RESEARCH REPORT



Anatomically ordered tapping interferes more with one-digit addition than two-digit addition: a dual-task fMRI study

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Abstract Fingers are used as canonical representations for numbers across cultures. In previous imaging studies, it was shown that arithmetic processing activates neural resources that are known to participate in finger movements. Additionally, in one dual-task study, it was shown that anatomically ordered finger tapping disrupts addition and subtraction more than multiplication, possibly due to a long-lasting effect of early finger counting experiences on the neural correlates and organization of addition and subtraction processes. How arithmetic task difficulty and tapping complexity affect the concurrent performance is still unclear. If early finger counting experiences have bearing on the neural correlates of arithmetic in adults, then one would expect anatomically and non-anatomically ordered tapping to have different interference effects, given that finger counting is usually anatomically ordered. To unravel these issues, we studied how (1) arithmetic task difficulty and (2) the complexity of the finger tapping sequence (anatomical vs. non-anatomical ordering) affect concurrent performance and use of key neural circuits using a mixed block/event-related dual-task fMRI design with adult participants. The results suggest that complexity of the tapping sequence modulates interference on addition, and that one-digit addition (fact retrieval), compared to

Handling Editor: Karl Friston, University College London. Reviewers: Roland Grabner, University of Graz; Marcie Penner-Wilger, King's University College. two-digit addition (calculation), is more affected from anatomically ordered tapping. The region-of-interest analysis showed higher left angular gyrus BOLD response for one-digit compared to two-digit addition, and in no-tapping conditions than dual tapping conditions. The results support a specific association between addition fact retrieval and anatomically ordered finger movements in adults, possibly due to finger counting strategies that deploy anatomically ordered finger movements early in the development.

 $\begin{array}{ll} \textbf{Keywords} & \text{Arithmetic} \cdot \text{Finger tapping} \cdot \text{fMRI} \cdot \text{Angular} \\ \text{gyrus} \cdot \text{Embodied cognition} \cdot \text{Numerical cognition} \\ \end{array}$

Introduction

Across different cultures, fingers play a role in representing and processing numbers. For example, most children and some adults count on their fingers when they are asked to do simple arithmetic. Multiple studies have shown that finger counting habits influence number processing performance (Domahs et al. 2010; Newman and Soylu 2014) and interact with visuospatial representations of numbers (Fischer 2008). Furthermore, there is evidence for adults' unconscious encoding of small numbers in the form of finger numeral representations (Badets et al. 2010) and finger counting patterns affecting arithmetic performance based on a sub-base-five effect (Klein et al. 2011). In multiple studies, it has been shown that finger sense (Fayol et al. 1998; Noel 2005) and fine motor ability (Luo et al. 2007) predict mathematical performance in young children. Additionally, finger and number processing were found to use overlapping neural resources both in adults (Andres



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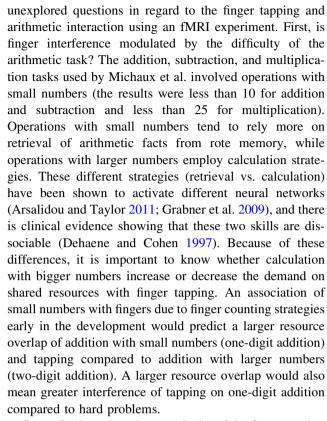
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et al. 2012; Rusconi et al. 2005; Zago et al. 2001) and in children (Krinzinger et al. 2011).

While there is considerable evidence for the relation between fingers and math, there is no consensus on what underlies this relation. There are mainly three approaches that explain the empirical findings on the finger and number processing relation. These are localizationist, functionalist (developmental), and redeployment (evolutionary) approaches (Penner-Wilger and Anderson 2013). According to the localizationist account (Dehaene et al. 2003), the co-occurrence of symptoms related to finger and number processing in neuropsychological cases (e.g., lesions in left angular gyrus) and evidence for neural overlap from neuroimaging studies are due to high anatomical proximity of crucial neural resources for finger and number processing, not due to a functional (casual) relationship between the finger and number processing systems. The functionalist approach explains the finger and number relation based on a developmental association due to the use of finger counting strategies in early numerical experiences, which permanently affects the neural organization for the number processing circuitry (Butterworth 1999). The massive redeployment hypothesis (MRH) provides an evolutionary explanation for the finger and number relation. According to MRH, new cognitive skills are acquired by redeployment of existing neural regions that originally participate in sensorimotor tasks (Anderson 2007). In the case of numerical processing, it is argued that the circuitry for mental representation of fingers was partially redeployed for number representation (Penner-Wilger and Anderson 2013).

From a performance-based perspective, both the functionalist and redeployment approaches predict that finger activity should interfere with numerical processes, particularly if the task relies on finger processes. For example, in a recent dual-task study, Michaux et al. (2013) found that anatomically ordered finger tapping interfered with addition and subtraction more than multiplication. They proposed that the finger counting-based calculation strategies used in childhood for simple addition and subtraction, but not for multiplication, can explain the selective interference based on an early grounding of addition and subtraction processes in finger representations, which still has influence on arithmetic processing in adulthood. In addition, they checked whether the selective interference on addition and subtraction was specific to finger movements, or was a general effect of motor activity. They compared the interference of finger movements with the interference of a feet movement task, where subjects were asked to produce a regular rhythm with their feet. The results showed that the selective interference on addition and subtraction was specific to finger tapping.

The current study extends the findings reported by Michaux et al. (2013), by pursuing three previously



Secondly, how does the complexity of the finger tapping sequence affect interference? Executing a complex as opposed to simple (following the anatomical order) finger tapping sequence has been shown to activate additional neural resources, particularly in the primary motor cortex (Gerloff et al. 1998). Since the interference effects during dual-task performance are modulated by the amount of neural overlap between two tasks (Klingberg and Roland 1997), finger tapping with a complex sequence may cause more interference on arithmetic performance. Another interesting sub-question is whether there is an interaction between addition difficulty and complexity of the finger tapping sequence. Finger counting strategies used in childhood for simple arithmetic involve anatomically ordered movement of fingers (e.g., no jumps from thumb to middle finger). It is possible that this leads to grounding of one-digit addition processes in circuits that are used for anatomically ordered tapping. This early grounding can yield to concurrent anatomical tapping interfering more with one-digit addition than two-digit addition.

The third focus of this paper is how addition difficulty, tapping, and tapping complexity affect and interact with neural processing. While we provide a whole-brain analysis exploring the effects of addition difficulty, tapping, and tapping complexity, we specifically focus on the angular gyrus (AG) with a region-of-interest (ROI) analysis based on previous experimental and neuropsychological evidence pointing to AG (particularly left) as a crucial site



for both arithmetic (Dehaene et al. 2003; Grabner et al. 2009) and finger processing (Ardila and Concha 2000; Roux et al. 2003). In Gerstmann's syndrome, left AG lesions were reported to cause disruption both in finger sense and arithmetic (Gerstmann 1940; Mayer et al. 1999). Two magnetic stimulation studies with healthy adults parallel findings from patient studies showing that stimulation of angular gyrus leads to disruptions both in number processing and in finger sense (Roux et al. 2003; Rusconi et al. 2005). However, Gerstmann's syndrome is controversial. The existence of such a condition is questioned both because it is hard to find a pure case of Gerstmann's syndrome and because the tetrad of symptoms does not have an obvious shared sub-function that can be affiliated with the angular gyrus (Rusconi et al. 2010).

Materials and methods

Participants

Thirteen right-handed, native English-speaking adults $(24.67 \pm 4.67 \text{ years old}, 6 \text{ females})$ participated in the experiment. None of the subjects reported a history of neurological or psychiatric disorders. The study was approved by the institutional review board, and participants gave written informed consent.

Task

A dual-task within-subjects study was conducted (Fig. 1). The primary task was addition and the secondary task finger tapping. The addition problem was presented at the top of the screen with three possible answers at the bottom. There were two levels of difficulty. One-digit questions (60 trials) involved addition of three numbers between 1 and 4 (e.g., 3+2+4; three instead of two operands were used to keep the RT differences minimal between one-digit and two-digit conditions, based on behavioral pilots with two and three operands), and two-digit questions (60 trials) involved the addition of two numbers between 11 and 88, excluding multiples of 5 (e.g., 41+37). The results of all two-digit addition questions were less than 100. The results

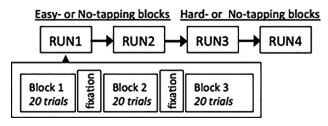


Fig. 1 Experiment design

of 23 one-digit questions were lower than 10, while the remaining 37 were between 10 and 12. The secondary task was finger tapping using the four fingers of the right hand (no little finger), with two levels of difficulty.

The easy-tapping sequence followed the anatomical order of fingers (ring, middle, index, and thumb), and the hard sequence followed the "ring, thumb, middle, and index" order (Fig. 2). Two fMRI button boxes (one for the left and one for the right hand) with five buttons on each were used to collect responses. Subjects used their right hands for the finger tapping task and their left hands to input responses for the addition questions. Three answer choices were presented in each trial. The ring, middle, and index fingers of the left hand matched with the choices A, B, and C, respectively.

There were six conditions (one-digit and two-digit notapping addition; one-digit and two-digit addition with easy-tapping: one-digit and two-digit addition with hardtapping). The filler task (sentence comprehension) was not included in the analyses; filler trials were randomly distributed. A mixed blocked/event-related design was used. The experiment was divided into four runs, and each run included one no-tapping and two tapping (easy or hard) blocks. Each run contained two 30-s fixation periods, used for the baseline condition, and located in between the first and second, and second and third blocks. The fixation periods involved passive viewing of a white cross hair centered on the screen. Each block started with a short practice of the finger tapping sequence to be used followed by a 10-s fixation. The blocks consisted of 20 trials of addition (no-tapping and dual tapping) and fillers. There were a total of 40 no-tapping, 40 easy-tapping, and 40 hard-tapping trials, divided evenly between one-digit and two-digit addition conditions. Finger tapping complexity was presented in two separate sets of runs such that the dual-task condition in one set involved tapping with the easy sequence while the other set involved the hard sequence (e.g., easy-tapping for runs 1 and 2, hard-tapping for runs 3 and 4). The order of the blocks was counterbalanced across participants.

Trial durations were fixed and were determined based on the mean RT values from the results of an earlier behavioral



Fig. 2 Easy and hard-tapping sequences



experiment that used the same stimulus set. The preset trial durations were as follows: one-digit (no-tapping: 3 s, easy-tapping dual: 4 s, hard-tapping dual: 5 s), two-digit (no-tapping: 4 s, easy-tapping dual: 5 s, hard-tapping dual: 6 s). The runs with easy-tapping took 772 s (\sim 13 min), and the runs with hard-tapping took 812 s (\sim 13.5 min). The intertrial interval (ITI) for even timed trials (4 or 6 s) was 10 s, and 11 s for odd timed trials (3 or 5 s).

fMRI acquisition and analysis

A Siemens TIM Trio 3.0 Tesla scanner with a 32-channel whole-head coil was used. Thirty-three oblique-axial images, providing whole-brain coverage, were captured. The images were collected using an echo-planar acquisition sequence, with TR = 2000 ms, TE = 30 ms, flip angle = 70° , with a voxel size of 3.4-mm \times 3.4-mm \times 3.8-mm with a 0-mm gap. Additionally, high-resolution structural images were also acquired using Siemens MPRAGE sequence (160 3DMPRAGE oblique-axial images were collected with TR = 2000 ms, TE = 3.34 ms, 7° flip angle, and a 256 \times 256 FOV, resulting in 1-mm³ voxels).

SPM8 (Friston and Penny 2003) together with xjView (http://www.alivelearn.net/xjview) and MarsBaR (http://marsbar.sourceforge.net/) toolboxes were used to analyze data. Images were corrected for slice acquisition timing, motion-corrected, spatially normalized to a standard EPI template (Evans et al. 1993), smoothed with a 8-mm Gaussian kernel to decrease spatial noise. Statistical analysis was performed on individual and group data by using the general linear model and Gaussian random field theory as implemented in SPM8. Comparisons between conditions were conducted with an uncorrected *p* value of .001 and a cluster size threshold of 22; this corresponds to a per-voxel false-positive probability of .041, determined by the Monte Carlo simulation (Ward 2000).

Results

Filtering

Trials with no responses (5.6 % of all trials) and with incorrect responses (1.6 %) were excluded from the behavioral analysis, except for task accuracy analysis where incorrect responses were included.

Behavioral results

Reaction time

A 3 \times 2 repeated measures ANOVA (Fig. 3) on RT (tapping: no-tapping vs. easy-tapping vs. hard-



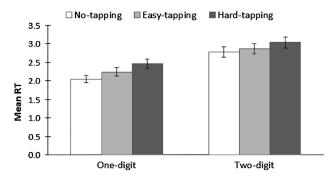


Fig. 3 Addition RT results. The *error bars* represent 95 % confidence intervals adjusted for within-subjects designs (Masson and Loftus 2003)

tapping × addition difficulty: one-digit vs. two-digit addition) showed a main effect of tapping, F(2,12) = 10.562, p < .001, partial $\eta^2 = .514$, and difficulty, $F(1, 12) = 90.691, p < .001, \eta p^2 = .901$. There was also a significant interaction between tapping and addition difficulty, F(2, 12) = 3.805, p = .04, $\eta p^2 = .276$. Mauchly's test indicated that the assumption of sphericity had not been violated, $\chi^2(2) = 2.808$, p = .246. To explore the main effect of tapping, we conducted post hoc pairwise comparisons using the Bonferroni correction on the averaged (across one-digit and two-digit conditions) RT values for each level of the tapping factor (no-tapping M = 2.41, SD = .21, easy-tapping M = 2.55, SD = .43, and hardtapping M = 2.75, SD = .38). The RT difference between no-tapping and easy-tapping was not significant (p = .37); however, there was a significant difference between notapping and hard-tapping (p < .001), and between easytapping and hard-tapping (p = .018) averaged values.

A test of simple effects was conducted to further explore the tapping and addition difficulty interaction. We conducted two one-way repeated measures ANOVAs with pairwise comparisons to explore the effect of tapping (notapping, easy-tapping, hard-tapping) separately for onedigit and two-digit addition RT. Both one-digit [F(1,(12) = 13.572, p < .001 and two-digit (F(1, 12) = 7.476,p = .003] ANOVAs showed an effect of tapping. The pairwise comparisons showed that both the no-tapping (M = 2.05, SD = .17) and easy-tapping (M = 2.24,SD = .41; p = .05), and easy-tapping and hard-tapping (M = 2.46, SD = .38; p = .015) differences were significant for one-digit addition. For two-digit addition, the no-(M = 2.78,SD = .27) and tapping easy-tapping (M = 2.86, SD = .50) difference was not significant (p = .366), while the easy-tapping and hard-tapping (M = 3.03,SD = .42) difference was (p = .004). These results suggest that the tapping and addition difficulty interaction is due to differential interference of easy-tapping on one-digit addition compared to

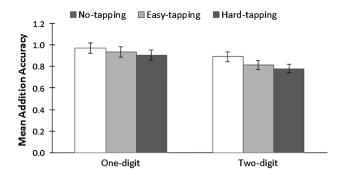


Fig. 4 Addition task accuracy results. The *error bars* represent 95 % confidence intervals adjusted for within-subjects designs (Masson and Loftus 2003)

two-digit addition, and that hard-tapping interference was similar for one- and two-digit addition conditions.

Task accuracy

A 3 × 2 repeated measures ANOVA (Fig. 4) on addition accuracy (tapping: no-tapping vs. easy-tapping vs. hard-tapping × addition difficulty: one-digit vs. two-digit addition) showed a main effect of tapping, F(2, 12) = 9.275, p = .001, $\eta p^2 = .481$, and addition difficulty, F(1, 12) = 11.311, p < .007, $\eta p^2 = .531$. Mauchly's test indicated that the assumption of sphericity had not been violated, $\chi^2(2) = 1.769$, p = .413. There was no interaction between tapping and addition difficulty, F(2, 12) = 1.414, p = .266, $\eta p^2 = .124$, which shows that one-digit and two-digit addition accuracy were similarly affected by the tapping manipulation.

Tapping performance

The tapping performance measure was the number of correct taps per second. A correct tap is one that follows the order of the assigned tapping sequence (e.g., middle finger stroke after the ring finger for easy-tapping). This measure combines both the speed and accuracy of tapping. A 2×2 repeated measures ANOVA on tapping performance (tapping complexity: easy-tapping vs. hard-tapping × addition difficulty: one-digit vs. two-digit) revealed no main effect of tapping complexity, F(2, 12) = 1.100, p = .300, p = .025, and addition difficulty, F(1, 12) = .723, p < .400, p = .017, showing that tapping complexity and task difficulty did not affect tapping performance. There was also no interaction between tapping complexity and addition difficulty, F(2, 12) = 1.203, p = .279, p = .027.

Whole-brain analysis

Simple contrasts for each condition were computed using the fixation as the baseline. Then, the individual first-level contrasts were used in a second-level group analysis to conduct a 3×2 (tapping: no-tapping vs. easy-tapping vs. hard-tapping \times addition accuracy: one-digit vs. two-digit addition) repeated measures ANOVA (see Henson and Penny 2005 for details on the procedure and how the contrast vectors were generated).

A t test contrast was used to test the main effect of addition difficulty. F test contrasts were used to test the main effect of tapping, and the tapping and addition difficulty interaction. The activation table shows results for the main effects and the interaction (Table 1).

Main effect of addition difficulty

A distributed frontoparietal network showed a main effect of addition difficulty (Fig. 5). Areas that showed a positive effect (two-digit > one-digit) included clusters in the left precentral, left supplementary motor, and bilateral inferior parietal areas. A bilateral inferior parietal network was previously suggested as a core neural correlate for numerical calculation, responsible for semantic knowledge about numerical quantities (Dehaene and Cohen 1997; Dehaene et al. 2003). Precentral and supplementary motor activations were also reported for arithmetic calculations versus retrieval tasks previously (Grabner et al. 2009); however, their functions are less clear. For the two-digit < one-digit contrast, activation was observed in the cingulate gyrus, left angular gyrus, left superior temporal, left supramarginal, right postcentral, right medial, and superior frontal areas. Left AG activation has consistently been found in single-digit arithmetic tasks and is theorized to reflect verbal rote memory retrieval (Dehaene et al. 1999; Grabner et al. 2009; Stanescu-Cosson et al. 2000). Left supramarginal activation has also been reported for retrieval compared to calculation tasks and is thought to reflect phonological processing together with AG (Stanescu-Cosson et al. 2000; Wu et al. 2009).

Main effect of tapping

Left precentral and bilateral posterior cingulate areas showed a main effect of tapping (Fig. 6).

Tapping versus addition difficulty interaction

The tapping and difficulty interaction showed a distributed network of clusters peaking at bilateral angular gyri, left postcentral (distributed over precentral), left inferior



Table 1 Results of the 3×2 ANOVA showing significant clusters of activation

Task	Region	Cluster size	Z	Peak MNI, x, y, z
Main effect of addition difficulty (<i>T</i> test; positive: two-digit > one-digit)	Left precentral	531	4.18	-40, 6, 30
	Left supp. motor area	302	3.92	-2, 18, 46
	Right inferior parietal	225	4.29	30, -54, 50
	Left inferior parietal	363	4.52	-28, -56, 54
Main effect of addition difficulty (<i>T</i> test: negative: one-digit > two-digit)	Cingulate gyrus	6831	5.40	-4, 40, 34
	Left angular gyrus	544	4.41	-44, -66, 40
	Left superior temporal	116	4.06	-42, -12, 0
	Left supramarginal	176	4.01	-56, -42, 28
	Right postcentral	72	3.59	60, -12, 24
	Right medial superior frontal	1127	4.56	6, 54, 36
Main effect of tapping (F test)	Left precentral	1481	7.13	-32, -24, 58
	Right posterior cingulate	31	3.74	18, -60, 6
	Left posterior cingulate	31	3.80	-2, -44, 16
Addition difficulty and tapping interaction (F test)	Right angular gyrus	138	4.50	48, -60, 34
	Left angular gyrus	49	4.16	-42, -68, 40
	Left postcentral	779	5.43	-36, -22, 54
	Left inferior parietal	203	4.10	-28, -56, 54
	Right medial superior frontal	57	3.67	8, 54, 42
	Left median cingulate gyrus	1074	4.74	-4, -40, 34
	Right superior temporal	41	3.73	38, -34, 14

Fig. 5 Main effect of addition difficulty: a One-digit addition compared to two-digit and b two-digit addition compared to one-digit

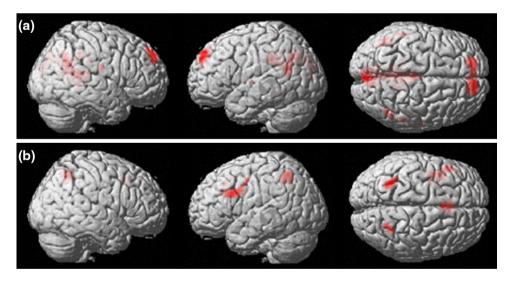
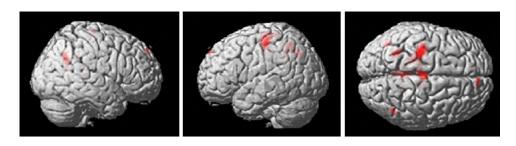


Fig. 6 Main effect of tapping





Fig. 7 Tapping versus addition difficulty interaction



parietal, left median cingulate, right medial superior frontal, and right superior temporal areas (Fig. 7). The ROI analysis focuses on bilateral AG.

No-tapping versus tapping comparison

To explore how additional tapping demand in the tapping conditions affected addition processing, we compared the two no-tapping conditions (one-digit and two-digit) with the four tapping conditions (one-digit and two-digit, easyand hard-tapping) for each participant at the first-level and used these contrasts to do a group analysis at the second level (Fig. 8). For the tapping versus no-tapping comparison, no region revealed significantly greater activation for the tapping compared to no-tapping conditions, except for an activation cluster in the left primary motor area, centered in precentral gyrus (Fig. 5a) due to the motor tapping movement. The no-tapping versus tapping comparison, however, showed distributed clusters of activation in bilateral angular gyri, occipital temporal cortex, middle frontal gyrus, and pre-SMA/anterior cingulate cortex (Fig. 5b). This effect is referred to as an underadditivity effect, characterized by reduced activations in dual conditions compared to single ones (i.e., tapping and no-tapping in this study), has been observed in previous dual-task studies (for example, Newman et al. 2007), and is further explored in the discussion.

Region-of-interest (ROI) analysis on bilateral angular gyri (AG)

A ROI time series analysis was conducted on the bilateral angular gyri (AG), using the AAL ROI library and the MarsBar toolbox (Brett et al. 2002). Time series were extracted and averaged across the voxels within the two ROIs. The time series were normalized, and percent signal change was calculated. The signal between the 4th and 8th seconds after the onset (three volumes, covering between one image before and after the peak, considering the 6-s hemodynamic delay) was averaged for each participant.

3 × 2 ANOVAs were conducted separately for left and right AG (Fig. 6). Mauchly's test indicated that the assumption of sphericity had not been violated for the left,

 $\gamma^{2}(2) = 2.687$, p = .261, and right AG, $\gamma^{2}(2) = 5.483$, p = .064, percent signal change data. The results showed a main effect of tapping for left AG, F(2, 12) = 4.263, p = .022, $\eta p^2 = .316$, but not for right AG, $F(2, \frac{1}{2})$ (12) = 1.958, p = .167, $\eta p^2 = .164$. There was a main effect of addition difficulty for left AG, F(1, 12) = 8.625, p = .015, $\eta p^2 = .463$, but not for right AG, $F(1, \frac{1}{2})$ 12) = 3.987, p = .074, $\eta p^2 = .285$. There were no significant interactions either for left, F(2, 12) = .507, p = .610, $\eta p^2 = .048$, or right AG, F(2, 12) = .221, p = .803, $\eta p^2 = .022$. To explore the main effect of tapping on left AG, we conducted post hoc pairwise comparisons using the Bonferroni correction on the averaged (across one-digit and two-digit conditions) percent signal change for each level of the tapping (no-tapping SD = .240; easy-tapping M = -.348, M = -.201. SD = .293; and hard-tapping M = -.347, SD = .239). The no-tapping mean was significantly different both from easy-tapping (p = .028) and hard-tapping (p = .048), while the easy-tapping and hard-tapping activation means were not different (p = .98). Overall, the results show that the left AG activates more in one-digit addition compared to two-digit addition, and in no-tapping conditions compared to easy- and hard-tapping conditions (Fig. 9).

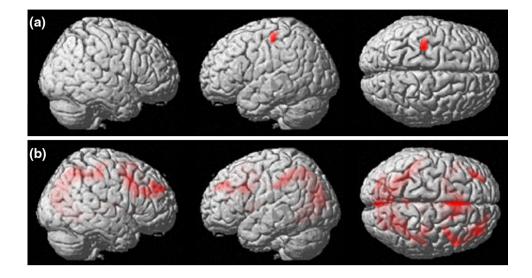
Discussion

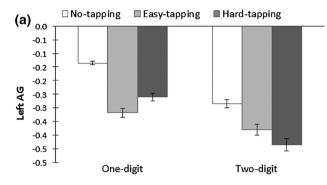
In this study, we investigated how addition difficulty, tapping, and tapping difficulty affect addition performance and the neural aspects of this interaction, with particular focus on the AG. The RT and task accuracy results showed that complex, non-anatomical tapping interfered more with addition than simple, anatomical tapping. We also observed an effect of addition difficulty and tapping on the left AG activation, but not on right AG, showing that both the difficulty and tapping manipulations impact the processing taking place in the left AG. Therefore, because the right AG did not produce any main effects and interactions, we will limit the discussion here to the participation of left AG in finger and arithmetic processing.

One of the goals of the current study was to determine whether one-digit addition, which relies on retrieval



Fig. 8 a Tapping vs. notapping comparison, with a single cluster in the left precentral area, and b notapping vs. tapping comparison





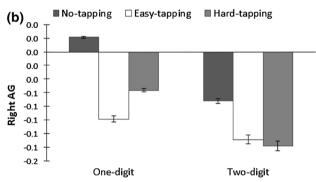


Fig. 9 Averaged activations (percentage change compared to baseline) in the left (a) and right (b) ROIs. The *error bars* represent 95 % confidence intervals adjusted for within-subjects designs (Masson and Loftus 2003)

mechanisms, would show differential finger tapping interference compared to two-digit addition, which relies more heavily on calculation procedures. RT results showed that anatomical tapping impacted one-digit addition more than two-digit addition, suggesting that one-digit addition and the simple finger tapping sequence have greater process overlap than does two-digit addition.

One possible explanation for this process overlap for one-digit addition and the simple finger tapping sequence is that there is a link between the sequential, anatomical ordering of the fingers and number representation. Some evidence in support of this idea can be seen in studies that show that finger counting habits influence number processing (e.g., Di Luca and Pesenti 2008; Newman and Soylu 2014). Additionally, it was shown that small (1–4) digits in a parity judgment task leads to excitability of right-hand muscles, and that the effect gets weaker for larger (6-9) digits. In this study, all subjects but two (14 out of 16) started finger counting with their right hands (right starters), hinting that the effect might be due to a mapping between fingers and digits grounded in finger counting practices (Sato et al. 2007). In a more recent study, Tschentscher et al. (2012) investigated the effect of finger counting habits on the laterality of number representation in an fMRI experiment. Participants included 15 right starters and 14 left starters. The results showed that the group of right starters revealed left-lateralized motor cortical activations, and the left starters showed right-lateralized activations, when presented with small numerals (1-5). Overall, these studies provide evidence for finger counting habits influencing neural correlates and organization for mental representation of single-digit numbers.

A developmental account for why the process overlap is greater between one-digit addition and the easy-tapping sequence is that early finger-based calculation strategies for addition and subtraction use anatomically ordered movement of fingers. The link between finger movement and number may be weakened when the fingers are not moved in a simple anatomical order, making the interference effect larger for simple sequence tapping than the complex sequence tapping. The previously reported selective interference of simple sequence tapping on one-digit addition and subtraction, but not on multiplication (Michaux et al. 2013), supports the idea that arithmetic operations that rely



on finger counting strategies (i.e., addition and subtraction) early in the development rely more on finger representations and possibly on the sequential activation of these representations with the anatomical order.

As it relates to the three alternative explanations for the interaction between finger processing and arithmetic-localizationist, developmental, and redeployment—the relation between anatomically ordered tapping and one-digit addition seems to favor the functionalist (i.e., developmental association) hypothesis over the localizationist one, since it is possible that the relation observed between onedigit addition and easy-tapping is due to a developmental association. However, this conclusion should be taken with some caution since the tapping complexity and addition difficulty interaction were not observed in the AG data. Furthermore, the one-digit addition task used involved addition of three single-digit numbers, as opposed to just two, to decrease the reaction time differences between onedigit and two-digit conditions. Therefore, while the onedigit addition does involve fact retrieval, it may also be expected to involve other processes like working memory. Further studies are necessary in order to adequately characterize the processing within the AG.

The role of angular gyrus in arithmetic and finger processing

Unlike the behavioral results, the ROI analysis failed to show a significant interaction between tapping and addition difficulty in bilateral AG even though the pattern of activation in left AG suggests one. The whole-brain analysis showed an interaction of tapping and difficulty in seven clusters, two of which had overlapping peaks with left and right AG. To avoid the problem of "double dipping" (Kriegeskorte et al. 2009), we did not use the coordinates for these clusters for the ROI analysis and instead used the anatomical descriptions from the AAL library (Brett et al. 2002) based on an a priori decision to focus on bilateral AG in the ROI analysis.

Left AG revealed significant effects of both tapping and addition difficulty. This is important and supports the region's role in both finger processing and arithmetic. Recall that one of the first indications of an overlap between these processes was made by Gerstmann (1940). The lesion responsible for Gerstmann's syndrome (GS) is located in the left AG and leads to four co-occurring symptoms: finger agnosia (loss of finger sense), acalculia (inability to carry out simple mathematical calculations), left–right disorientation, and agraphia (inability to write). Even though Gerstmann proposed that a single cognitive process was shared by the four skills affected, there has been little evidence to support this hypothesis, and there is no obvious shared sub-function that is affiliated with

angular gyrus (Rusconi et al. 2010). One potential explanation, at least to explain the relationship between finger sense and number processing, is that number processing uses finger schemas, and there is some evidence supporting this claim, for example in a study where excitability in the hand muscles was measured during a visual parity judgment task, involving numbers between 1 and 9. Modulation of right-hand muscles, but not the left hand, was found with right-handed subjects (14 out of 16 started finger counting with their right hands). The effect was stronger for numbers between 1 and 4 (Brett et al. 2002). In another study, enumeration of dots on the screen both with numbers and letters was found to increase the corticospinal excitability of hand muscles (Sato et al. 2007). Because the effect was found both for enumeration with numbers and letters, the authors proposed that hand motor circuits are involved whenever a set of items have to be matched with the elements of an ordered series.

Here, the RT data show that one-digit addition is more affected from easy-tapping compared to two-digit addition, implying a specific association (possibly developmental) between retrieving arithmetic facts from rote memory and activating anatomically ordered finger schemas. The trends in bilateral AG activation suggest a similar, albeit non-significant, interaction, with further deactivation during easy-tapping with one-digit addition but not with two-digit addition (compared to hard-tapping). Given that this interaction is not significant, we are cautious about relating the RT findings with AG activation. However, these preliminary findings indicate that perhaps it is not single, finger representations that are activated during retrieval of number facts, but rather finger schemas, a combination of ordinal finger configurations.

The angular gyrus and the default mode

The ROI analysis showed negative activation compared to a fixation baseline across all conditions, except for notapping, one-digit addition in the right AG. Negative AG activation in cognitive (Humphries et al. 2007; Mazoyer et al. 2001) and finger tapping tasks (Liu et al. 2011) has been consistently observed in previous studies, and this phenomenon is attributed to AG's participation in the default mode network (DMN; Raichle et al. 2001). DMN constitutes a group of regions that are active during rest, and they typically show negative activation during cognitive tasks. For example, in a PET study, nine different cognitive tasks, compared to rest, all showed negative activation in AG together with a set of other regions that are proposed to constitute the DMN (Mazoyer et al. 2001). Aligned with this, bilateral AG negative activation during arithmetic was reported in two previous studies (Rickard et al. 2000; Wu et al. 2009). Wu et al. (2009) explained



deactivation of, particularly left, AG during arithmetic tasks based on AG overlap with DMN, noting the need for more careful analysis of magnitude and sign of activation changes in the AG for different mathematical tasks.

Dual-tasking and underadditivity

The ROI analysis results showed lower activation for tapping conditions, compared to matching no-tapping conditions. In dual-task studies, an underadditive response for dual conditions, which is characterized by lower activation in dual-task conditions compared to the activation from single tasks, has been observed previously (Goldberg et al. 1998; Just et al. 2001; Newman et al. 2007). Underaddivity was proposed either to be due to an upper threshold of brain activation in association and sensory areas or due to a limit on how much attention can be distributed over more than one task (Just et al. 2001). In fact, Newman et al. (2007) found similar results using a dual-tasking study with auditory sentence comprehension and visual mental rotation tasks. No significant increase in prefrontal activation was found for the dual-task condition, and there was increased activation in the task-specific regions for the single-task condition compared to the dual-task condition. The explanation provided was related to automaticity. It may be that the finger tapping task becomes relatively automatic, even the more difficult tapping sequence. Additionally, the addition processes are also altered to eliminate any supplementary processes like fact checking. Together, this pared down processing may result in decrements in performance but allows for the ability to perform the tasks simultaneously.

Conclusion

Based on a previous study (Michaux et al. 2013) showing that finger tapping selectively interfered with addition and subtraction, but not with multiplication and that the effect was specific to finger tapping, we explored how the tapping and addition difficulty modulated the dual-task interference, and explored the neural aspects of the interference. The RT results show that the tapping modulates the interference across all conditions. We also found that one-digit addition is more prone to interference from easy-tapping sequence compared to two-digit addition, possibly due to an early association between addition and anatomically ordered finger movements during finger-based calculation strategies. The ROI analysis showed a similar effect. We explained this effect based on a greater process overlap between one-digit addition and the easy finger tapping sequence within the AG. We, albeit cautiously, argue that the retrieval of addition facts relies more on finger representations, compared to calculation, and interference of tapping on one-digit addition is higher with the easy-tapping sequence due to a link between the activation of anatomically ordered finger schemas and arithmetic fact retrieval.

Future studies should also focus on interference of finger sense/recognition on arithmetic tasks. Clinical (Mayer et al. 1999), developmental (Noel 2005), and cortical stimulation (Roux et al. 2003; Rusconi et al. 2005) studies point to a relation between finger sense and number representation. However, no dual-task study has focused on the stimulation of fingers during a number task to explore the interference effects. It is possible that the relevance of finger sense in number processing is due to mental representation of fingers, which would be shared with finger tapping, or due to some other non-shared process.

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