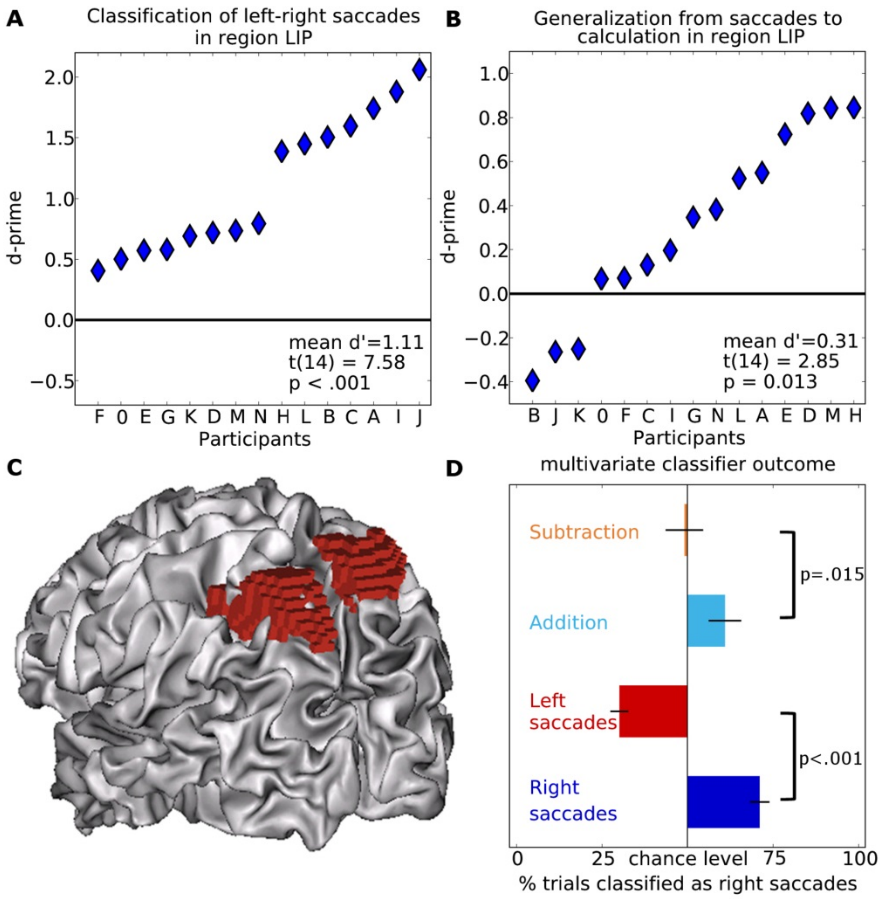

Figure 5: A, classification performance (d-prime) for each participant in the saccades task (participants sorted according to d-prime). B, classification performance (d-prime) per participant for generalization of the classifier trained on left/right saccades to subtraction/addition trials. C, voxel clusters in left and right PSPL region that resulted from the saccade localizer task and served as ROI for the classifier, rendered on white matter/grey matter boundary. D, percentages of trials classified as right saccades for subtraction (orange), addition (light blue) and left and right saccades (red and blue, respectively). Figure 5 corresponds to Figure 2 in Study 4.

The observed generalization implies that mental arithmetic superimposes on a parietal circuitry originally associated with spatial coding. Our results confirm the above hypothesis that mental calculation can be likened to a spatial shift along a mental “number line”. In a certain sense, when a Western participant calculates 18+5, the activation moves “rightward” on the MNL from 18 to 23. This spatial shift recycles neural circuitry in PSPL shared with those involved in updating spatial information during saccadic eye movements and therefore confirms prediction P2. The idea is that human mathematics builds from foundational concepts (space, time, and number) by progressively co-opting cortical areas whose prior organization fits with the cultural need. The PSPL area, perhaps because of its capacity for vector addition during eye movement computation (Pouget, Deneve, & Duhamel, 2002), appears to have a connectivity or internal structure relevant to arithmetic.

Studies 1 through 4 can be summarized as follows. First, symbolic approximate addition and subtraction share with non-symbolic addition and subtraction a number of cognitive signatures. Performance in both notations follows Weber's law. This can be interpreted as support for the grounding of higher mathematical competencies in the basic numerical core system, the ANS. Performance in approximate mental arithmetic problems was significantly modulated by the arithmetic operation at hand. Addition led to significantly larger response compared to subtraction. This OM effect has been replicated in several experiments with different stimuli and paradigms. Finding a shared effect suggests shared cognitive sub-processes in non-symbolic and symbolic arithmetic. Second, hitherto gathered evidence from Study 3 and Study 4 suggests that attentional shifts play a crucial role during mental arithmetic and may give rise to the OM effect. Third, Study 4 shows for the first time the involvement of low-level visual processes in higher-order cognition on a neural level. The cortical activation pattern elicited by saccades (which, in turn, are accompanied by shifts of spatial attention) was predictive for the type of arithmetic operation. The most plausible explanation for this finding implies that the neural circuits involved in spatial shifts of attention contribute to mental arithmetic in a comparable manner. Hence, mental arithmetic may have co-opted parietal areas and recycled their original function in the context of new cultural needs.

5. Sharing resources does not come for free – consequences of cultural recycling.

- **Study 5 -** Huckauf, A., **Knops, A.**, Nuerk, H.-C., & Willmes, K. (2008). Semantic processing of crowded stimuli? *Psychological Research*, *72*(6): 648 – 656.
- **Study 6 -** Koten, J.W.*, Lonnemann, J., Willmes, K., & **Knops, A.*** (2011) Micro and macro pattern analyses of fMRI data support both early and late interaction of numerical and spatial information. *Frontiers in Human Neuroscience*. 5:115. [doi:10.3389/fnhum.2011.00115]
- **Study 7 -** Lonnemann, J., Krinzinger, H., **Knops, A.**, & Willmes, K. (2008). Spatial representations of numbers in children and their connection with calculation abilities. *Cortex, 44*(4), 420-428.

  * equal contribution

Studies 1 to 4 suggest that mental arithmetic co-opts brain circuits that have evolved for spatial navigation, spatial perception and acting in space. The functional architecture of these brain areas appears to fit with the cultural needs. Formal mathematical reasoning is a relatively young cultural achievement. Although ancient traces of numerical information transmission date back thousands of years, the human brain only had a few hundred years to adapt to modern mathematics using Arabic numbers in a place-value system, including the concept of zero. From an evolutionary point of view this is far from enough time for developing dedicated cortical circuits. Cultural recycling does not co-opt existing cortical circuits by replacing their initial function. Instead, the initial functional scope is enlarged to the new culturally defined needs. In chapter 1 I demonstrated that this process can be observed using appropriate behavioral and functional imaging paradigms. I demonstrated that mental arithmetic 'inherited' performance signatures that characterize the ANS, e.g. Weber's law. In chapter 2 I will examine the putative costs of cultural recycling in the context of numerical-spatial interaction. In particular, enlarging the functional scope of a given brain area may come at the expense of fast and error-free performance because it leads to representational overlap and interference.

Large parts of the human brain are dedicated to the analysis of visual information and the guidance of motor behavior. The extraction of spatial and metric characteristics of the objects in a visual scene is crucial for successful motor actions. According to the widely accepted theory by Milner & Goodale (Goodale & Milner, 2004) visual perception results from integrating the output of two relatively independent processing streams: the ventral stream in temporal cortex subserves conscious recognition of visual objects ("vision for perception"), while the dorsal stream in parietal cortex (PC) is associated with visuomotor processes ("vision for action"). Interestingly, patient studies have shown that metric information from dorsal stream informs manual movements despite the absence of complete conscious access to this information (patient DF). This suggests that lack of complete conscious access does not entail temporal decay of numerical information processed in dorsal stream (Kouider & Dehaene, 2009). In Study 5 we explicitly tested this assumption in a crowding paradigm. Crowding describes the impairment of peripheral target perception by nearby flankers. Currently prevailing theories of crowding mainly rely on low-level visual or attentional mechanisms to explain the phenomenon. Higher-level processing of semantic information should hence not be possible since the visual input itself is impaired and cannot propagate to semantic levels (He, Cavanagh, & Intriligator, 1996; Pelli, Palomares, & Majaj, 2004). If, however, semantics of a given stimulus is processed in dorsal stream which has been demonstrated to affect manual movements in brain damaged patients, we reasoned that numerical information too may leave a semantic trace in a crowding regime.

In Study 5 participants were presented with laterally presented Arabic digits (target, e.g. 3) flanked by other Arabic digits (flankers, e.g. 4, yielding 434). In two experiments participants were asked to either judge the identity of the target (identification) or to decide whether the target is numerically smaller or larger than five (magnitude comparison). We observed semantic congruity effects in the magnitude comparison task. Performance to targets with congruent flankers (e.g. 434, both target (3) and flankers (4) are smaller than 5) was better compared to incongruent flankers (e.g. 636, while target (3) is smaller than 5, flankers (6) are larger). Moreover, variation of stimulus onset asynchrony (SOA) between target and flankers yielded so-called type-B priming effects (see Figure 6), indicative of interference from high levels of processing (Di Lollo, Enns, & Rensink, 2000; but see also Francis & Herzog, 2004). Hence, Study 5 suggests that in healthy participants, too, numerical information from dorsal stream influence performance. This argues against theoretical accounts of crowding that assume impaired visual information propagation to and from ventral stream areas. Study 5 demonstrates that participants must have had (nonconscious) access to target identity information (most likely processed in inferior temporal cortex) which has reached and activated number processors (in hIPS). This is in line with earlier findings of notation-independent number priming effects (Naccache & Dehaene, 2001) and implies that due to the implementation in parietal cortex numerical information does not rely on conscious access to inform other cognitive instances in a given task. Hence, numerical information inherit the functional features from ‘hosting‘ cortical circuits, in this case the capability to modulate overt behaviour even under a crowding regime. This is also in line with recent findings of automatic non-conscious access numerical information (Bahrami et al., 2010).

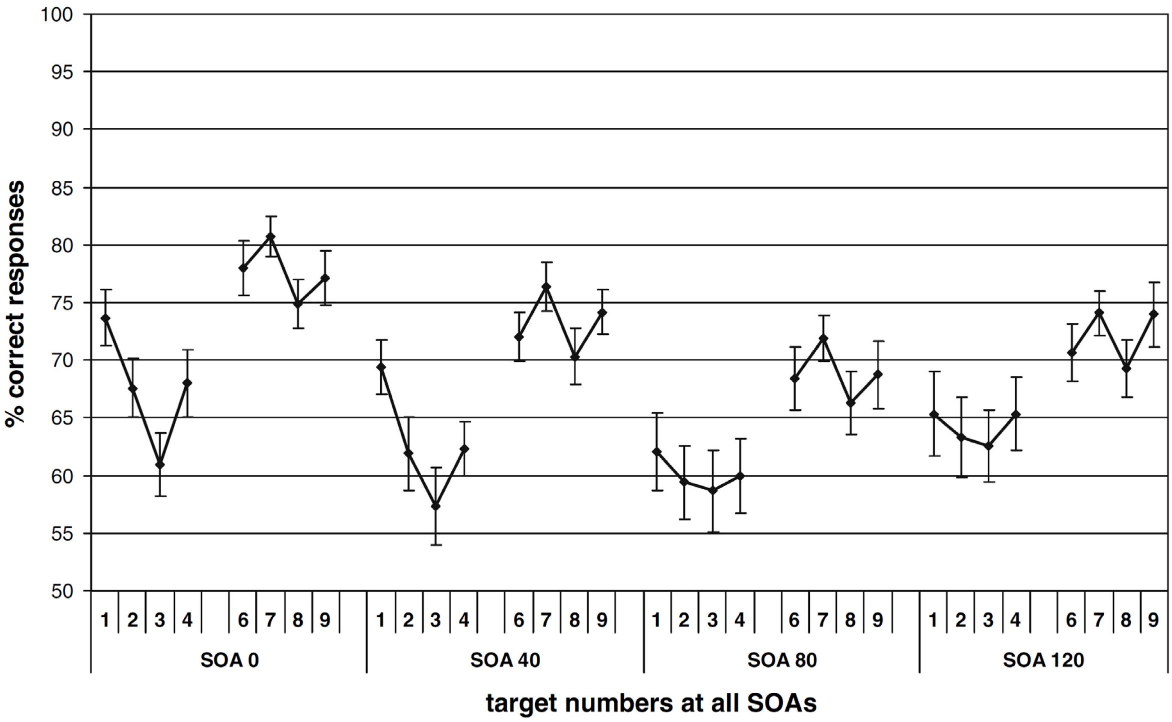

Figure 6: Mean proportion of correct responses and standard errors for each target in Experiment 2, separately for the different SOAs. The decreasing performance with increasing SOA characterizes Type B priming. Figure 6 corresponds to Figure 5 in Study 5.

A number of visual properties such as contrast, color or orientation are automatically extracted from the visual scene. Similarly, physical size has been demonstrated to automatically interfere with numerical magnitude information. Comparing two Arabic digits in terms of physical and numerical size/magnitude takes longer and is more error prone when the two dimensions lead to contradictory information, for example 1_9. Although being numerically larger than 1 the digit 9 is physically smaller. This size congruity effect is one instantiation of numerical-spatial interactions. Recent theoretical frameworks attribute these interactions either to representational overlap at the central semantic stage of information processing (Schwarz & Heinze, 1998) or to interfering motor responses later in the cascade of cognitive events (Cohen Kadosh et al., 2007).

In Study 6 we used fMRI to investigate the functional and cortical locus of numerical-spatial interactions using a numerical landmark task. Participants were presented with three horizontally arranged two-digit numbers at a time (e.g. 12__25__84). The task was to decide which numerical interval was numerically smaller, the interval between the leftmost and the middle number (12_25) or the interval between the middle number and the rightmost number (25_84). Orthogonal to the numerical distances/intervals we manipulated the physical distances by changing the spatial position of the middle number. In one third of the trials physical intervals and numerical intervals were congruent (e.g. 12_25___84), in one third intervals were neutral (see first example), and in one third intervals were incongruent (e.g. 12___25_84). Additionally, a saccade localizer and a calculation localizer were administered to identify regions of interest in parietal cortex (AIP, hIPS, and PSPL).

Standard General Linear Model (GLM) analyses revealed a large overlap in bilateral parietal areas between congruent and incongruent trials (see Figure 7A; green). These regions also overlapped with saccade-related regions (pink) and calculation-related regions (blue). However, merely overlapping activation between two conditions does not necessarily imply shared processed. More information can be extracted from the functional brain maps when analyzing the spatial pattern of activation across voxels. GLM analysis lacks the capacity to integrate the numerous relations between vertices in a given region of interest (ROI) that form specific spatial or temporal patterns of activations. Recent approaches to the analysis of multivariate brain imaging data emphasize that different tasks, conditions, and even stimuli give rise to distinct and recognizable patterns of activations even in situations when the GLM approach is not sensitive enough to reveal amplitude differences (O'Toole et al., 2007; Peelen, Wiggett, & Downing, 2006). Here, we used across voxel correlations (AVC) to analyze in detail the functional patterns associated with a given task or condition. We extracted the beta weights from the contrasts in the GLM analysis from 12 ROIs. Those beta weights were then correlated across vertices. The resulting across vertex correlation (AVC) matrices reflect the micro-organization of the vertices within the 12 ROIs (see Figure 7B) in the course of the four cognitive tasks.

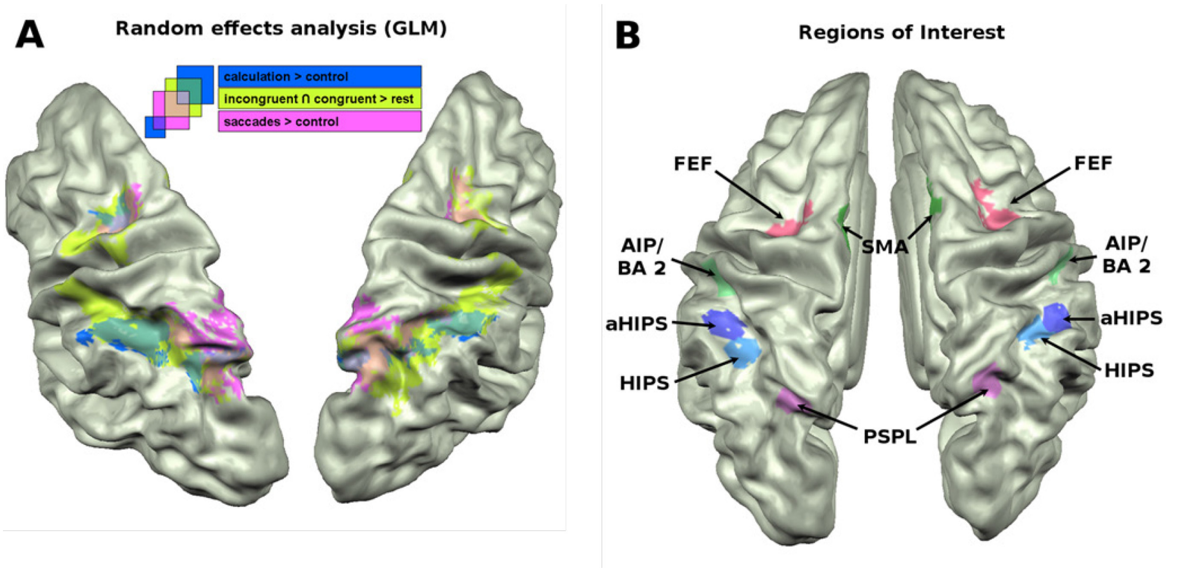

Figure 7: A, brain activation data of the GLM analysis (p = .005, uncorrected) projected on the cortex-based aligned average anatomy of the sample. Mapped contrasts: conjunction of incongruent and congruent vs. baseline (greenish); subtraction vs. control (blue); saccades vs. control (pink). B, The 12 ROIs selected based on activation data shown in A. Figure 7 corresponds to Figure 2 in Study 5.

Figure 8 exemplifies the difference between amplitude-based GLM analyses and spatial pattern-based AVC. Since analyzing spatial patterns of activation (e.g. using AVC) or GLM may lead to completely different results using both types of data analysis offers a comprehensive analysis approach.

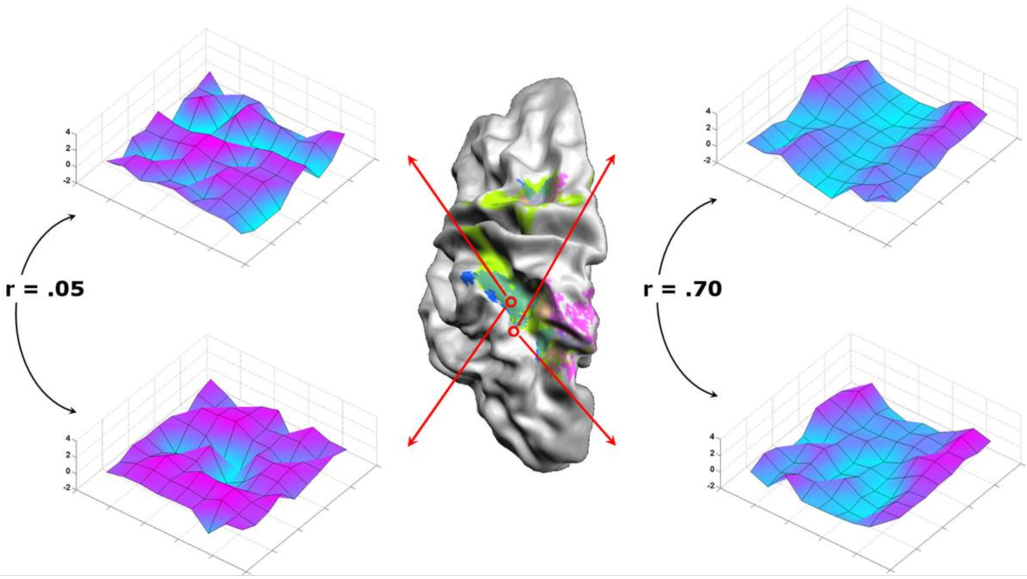

Figure 8: Activation patterns from two different contrasts sampled from two ROIs (red circles) in the left hemisphere (middle, top view). Top row depicts shows contrast A, bottom row shows contrast B. On the left both contrasts show overlap in left intraparietal cortex. However, the spatial patterns associated with contrasts A and B are completely different (r = .05). This indicates that the voxels in this ROI are differentially involved in both situations. On the right we see the reverse situation, where the spatial pattern between contrasts is high (r = .70) but no significant activation was observed.

Extent of the AVC in the 12 ROIs is shown in Figure 9A as color-coded link between nodes referring to the activation from congruent, incongruent, arithmetic, and saccades. Blue and green colors indicate low correlations, followed by yellow/orange and red for medium and high correlations, respectively. In all ROIs congruent and incongruent trials elicited highly correlated patterns of activations. Together with the overlapping activation in incongruent and congruent trials this supports the notion that both types of trials rely on spatially overlapping neural circuits with highly correlated patterns of activity. We subjected the AVC matrices to a cluster analysis to reveal the macro-organization of brain activity (Figure 9A). The results suggest two large-scale networks – a motor-related network and a network devoted to saccades and numerical information. The analysis of the micro and macro-organization of the different tasks in the different ROIs suggest a subdivision of the areas along the HIPS and a differential involvement of the areas defined here in the resolution of the conflict occurring when spatial and numerical information do not converge on the same response.

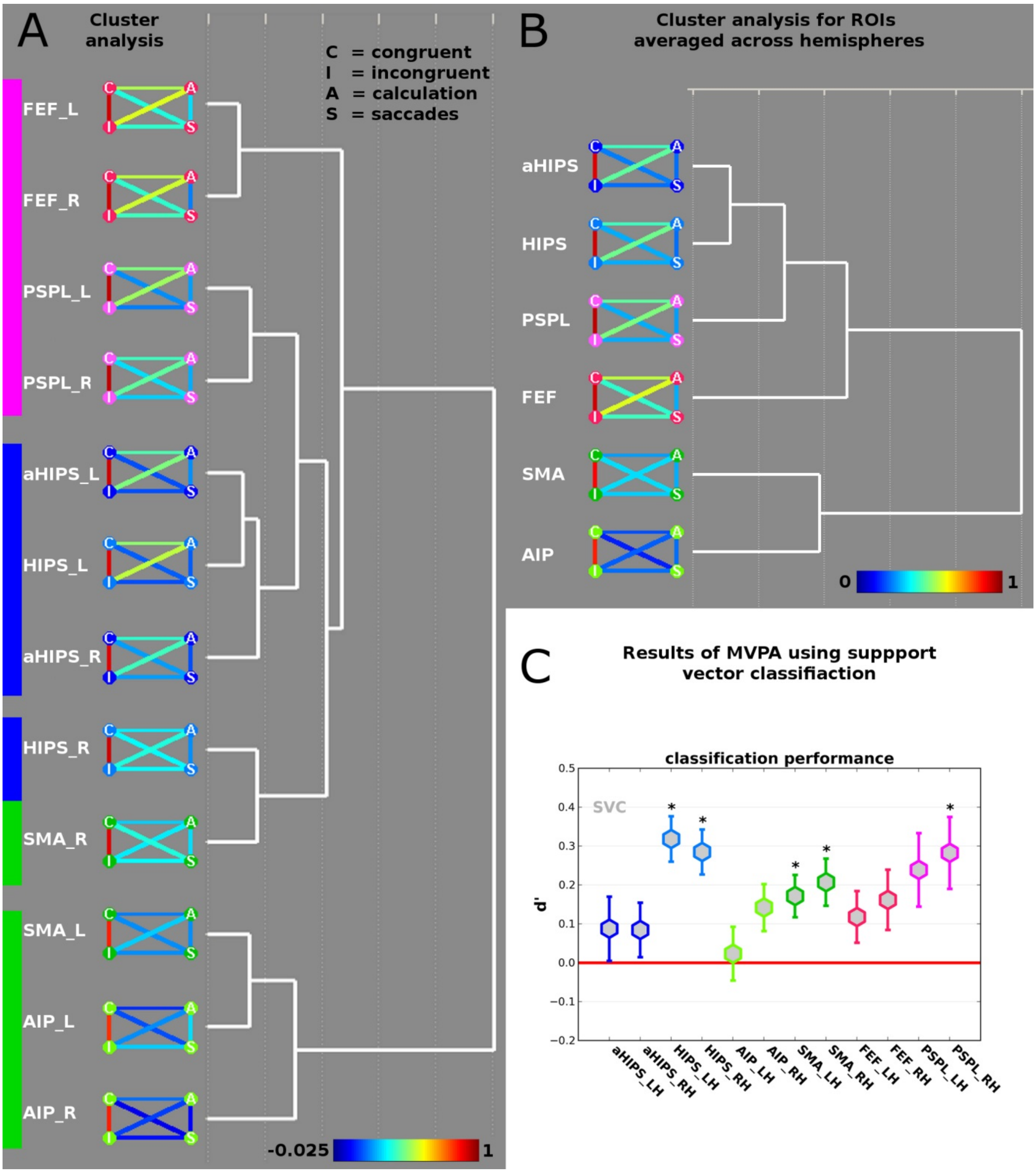

Figure 9: A, results of the cluster analysis of the AVC between congruent, incongruent and the two localizer tasks (saccades and calculation) in the 12 ROIs. The four corners represent congruent (C), incongruent (I), calculation (A) and saccades (S) contrasts. The color of the connecting lines indicates height of respective correlation in the ROI (see bottom for scale). B, results of the cluster analysis of the 12 ROIs collapsed across hemispheres. C, results of the decoding analysis differentiating incongruent from congruent trials in the different ROIs. Coefficient d-prime was computed by defining correct classification of congruent trials as congruent as true positive and classification of incongruent trials as incongruent as true negative. Stars indicate d-prime significantly larger than zero (red line) at p<.05 (corrected for multiple comparisons). Error bars represent standard error of the mean. Figure 9 corresponds to Figure 3 in Study 5.

To further investigate the implication of the different clusters (and the ROIs therein) in the context of the numerical landmark task we used a support vector machine classifier to differentiate congruent from incongruent trials (see Figure 9C). Importantly, in ROIs from each of the two large-scale networks the spatial activation patterns allowed for a better-than-chance distinction between congruent and incongruent trials. Combining prior knowledge about the different ROIs' functional scope with their network-structure allows differentiating between central-semantic levels of information processing and response-related levels. Finding that ROIs at both levels of information processing carried information that allowed disentangling congruent and incongruent trials suggests that the numerical-spatial interference arises both at early and late levels of information processing.

In Study 7 we administered the same paradigm to 8- and 9-year-old children and observed a strong distance-congruity effect which was present over the entire temporal range of the reaction time distribution (from early to late RT bins). These results demonstrate that the comparison of numerical distances was strongly influenced by the spatial arrangement of the stimuli. This constitutes further evidence for the involvement of spatial representations in the context of numerical tasks, even in third graders. Together with the observed correlations with calculation abilities in boys this supports the close link between numerical and spatial processes and point to an early ontogenetic onset.

Together, these results imply that cultural recycling of parietal areas in the course of numerical cognition may lead to cognitive costs when information from the numerical and spatial domain is contradictory, as stipulated by prediction P3. Study 6 demonstrates that the interference arises at central semantic stages of information processing in areas that are frequently found in studies investigating mental arithmetic or number processing. Interestingly, anterior parietal areas related to hand movements and functionally different from the saccades/number cluster also carry congruity conflict information. In combination with the findings from saccade-related areas this lends further support to the notion made by Hubbard and colleagues (2005) that the numerical-spatial interaction may be due to the interaction at the motor programming level. Future studies should further investigate how the functional and cortical dynamics during hand- and eye-movements contribute to spatial-numerical interactions and mental arithmetic.

6. Numerical ordering – the missing link between the approximate number system and mental arithmetic?

Study 8 - Knops, A. & Willmes, K. (2014). Numerical ordering and symbolic arithmetic share frontal and parietal circuits in the right hemisphere. *Neuroimage, 84*, 786 – 795.

In chapters1 and 2 I have argued for a cultural recycling of cortical circuits in parietal cortex for numerical processing. This does not come 'for free' but entails specific performance characteristics. First, mental arithmetic carries functional signatures from the underlying cortical structures. In particular we see that numerical processing and mental arithmetic follow Weber's law. We also found evidence for an influence of attentional shifts during mental arithmetic, a core candidate mechanism underlying the operational momentum effect in addition and subtraction. Finally, we observed that much like spatial information numerical magnitude is processed automatically and interferes with spatial information at both central and response-related stages. Together, this is line with the assumption that the ANS can be understood as a core capacity that provides us with a start-up tool for acquiring mental arithmetic (Piazza, 2010). Put differently, mental arithmetic is grounded in the approximate number system. How does this come about? What are the particular mechanisms that instantiate this process? A recent proposition emphasizes the role of numerical ordering in this context. Lyons and Beilock recently demonstrated that the correlation between core ANS parameters (i.e. the Weber fraction) and mental arithmetic performance was statistically mediated by numerical ordering abilities in a large sample of highly educated college students (Lyons & Beilock, 2011).

Study 8 investigated the neural correlates of the relation between mental arithmetic and numerical ordering. We administered a mental calculation task (additions & subtractions), as well as an ordinality judgment task ("Is the sequence 1_5_3 numerically ascending or not?") to participants while measuring their brain activity with an MR system. We augmented standard GLM analyses, revealing largely overlapping activity in a fronto-parietal network for both tasks, with a correlation-based analysis of the spatial pattern of activation (AVC, see chapter 2).

We defined three criteria for areas that functionally link the processing of order information to mental arithmetic: First, the area must be active in both ordering and mental arithmetic. Second, the spatial activation pattern elicited by ordering should be similar to the spatial pattern elicited by mental arithmetic and this correlation should be consistently found in the majority of participants (i.e. be significant at the group level). Third, we hypothesized that those arithmetic operations, which are more demanding in terms of numerical competencies and for which ordering abilities are more important, also exhibit a stronger correlation with ordering ability. A right-hemisphere network comprising anterior aspects of the intraparietal sulcus as well as Brodmann area 44 (BA 44) was identified that met all criteria to be considered a candidate region for establishing the behaviorally observed link between the ANS and symbolic calculation abilities.

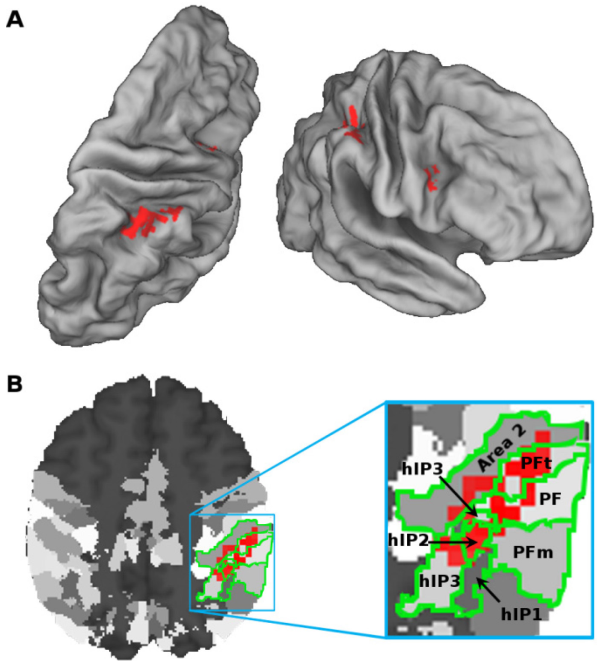

Figure 10: A, right hemispheric regions fulfilling all criteria (1-3) as defined in the introduction projected on posterior-superior (left) and lateral-frontal (right) views of the brain. B, projections on horizontal plane (z = 49.5) of cytoarchitectonically defined parcellation of the brain in SPM (Anatomy toolbox (Eickhoff et al., 2007)) with a zoom on the activated regions (blue box) on the right. Borders of labeled areas in right parietal lobe are depicted in green; all FDR-corrected ($p < .05$) and inclusively masked by the contrasts as specified in the text. Figure 10 corresponds to Figure 3 in Study 8.

We propose that this network operates on a spatial code and can be considered the right hemisphere counterpart of the well-known left-hemisphere network engaged in processing of order information in language and action processing (Meyer, Obleser, Anwander, & Friederici, 2012). For the first time we provide a plausible functional interpretation of right hemisphere BA 44 activity that has frequently been reported in mental arithmetic. This may be understood as another instantiation of cultural recycling of brain circuits evolved for the understanding of ordinal relations in concrete and abstract series of events such as language in the left hemisphere and space in the right hemisphere.

7. Exact versus approximate calculation – a conceptually warranted but empirically elusive distinction.

- **Study 9 -** Klein, E., Nuerk, H.-C., Wood, G., **Knops, A.** & Willmes, K. (2009). The exact vs. approximate distinction in numerical cognition is not exact, but only approximate: How different processes work together in multi-digit addition, *Brain and Cognition, 69*, 369 – 381.

In the previous chapters I discussed the characteristics of approximate arithmetic and its implementation in the human brain. Importantly, I argued that the ANS crucially contributes to this process. One key finding is that the influence of the ANS on mental arithmetic is more pronounced in the context of approximate operations. Using symbolic notation, for example, we observed a smaller operational momentum effect compared to non-symbolic notation. Yet, even in the symbolic notation one may distinguish between approximate and exact calculation. The question arises, though, how to distinguish between these processes. A frequent approach to probe approximate calculation is to present participants with two incorrect response alternatives in the context of mental addition problems (Stanescu-Cosson et al., 2000). For example, for the problem 1 + 2 = ? participants are presented with the alternatives 4 and 8. Even without retrieving the exact result participants are supposed to readily reject 8 since the numerical distance to the correct response is large and, more importantly, larger than the distance of the second incorrect response alternative. Exact calculation, however, is triggered using the correct result and a close but incorrect response alternative, for example, 3 and 5 for the above problem. While problem size is expected to exert a huge impact on exact calculation, using approximation should be relatively unaffected by problem size. Indeed, this is exactly what Stanescu-Cosson and colleagues (Stanescu-Cosson et al., 2000) observed. However, as becomes obvious from the above examples, the exact-approximate distinction is undermined by confounds in the stimulus material. For example, target and distractor distance (distance of target and distractor to correct result) is smaller in exact problems (0 and 2 for exact versus 1 and 5 in the approximate), potentially leading to more difficult distinction between response alternatives due to smaller numerical distances. From the above it follows that the approximate condition exclusively contained non-identical (NIT) trials with large distractor distance (e.g., ‘‘1 + 2 = 4 or 8”), while the exact calculation condition exclusively contained identical (IT) trials with small distractor distance (e.g., ‘‘1 + 2 = 3 or 4”). Thus, rather than the distinction between exact and approximate calculation an interaction between target identity and distractor distance was investigated: NIT with large distractor distance (‘‘approximate calculation”) and IT with small distractor distance (‘‘exact calculation”, see arrows in Figure 11). Hence, the exact-approximate distinction would be confounded with the hallmark effect in numerical cognition, the distance effect. Additionally, carry-over effects were confounded in the Stanescu-Cosson (Stanescu-Cosson et al., 2000) study with the exact-approximate distinction.

In Study 9, we sought to disentangle the exact-approximate distinction from the above mentioned confounds in target and distractor distance, problem size, and carry-over. Participants had to solve two-digit addition problems. Target distance was orthogonally manipulated with respect to distractor distance while carry-over and problem size were matched across stimulus groups.

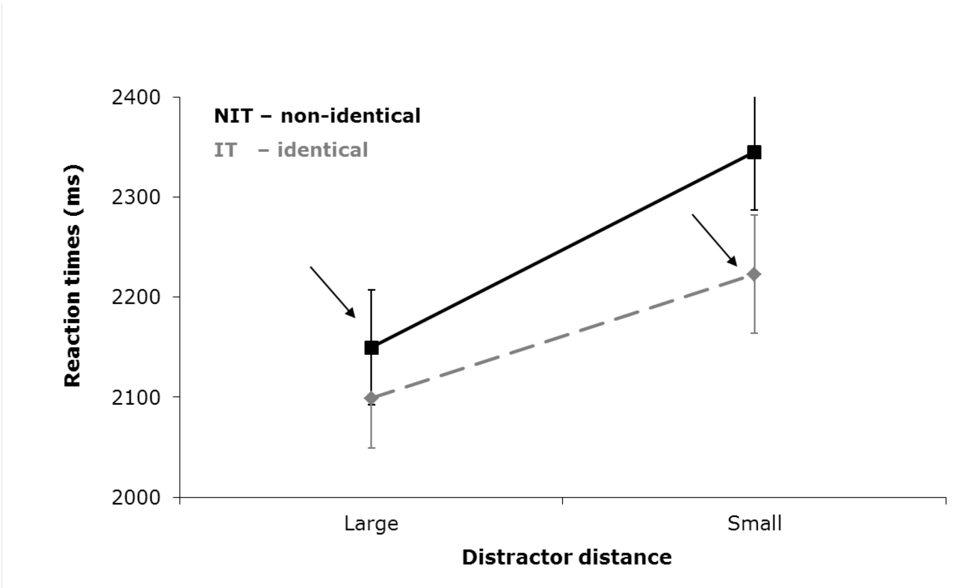

Figure 11: Identical (IT) vs. non-identical (NIT) target (target distance = 0 vs. target distance > 0) with large and small distractor distances. Error bars indicate standard error of the mean. The conditions actually compared in Stanescu-Cosson et al. (2000) are marked by arrows: obviously, RT effects are reduced in this comparison. Figure 11 corresponds to Figure 1 in Study 9.

Our results indicate that previous results may have overgeneralized findings that were due to particular stimulus configurations. In particular, we observed an interaction between target identity and distractor distance in the absence of a statistically significant difference between previous stimulus configurations. Also, the faster responses in the IT trials (previously assumed to trigger exact calculation) compared to NIT trials challenged the notion of approximation as a fast calculation process. Brain imaging results revealed no evidence either for distinct mental codes underlying these tasks or for any specific fMRI activation in NIT or IT calculation. Furthermore, the activation in parietal cortex was accounted for by the factor distractor distance, even within the NIT condition itself, as well as within the IT condition itself. Hence, problems with identical and problems with non-identical response alternatives rely on highly overlapping brain areas, modulated by target distance and distractor distance. These activity modulations, though, were previously attributed to the differential involvement of parietal cortex in exact versus approximate calculation.

While these results underline the importance of controlling task-relevant stimulus dimensions which may be confounded with the stimulus dimension under investigation it is important to note that they do not speak against the distinction between exact and approximate mental arithmetic *per se*. Future research needs to address the issue to what extent these theoretically and conceivably different operations do rely on overlapping and/or distinct neural circuits. First evidence comes from Study 4. Given that non-symbolic calculation relies to a larger amount on approximate numerosity estimates than symbolic calculation which may be verbally mediated, Study 4 demonstrates largely overlapping activations in parietal cortex in both symbolic and non-symbolic calculations. Furthermore, attentional operations in posterior parietal cortex were comparably involved in both notations as indexed by successful cross-notational generalization. Since both notations used the same arithmetic problems, stimulus set differences can be excluded in the interpretation of activation overlap.

8. Conclusions and outlook

In four chapters I argued for a grounding of mental arithmetic in the approximate number system (ANS) that can be interpreted as cultural recycling of parietal neural circuits which initially evolved for spatial navigation, perception, and action. In part 1 I demonstrated how approximate mental arithmetic is influenced by the functional characteristics of the co-opted parietal system: In Study 1, mental addition and subtraction in both symbolic and non-symbolic notation exhibits basic psychophysical characteristics of the ANS. Additionally, a common cognitive bias (operational momentum effect) was found in both notations, implying partially overlapping sub-processes. As shown in Study 2, the operational momentum effect (OM) cannot be accounted for by the inherent features of the ANS. Rather, it seems to be linked to the attentional system, as indicated by Studies 3 and 4. The neural correlates of basic perceptual processes (i.e. saccades) in posterior parietal cortex (PSPL) were found to be predictive of higher-order cognitive processes, namely addition and subtraction. Together, this underlines the idea that mathematical capacities are grounded in the basic numerical understanding mediated by the ANS. It is also in line with the notion of Hubbard and colleagues (2005) who conceived of mental arithmetic as interplay between hIPS and PSPL. Part 2 showed how numerical cognition inherits functional characteristics from parietal cortex: Study 5 showed that numerical information escapes from temporal decay even under a regime of non-conscious processing and can exert response-relevant influence in crowded presentation. Studies 6 and 7 demonstrated that co-opting parietal circuits comes at the expense of interference between spatial and numerical information. Combining multivariate analysis approaches in a new and innovative way revealed a central-semantic and response-related origin of numerical-spatial interaction. Carrying the map-based analysis approach from Study 6 to three-dimensional space, Study 8 argues for a mediating role of a right parieto-frontal network comprising anterior parietal areas and the right homologue of Broca's area (BA 44) in linking symbolic arithmetic to the ANS. The identified right-hemispheric network may form a contralateral homologue in the spatial domain to the left-hemispheric network which is thought to process ordinal aspects in the language domain. In Study 9 I described some of the stimulus-related pitfalls in the empirical investigation of the distinction between exact and approximate calculation.

The experimental work and the conceptual framework presented here may contribute to future work in several ways.

First, the conceptual framework presented in Study 4 may fruitfully be applied to other cognitive domains to decipher the contribution of particular neural structures to a given cognitive process at hand. For example, it has been reasoned that spatial and verbal working memory contribute preferentially to subtraction and multiplication, respectively (Lee & Kang, 2002). This notion lends itself to testing using the above sketched framework. By applying the framework to empirical methods with superior temporal resolution like MEG one may trace up to the millisecond at what point in time which cognitive processes manifests itself where in the brain (King & Dehaene, 2014). In general, demonstrating how low-level perceptual processes contribute to high-level cognition is in reach with the given conceptual framework and may bring psychologists one step further in elucidating the neural basis of cognition and delineating the cognitive components. Future studies need to investigate in more detail what conditions render a given cortical area's connectivity or internal structure favourable to certain cognitive functions.

Study 5 raises questions concerning the nature and neural fate of non-conscious numerical information in a crowding regime. What is the origin of crowding? What determines if a given piece of information exerts response-related influence or not? These questions need to be addressed. In this respect the numerical domain offers interesting opportunities. It may be hypothesized that compared to ventrally processed information for dorsally processed information it is easier to influence overt behavior because the dorsal stream is largely occupied with action–related processes. It would be highly disadvantageous, for example, if every aspect of grasping an object with the hand (distance to object, trajectory of the hand, speed of the movement, finger aperture, initiation of closing to grasp, etc.) would require conscious processing. The reader may remember how much cognitive control and effort was initially required to stir a car. Thus, the results from Study 5, too, could be interpreted as the consequence of numbers co-opting parietal cortex.

The analysis of spatial patterns of activity presented in Studies 6 and 8 goes well beyond the mere report of overlapping activation. This is an interesting approach to tackle the question what the particular role of given cortical area in a process may be. This is especially relevant for domain-general cortex areas such as parietal cortex which is involved in a number of processes (working memory, number processing, action planning, eye movement, multisensory integration).

Study 9 suggests that more work with rigorously controlled stimulus sets is needed to empirically disentangle the theoretically motivated concepts of approximate and exact calculation.

9. References

Arsalidou, M., & Taylor, M. J. (2011). Is 2+2=4? Meta-analyses of brain areas needed for numbers and calculations. *Neuroimage, 54*(3), 2382-2393. doi: 10.1016/j.neuroimage.2010.10.009

Bahrami, B., Vetter, P., Spolaore, E., Pagano, S., Butterworth, B., & Rees, G. (2010). Unconscious Numerical Priming Despite Interocular Suppression. *Psychological Science, 21*(2), 224-233. doi: Doi 10.1177/0956797609360664

Barth, H., Beckmann, L., & Spelke, E. S. (2008). Nonsymbolic, approximate arithmetic in children: abstract addition prior to instruction. *DevelopmentalPsychology., 44*(5), 1466-1477.

Barth, H., La Mont, K., Lipton, J., Dehaene, S., Kanwisher, N., & Spelke, E. (2006). Non-symbolic arithmetic in adults and young children. *Cognition, 98*(3), 199-222. doi: 10.1016/j.cognition.2004.09.011

Burr, D., & Ross, J. (2008). A visual sense of number. *Current Biology, 18*(6), 425-428.

Butterworth, B., Varma, S., & Laurillard, D. (2011). Dyscalculia: from brain to education. *Science, 332*(6033), 1049-1053.

Carrasco, M. (2011). Visual attention: the past 25 years. *Vision Research, 51*(13), 1484-1525. doi: 10.1016/j.visres.2011.04.012

Cohen Kadosh, R., Cohen Kadosh, K., Linden, D. E., Gevers, W., Berger, A., & Henik, A. (2007). The brain locus of interaction between number and size: a combined functional magnetic resonance imaging and event-related potential study. *Journal of Cognitive Neuroscience, 19*(6), 957-970.

Dehaene, S. (2003). The neural basis of the Weber-Fechner law: a logarithmic mental number line. *Trends in Cognitive Science, 7*(4), 145-147.

Dehaene, S., & Cohen, L. (2007). Cultural recycling of cortical maps. *Neuron, 56*(2), 384-398.

Dehaene, S., Spelke, E. S., Pinel, P., Stanescu, R., & Tsivkin, S. (1999). Sources of mathematical thinking: behavioral and brain-imaging evidence. *Science, 284*(5416), 970-974.

Di Lollo, V., Enns, J. T., & Rensink, R. A. (2000). Competition for consciousness among visual events: the psychophysics of reentrant visual processes. *Journal of Experimental Psychology: General, 129*(4), 481.

Fias, W., Lammertyn, J., Reynvoet, B., Dupont, P., & Orban, G. A. (2003). Parietal representation of symbolic and nonsymbolic magnitude. *Journal of Cognitive Neuroscience, 15*(1), 47-56.

Francis, G., & Herzog, M. H. (2004). Testing quantitative models of backward masking. *Psychonomic Bulletin & Review, 11*(1), 104-112. doi: Doi 10.3758/Bf03206468

Freyd, J., & Finke, R. A. (1984). Representational momentum. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 10*, 126 - 132.

Gallistel, C. R., & Gelman, R. (1992). Preverbal and Verbal Counting and Computation. *Cognition, 44*(1-2), 43-74. doi: Doi 10.1016/0010-0277(92)90050-R

Goodale, M. A., & Milner, A. D. (2004). *Sight Unseen: An Exploration of Conscious and Unconscious Vision*. New York: Oxford University Press.

Gross, J., Hudson, C., & Price, D. (2009). *The long term costs of numeracy difficulties.* . London (UK): Every Child a Chance Trust and KPMG.

Halberda, J., Ly, R., Wilmer, J. B., Naiman, D. Q., & Germine, L. (2012). Number sense across the lifespan as revealed by a massive Internet-based sample. *Proceedings of the National Academy of Sciences U S A, 109*(28), 11116-11120. doi: 10.1073/pnas.1200196109

Halpern, A. R., & Kelly, M. H. (1993). Memory biases in left versus right implied motion. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 19*(2), 471-484.

Harvey, B. M., Klein, B. P., Petridou, N., & Dumoulin, S. O. (2013). Topographic Representation of Numerosity in the Human Parietal Cortex. *Science, 341*(6150), 1123-1126. doi: DOI 10.1126/science.1239052

He, S., Cavanagh, P., & Intriligator, J. (1996). Attentional resolution and the locus of visual awareness. *Nature, 383*(6598), 334-337. doi: 10.1038/383334a0

Hubbard, E. M., Piazza, M., Pinel, P., & Dehaene, S. (2005). Interactions between number and space in parietal cortex. *Nature Reviews Neuroscience, 6*(6), 435-448.

Hubbard, T. L. (2005). Representational momentum and related displacements in spatial memory: A review of the findings. *Psychonomic Bulletin & Review, 12*(5), 822-851.

Kerzel, D. (2003). Attention maintains mental extrapolation of target position: irrelevant distractors eliminate forward displacement after implied motion. *Cognition, 88*(1), 109-131.

King, J. R., & Dehaene, S. (2014). Characterizing the dynamics of mental representations: the temporal generalization method. *Trends in Cognitive Sci*ence doi: 10.1016/j.tics.2014.01.002

Knops, A., Thirion, B., Hubbard, E. M., Michel, V., & Dehaene, S. (2009). Recruitment of an area involved in eye movements during mental arithmetic. *Science, 324*(5934), 1583-1585.

Kouider, S., & Dehaene, S. (2009). Subliminal number priming within and across the visual and auditory modalities. *Experimental Psychology, 56*(6), 418-433.

Lee, K. M., & Kang, S. Y. (2002). Arithmetic operation and working memory: differential suppression in dual tasks. *Cognition, 83*(3), B63-B68. doi: Pii S0010-0277(02)00010-0

Doi 10.1016/S0010-0277(02)00010-0

Lyons, I. M., & Beilock, S. L. (2011). Numerical ordering ability mediates the relation between number-sense and arithmetic competence. *Cognition, 121*(2), 256-261. doi: 10.1016/j.cognition.2011.07.009

McCrink, K., Dehaene, S., & Dehaene-Lambertz, G. (2007). Moving along the number line: operational momentum in nonsymbolic arithmetic. *Perception &Psychophysics, 69*(8), 1324-1333.

Meyer, L., Obleser, J., Anwander, A., & Friederici, A. D. (2012). Linking ordering in Broca's area to storage in left temporo-parietal regions: the case of sentence processing. *Neuroimage, 62*(3), 1987-1998. doi: 10.1016/j.neuroimage.2012.05.052

Molko, N., Cachia, A., Riviere, D., Mangin, J. F., Bruandet, M., Le, B. D., . . . Dehaene, S. (2003). Functional and structural alterations of the intraparietal sulcus in a developmental dyscalculia of genetic origin. *Neuron, 40*(4), 847-858.

Naccache, L., & Dehaene, S. (2001). The priming method: imaging unconscious repetition priming reveals an abstract representation of number in the parietal lobes. *Cerebral Cortex, 11*(10), 966-974.

O'Toole, A. J., Jiang, F., Abdi, H., Penard, N., Dunlop, J. P., & Parent, M. A. (2007). Theoretical, statistical, and practical perspectives on pattern-based classification approaches to the analysis of functional neuroimaging data. *Journal of Cognitive Neuroscience, 19*(11), 1735-1752.

Park, J., & Brannon, E. M. (2013). Training the Approximate Number System Improves Math Proficiency. *Psychological Sci*ence doi: 10.1177/0956797613482944

Peelen, M. V., Wiggett, A. J., & Downing, P. E. (2006). Patterns of fMRI activity dissociate overlapping functional brain areas that respond to biological motion. *Neuron, 49*(6), 815-822.

Pelli, D. G., Palomares, M., & Majaj, N. J. (2004). Crowding is unlike ordinary masking: distinguishing feature integration from detection. *Journal of Vision, 4*(12), 1136-1169. doi: 10:1167/4.12.12

Piazza, M. (2010). Neurocognitive start-up tools for symbolic number representations. *Trends in Cognitive Science, 14*(12), 542-551.

Piazza, M., Pinel, P., Le Bihan, D., & Dehaene, S. (2007). A magnitude code common to numerosities and number symbols in human intraparietal cortex. *Neuron, 53*(2), 293-305.

Pouget, A., Deneve, S., & Duhamel, J. R. (2002). A computational perspective on the neural basis of multisensory spatial representations. *Nature Reviews Neuroscience, 3*(9), 741-747. doi: Doi 10.1038/Nrn914

Reyna, V. F., Nelson, W. L., Han, P. K., & Dieckmann, N. F. (2009). How numeracy influences risk comprehension and medical decision making. *Psychological Bulletin, 135*(6), 943-973. doi: 10.1037/a0017327

Rickard, T. C., Romero, S. G., Basso, G., Wharton, C., Flitman, S., & Grafman, J. (2000). The calculating brain: an fMRI study. *Neuropsychologia, 38*(3), 325-335. doi: Doi 10.1016/S0028-3932(99)00068-8

Roggeman, C., Verguts, T., & Fias, W. (2007). Priming reveals differential coding of symbolic and non-symbolic quantities. *Cognition, 105*(2), 380-394. doi: 10.1016/j.cognition.2006.10.004

Schwarz, W., & Heinze, H. J. (1998). On the interaction of numerical and size information in digit comparison: a behavioral and event-related potential study. *Neuropsychologia, 36*(11), 1167-1179.

Stanescu-Cosson, R., Pinel, P., van De Moortele, P. F., Le, B. D., Cohen, L., & Dehaene, S. (2000). Understanding dissociations in dyscalculia: a brain imaging study of the impact of number size on the cerebral networks for exact and approximate calculation. *Brain, 123 (Pt 11)*, 2240-2255.

10. Appendix - Submitted manuscripts

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