MORE THAN FINGER COUNTING:

SHARED RESOURCES BETWEEN FINGER TAPPING AND ARITHMETIC

Fırat Soylu

Submitted to the faculty of the University Graduate School
in partial fulfillment of the requirements
for the degree
Doctor of Philosophy
in Instructional Systems Technology and Cognitive Science
Indiana University
November, 2011

Accepted by the Graduate Faculty, Indiana University, in partial fulfillment of the

requirements for the degree of Doctor of Philosophy.

Doctoral Committee

<div style="text-align: right;">

_____

Frank K. Lester, Jr., PhD

_____

SharleneD. Newman, PhD

_____

Elizabeth Boling, MFA

_____

Robert L. Appelman, PhD

</div>

Acknowledgements

I owe gratitude to everyone who has supported me in various ways during my graduate studies, which led up to this dissertation.

My deepest gratitude is to my advisor Sharlene Newman, who dedicated countless hours to my dissertation study, for her wisdom, patience and kindness.

I owe many thanks to Frank Lester for overseeing my dissertation process, for fruitful discussions, and for his continuous support and encouragement.

I am thankful to Elizabeth Boling and Robert Appelman for supporting my interdisciplinary interests and for accommodating the unusual path I followed during my graduate studies.

I am grateful to my cousin, friend, and mentor Buğrahan Yalvaç for helping me in every stage of my education, having endless belief in me, encouraging me, for all the ever expanding discussions about research and for always being there in the good and bad times.

My life would have followed a different path if it wasn't for Kürşat Çağıltay. I am indebted to him for being a model and mentor during my undergraduate studies and encouraging me to pursue graduate work abroad.

Thanks to Bahar Tabakoğlu, Craig Howard, Daniel Yurovsky, Emel Gençer, Erdem Yücel, Evie Malaia, Mark Millard, Murat Özbilgi, Murat Ulubay, Nate Shannon, Robert Goldstone, Srikanth Padmala, Steve Green, Taylan Şengül, Thomas Duffy and Turgay Bayraktar, for contributing to my intellectual development through informal discussions over the years or for helping me in my dissertation work in some way.

I very much appreciate the research awards granted to me for my dissertation study by the Cognitive Science Program, the Achasa Beechler Fund, the University Graduate School, and

Fırat Soylu

More Than Finger Counting: Shared Resources between Finger Tapping and Arithmetic

Arithmetic is a branch of mathematics upon which many other mathematical content areas are built. The study of the mechanisms underlying arithmetic is crucial for understanding cognition in other domains of mathematics, as well as higher-level cognition. Recent advances in the study of embodied cognition have yielded to a new interest in how mathematical thinking relates to our body and the sensorimotor system. Abundant behavioral, neuroimaging, and neuropsychological evidence have accumulated over the last two decades showing a relationship between number processing and sensorimotor processes. In addition, considerable evidence has been presented that suggest precursors of arithmetic skills in animals. This shows that arithmetic is not uniquely human and some of the relevant mechanisms may exist independent of language. In this dissertation a combination of behavioral and neuroimaging methods were used to explore the embodiment of arithmetic processing, with particular focus on the relation between finger movements and addition. In addition, how bodily measures (e.g. handedness, finger counting habits, finger tapping ability) interact with cognitive measures (e.g. math ability, digit span, spatial ability) was investigated. The results provide evidence for a finger-based representation of numbers, and show that bodily measures can predict elementary numerical skills.

Keywords: embodied cognition, number processing, arithmetic, finger tapping, angular gyrus, fMRI

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Chapter 1 - Introduction

Humans' mathematical ability goes far beyond the numerical abilities of any other animal. The extent to which humans can do mathematics is unique, but having a sense of quantity and doing simple arithmetic is not. There is considerable evidence for different animal species having a number sense and carrying out simple arithmetic calculations (Dehaene, Dehaene-Lambertz, & Cohen, 1998). However, building on simple notions of numerosity and through a learning process supported by verbal language, humans can develop higher mathematical skills. Understanding the base components that provide the grounding for higher mathematics is essential in understanding mathematical cognition.

The cognitive revolution brought about a view of the mind as a symbol processing machine (Fodor, 1983; Newell & Simon, 1976). The cognitivist perspective advocated a disembodied view of the mind, according to which cognitive processes were independent from bodily dynamics. An alternative view emerged in the early 1980s when Lakoff and Johnson (1980) argued that conceptual content and structure in human languages are grounded in bodily experiences. Following that, Maturana and Varela (1987) have provided a neurobiological account of how simple bodily processes interconnect in complex ways resulting in the emergence of higher level cognitive processes. These early studies initiated the embodied cognition research program. According to the embodied view sensory and motor mechanisms, which underlie bodily perception and action, are the grounding for higher level cognitive processes. This idea resonates with earlier attempts to link bodily development with abstract thinking. For example, in Piaget's stages of cognitive development, sensorimotor development precedes and constitutes the grounding for later stages, which ultimately lead to higher-order, abstract thinking (Piaget, 1954).

1

Embodied approaches to cognition also initiated a new approach to the origins of human mathematical ability.

According to the embodied orientation we make sense of mathematical concepts based on our non-conceptual, bodily experiences (Lakoff & Nunez, 2000). Mathematical processes take place on sensorimotor systems that originally evolved for other purposes, for example tool use in the case of hands. Arithmetic, being the most elementary domain of mathematics, has been one of the foci of studies on the bodily foundations of mathematics.

In a talk given on April 7, 2008, titled "How Hands Help Us Think," Susan Goldin-Meadow presented her behavioral research focusing on how hand gestures relate to teaching and learning mathematics as well as how gestures play a role in mathematical thinking. This was a time when I was trying to refine my dissertation topic. Throughout the talk, I could not stop thinking about how Dr. Goldin-Meadow's research related to embodiment and sensorimotor foundations of higher thinking. In my mind I was developing explanations as to how a simulation system grounded in the sensorimotor system might underlie mathematical thinking and how gestures might be represented within the same system. During the talk, Goldin-Meadow was asked how she would explain the gestures and mathematics relation in terms of what is happening in the brain. She said that she was not a neuroscientist and that we needed imaging research to understand how mathematical cognition relates to hands and gesture processing. This was the defining moment for my dissertation study topic.

In my dissertation, I studied the embodiment of arithmetic, with particular focus on shared use of resources between addition and finger movements. Based on previous

studies providing evidence for a finger-based representation of numbers (Fischer, 2008; Noel, 2005; Penner-Wilger et al., 2007; Rusconi, Walsh, & Butterworth, 2005; Sato, Cattaneo, Rizzolatti, & Gallese, 2007; Sato & Lalain, 2008; Zago et al., 2001), I hypothesized that arithmetic processing takes place on a neural circuit that is originally responsible for finger related sensorimotor functions. This hypothesis was tested through a behavioral and neuroimaging experiment both using a dual-task paradigm. The dual-task paradigm was used to investigate interference effects of finger tapping on addition and on a control task during concurrent performance. In the behavioral experiment the degree of interference was used as an indicator of shared resource use. The fMRI experiment was conducted to investigate, first the neural overlap between finger tapping and addition, and second, how the two processes (finger tapping and addition) interact when they are performed together. These two experiments focused on a specific relation between finger tapping and addition. However, since the number/finger relation probably extends to other modes of finger processing and domains of numerical cognition, I conducted a third, exploratory study. In the third study, I investigated the relationship between a range of bodily measures (sequential finger tapping ability, finger counting habits, handedness) and cognitive measures (arithmetic and spatial ability and working memory capacity), to see if certain bodily capacities can predict cognitive performance.

In the following pages a review of previous studies and current discussions on the embodiment of number processing is presented. Since both the behavioral and fMRI experiments utilize a dual-task paradigm, I present a detailed account of previous research on dual-task performance. Dual-task designs present an innovative way for testing claims of embodiment, since interference can be a reliable measure of shared use of neural

3

resources between two processes (Roland & Zilles, 1998). Nevertheless, as one would expect from the most complicated system known to man, the human brain, dual-tasking represents many idiosyncrasies, which need to be explained to make better sense of the later presented experiments.

Background

Gerstmann's Syndrome

The first scientific study that points to a relationship between fingers and number processing goes back to the early 20th century. In 1924 Josef Gerstmann diagnosed an adult patient who was not able to name her own fingers or point to them on request. Gerstmann named this condition "finger agnosia." Tests on this patient also revealed that she had difficulty differentiating between her right and left hand, or another person's right and left hands. In addition, she performed poorly on calculation tests and had impairments in spontaneous writing, a condition referred to as "agraphia." He studied more patients with the same four co-occurring symptoms, finger agnosia, acalculia, left-right disorientation and agraphia, and described a condition now named Gerstmann's Syndrome. He hypothesized that the main source of the symptoms was "a lesion located in the parieto-occipital region of the brain, namely, in that part which corresponds to the angular gyrus in its transition to the second occipital convolution" (Gerstmann, 1940, p. 399). Gerstmann believed that the main symptom was finger agnosia, a specific type of body schema impairment (autopagnosia) affecting specifically the representation of hands and fingers. He proposed that the loss of finger sense combined with the left-right disorientation caused acalculia (Butterworth, 1999b, p. 219).

According to another theory, Gerstmann's Syndrome is due to an impairment in mental manipulation of images and not to a deficit in the mental representation of hands and fingers (Mayer et al., 1999). Roux, Boetto, Sacko, Chollet and Tremoulet (2003) used direct brain mapping to study a series of patients who had tumors in and around the angular gyrus. They reported that areas producing impairments in writing, calculating, and finger recognition were found in the angular gyrus, which may or may not have been associated with object-naming, color-naming, or reading sites. In a study conducted with healthy subjects, Rusconi, Walsh, & Butterworth (2005) found that rTMS over the left angular gyrus disrupted tasks requiring access to the finger schema and number magnitude processing in the same group of participants; providing additional support for Gerstmann's Syndrome impairing access to the body schema, particularly finger representation. A series of behavioral studies have consistently shown that finger gnosia (sense of fingers - this is different from agnosia which indicates a lack of finger sense) in younger children is a predictor of numerical abilities; pointing to a functional relation between representation of fingers and number processing (Noel, 2005; Penner-Wilger, et al., 2007). To summarize, there is extensive evidence to support an association between finger perception and number processing.

Is Number Processing Body Based?

The fact that an impairment in body-schema co-occurs with calculation deficits in Gerstmann's Syndrome provides preliminary support for number processing being, at least partially, embodied. However, contrary to the body schema explanation, Gobel, Walsh, and Rushworth (2001) argued that the angular gyrus supports a visuo-spatial representation of numbers. They supported this argument with an experiment in which

rTMS was applied to the angular gyrus of healthy subjects and found that it disrupted both a visual search and a number comparison task (Gobel, et al., 2001). This study, along with others, demonstrates that the debate regarding the embodiment of number processing is an on-going one. For example, multiple studies have reported an association of small numbers with the left visual field and big numbers with the right visual field (see Fias & Fischer, 2005 for review) with some suggesting that this effect supports a visuo-spatial link. In their original identification of this phenomenon, Dehaene, Bossini, and Giraux (1993) measured the response time for parity judgment of single digit numbers by varying the response rule (right button for even, left button for odd and vice versa). They found that right button responses were faster for large numbers and left button responses were faster for small numbers. The effect was named "spatial-numerical association of response codes" (SNARC). A series of studies inquired if the SNARC effect is universal, and if it is modality specific (vision-only). Fischer (2008) explored whether finger-counting habits contribute to the SNARC effect and found that subjects who are left-starters, people who start counting from their left hands, show a SNARC effect significantly more than right-starters. Di Luca, Grana, Semenza, Seron and Pesenti (2006) used an experimental design to demonstrate that the SNARC effect was body-based. In their study subjects were asked to identify Arabic digits by pressing one of 10 keys with all 10 fingers. The configuration of response buttons varied both in terms of the global direction of the hand-digit mapping and the direction of the finger-digit mapping within each hand, from small to large digits or vice versa. The results showed that subjects performed better when there was a congruency between reported finger-counting strategy of the subject and the mapping of the response buttons, compared to a mapping congruent with a left to right oriented mental

6

number line, both in palm-down and palm-up postures of the hands. Both Di Luca, et al. (2006) and Fischer (2008) provide evidence for the dominance of a finger-based number representation compared to a spatial one. This data can all easily be interpreted as support for a dominant link between finger perception, as opposed to visuo-spatial processing, and number processing.

Brozzoli et al. (2008) provided contrary evidence and proposed the dominance of spatial over finger-based representation of numbers. In their experiment, subjects detected tactile stimuli on their right-hand, thumb or little finger, either in palm up or palm down posture. The responses were recorded with a foot pedal. The results showed that subjects performed better when reporting tactile stimuli delivered to the little finger after the presentation of number "5" than number "1," with the hand resting palm-down. When the hand is in a palm-up posture (the thumb is on the right and the little finger on the left) the pattern reverses, with better performance after presentation of number "1" than "5." This suggests that it is the spatial information and not finger specific information that is guiding the effect.

In all of the aforementioned studies, the SNARC effect was studied based on motor responses with hands. If the spatial representation of numbers, in the form of a left to right extending mental number line, was the most dominant mode, this effect should also be observed with automatic saccadic eye responses. Schwarz and Keus (2004) compared manual and saccadic responses in a parity judgment test. Consistent with previous studies, manual responses showed the SNARC effect. However, saccadic responses showed a vertical effect in which performance was better when bigger numbers were presented in the upper visual field. Based on these results Schwarz & Keus

interpreted the SNARC effect as an overlearned motor association between numbers and manual responses, like in typewriters and computers. The effect might also be due to the direction of writing in the Latin alphabet. In the original study by Dehaene, Piazza, Pinel and Cohen (2003), in which the SNARC effect was identified for the first time, it was found that the likelihood of Iranian subjects showing the SNARC effect increased with the amount of time they lived in France. The reason given for the effect was based on the direction of writing in the Persian alphabet (right to left). A similar result was found when Arabic and English speakers were compared in terms of the mental number line direction (Zebian, 2005). While these results do not speak directly to the involvement of fingers in number processing, they do suggest a significant role of the sensorimotor system.

Overall, while there is common agreement that finger configuration plays a role in number representation, the extent of this role is open to debate. In his book *What Counts*, Butterworth (1999b) discussed why fingers and not another body part play this specific role. One explanation given was that the finger-number relationship is based on an association made during early experiences with number processing. Children across cultures spontaneously develop finger configurations that match numbers, and use their fingers to count. These experiences may create an early association between fingers and numbers, thus shaping the neural circuit in which number processing takes place. Nevertheless, this theory does not explain why children who are born with finger agnosia are likely to develop acalculia. Similarly children with Spina Bifida, a neurodevelopmental disorder that causes deficits in fine motor ability, among other things, show difficulties in number processing in early development persisting through adulthood (Barnes, Smith-Chant, & Landry, 2005). Following Butterworth's (1999a, 1999b, 2005)

8

proposal that subitizing (innate capacity to represent small numerosity), fine motor ability and the ability to mentally represent one's fingers are all related, Penner-Wilger et al. (2007) tested whether subitizing, finger tapping (measure of fine motor processing), and finger gnosia predict the math abilities of first grade children. The results showed that subitizing is a predictor of both number system knowledge and calculation skill directly, while finger gnosia and finger tapping are direct predictors of number system knowledge and indirect predictors of calculation skill through number system knowledge. It is also notable that there were no correlations between these three measures, compatible with Butterworth's proposal that, while they may all interact, the systems for subitizing, finger gnosia, and fine motor ability are separate and independent (Butterworth, 1999a).

Another aspect of the finger-number relationship is the representation of magnitude. Considerable behavioral and neuroimaging evidence provide support for a common representation of magnitude across different notations and modalities (see Cohen Kadosh, Lammertyn, & Izard, 2008, for a comprehensive review of magnitude representation research). Andres, Ostry, Nicol and Paus (2008) used a task in which the subjects needed to reach and grasp a wooden block after reading small or big single digit numbers. The grip aperture was measured using infrared emitting diodes placed on the thumb and index finger. The grip aperture was larger when the movement was towards a block with a large number on it, compared to a movement towards the same block with a small number on it. While this study revealed an interaction between magnitude processing and object grasping, the question of whether the interaction happens during the estimation of object size, or directly during the grasping movement still remains unanswered. Badets, Andres, Di Luca, and Pesenti (2007) addressed this question. They

explored the effect of number magnitude on the capacity to judge a potential grasping action without performing it. Subjects were asked to grasp rectangles of different sizes after being shown a small or a large digit. Similar to the Andres et al. (2008) study, the results showed that the size of rectangles that the subjects judged as ungraspable were larger, when small digits were shown before displaying the rectangles, and vice versa for large digits. This study showed that the interaction between numbers and object-size estimates is the source of interference between number magnitude and grip aperture. This result is compatible with the size congruity effect observed when numerical and physical dimensions are varied independently (Algom, Dekel, & Pansky, 1996; Cohen Kadosh, Kadosh, & Henik, 2008; Fulbright, Manson, Skudlarski, Lacadie, & Gore, 2003; Pinel, Piazza, Le Bihan, & Dehaene, 2004). For example, when two digits are presented to be compared in terms of their physical dimensions, participants could not ignore the numerical values, which interfere with their physical judgments. The same effect is observed in the reverse condition, when subjects are asked to ignore the physical dimensions of digits and compare the numerosities. Together, this data seems to clearly demonstrate a link between magnitude estimation and finger processing.

Neural Dynamics of the Finger and Number Processing Interaction

Neuropsychological and brain imaging studies on number processing support a distinction between exact arithmetic and magnitude processing for approximate calculations (Sato, et al., 2007). A frontoparietal network has been found to underlie number processing, frontal processing being more related to the retrieval of arithmetic facts and exact calculation, and parietal areas being responsible for magnitude representation. Among the frontal areas the precentral gyrus and pre-motor regions are the

most relevant (Dehaene, et al., 2003). In terms of the role of parietal regions in number processing, two areas consistently have been found to be active in number processing tasks; the intraparietal sulcus (IPS) and the angular gyrus (Dehaene, et al., 2003; Dehaene, Spelke, Pinel, Stanescu, & Tsivkin, 1999; Houdé & Tzourio-Mazoyer, 2003; Hubbard, Piazza, Pinel, & Dehaene, 2005). There are conflicting results concerning the role the IPS and angular gyrus play in number processing. Cappelletti, Barth, Fregni, Spelke and Pascual-Leone (2007) reported that stimulation of the angular gyrus did not modulate performance in a number comparison task involving double digit integers, while the stimulation of left IPS reduced performance, showing that IPS, and not the angular gyrus, is related to magnitude estimation. However, Gobel et al. (2001) found that stimulation of the angular gyrus disrupted both number comparison with single digits, and a visual search task. IPS has consistently been found active during number comparison tasks in a series of neuroimaging studies, yielding to the result that IPS is used for common representation of magnitude for numerical processing, both symbolic and non-symbolic (Cappelletti, et al., 2007; Cohen Kadosh, Lammertyn, et al., 2008; Pinel, et al., 2004). symbolic and non-symbolic (Cappelletti, et al., 2007; Cohen Kadosh, Lammertyn, et al., 2008; Pinel, et al., 2004). The existence of a frontoparietal network for number processing has been associated with different functional accounts. According to a theory proposed by Dehaene et al. (Dehaene, 1992; Dehaene & Cohen, 1995; Dehaene, et al., 2003), frontal regions active in number processing underlie numerical facts and exact calculation, while parietal regions play a role in visuo-spatial processing during approximation. But which parietal region, IPS or angular gyrus, plays a role in visuo-spatial processing during approximation? On the other hand, it was pointed out that the frontoparietal network

overlaps with the neural circuitry active during finger movements, leading to the theory that the early association between number processing and fingers during development might shape the neural substrate of number processing; situating it on a network originally used for finger movements (Butterworth, 1999a; Pesenti, Thioux, Seron, & Volder, 2000; Sato, et al., 2007).

Neuroimaging studies also show an overlap between finger movement control and number processing. Studies on the neural correlates of number processing (Crozier et al., 1999; Dehaene, et al., 2003; Houdé & Tzourio-Mazoyer, 2003; Hubbard, et al., 2005) and of hand motor abilities (Binkofski et al., 1999; Chong, Cunnington, Williams, Kanwisher, & Mattingley, 2008; Corina & Knapp, 2006; Sakata & Taira, 1998) point to the importance of an overlapping prefrontal and intraparietal circuit. Zago et al. (2001) found activation of a finger representation circuit in the left parietal lobe during adults' performance of basic arithmetic. Increased activation was observed in the premotor strip at the coordinates for finger representation during performance of single-digit multiplication compared to a digit reading condition. Sato et al. (2007) used rTMS to measure changes of excitability in hand muscles while participants performed a visual parity judgment task on single digit numbers. While no modulation was observed for the left hand muscles, an increase in amplitude of motor evoked potentials was found for the right hand muscles, particularly for smaller digits (1 to 4).

Theoretical Perspectives

Although it is clear that there is a relationship between mental representation of fingers (finger gnosis), fine motor processing, and mathematical ability, there are varied interpretations as to what this really means. Dehaene et al. (2003) proposes that finger

gnosia and math ability are related because the two abilities are supported by closely neighboring brain regions in the parietal lobe. According to this *localizationist* account, the predictive power of finger gnosia for math ability is due to common developmental trajectories of neighboring regions. From a *functionalist* perspective, the relationship between finger related activity and mathematical ability is due to a learned association. Fingers are used to represent numbers during mathematical development across cultures. Therefore, the co-existence of finger agnosia and acalculia in Gerstmann's Syndrome, and the relationship between finger gnosia, fine motor processing, and math ability is due not only to the close proximity of their neural substrates but also a learned association (Butterworth, 1999a, 1999b; Zago, et al., 2001). In an alternative account, Anderson and Penner-Wilger (2007) propose that part of the neural circuit supporting finger gnosia has been redeployed for magnitude representation during the evolutionary process. From a *computationalist* perspective, one of the foundational elements of a calculation circuit is a register that can independently store numbers to be manipulated by use of a series of switches. Whether fingers are used as the register or the switches is unclear. However, the evidence thus far suggests that the same circuit used to represent fingers is also used to represent numerical magnitudes.

One way to test the claim of an overlapping finger sensorimotor and arithmetic system is to look at the mutual interference of finger movements and an arithmetic task during concurrent performance. Use of this approach requires a thorough understanding of dual-task performance in the human brain. The next section reviews what we know about dual-task performance.

Dual-Task Performance

People often perform two tasks at the same time. We can talk and drive, or eat and read at the same time. However, we cannot read and write at the same time. Therefore, the nature of two tasks affects if and how they can be done together. The opposite is also true. The interference of two tasks on each other tells us about the nature of these tasks. Experimental designs where participants are asked to perform two tasks simultaneously are called *dual-task paradigms*. A dual-task paradigm is characterized by a resource-demanding secondary task performed concurrently with a primary task, in order to be compared with single-task conditions. The dual-task interference is mostly measured based on an increase in RT and/or in task error rates.

Telford (1931) showed for the first time that when participants are asked to respond to two successive stimuli, the response to the second stimuli is delayed, and the amount of delay is modulated by the time interval between the stimuli. With an analogy with the refractory period of neurons, Telford named this *psychological refractory period* (PRP). The PRP effect was observed in a variety of response modalities (Pashler, 1994), and even when the two tasks use different modalities, for example manual and eye movement responses (Pashler, Carrier, & Hoffman, 1993). The PRP effect constitutes a special case for dual-task interference, and it is observed only when the time interval between two stimuli is under a certain threshold. In a more recent study involving simple visual and somatosensory RT tasks, it was found that the delay for the second response disappeared when the time interval between two stimuli was more than 300 msec. As the time interval decreased the delay time increased. In the same study, using fMRI, it was found that right interior frontal gyrus activated only when the PRP effect was observed

(Herath, Klingberg, Young, Amunts, & Roland, 2001). This shows that when the time pressure to process two separate sets of stimuli is beyond a certain level additional neural resources are recruited.

In this study a dual-task paradigm is used as a way to study shared use of resources between finger movements and number processing. The amount of dual-task interference is an indicator of shared use of resources between two tasks. This argument has previously been empirically validated (Klingberg & Roland, 1997; Roland & Zilles, 1998). Nevertheless, dual-task performance is a complex phenomenon that goes beyond the simple metaphor of two agents demanding use of the same resources and therefore interfering with each other's work.

Earlier approaches to dual-task interference had a dominant information processing focus. Dual-task interference has been proposed to be either due to a competition for attentional resources (Friedman, Polson, Dafoe, & Gaskill, 1982) or due to shared demand on limited information processing systems (Kinsbourne & Hicks, 1978). These explanations assume a separation of perceptual, motor and cognitive processing systems and, therefore they are not compatible with the embodied viewpoint proposed here. The central thesis in this study is that cognitive processes, particularly number processing, are grounded in sensorimotor systems. Therefore we do not assume a separation of sensory and motor modalities from each other and from cognitive processing as well. Recent research on multisensory integration supports the idea that brain systems are not neatly demarcated for specific sensory modalities and that motor processing is not independent from sensory systems (Allman, Keniston, & Meredith, 2009; Pascual-Leone & Hamilton, 2001; Stein & Stanford, 2008). Nevertheless earlier studies provide valuable insights

about behavioral indicators of dual-task interference and provide a historical context for current neuroimaging research. Therefore, a review of earlier research on dual-task interference is provided.

Recent research on dual-task performance focused not only on behavioral measures, such as reaction time and accuracy, but also brain data: how the brain handles additional demand on limited resources. This particular field of study is very important in interpreting the fMRI data in this study. Although the interference of finger movements on number processing has never been studied, previous neuroimaging research on dual-task performance provides new implications for what some traditional concepts, like attention, might mean in terms of its representation in brain dynamics. In addition, methodological issues related to studying the brain dynamics of dual-task interference is answered in previous research.

Earlier approaches to dual-task interference.

Earlier theories of dual-task interference can be grouped into three categories (Pashler, 1994):

Capacity sharing.

Capacity sharing refers to the idea that multiple independent cognitive processes use a shared processing capacity when they are performed together. Casual observations show that people can continue to perform two tasks, for example driving and conversing, at the same time until one of the tasks becomes more demanding, like when traffic becomes more busy, which causes a decrease in performance in either or both of the tasks.

Bottleneck Models.

According to the bottleneck models dual-task interference happens when two processes demand the same particular resource at the same time, making parallel processing impossible. The bottleneck models were initially proposed to explain the psychological refractory period (PRP) results (Welford, 1952). However these models were also used to explain the dual-task interference of two continuous tasks.

Cross-Talk Models

While the previous two models do not concern the content of the information processed, cross-talk models suggest that the content of the information being processed may modulate the interference either positively or negatively. This can happen when the processing of the first task produces outputs or side effects that disturb the processing of the second task. Called "outcome conflict" (Navon, 1985), this phenomenon is best observed in the Stroop-effect and its derivatives. The Stroop effect refers to the original observation that naming a color word takes a longer amount of the time when the color word and the color of the ink used are not congruent (Logan, 1980; Stroop, 1935).

Earlier attempts to explain the brain dynamics of dual-task performance have also made use of cross-talk models. For example, it was proposed that task interference is modulated by the cerebral distance between the processing loci for the two tasks (Kinsbourne & Hicks, 1978). The more similar the tasks are the closer their processing loci, which results in more interference (Kinsbourne, 1981)

Neural dynamics of the dual-task performance.

What happens in the brain when two tasks are performed at the same time? The answer to this question mostly focuses on how the brain handles increased demand on

shared resources as well as on how executive mechanisms function to manage the limited resources. This section is structured based on the shared principles/hypotheses that have been proposed in multiple studies on the brain dynamics of dual-task performance. In addition, differences in findings from various studies on dual-task performance are discussed.

The amount of dual-task interference is modulated by the proximity and overlap of the neural correlates for single task

The idea that cortical proximity might determine the amount of interference between two tasks being performed together was also previously proposed (Kinsbourne, 1981; Kinsbourne & Hicks, 1978). Initially, this hypothesis had only behavioral support from dual-task experiments with right handed subjects, where a hand/finger motor task interfered with a language task more when it was executed with the right hand, compared to the left hand (Keefe, 1985; Kinsbourne & Cook, 1971). It was argued that this is because the cortical overlap between the two tasks is more between right hand movements and language, which is known to be left lateralized.

One current neurobiological theory that explains the dual-task interference is the cortical field hypothesis (CFH). According to the CFH, if two tasks use extensively overlapping brain regions, performing them concurrently would result in significant errors or increases in latency (Roland & Zilles, 1998). The advancement of neuroimaging techniques made it possible to investigate the effects of cortical proximity at a more refined level that goes beyond hemispheric dominance. In the first neuroimaging study on dual-task interference, using PET (positron emission tomography) Klinberg and Roland (1997) tested the hypothesis that two tasks interfere because they use overlapping areas of

18

the cortex. They measured interference between two go/no-go (visual and auditory) and two short-term memory (STM) tasks (visual and auditory). Although both go/no-go and STM tasks showed significant interference in performance, STM tasks showed significantly more increase in reaction time during dual-task performance compared to go/no-go tasks. The brain data showed that the volume overlap between the single conditions for STM tasks were larger compared to go/no-go tasks. The results provide support for the idea that increased interference, as it is indicated with RT, is due to the larger neural overlap between the two STM tasks.

Dual-task activations show underadditivity

Underadditivity refers to the condition where the activation for a dual-task condition is significantly less than the sum of the single-task activations. In studies where the two single tasks activate overlapping cortical regions (Rees, Frith, & Lavie, 1997; Vandenberghe et al., 1997), the activation associated with a particular task decreases in dual-conditions (Klingberg & Roland, 1997). Just et al. (2001) investigated the underaddivitiy principle for two tasks (auditory sentence comprehension and mental rotation) that do not cortically overlap in a significant way. The fMRI results showed that the association cortex most involved in each of the tasks (e.g., temporal cortex for language and parietal areas for mental rotation) dual-task activation was significantly less than the sum of activation for the two single tasks. A similar result was also observed in the sensory areas. The underadditivity effect was observed both for signal intensity and activation volume, albeit more significantly for activation volume. Although both single tasks showed very small activation in the pre-frontal areas, this activation was additive in the dual-task condition. The underaddivity was proposed to be either due to an upper

19

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. Alternatively these two explanations might overlap, given that limitations on attentional resources might be due to a limit on brain activation.

Underadditivity of dual-task activations was also observed in another study where subjects attended either a sentence comprehension or mental rotation task, or both of them at the same time (Newman, Keller, & Just, 2007). The dual-task activation was found to cause less activation than the sum of the attend sentence and attend rotation conditions. Particularly, the language related activation in temporal areas was considerably lower in the dual-task condition compared to the sentence comprehension only condition. In this study another possible explanation for underadditivity was proposed. During single task performance there are resources available to perform additional elaborations, particularly during language. For example, if time permits and resources are available, when reading a sentence subjects may generate a visual image of the actions described or generate inferences regarding the implications of those actions. This type of elaboration does not occur when resources are limited.

While activation in sensory and association cortex appears to show underadditivity, activation in prefrontal regions show additivity. In a dual-task study, where the focus was on working memory demands on prefrontal areas, Goldberg et al. (1998) found that the activation in prefrontal areas was less in the dual-task condition, compared to the single-task condition. However, Jaeggi et al. (2003) found that during both single and dual-tasks the prefrontal activation increases as a function of the working memory load. In addition, the prefrontal activation during the dual-task exceeded the

activations in single-task conditions. In another study, concurrently performed visual and somatosensory reaction time tasks activated regions that correspond to the sum of the single-task activations, which fails to show the underadditivity effect (Herath, et al., 2001)

Overall, how underadditivity contributes to processing of dual-task demands and why it is not observed in all dual-task conditions is still not clear. It is probable that multiple factors contribute to underadditivity, such as the nature of the tasks, temporal aspects of stimuli presentation and response modes.

Dual-task demands activate a combination of prefrontal and parietal regions

There are conflicting results from multiple studies on whether dual-task performance relies only on the brain activity that constitutes the dual-task or recruits cortical areas in excess of those required by the single tasks. In a number of studies involving varied tasks such as, auditory and visual working-memory (Klingberg, 1998), card sorting and auditory verbal shadowing (Goldberg, et al., 1998), and auditory sentence comprehension and mental rotation (Just, et al., 2001) tasks, no additional regions of activation where found for the dual-tasks.

Notwithstanding these results, in a study that involved two non-working-memory tasks, semantic-judgment and spatial rotation, the dual-task condition activated bilateral dorsolateral prefrontal cortex (DLPFC), and the anterior cingulate cortex (ACC, D'Esposito et al., 1995). Both of these areas did not show activation in the single-tasks. The authors hypothesized that DLPFC is involved in allocation and coordination of attentional resources, which is part of the central executive system (CES). ACC was also proposed to be part of the same CES network, and to be involved in response selection among competing, complex contingencies. In another study where the concurrent

performance of a somatosensory and visual RT task was investigated, the dual-task activated bilateral superior frontal cortex, the frontal eye fields, the intraparietal sulcus (IPS), and the supramarginal gyri (Herath, et al., 2001). These areas were not activated in the single tasks.

The discrepancy between the results on if dual-task performance recruits additional regions can be explained in two ways: First, previous studies reported DLPFC and cingulate cortex activations for WM sensory stimuli (Jonides et al., 1993; Klingberg & Roland, 1997; Petrides, Alivisatos, Meyer, & Evans, 1993). Therefore, it is possible that the WM demand is due to the coordination of two non-WM tasks during the dual-task performance. Processing a stimulus from one task might be delayed because of the demands for the second task inducing a WM requirement. (Detweiler & Schneider, 1991; Klingberg, 1998). Second, the lack of additional regions of activation in dual-tasks for some studies (Goldberg, et al., 1998; Just, et al., 2001; Klingberg, 1998) can be reconciled by the fact that the tasks involved in these studies were relatively complex paradigms. It is possible that these tasks activated areas in the frontal and parietal cortices that are found to be activated in dual-tasks. Therefore the dual-tasks in these studies may have just increased the activation that was present for the single tasks (Herath, et al., 2001).

The overarching argument in this study is that number processing is embodied. An important follow-up to this argument is that numerical processes and sensorimotor processes share neural resources. The first study (Chapter 2) tests if addition and finger tapping use shared resources using a behavioral dual-task experiment. According to CFH (Cortical Field Hypothesis) (Klingberg & Roland, 1997) dual-task interference is modulated by the amount of neural resources shared by two processes. Therefore, it was

hypothesized that finger tapping interference would be more on addition compared to the control, sentence comprehension, task. In addition, complexity of the tapping sequence was hypothesized to modulate the interference. In the second study (Chapter 3) the neural dynamics of the interaction between tapping and addition was investigated. Based on the behavioral findings from the first study it is argued that areas that are known to be essential for arithmetic would activate for finger tapping as well. In addition through a series of contrasts, hypotheses about how tapping complexity and task difficulty would affect the finger and number processing interactions were tested. Finally, how the brain handles concurrent demand on shared resources during dual-task finger tapping and addition performance was investigated. The experiments in the first and second study are unique, in the sense that they investigate embodiment of arithmetic from a performance based perspective. These two studies use a dual-task design as an innovative way to investigate embodiment of higher-thinking. The third study (Chapter 4) explores relations between an array of bodily and cognitive measures, to find out if and how bodily measures can be used as predictors of cognitive ability. In Chapter 5 I provide a new theoretical approach to mathematical cognition, namely embodied simulations. I argue that approaching mathematical processes as sensorimotor simulations make it possible to build bridges among disparate findings and provide a unified explanation of how mathematics emerges from the embodied mind. This theoretical investigation complements the empirical findings in the previous three chapters.

In Chapters 2, 3, and 4 first-person plural pronoun is used because each chapter was originally co-authored as a separate research article by me and Dr. Sharlene D. Newman. In the remaining chapters first-person singular pronoun is used.

Chapter 2 - Behavioral Indicators for Shared Resource Use Between Finger Tapping and Arithmetic

Abstract

We propose that the unique ability of humans to have separate mental representations for each finger and to move them in different sequential orders is used for arithmetic. We tested our hypothesis with a behavioral dual-task experiment, where participants (n=46) solved addition problems (primary task) and performed a sentence comprehension task (control task), while concurrently tapping their fingers (secondary task). We examined two sequential finger tapping tasks: one that was more automatic and followed the anatomical finger order (simple) and one that relied heavily on sequence processing (complex). We found that both simple and complex finger tapping differentially interfered with addition compared to sentence comprehension. These results provide support for shared use of resources between addition and finger tapping and for the idea that finger processing plays a role in simple addition, even for adults who do not rely on finger counting strategies.

Introduction

A relation between fingers and number processing was first formulated in 1924 when Josef Gerstmann diagnosed a condition, now named Gerstmann's Syndrome, with 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). Gerstmann found that the condition was most commonly due to a lesion in the left angular gyrus (Gerstmann, 1940). He believed that the main symptom was finger agnosia, a specific type of body schema impairment (autopagnosia) affecting the mental representation of hands and fingers. He proposed that the loss of finger sense combined with the left-right disorientation caused acalculia, (Butterworth, 1999b, p. 219). There have been a number of studies reporting data to support Gerstmann's theory. For example, a study examining patients with tumors in and around the angular gyrus found that these patients had impairments in writing, calculating, and finger recognition (Roux, et al., 2003). Also, in an rTMS study of healthy participants it was found that disruption of the left angular gyrus impaired access to the finger schema and number magnitude processing (Rusconi, et al., 2005). Additionally, a series of behavioral studies have consistently shown that finger gnosia in younger children is a predictor of numerical abilities; pointing to a functional relation between finger representation and number processing (Noel, 2005; Penner-Wilger, et al., 2007).

While there is evidence to support Gerstmann's theory, an opposing theory suggests that acalculia in Gerstmann's Syndrome is due to an impairment in mental manipulation of images and not due to a deficit in the representation of hands and fingers (Mayer, et al., 1999). In a study with healthy patients rTMS to the angular gyrus disrupted

both a visual search and a number comparison task (Gobel, et al., 2001). However, this finding only partially supports the opposing theory because the effects of rTMS on finger schema representation were not tested.

The question of whether acalculia in Gerstmann syndrome is due to finger representation or visuo-spatial processing impairments characterizes a general discussion: To what extent is number representation body-based?

Fischer (2008) explored whether finger-counting habits interact with the SNARC (Spatial-Numerical Association of Response Codes) effect, which is an association of small numbers with the left visual field and big numbers with the right visual field (Dehaene, et al., 1993). The results revealed that participants who are left-starters show a SNARC effect significantly more than right-starters. Di Luca, Grana, Semenza, Seron and Pesenti (2006) asked participants to identify Arabic digits by pressing one of 10 keys with all 10 fingers. The configuration of response buttons varied both in terms of the global direction of the hand-digit mapping and the direction of the finger-digit mapping within each hand, from small to large digits or vice versa. The results showed that participants performed better when there was a congruency between the reported finger-counting strategy of the participant and the mapping of the response buttons. Both studies (Di Luca, et al., 2006; Fischer, 2008) provide evidence for the dominance of a finger-based number representation compared to a spatial one.

In order to explore shared processes between number and finger processing, the current study focused on sequence processing. Sequence processing is defined as action on or manipulation of a set of ordered items. It therefore involves at least two sub-processes: action sequencing or the motor-related activity necessary to manipulate the items; and rule

monitoring which is monitoring of the item order. Arithmetic, and more generally number processing, involves sequential processing. Some evidence to support this idea comes from neuroimaging studies which suggest an overlap between visual-motor sequencing (Buhusi & Meck, 2005) and number processing (Dehaene, et al., 1999), in cerebellum and intraparietal sulcus (Sakai, Ramnani, & Passingham, 2002). Additionally, Arsalidou and Taylor (2010) propose that both visuo-spatial and motor simulation strategies used in calculation require sequencing under conditions with time constraints.

The aim of the current study was to test claims of a finger-based representation of numbers. This was done by examining a simple arithmetic function, addition, within a dual-task paradigm. The secondary task was a sequential finger tapping task. If number processing is grounded in a system that is also used for finger processing, then we hypothesize that finger movements should interfere more with number processing compared to a non-numerical control task. Here, the difficulty of the addition problems as well as the finger tapping sequence, was manipulated. Addition difficulty was manipulated in order to determine whether finger-based representations are differentially involved in rote retrieval of arithmetic facts compared to calculation strategies. The finger tapping sequence difficulty was manipulated by varying the difficulty of the sequence rule. The easy sequence is the anatomical order of the fingers and requires action/motor sequencing but very little rule monitoring while the hard sequence places demands on both of the component sequence processes. As a result, it was predicted that if the overlap between finger and number processing is due to the use of a shared sequence processing system, then the level of interference between tapping and addition would be a function of tapping difficulty.

Methods

Participants

46 adults (age 18-28, M=19.90, 35 females, all right handed) were recruited from the Indiana University community. All were native English speakers and none of the participants reported any neuropsychological conditions except one with dyslexia. All participants gave written, informed consent approved by the Indiana University institutional review board.

Stimuli

The experiment utilized a dual-task paradigm. The primary task was addition. The addition problem was presented at the top of the screen with 4 possible answers at the bottom. There were two levels of difficulty. Easy questions involved addition of three numbers between 1 and 4, and hard questions involved the addition of two numbers between 11 and 99, excluding multiplies of 5. The secondary task was finger tapping involving the four fingers of the right hand (no little finger), with two levels of complexity. The simple sequence followed the anatomical order of fingers (ring, middle, index and thumb), and the complex sequence followed the "ring, thumb, middle and index" order. It was previously shown that learning to tap sequentially at a given rhythm allocates additional resources compared to sequential tapping with an uncontrolled rhythm (Sakai, et al., 2002). Therefore, the participants were told to tap rhythmically at a self-controlled and comfortable pace. We had a control non-numeric task - a sentence comprehension task. In the comprehension task participants were presented with a sentence at the top of the screen, and a true/false comprehension probe at the bottom. The

comprehension task also had two levels of difficulty, with active sentences comprising the easy condition and passive sentences the hard (Slobin, 1996).

Finger tapping complexity was presented in two separate blocks. The dual-task condition in one block involved tapping with the simple sequence while the other block involved the complex sequence. The order of the blocks was counterbalanced across participants. Each block consisted of 20 trials of single addition, single comprehension, dual addition-tapping and dual comprehension-tapping conditions. The single finger tapping trials consisted of 15 sec of tapping while a fixation crosshair was presented on the screen.

While finger tapping was performed with the right hand, participants responded to the addition and comprehension trials with their left hands. Participants responded to the addition trials by pressing the "a," "s," "d," and "f" buttons on the keyboard (matching with A, B, C, D choices), using their little, ring, middle and index fingers respectively. They used "a" (true) and "s" (false) keyboard buttons, matching with middle and index fingers respectively, to respond to the comprehension probe.

We designed a task to test if having four response buttons for addition and two response buttons for comprehension is a confound in terms of the interaction between the left hand finger movement to give a response and the right hand finger tapping. We thought that having four choices might interfere more with finger tapping than having two. During the task the participants (n=10) were presented with either four ("A, B, C, D") or two ("T, F") choices. After choices stayed on the screen for 3 sec one of them turned yellow and the participant clicked on the button for that choice. Participants were also asked to tap their fingers both with the simple and complex finger tapping sequences in

two separate blocks. There were 30 trials per condition with a total of 120 trials. The results showed that there were no significant differences between four and two choice conditions in terms of RT, response accuracy, and tapping performance, across both tapping complexities (Table 1). Based on the results we concluded that having different response settings for the two task conditions had little impact on the results.

Table 1 - *Results from the confound task*

	Simple				Complex			
	ABCD		True/False		ABCD		True/False	
	M	SD	M	SD	M	SD	M	SD
RT	3.62	0.58	3.65	0.56	3.76	0.73	3.89	0.48
Accuracy	0.93	0.26	0.9	0.3	0.93	0.25	0.91	0.29
Tap Perf.	4.77	1.82	4.66	2.44	2.83	0.87	2.82	0.76

Procedure

After participants were given general information about the experiment, they went through a training session where they were presented with a shortened version of the experiment. The finger tapping combination used during the training was different than the two tapping combinations used in the experiment. Before each experimental block participants completed a finger tapping training where they finger tapped at a rhythmic and comfortable pace using the sequence for block that block. A blinking green ellipse, was presented when they completed a sequence correctly. They were to complete 25 consecutive tapping sequences successfully before the training ended.

Before the experiment started the participants were told to tap their fingers as rhythmically as possible in a comfortable pace. They were also reminded that there were no time constraints and accuracy was more important than speed. They were instructed that during the dual trials they were to continuously tap, even when responding to the addition and comprehension trials.

We use the terms "simple" and "complex" to refer to the complexity of the tapping sequence, and "easy" and "hard" to indicate the task difficulty for addition and comprehension. For example, dual-complex refers to the dual conditions where the participants answered addition or comprehension questions while tapping the complex sequence.

Filtering

All trials with RT values outside the M ±2 SD range were filtered and not included in the analysis (6%) to exclude outliers. The range was calculated separately for each participant/block. Dual trials in which the participant did not tap fingers were also filtered (1.4%). Finally, trials with incorrect responses were filtered from analysis of RT and tapping performance (9.7%).

Reaction Time
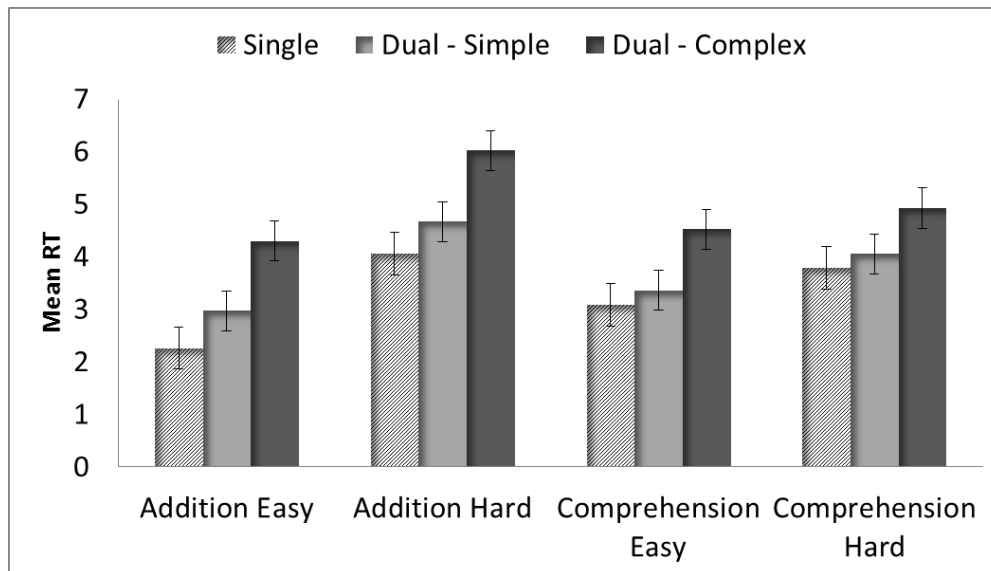
Figure 1. Mean reaction time values (sec) for each condition.

For the simple tapping condition, we performed a 2 (single vs. dual-simple) x 2 (addition vs. comprehension) x 2 (easy vs. hard) within participants ANOVA on reaction time (Fig. 1). Analysis revealed a main effect of single/dual such that RT was higher for dual compared to the single conditions [$F(1,45)=20.67$, $p<0.0001$]. There was also a main effect of difficulty, hard questions taking longer than easy questions: [$F(1,45)=310.28$, $p<0.0001$]. A significant interaction between single/dual-simple and task [$F(2,45)=13.51$, $p<0.001$] was found. Post-hoc analysis revealed that the difficulty-collapsed single and dual-simple RT values were significantly different both for addition [(M=3.15, SD=0.75), (M=3.76, SD=0.97)] and comprehension [(M=3.41, SD=0.78), (M=3.70, SD=0.99)]. The effect size was bigger for addition (0.85) compared to comprehension (0.38), showing that, based on RT, the dual-task demands of simple tapping interfered more with addition than comprehension. There was also a significant interaction between task and difficulty [$F(2,45)=80.59$, $p<0.0001$]. According to the post-hoc analysis the single/dual-simple collapsed averages were significantly different between easy (M=2.63, SD=0.54), and hard (M=4.35, SD=1.14) addition, and easy (M=3.24, SD=0.72) and hard (M=3.90, SD=0.91) comprehension. The effects size for addition (2.29) was bigger than it was for comprehension (1.08) showing that the interaction was due to a bigger difference between easy and hard conditions for addition.

We conducted a 2 (single vs. dual-complex) x 2 (addition vs. comprehension) x 2 (easy vs. hard) within participants ANOVA to investigate the effects of complex tapping. The analysis revealed a main effect of single/dual-complex [$F(1,43)=72.75$, $p<0.0001$] with single conditions showing longer RT; and of difficulty [$F(1,45)=110.29$, $p<0.0001$] with easy trials having a longer RT. A significant interaction between single/dual-simple

32

and task [F(2,45)=21.57, p<0.0001] was found. Post-hoc analysis revealed that the difficulty-collapsed single and dual-complex RT values were significantly different both for addition [(M=3.15, SD=0.75), (M=5.17, SD=1.62)] and comprehension [(M=3.41, SD=0.78), (M=4.72, SD=1.49)]. The effect size was larger for addition (1.50) compared to comprehension (0.94), showing that, based on RT, the dual-task demands of complex tapping interfered more with addition than comprehension. There was also a significant interaction between task and difficulty [F(2,45)=37.65, p<0.0001] due to a larger difference between easy and hard conditions for addition.

A 2 (dual-simple vs. dual-complex) x 2 (addition vs. comprehension) x 2 (easy vs. hard) within participants ANOVA was used to investigate the effects of sequence processing load on RT (Fig. 1). Main effects of complexity [F(1,43)=73.22, p<0.0001] and difficulty [F(1,43)=91.88, p<0.0001] were found, hard and dual-complex conditions having higher RT than easy and dual-simple conditions respectively. An interaction between complexity and task was found [F(1,43)=2.401, p=0.043]. Post-hoc analysis showed that the difficulty-collapsed dual-simple and dual-complex RT values were significantly different both for addition [(M=3.76, SD=0.97), (M=5.17, SD=1.62)] and comprehension [(M=3.70, SD=0.99), (M=4.71, SD=1.49)]. However, the effect size was bigger for addition (1.33) compared to comprehension (0.92), showing that, in terms of RT, the additional sequence processing demand in complex tapping interfered more with addition than comprehension. Additionally, there was an interaction between task and difficulty [F(1,43)=34.22, p>0.0001] due to the bigger RT difference between easy and hard for addition compared to comprehension.

Task Accuracy
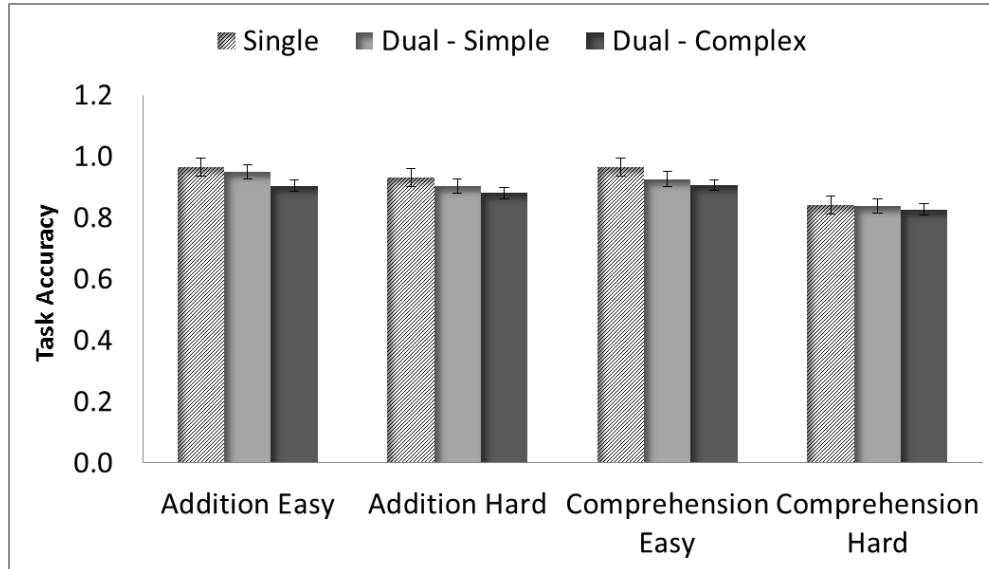
Figure 2.Mean task accuracy values (Number of correct responses / Number of total responses) for each condition.

We performed a 2 (single vs. dual-simple) x 2 (addition vs. comprehension) x 2 (easy vs. hard) within participants ANOVA on task accuracy to investigate the effects of simple finger tapping on accuracy (Fig. 2). The analysis revealed a main effect of single/dual-simple [$F(1,45)=7.46$, $p=0.009$] with single conditions showing higher accuracy; of task [$F(1,45)=18.40$, $p<0.0001$] with addition having higher accuracy; and of difficulty [$F(1,45)=48.82$, $p<0.0001$] with easy trials having a higher accuracy. There was a significant interaction between task and difficulty [$F(2,45)=18.40$, $p<0.0001$]. According to the post-hoc analysis while there was no significant difference between single-dual collapsed averages of easy (M=0.96, SD=0.04) and hard (M=0.95, SD=0.05) addition, the difference was significant for easy (M=0.92, SD=0.07) and hard (M=0.84, SD=0.12) comprehension. Notably there was no interaction between single/dual and task [$F(2,45)=0.006$, $p=0.941$] showing that both addition and comprehension accuracy were affected similarly from simple finger tapping compared to single conditions.

34

We conducted a 2 (single vs. dual-complex) x 2 (addition vs. comprehension) x 2 (easy vs. hard) within participants ANOVA to investigate the effects of complex tapping on accuracy (Fig. 2). We found a main effect of single/dual-complex [$F(1,43)=30.207$, $p=<0.0001$] with single conditions having higher accuracy; of task [$F(1,45)=7.02$, $p=0.011$] with addition showing greater accuracy; and of difficulty [$F(1,45)=30.68$, $p=0.009$] due to easy conditions having higher accuracy. The only significant interaction was between task and difficulty [$F(1,45)=9.18$, $p=0.004$] due to larger accuracy difference between easy and difficulty comprehension conditions compared to addition.

A 2 (dual-simple vs. dual-complex) x 2 (addition vs. comprehension) x 2 (easy vs. hard) within participants ANOVA was conducted to investigate the effects of sequence processing load on accuracy (Fig. 2). The results revealed main effects of complexity [$F(1,43)=12.99$, $p=0.001$], task [$F(1,43)=8.05$, $p=0.007$], and difficulty [$F(1,43)=40.23$, $p<0.0001$]. There was an interaction between task and difficulty [$F(2,45)=4.593$, $p=0.038$]. Notably, there was no interaction between complexity and task [$F(1,43)=0.62$, $p=0.436$], showing that the sequence processing load affected addition and comprehension accuracy similarly.

Tapping Performance
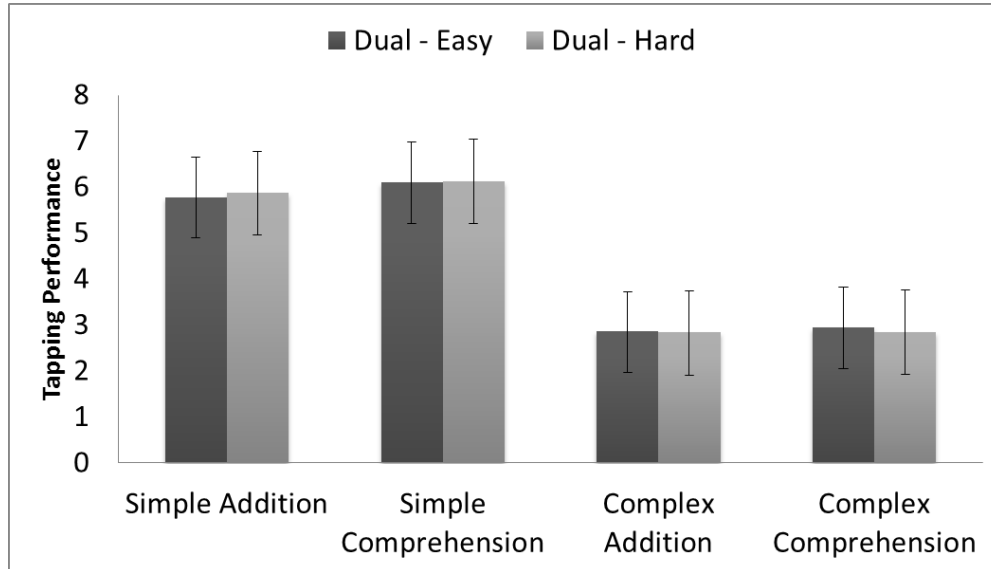
Figure 3. Tapping performance (Number of corrects taps / RT).

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. This measure combines both the speed of tapping and accuracy. We performed a 2 (simple vs. complex tapping) x 2 (addition vs. comprehension) x 2 (easy vs. hard) within participants ANOVA on tapping performance to investigate the effects of sequential processing load on tapping performance. The analysis revealed a main effect of complexity [$F(1,45)=123.99$, $p<0.0001$] and task [$F(1,45)=12.28$, $p=0.001$] (Fig. 3).

There was an interaction between complexity and task [$F(2,45)=0.320$, $p=0.574$].The post-hoc analysis revealed that while there was a significant difference between difficulty collapsed tapping performance averages for simple tapping addition (M=5.76, SD=2.24) and comprehension (M=6.06, SD=2.20) values, there were no significant differences between addition (M=2.82, SD=0.87) and comprehension (M=2.87,

SD=0.84) for complex tapping conditions. Therefore the interaction is due to the relatively bigger interference of addition on simple-finger tapping compared to comprehension.

Discussion

The primary aim of this study was to explore the embodiment of number processing. We aimed to determine whether arithmetic shares resources with finger movement processes from a performance-based perspective. Within a dual-task paradigm we compared addition to a control, sentence comprehension task. The results presented here suggest that there are overlapping processes between finger movement and arithmetic, at least for addition. Here, we found that finger tapping, with both the easy and difficult sequences, interfered with addition, for both the easy and hard addition problems. Furthermore, the interference observed for addition was significantly greater than that observed for sentence comprehension. Below is a discussion of the results and their implications for the embodiment of number processing.

One of the predictions was that addition would be differentially affected by both simple tapping and complex tapping compared to sentence comprehension. This was observed here. For both the simple tapping and complex tapping a significant interaction between dual/single and task was observed which indicated that addition performance was more affected by tapping. We hypothesize that one reason for this increased interference is that both finger tapping and addition rely on a finger-based representation. The participants in this study were all adult, college students; therefore it is not likely that they used finger counting strategies to solve the addition problems. Instead, we argue that finger representation is tied to and facilitates number processing. The data presented here does provide some support for this idea. Finger tapping, specifically the simple sequence,

affected both the easy, memory retrieval-based, and hard, calculation-based, conditions. While sequence processing may be expected to interfere with calculation, it is not expected to interfere with memory retrieval. Memory retrieval is involved in the comprehension task and it could be argued that the comprehension task requires more memory processing (each word is accessed in memory) than addition. However, the finger tapping task interfered less with the comprehension task. Therefore, finding significant interference for the easy addition problems suggest that it is not necessarily the sequence processing aspect of the finger tapping that is interfering but it is the involvement of the fingers.

Second, we predicted that when the demand on sequence processing increased in the finger tapping task the interference with addition would also increase. This was also observed. This prediction was made because rule monitoring was thought to be an aspect of sequence processing that would additionally overlap with calculation procedures. However, as discussed, both easy and hard addition were affected by the additional sequencing load. One possible explanation is that although the majority of the operations taking place in easy addition involve rote memory retrieval, the solution may still involve some overlapping processes with the complex sequence, namely working memory processes. The complex sequence has a significantly greater working memory load than the simple sequence and this additional process may be responsible for the increased interference.

It should also be noted that aspects of sentence processing also involve sequence processing, particularly syntactic processing. For example, Pulvermuller (2003) suggests that syntax is built on serial-order mechanisms. Here, the sub-component of sequence

processing that was expected to overlap most with syntactic processing is rule monitoring. Given that syntax is defined as the set of rules that govern how words are combined to create sentences, we expected the complex sequence to interfere with comprehension, particularly the hard passive sentences.

The increase in process overlap between finger tapping and addition compared to comprehension implies that these two tasks may also share neural resources. Previous neuroimaging research showing shared neural resource allocation for finger representation and number processing supports this interpretation (Sato, et al., 2007; Zago, et al., 2001). From a functional standpoint the results provide support for the previously established relation between the mental representation of fingers and numerical quantity (Noel, 2005; Penner-Wilger, et al., 2007). In addition, we propose that sequence processing resources are also shared between finger motor processes and number processing.

Limitations & Future Directions

An alternative interpretation for the results would be that addition is more prone to dual-task interference compared to sentence comprehension, independent of the nature of the secondary task. Therefore future experiments should focus on testing if other motor tasks (e.g. jumping) would also show differential interference for addition. Based on our hypotheses we would predict that a non-hand or finger related secondary motor task would not cause differential interference for addition. Additionally, a double dissociation of addition and comprehension can be established by finding a motor task that differentially interferes with comprehension, which would provide further support for our claims. Nevertheless, there are practical limitations about capturing non-hand related motor movements. Also due to lack of previous research on motor task interference in

mathematics or sentence comprehension it is challenging to narrow down the secondary task possibilities.

Previous research shows that the motor system is involved in semantic language processing (Buccino et al., 2005; Kemmerer & Gonzalez-Castillo, 2008), therefore it is possible that finger tapping interference is modulated by the relevance of sentence semantic content to hand/finger related movements. Although we did not control for the semantic content, none of the sentences involved hand/finger related verbs (e.g. grasp, tap, squeeze).

The differential interference of complex tapping on addition constitutes partial evidence for shared use of sequence processing resources. The effect can also be attributed to shared use of finger representations independent of sequence processing. However, it is difficult to separate the contribution of sequence processing and finger representation to number processing. There may be two ways to investigate this: 1) using a non-finger related sequential motor task to quantify the influence of sequence processing independent of finger processing and 2) using a task that uses finger representations without a motor or sequence task. Both present practical challenges.

Conclusion

Mathematics is a highly abstract knowledge domain presenting challenges for the idea of embodied cognition. In this study we explored the embodiment of arithmetic by investigating the shared resource usage between addition and finger tapping. We found evidence for shared use of resources between addition and finger tapping at different levels of complexity. This study is unique in two aspects: First, we focused on the role of sequence processing in the interaction between finger movements and arithmetic, which

40

has not been studied before. Second, by studying dual-task interference we adopted a performance-based approach to explore the interaction between motor and arithmetic processes.

Chapter 3 - Neural Dynamics of Shared Resource Use Between Finger Tapping and Arithmetic

Abstract

In a previous behavioral dual-task study we showed that sequential finger tapping interferes more with addition compared to a control sentence comprehension task (Soylu & Newman, 2011). Based on this study, we investigated the neural dynamics of the dual-task interference between addition and finger tapping to explore the shared neural resources between two tasks and how the brain handles additional demand on these shared resources. Results revealed that neural correlates of addition overlap with a frontoparietal network that is also used by finger tapping. The angular gyrus was deactivated, compared to a fixation baseline, across all conditions. The deactivation was modulated by both difficulty and tapping complexity. We also found evidence for angular and supramarginal gyri having different functional roles in arithmetic processing. Based on the results we inferred that bilateral angular gyri participate in mental representation of fingers where left supramarginal gyrus mediates sequential activation of finger representations, such as in finger tapping. Overall, the results further our understanding of the shared use of neural resources between arithmetic and the sensorimotor system, and make a strong case for the embodiment of arithmetic.

Introduction

Although there is evidence for some non-human animals having a number sense and the ability to do simple arithmetic (see Dehaene, et al., 1998) humans' mathematical ability is unprecedented. Yet still mathematics, in addition to other higher level cognitive skills, is processed in a brain that originally evolved for lower level sensorimotor tasks. The idea that mathematical cognition is grounded in sensorimotor processes resonates with the embodied approach to cognition, according to which cognition is grounded in bodily processes and in our interactions with the environment. Since embodied approaches to cognition explain cognitive skills in terms of their sensorimotor groundings, evolution of cognition is viewed as a process where higher cognition emerges from systems that have already developed for other, lower level functions. One theory that explains how low level sensorimotor systems are adapted for higher level thinking (e.g. verbal communication, mathematics) is the *massive redeployment theory* (MRT) (Anderson, 2006). Anderson argues that higher cognition is possible through redeployment of existing neural systems for new functions. Based on previous neuroimaging research in different domains of cognition he formulated three principles for redeployment: 1) A single brain region is used for many cognitive functions, 2) evolutionarily older brain areas are affiliated with more cognitive functions, and 3) newer cognitive functions utilize more distributed brain areas (Anderson, 2007). Compatible with MRT, neuroimaging studies on the neural correlates of number processing show a widely distributed frontoparietal network. The existence of a frontoparietal network for number processing has been associated with different functional accounts. According to a theory proposed by Dehaene et al. (1992; Dehaene & Cohen, 1995; Dehaene, et al., 2003), frontal regions active in

number processing underlie numerical facts and exact calculation, while parietal regions play a role in visuo-spatial processing during approximation. On the other hand, the frontoparietal network overlaps with the neural circuitry active during finger movements, which lead to the theory that numbers are represented on a circuit that was originally developed to represent fingers (Anderson & Penner-Wilger, 2007; Andres, Seron, & Olivier, 2007; Penner-Wilger & Anderson, 2008, 2011; Penner-Wilger, et al., 2007). In a previous behavioral dual-task study, where addition was the primary and sequential finger-tapping was the secondary task, we found that finger-tapping interference on addition was significantly greater than that observed for the control task (Soylu & Newman, 2011). According to the *cortical field hypothesis* (CFH), the amount of dual-task interference is modulated by the proximity and overlap of the neural correlates for single tasks (Klingberg & Roland, 1997; Roland & Zilles, 1998). Based on CFH we inferred that differential interference of tapping on addition also implies that these two tasks use overlapping neural resources. In this paper we followed up on this claim and investigated the interaction between addition and sequential finger tapping at the neural level using a dual-task paradigm. This design made it possible to investigate the neural systems that support finger tapping and arithmetic separately, in addition to how the brain handles the extra demand when the two tasks are performed concurrently. The results of this study contribute to a line of research focusing on the finger and number relation, starting with the identification of a neurological syndrome in the early 20th century.

The relationship between fingers and number processing

In 1924 Josef Gerstmann diagnosed an adult patient who had "an isolated disturbance in the recognition, naming, choosing, and differential exhibition of the various

fingers of both hands-one's own fingers as well as those of another person..." and he named this condition 'finger agnosia.' Tests on this patient also revealed that she had difficulty differentiating between her right and left hand, or another person's right and left hands. In addition, she performed poorly on calculation tests and had impairments in spontaneous writing, a condition referred to as 'agraphia.' He studied more patients with the same four co-occurring symptoms, finger agnosia, acalculia (an inability to perform arithmetic calculation), left-right disorientation and agraphia, and described a condition now named Gerstmann's Syndrome. He explained the main source of the symptoms as "a lesion located in the parieto-occipital region of the brain, namely, in that part which corresponds to the angular gyrus in its transition to the second occipital convolution (Gerstmann, 1940, p. 399). Gerstmann believed that the main symptom was finger agnosia, a specific type of body schema impairment (autopagnosia) affecting specifically the representation of hands and fingers. He proposed that the loss of finger sense combined with the left-right disorientation caused acalculia (Butterworth, 1999b, p. 219). According to another theory, Gerstmann's Syndrome is due to an impairment in mental manipulation of images and not to a deficit in the mental representation of hands and fingers (Mayer, et al., 1999). Roux, Boetto, Sacko, Chollet and Tremoulet (2003) used direct brain mapping to study a series of patients who had tumors in and around the angular gyrus. They reported that areas producing impairments in writing, calculating, and finger recognition were found in the angular gyrus, which may or may not have been associated with object-naming, color-naming, or reading sites. In a study conducted with healthy subjects, Rusconi, Walsh, & Butterworth (2005) found that rTMS over the left angular gyrus disrupted tasks requiring access to the finger schema and number magnitude

processing in the same group of participants; providing additional support for Gerstmann's Syndrome impairing access to the body schema, particularly finger representation. A series of behavioral studies have consistently shown that finger gnosia in younger children is a predictor of numerical abilities; pointing to a functional relation between representation of fingers and number processing (Noel, 2005; Penner-Wilger & Anderson, 2008, 2011; Penner-Wilger, et al., 2007).

Neural Dynamics of the Interaction Between Fingers and Number Processing

Neuropsychological and brain imaging studies on number processing support a distinction between exact arithmetic and magnitude processing for approximate calculations (Sato, et al., 2007). A frontoparietal network has been found to underlie number processing, frontal processing being more related to retrieval of arithmetic facts and exact calculation, and parietal areas being responsible for magnitude representation. Among the frontal areas, the precentral gyrus and pre-motor regions are the most relevant (Dehaene, et al., 2003). In terms of the role of parietal regions in number processing, two areas consistently have been found to be active in number processing tasks; the intraparietal sulcus (IPS) and the angular gyrus (Dehaene, et al., 2003; Dehaene, et al., 1999; Houdé & Tzourio-Mazoyer, 2003; Hubbard, et al., 2005). There are conflicting results concerning the role the IPS and angular gyrus play in number processing. Cappelletti et al. (2007) reported that stimulation of the angular gyrus did not modulate performance in a number comparison task involving double digit integers, while the stimulation of left IPS reduced performance, showing that IPS, and not the angular gyrus, is related to magnitude estimation. However, Gobel, Walsh and Rushworth (2001) found that stimulation of the angular gyrus disrupted both number comparison with single digits,

and a visual search task. IPS has consistently been found active during number comparison tasks in a series of neuroimaging studies, yielding to the result that IPS is used for common representation of magnitude for numerical values, both symbolic and non-symbolic (Cappelletti, et al., 2007; Cohen Kadosh, Lammertyn, et al., 2008; Pinel, et al., 2004). The existence of a frontoparietal network for number processing has been associated with different functional accounts. According to a theory proposed by Dehaene et al. (Dehaene, 1992; Dehaene & Cohen, 1995; Dehaene, et al., 2003), frontal regions active in number processing underlie numerical facts and exact calculation, while parietal regions play a role in visuo-spatial processing during approximation. In an alternative account, the frontoparietal network overlaps with the neural circuitry active during finger movements, leading to the theory that the early association between number processing and fingers during development might shape the neural substrate of number processing; situating it on a network originally used for finger movements (Butterworth, 1999a; Pesenti, et al., 2000; Sato, et al., 2007).

Neuroimaging studies also show an overlap between finger movement control and number processing. Studies on the neural correlates of number processing (Crozier, et al., 1999; Dehaene, et al., 2003; Houdé & Tzourio-Mazoyer, 2003; Hubbard, et al., 2005) and of hand motor abilities (Binkofski, et al., 1999; Chong, et al., 2008; Corina & Knapp, 2006; Sakata & Taira, 1998) point to the importance of an overlapping prefrontal and intraparietal circuit. Zago et al. (2001) found activation of a finger representation circuit in the left parietal lobe during adults' performance of basic arithmetic. Increased activation was observed in the premotor strip at the coordinates for finger representation during performance of single-digit multiplication compared to a digit reading condition. Sato et

al. (2007) used rTMS to measure changes of excitability in hand muscles while participants performed a visual parity judgment task on single digit numbers. While no modulation was observed for the left hand muscles, an increase in amplitude of motor evoked potentials was found for the right hand muscles, particularly for smaller digits (1 to 4).

Methods

This experiment is designed to explore the overlap of the neural network that supports both sequential finger tapping and addition. In addition, the effects of tapping complexity and task difficulty are investigated. To do that, a previously conducted behavioral experiment (Soylu & Newman, 2011) was adapted for the fMRI environment.

Participants

13 adults (age 23-39, M=24.67, 6 females, 7 males, all right handed) were recruited from the Indiana University community. All were native English speakers (4 bilingual) and none of the participants reported any neuropsychological conditions. All participants gave written, informed consent approved by the Indiana University institutional review board.

Stimuli

The fMRI experiment involved two main parts: 1) Sequential finger tapping task, which was designed as a functional localizer and involves one run, and 2) the main experiment, which was divided into four runs.

Sequential Finger Tapping (SFT) Task: The SFT task was designed to localize, first, areas activated during sequential finger tapping, and second, the areas involved in

sequence processing. This task used a block-design. In each block participants were shown a finger tapping sequence twice on the screen, and then were asked to execute this sequence as fast as they can for 16 sec. There were four types of sequences. All sequences involved tapping with four fingers of the right hand (all but the little finger). The two simple sequences, which followed the anatomical order of fingers were: "ring - middle - index - thumb" and "thumb - index - middle - ring." The two complex sequences involved: "*ring - thumb - middle - index*" and "*index - ring - middle - thumb.*"

Main Experiment Part: A mixed design was used such that there were blocks of single and dual conditions but within each block the trials were presented using a rapid-event related design. The inter-trial interval (ITI) was 10 sec to allow for the hemodynamic response to approach baseline. Trial durations were fixed and were determined based on the mean RT values for the same conditions from a previous self-paced behavioral experiment that used the same stimuli (Soylu & Newman, 2011). The preset trial durations were: Easy (single: 3s, simple dual: 4s, complex dual: 5s), hard (single: 4s, simple dual: 5s, complex dual: 6s). The experiment was divided into four runs to ensure that no run was longer than 15 min to allow subjects some time to rest between runs. Each scan was approximately 1.5 hours in duration.

There were two levels difficulty for addition, and finger tapping. There were 30 trials per condition and a within subjects design is used. As a result there were 6 conditions (2 single task conditions: easy and hard addition; 2 easy and hard addition dual-task conditions with easy finger tapping; 2 easy and hard addition dual-task conditions with hard finger tapping). A filler condition, which was not included in the analysis, included sentence comprehension trials randomly distributed among the addition trials.

Finger tapping complexity was presented in two separate blocks. The dual-task condition in one block involved tapping with the simple sequence while the other block involved the complex sequence. The order of the blocks was counterbalanced across participants. Each block consisted of 20 trials of single addition, single comprehension, dual addition-tapping and dual comprehension-tapping conditions. The single finger tapping trials consisted of 15 sec of tapping while a fixation crosshair was presented on the screen.

While finger tapping was performed with the right hand, participants responded to the addition trials with their left hands. Participants responded to the addition questions by pressing the "a," "s," and "d" buttons on the keyboard (matching with A, B, C choices), using their ring, middle and index fingers respectively.

Procedure

The fMRI experiment was conducted on a Siemens TIM Trio 3.0 Tesla scanner located in the Imaging Research Facility at Indiana University, Bloomington. A 32-channel whole-head coil was used, which allows for improved SNR and spatial resolution. The fMRI protocol included capturing 33 axial images providing whole brain coverage. The images were collected using an echo-planar acquisition sequence, with TR=2.0 sec, TE=25 ms, flip angle=70°, with a voxel size of 3.4-mm x 3.4-mm x 3.8-mm with a 0mm gap. Additionally, high-resolution structural images were also be acquired using Siemens MPRAGE sequence (160 3DMPRAGE oblique-axial images were collected with TR=2000 ms, TE=3.34 ms, 7º flip-angle, and a 256×256 FOV, resulting in 1-mm^3 voxels).

Functional MR data was analyzed using SPM8 (Friston & Penny, 2003) installed on a Ubuntu GNU/Linux computer. 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 0.001 and a cluster size threshold of 22; this corresponds to a per-voxel false-positive probability of 0.041, determined by Monte Carlo simulation (see program AlphaSim by D. Ward in AFNI software. Parameters were: single voxel P value=0.001, FWHM=8 mm.

A series of contrasts were performed. First, the main effects of difficulty and single/dual were examined. 2x2 (tapping complexity; easy vs. hard) ANOVAs were also performed.

Results

Behavioral Results

Trials with no responses (6% of all trials) and incorrect responses (12% of all responded trials) were excluded from analysis, except for accuracy analysis. One subject completed only the complex tapping runs.

Task accuracy.
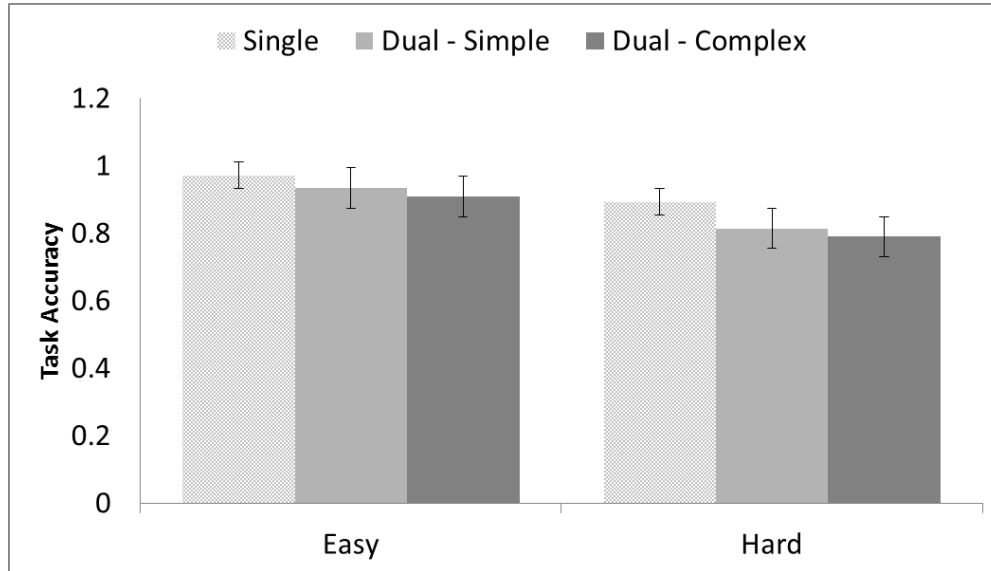
Figure 1. Mean task accuracy values.

We performed a 2 (single vs. dual-simple) x 2 (easy vs. hard) within participants ANOVA on task accuracy to investigate the effects of simple finger tapping on accuracy (Fig. 1). There were no significant main effects. There was a significant interaction between single/dual and difficulty [$F(1,12)=6.07$, $p=0.032$]. Post-hoc analysis revealed that while there were no significant differences between single easy (M=0.84, SD=0.13) and hard conditions (M=0.82, SD=0.12), there was a significant difference between easy (M=0.90, SD=0.08) and hard (M=0.79, SD=0.13) dual simple-tapping conditions. This shows that tapping interference was more for hard addition compared to easy.

A second 2 (single vs. dual-complex) x 2 (easy vs. hard) ANOVA was conducted to investigate the effects of complex tapping on accuracy. We found a main effect of difficulty [$F(1,11)=4.86$, $p=0.048$], such that accuracy was higher for the easy condition. There was also a significant interaction between single/dual and difficulty [$F(1,11)=4.46$, $p=0.056$]. Post-hoc analysis revealed that while there were no significant differences

between single easy (M=0.84, SD=0.13) and hard conditions (M=0.82, SD=0.12), there was a significant difference between easy (M=0.90, SD=0.08) and hard (M=0.77, SD=0.12) dual complex-tapping conditions. Similar to simple tapping, the complex tapping interference was more for hard addition compared to easy.

Finally, a 2 (dual-simple vs. dual-complex) x 2 (easy vs. hard) ANOVA was conducted to reveal the effects of tapping complexity on the accuracy of dual-task trials. There was a main effect of difficulty [$F(1,11)=14.32$, $p=0.003$], due to higher accuracy during easy trials. There were no interactions, showing that simple and complex tapping affected accuracy similarly.

Tapping performance.

The tapping performance measure was the number of correct taps per second. A correct tap (one finger stroke) is one that follows the order of the assigned tapping sequence based on the previous stroke. This measure combines both the speed of tapping and accuracy.

A 2 (dual-simple vs. dual-complex) x 2 (easy vs. hard) ANOVA was performed to investigate the effects of sequential processing load on tapping performance. Results revealed no main effects and interactions, showing that task difficulty and tapping complexity did not affect tapping performance in a significant way.
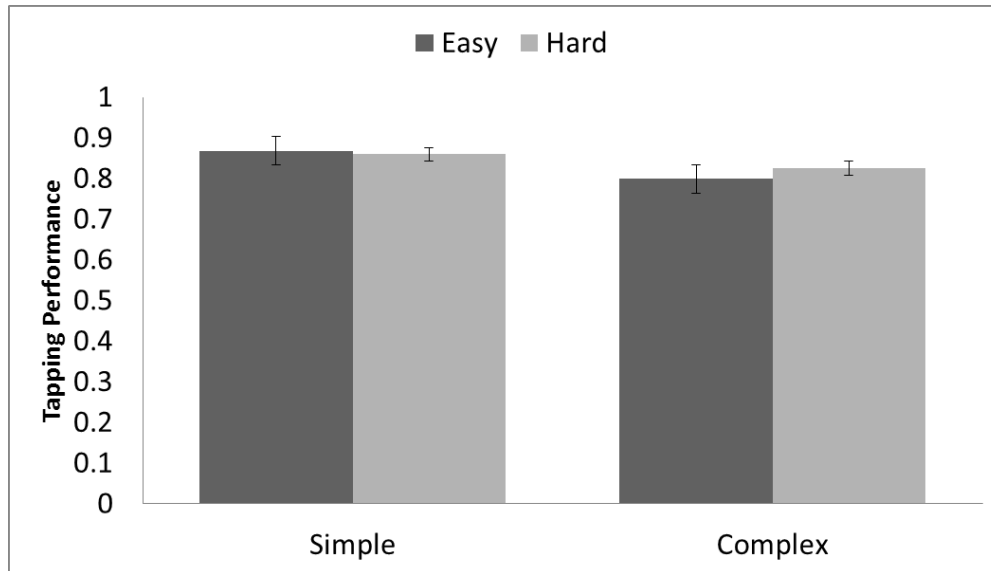
Figure 2. Tapping performance values.

Brain Imaging Results

Sequential finger tapping task (localizer) results.

All subjects (n=13) completed the sequential finger tapping (SFT) localizer task successfully; with less than 3 mm head movement.

The tapping conditions (simple and complex combined) contrasted with fixation revealed bilateral precentral, inferior frontal and prefrontal activations. Simple tapping showed right cerebellum, and bilateral thalamus, precentral and postcentral activations. Complex tapping showed, in addition to activations for simple tapping, activation in the right insula. The comparison of complex tapping with simple tapping revealed significant bilateral angular gyrus activation (Fig. 3, Table 1).

a   Tapping (simple and complex combined) - fixation

b   Simple tapping -fixation

c   Complex tapping -fixation

d   Complex tapping - Simple tapping
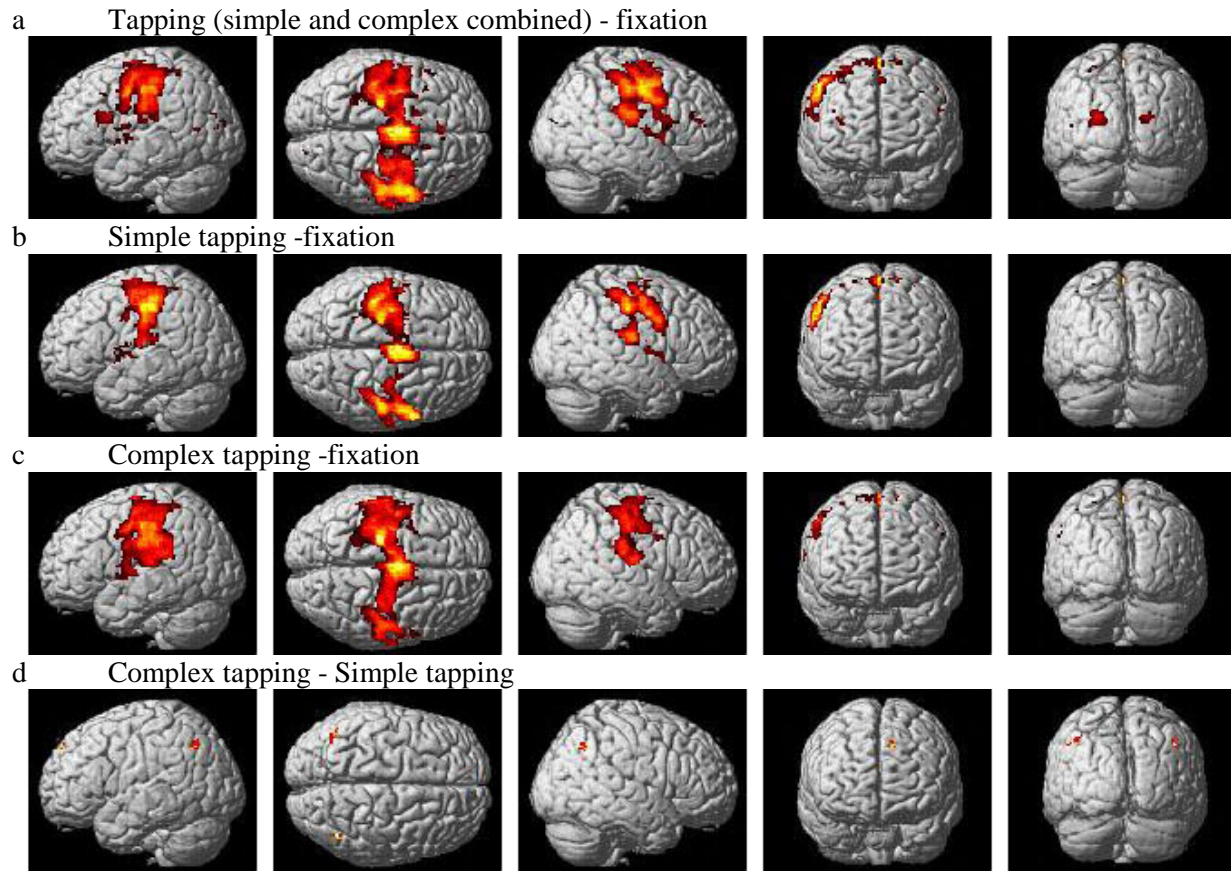
Figure 3. Activations revealed from the localizer (sequential finger tapping task).

Table 1 - *Sequential finger tapping localizer*

Contrast	Region	BA	Cluster Size	Z	MNI, x,y,z
Tap - Fix (simple and complex combined)					
	Vermis (4/5)		998	4.81	4 -54 -16
	Left lingual		166	4.50	-18 -80 -6
	Right thalamus		178	3.79	14 -20 4
	Left thalamus		845	4.18	-18 -16 4
	Left supp. motor		10633	5.07	0 -4 68
	Left middle occipital		169	3.66	-20 -86 18
	Right superior occipital		75	3.61	20 -84 16
	Left inferior frontal operculum		115	3.64	-50 14 20
	Right middle frontal		33	3.21	36 38 18
	Left superior medial frontal		43	3.34	0 28 52
Simple Tapping - Fixation					
	Right cerebellum (4/5)		819	4.94	8 -50 -14
	Right thalamus		226	4.11	16 -16 2
	Left thalamus		448	4.19	-16 -18 2
	Left postcentral		4489	5.1	-44 -26 46
	Right insula		423	4.09	38 4 10
	Right precentral		1659	4.95	56 6 34
	Sub-gyral		47	3.3	-20 -2 46
Complex Tapping - Fixation					
	Vermis (4/5)		1025	5.05	4 -54 -16
	Extra nuclear		314	4.09	22 -24 18
	Left precentral		12885	5.64	-26 -24 62
	Right insula		85	3.74	34 0 12
	Right precentral	9	27	3.58	56 6 34
Complex Tapping - Simple Tapping					
	Right angular gyrus		13	2.83	44 -62 42
	Left angular gyrus		16	2.71	-44 -64 42

Notes: Anatomical name and MNI locations of peak points, and size of clusters.

We conducted a ROI (Region of Interest) time series analysis, using MarsBar toolbox on SPM (http://marsbar.sourceforge.net/), based on the two AG clusters revealed in the localizer. The ROIs were limited to 10 mm spheres centered on the peak point of activations. Activation was normalized based on the baseline and percentage changes were

calculated. The activation for the 4th and 5th time points (the first three time points were disregarded considering the 6 sec hemodynamic peak latency) was averaged for each subject.

2 2x2 ANOVAs, based on the activation percentage value calculated for each participant, were conducted for each ROI (Fig. 4). The results of the first set of ANOVAs (difficulty X single/simple dual) showed a main effect of single/simple dual for both regions (Left AG [F(1,10)=9.04, p=0.011], Right AG [F(1,10)=9.37, p=0.012]), there was a main effect of difficulty only for left AG [F(1,10)=4.78, p=0.049]. There were no interactions. The second set of ANOVAs (difficulty X single/complex dual) showed a main effect of single/complex dual [F(1,10)=0.008, p=0.049] only for left AG. There were no interactions.

We also examined the activation correlation between right and left AG across all subjects and conditions. Results revealed significant correlations between right and left AG activations across all conditions (Table 2).

a.   Left AG
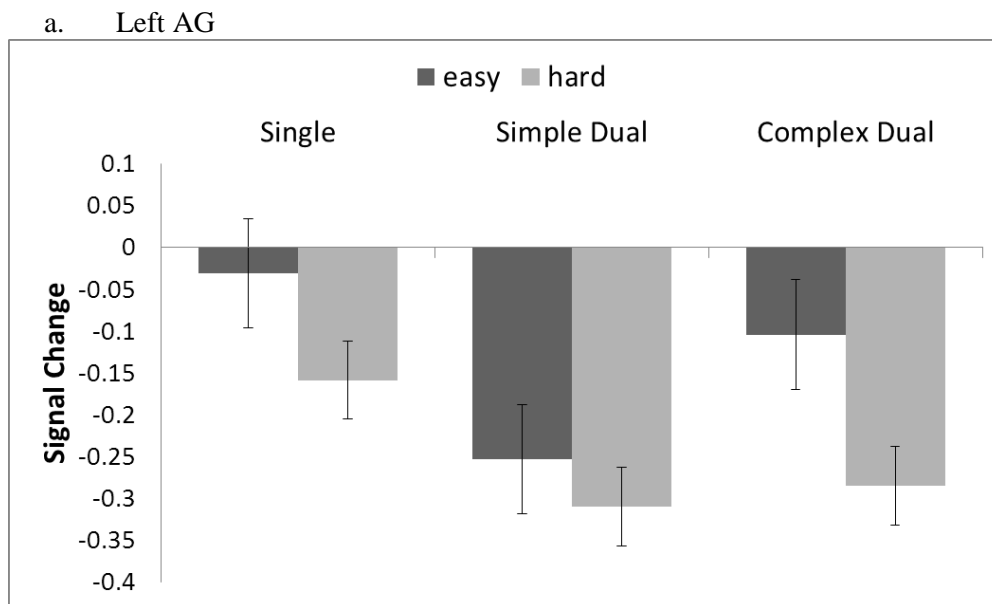
b.   Right AG
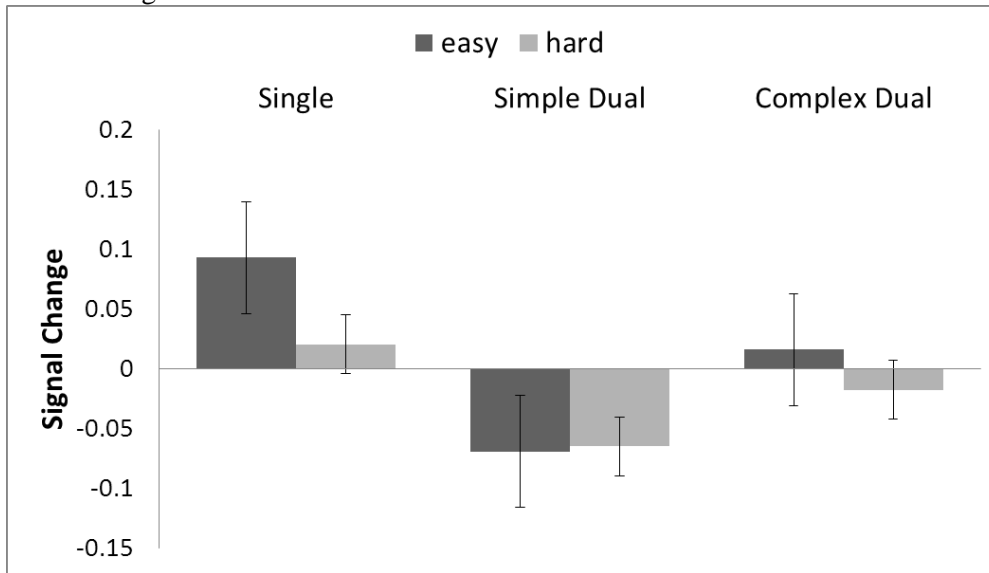
Figure 4. Averaged levels of activation (percentage change compared to baseline) in left (a) and right (b) angular gyrus for easy and hard, single and, simple and complex tapping dual addition conditions.

Table 2

		R-AG_sae	R-AG_sah	R-AG_dsae	R-AG_dsah	R-AG_dcae	R-AG_dcah
L-AG_sae	R	.838**	.607*	0.484	.608*	0.161	0.471
	P	0.000	0.028	0.132	0.047	0.600	0.104
L-AG_sah	R	.738**	.888**	0.582	0.356	0.186	0.351
	P	0.004	0.000	0.060	0.283	0.542	0.240
L-AG_dsae	R	.604*	.698**	.853**	0.288	0.395	0.328
	P	0.029	0.008	0.001	0.391	0.181	0.274
L-AG_dsah	R	.690**	.730**	.617*	.729*	.619*	0.445
	P	0.009	0.005	0.043	0.011	0.024	0.128
L-AG_dcae	R	0.313	0.365	0.270	.835**	.679*	0.432
	P	0.297	0.220	0.423	0.001	0.011	0.140
L-AG_dcah	R	.779**	.592*	0.501	0.513	0.462	.900**
	P	0.002	0.033	0.117	0.106	0.112	0.000

Notes: Signal change correlations between two ROIs, left and right angular gyrus (AG) across all conditions (* $p < 0.05$, ** < 0.01). (L-AG: left AG, R-AG, right AG, sae: single addition easy, sah: single addition hard, dsae: simple dual addition easy, dash, complex dual addition hard, dcae: complex dual addition easy, dcah: complex dual addition hard)

Main experiment results.

One subject did not complete the two complex tapping runs. Data from another subject for the two complex tapping runs were excluded due to excessive (more than 10 mm) head movement. Therefore data from 13 subjects for the two simple tapping runs and from 11 subjects for the complex tapping runs is reported.

Conditions compared to fixation.

The single easy addition condition showed right precuneus, left supplementary motor (SMA), bilateral middle frontal, and bilateral thalamus activation. Both middle frontal and thalamus activations were right lateralized. For single hard addition condition bilateral, right lateralized activation was observed in the SMA, thalamus and putamen, in addition to the right rolandic operculum activation. Simple tapping easy addition resulted with left precentral, right postcentral, left cerebellum, right pars triangular (of the inferior frontal gyrus) and right inferior frontal operculum activation. Simple tapping hard addition activated right medial superior frontal area, right precentral area, the right inferior frontal operculum and the left precentral area. Complex tapping easy addition revealed left precentral, right postcentral, cerebellar vermis (4/5) and bilateral ventral anterior nucleus (thalamus) activations. Finally, complex tapping hard addition showed significant activations in right supplementary motor area, right precentral area, right fusiform and left thalamus. Table 3 provides further details concerning the regions activated in each of these conditions. Figure 5 shows the surface rendering for the four conditions where significant clusters of activation were found.

a   Single easy addition - fixation

b   Simple tapping easy addition - fixation

c   Complex tapping easy addition - fixation

d   Single hard addition - fixation

e   Simple tapping hard addition - fixation

f   Complex tapping hard addition - fixation
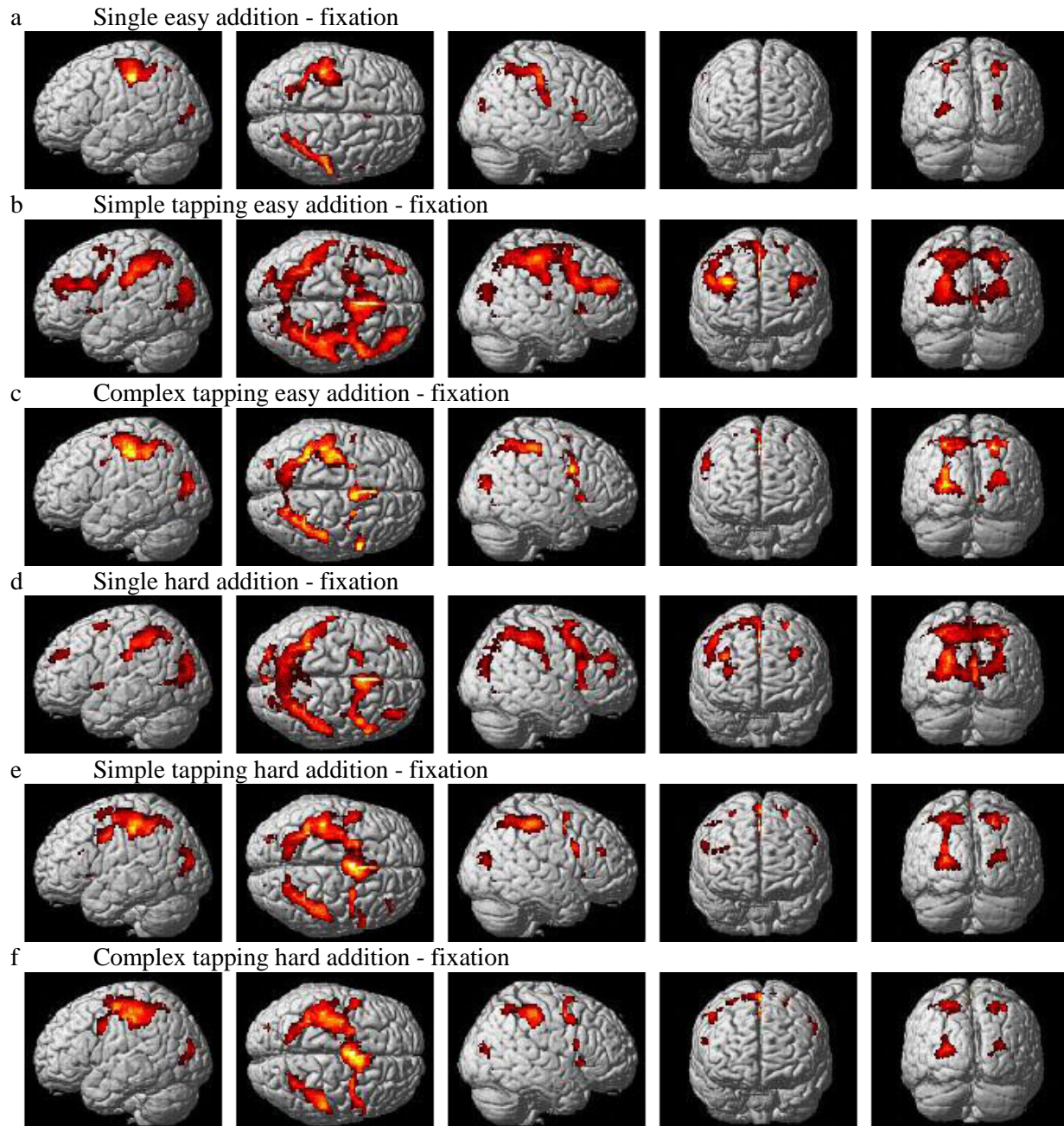
Figure 5. Areas of activationacross all conditions compared to fixation.

Table 3 - *Each condition compared to fixation.*

Task	Region	BA	Cluster Size	Z	
Easy Addition (no tapping) - fixation					
	Right precuneus	7	10621	5.54	24, -52, , 44
	Right thalamus		929	4.44	12 , -4, 10
	Left thalamus		46	4.25	-24, -28, -2
	Left insula	13	55	3.80	-44, 6, 0
	Left supp. Motor		4674	5.35	2, 18, 44
	Right middle frontal		336	4.04	34, 44, 12
	Supramarginal		83	3.79	50, -22, 26
	Left middle frontal		146	3.64	-32, 54, 30
Hard Addition (no tapping) - fixation					
	Right supp. motor area	6	20279	5.43	4, 4, 52
	Right thalamus		2893	5.25	20, -24, 0
	Right putamen		259	4.51	30, 18, 0
	Right rolandic operculum	43	33	3.6	54, -16, 14
Simple Tapping Easy Addition - fixation					
	Left cerebellum		500	4.68	-6, -64, -12
	Right insula		36	3.57	36, 4, 0
	Left middle occipital		99	4.29	-26, -88, 14
	Right pars triangular	45	78	3.73	50, 20, 4
	Right middle occipital	19	61	3.85	30, -82, 16
	Extra-nuclear		42	3.39	2, -16, 12
	Right postcentral		1152	4.14	46, -30, 52
	Right inferior frontal operculum		23	3.32	52, 12, 20
	Left precentral	4	1187	4.89	-38, -20, 58
	Right supp. Motor		25	3.69	4, 16, 48
Simple Tapping Hard Addition - fixation					
	Left middle occipital		5057	5.29	-26 -84 10
	Right middle occipital gyrus		572	4.68	30 -80 10
	Thalamus		38	3.98	24, -28, -2
	Right inferior frontal operculum		77	3.83	50, 16, 2
	Right precentral		299	3.86	42, 6, 30
	Right medial superior frontal		980	4.70	2, 20, 42
	Left precentral		31	3.38	-54, 2, 36
Complex Tapping Easy Addition - fixation					
	Right vermis 4/5		192	4.07	2, -54, -14
	Left lingual		314	4.65	26, -74, 0

Left occipital sub-gyral		412	5.06	-30, -74, -4
Left occipital sub-gyral		46	3.76	-38, -58, -8
Right extra-nuclear	47	75	3.69	34, 20, 0
Left ventral anterior nucleus		55	3.50	-12, -6, 8
Right ventral anterior nucleus		30	3.78	12, -4, 8
Right inferior frontal operculum		42	3.84	58, 12, 18
Left precentral		5409	5.12	-36, -22, 56
Right postcentral		1202	4.14	50, -28, 50
Complex Tapping Hard Addition - fixation				
Right supp. motor area		6237	5.49	8, 6, 56
Left vermis 4/5		154	3.87	-2, -60, -12
Right fusiform		388	4.97	26, -78, -2
Left insula		67	3.79	-32, 18, 2
Right putamen		69	4.5	26, 20, 4
Left thalamus		205	4.13	10, -8, 8
Right inferior frontal operculum		140	3.47	48, 10, 28
Right middle frontal		49	3.45	34, 36, 24
Left pars triangular		27	3.48	-40 24 24
Right superior occipital	7	1502	4.98	24, -62, 44
Right precentral	6	243	4.04	42, 0, 46

Notes: Anatomical name and MNI locations of peak points, and size of clusters.

Main effect of difficulty.

We compared areas of activation in hard addition to easy addition. We first collapsed across the single, and dual simple and complex tapping conditions to see the regions activated when the addition difficulty was increased. Significant activation was found in large clusters in both left and right inferior parietal areas (more for left), in left frontal gyrus (particularly pars triangular), both left and right precentral (more for left), and right middle cingulum (see Table 4, and Fig. 6 for details). For single addition, hard compared to easy activated both left and right inferior parietal, and left precentral areas in addition to right middle cingulum. Comparison of hard to easy for simple addition revealed both right and left occipital in addition to left superior parietal activations.

Complex tapping hard addition compared to easy activated, left middle occipital areas, inferior frontal gyrus (particularly the operculum) and the right angular gyrus.

a   Addition (Hard - Easy) (single, simple & complex tapping combined)

b   Single addition (Hard - Easy)

c   Simple tapping addition (Hard - Easy)

d   Complex tapping addition (Hard - Easy)

Figure 6. Main effect of difficulty (Hard-Easy): Brain areas that showed significantly greater activation during hard addition conditions contrasted to easy addition conditions.

Table 4 - *Main effect of difficulty.*

Task	Region	BA	Cluster Size	Z	
Addition(hard-easy combined across all single & dual conditions)					
	Midbrain		63	4.03	0, -28, -8
	Left inferior parietal		1985	4.95	-32, -60, 50
	Right inferior parietal	40	1286	4.70	38, -44, 52
	Left thalamus		92	3.94	-8, -14, 0
	Right thalamus		28	3.67	12, -14, 0
	Left pars triangular		1489	4.93	-38, 24, 22
	Left extra-nuclear		29	3.51	-16, -4, 12
	Right pars triangular		23	3.33	50, 30, 20
	Right precentral		99	3.65	46, 8, 30
	Right middle cingulum		1352	4.2	8, 20, 36
	Right pars triangular		35	3.38	52, 24, 30
	Right precentral	6	80	4.4	38, -4, 38
	Right precentral	6	27	3.3	28, -2, 48
	Right precentral		112	3.77	32, -22, 62
Single Addition (hard - easy)					
	Occipital (sub-gyral)		102	3.53	-28, -74, -2
	Cuneus		25	3.38	22, -82, 2
	Left pars triangular		22	3.43	-34, 42, 12
	Frontal (sub-gyral)		1113	4.49	-26, -2, 44
	Right pars triangular		147	3.66	40, 28, 28
	Left inferior parietal		1321	4.50	-30, -46, 44
	(sub-gyral)		103	3.76	34, 10, 26
	Left postcentral		38	3.85	-52, -20, 32
	Right precentral	6	28	3.94	60, 2, 34
	Right middle cingulum	32	1082	4.17	8, 22, 38
	Right inferior parietal	40	810	4.13	36, -44, 52
	Right precentral	6	171	4.48	38, -2, 38
	Right precentral		77	3.40	32, -22, 56
Simple Tapping Addition (hard - easy)					
	Left superior occipital		519	4.38	-24, -70, 26
	Right middle occipital		111	3.76	28, -70, 22
	Left frontal (sub-gyral)		78	3.84	-32, 22, 24
	Left precentral		23	3.36	-36, 4, 36
	Right middle cingulum	32	32	3.36	4, 22, 34
	Right superior occipital		337	3.90	22, -66, 46
	Left superior parietal		359	4.22	-26, -60, 56
	Left precentral		44	3.51	-30, -20, 60

Complex Tapping Addition (hard - easy)

Left temporal sub-gyral		40	4.17	-38, -58, -4
Left middle occipital		755	4.54	-28, -70, 28
Left pars triangular		400	4.16	-46, 28, 26
Right inferior frontal operculum		38	3.68	44, 8, 28
Right angular	7	193	4.34	24, -62, 48
Left middle frontal		34	3.49	-22, 8, 58

Notes: Anatomical name and MNI locations of peak points, and size of clusters.

Main effect of single/dual.

Dual conditions (collapsed across simple and complex) compared to single activated a left precentral cluster (Fig. 7, Table 5). Separate comparisons of dual conditions to single for both simple and complex showed similar left precentral activations. The left precentral activation was obviously due to the additional finger motor activity in the dual conditions. We also investigated areas activated in single conditions compared to dual. The difficulty collapsed single-dual comparison revealed a very large cluster peaking in right middle cingulum and including bilateral middle frontal and inferior parietal, and left insula activations. The comparison of single to dual separately for simple and complex tapping conditions showed large clusters of activation in middle occipital as well as inferior parietal and middle frontal activations. The comparison activations were stronger for the complex tapping condition. The large scale decrease in activations for dual conditions is compatible with the underaddivity effect that was found in previous studies focusing on dual-task performance (Klingberg, 1998; Klingberg & Roland, 1997; Roland & Zilles, 1998).

a   Single addition - Dual addition (simple/complex (for dual) and easy/hard combined)

b   Single addition - Simple tapping addition

c   Single addition - Complex tapping addition

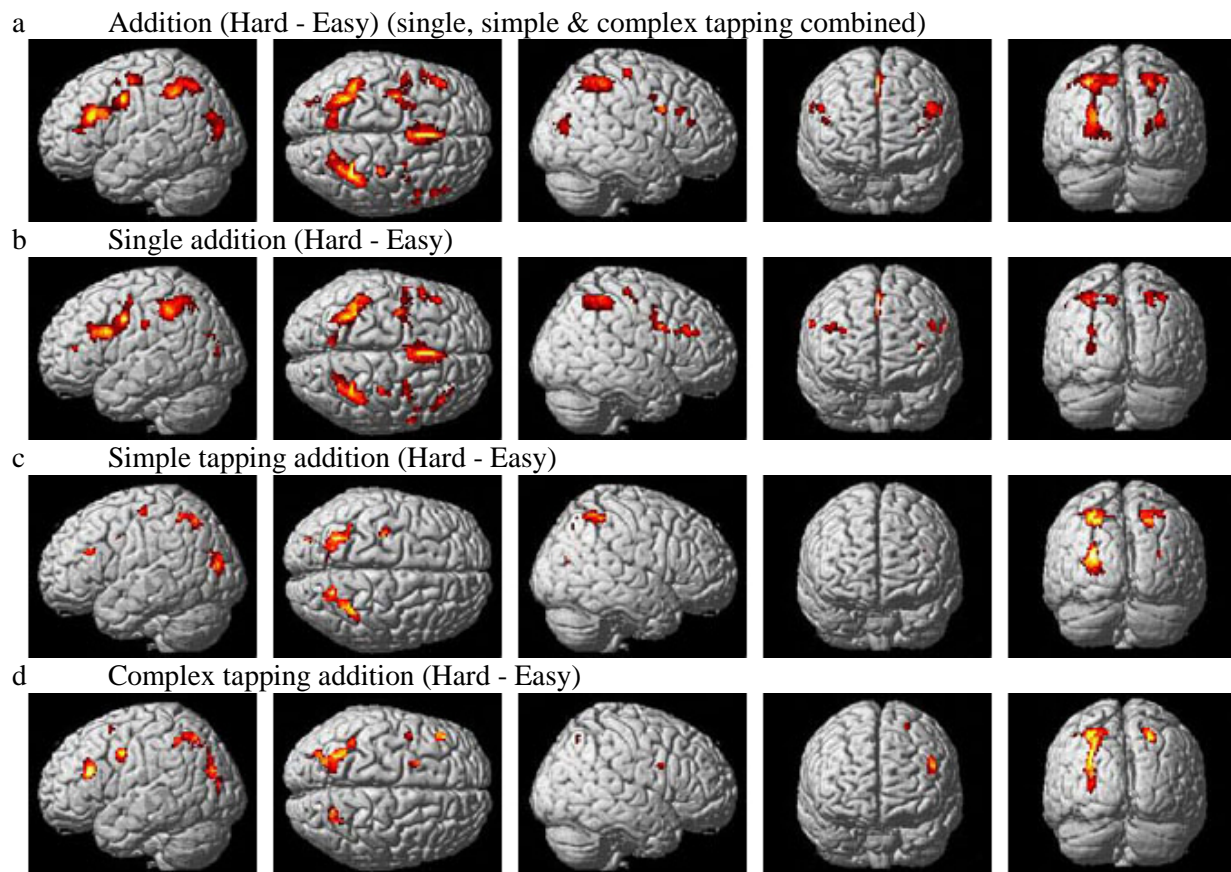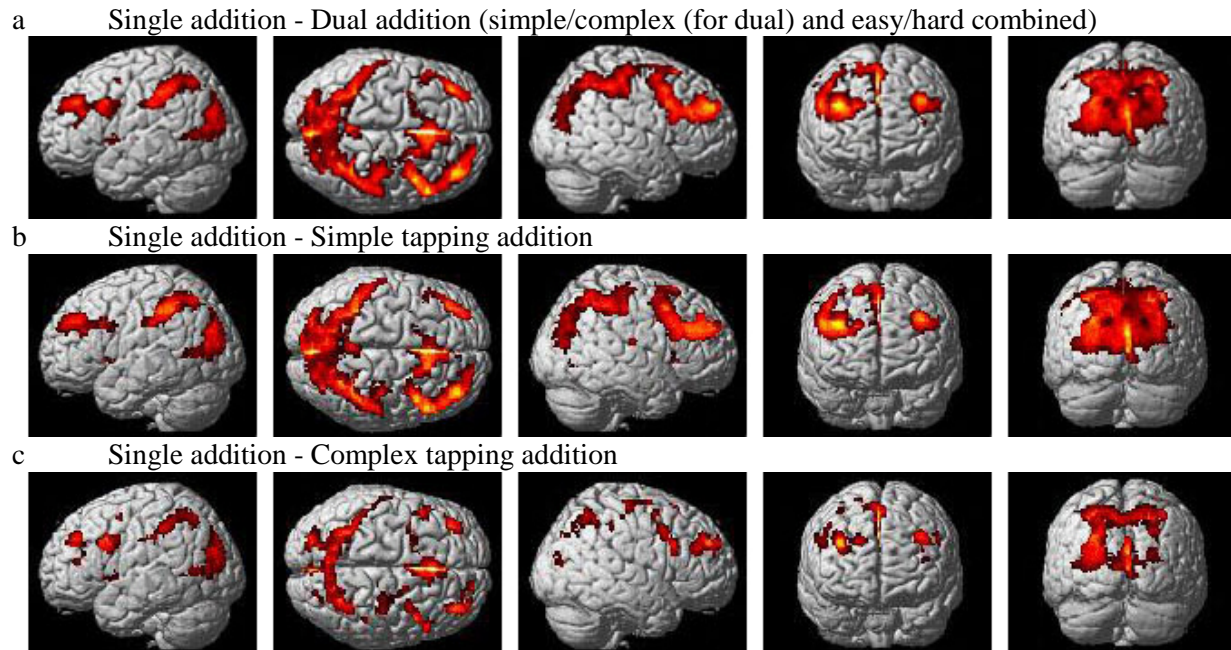*Figure 7.* Main effect of single/dual: Brain areas that showed significantly greater activation during dual conditions contrasted to single conditions.

Table 5 - *Main effect of single/dual*

Task	Region	BA	Cluster Size	Z	
Dual > Single					
Addition (dual - single combined across all easy and hard conditions)					
	Left precentral		225	4.03	-32, -24, 56
Simple Tapping Addition (dual - single)					
	Left precentral		228	4.09	-32, -24, 58
Complex Tapping Addition (dual - single)					
	Left precentral		230	4.08	-34, -24, 56
Single > Dual					
Addition (single - dual combined across all easy and hard conditions)					
	Right middle cingulum	24	29540	6.03	4, -2, 36
	Left insula		371	3.51	-40, 6, 2
Simple Tapping Addition (single -dual)					
	Right calcarine		8706	5.24	18, -66, 6
	Right thalamus		340	3.78	22, -26, -2
	Left insula		50	3.33	-40, 6, 2
	Right middle cingulum		4930	5.00	2, 24, 36
	Right caudate		71	3.78	10, 4, 12
	Left middle frontal		211	4.34	-40, 38, 34
	Right middle frontal	10	391	4.29	38, 52, 28
	Right precentral		274	3.78	40, 6, 42
	Right supramarginal		27	3.48	44, -36, 42
	Right middle cingulum		23	3.40	6, -28, 46
	Right precentral		145	3.87	26, -22, 66
	Right middle frontal		56	3.62	32, 2, 54
Complex Tapping Addition (single -dual)					
	Left middle cingulum		24340	5.82	0, 24, 34
	Left insula		70	3.43	-38, 14, 0
	Right rolandic operculum	43	38	3.64	52, -18, 16
	Right middle frontal	10	2091	4.46	40, 48, 28

Notes: Anatomical name and MNI locations of peak points, and size of clusters

Task difficulty and single/dual interactions.

We found significant activations only for the interaction of difficulty and single/dual for the dual complex tapping addition condition. The analysis revealed a single cluster encompassing the left supramarginal gyrus. We conducted a ROI time series analysis on this region. We averaged the activations for the 4th and 5th time points (the first three time points were disregarded considering the 6 sec hemodynamic peak latency) for each subject. The averaged activations revealed that while the task difficulty increase (from easy to hard) results with increased activity in supramarginal gyrus for single conditions, the opposite, a decrease in activity, occurs for the complex tapping conditions (Figure 8).
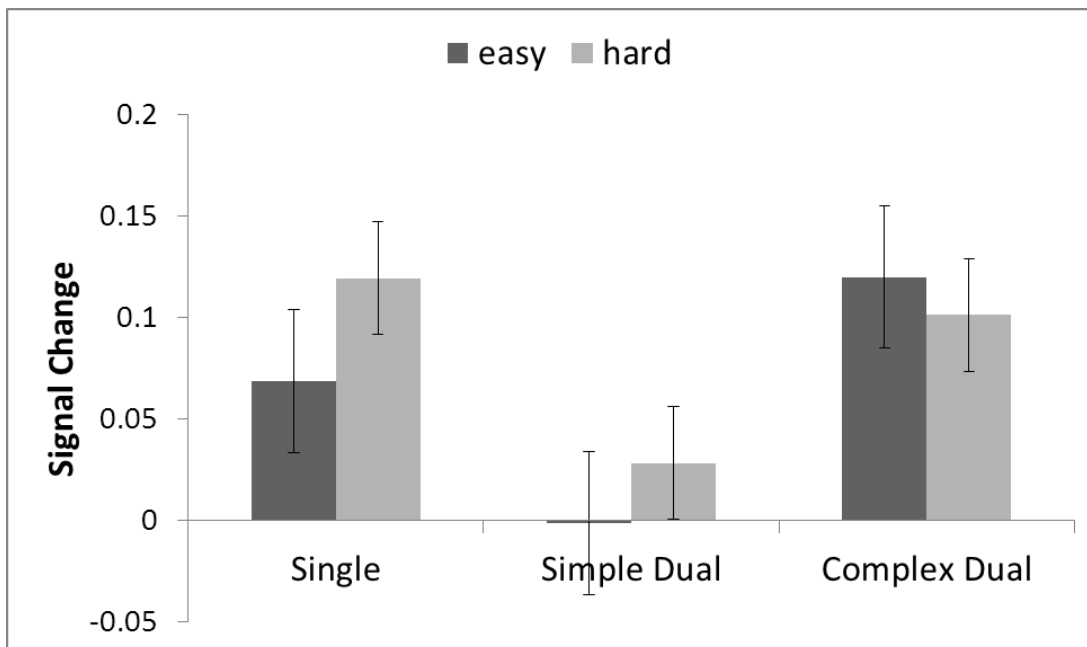
Figure 8. Averaged levels of activation (percentage change compared to baseline) in left supramarginal gyrus for easy and hard, single and, simple and complex tapping dual addition conditions.

<center>**Discussion**</center>

In this study we studied the neural dynamics of the interaction between finger tapping and addition. The findings showed that finger tapping and addition use overlapping neural resources particularly in the inferior frontal and superior parietal areas. In addition, we found that the angular gyrus is more activate in complex finger tapping (as opposed to simple) and in easy addition (compare to hard addition). Finally, the data revealed different patterns of activation for angular gyrus (AG) and supra marginal gyrus (SMG). We interpret these patterns of functional to explore the different functional contributions of AG and SMG to addition.

Single Task Performance and the Role of Angular Gyrus

Angular gyrus (AG) is often cited as one of the key areas in neuroimaging studies of mathematical cognition (Dehaene & Cohen, 1997; Dehaene, et al., 2003; Dehaene, et al., 1999; Gobel, et al., 2001; Grabner et al., 2009; Roux, et al., 2003; Rusconi, et al., 2005; Wu et al., 2009). Nevertheless, there are controversies around both its functional contribution to number processing and the mechanism with which it contributes. One widespread theory posits that left AG participates in verbal processing of numerical information and particularly functional in retrieval of arithmetic facts or in automated number processing (Dehaene & Cohen, 1995; Dehaene, et al., 2003; Dehaene, et al., 1999; Grabner, et al., 2009). This argument is based on the finding that fact retrieval compared to actual calculation shows positive AG activation and AG is known to be part of the perisylvian language network (Dehaene & Cohen, 1995; Dehaene, et al., 1999). On the contrary Zago et al. (2001) found that arithmetic fact retrieval did not engage perisylvian language network areas, and when compared to reading digits there was a significant

<center>69</center>

premotor activation, which was proposed to be a developmental trace of finger counting strategy facilitating numerical processing for adults. When compared to rest, language areas, including AG, was found to be deactivated during both retrieval and calculation. Zago et al. concluded that the previously attributed role for AG in participating in a verbal representation of numbers is misleading given that it is deactivated during both retrieval and calculation. Nevertheless, a finger-based account of number processing without AG is also incomplete. In numerous studies a lesion in AG was found to disrupt both number processing and mental representation of fingers, as it is identified in Gerstmann's Syndrome (Gerstmann, 1940; Martory, et al., 2003; Mayer, et al., 1999). Furthermore, separate rTMS studies showed that: stimulation of left AG was found to disrupt both number processing as well as access to finger representations (Rusconi, et al., 2005) and bilateral stimulation of AG caused disruptions in a visual search task as well as a number comparison task. These studies provide solid evidence for contribution of AG in mathematical cognition. However, the deactivation of AG during numerical tasks (as reported in Zago, et al., 2001) requires further explanation. In spite of the numerous studies reporting activation of AG in fact retrieval when compared to actual calculation, AG deactivation was shown in two other studies (Rickard et al., 2000; Wu, et al., 2009). Wu et al. (2009) explained deactivation of AG during arithmetic tasks based on AG overlap with the default mode network (DMN) (also see Seghier, Fagan, & Price, 2010; Sestieri, Corbetta, Romani, & Shulman, 2011). DMN constitutes a group of regions that are typically deactivated during cognitive tasks, compared to resting state, across different domains and the level of deactivation tends to increase with the difficulty of the task (Greicius & Menon, 2004). Using an fMRI paradigm Wu and colleagues found that the

part of AG that deactivates during numerical tasks overlaps with the DMN. Therefore a comparison of automated calculation (e.g. fact retrieval) as opposed to actual calculation shows positive activation, although when compared to baseline both tasks show negative activations. In addition, they found that the left AG deactivates more than right AG. Bilateral AG and supramarginal gyrus (SGM) deactivation, compared to baseline, was also reported in a study with a simple multiplication task (Rickard, et al., 2000).

Our results mostly support these findings, except for the deactivation of supramarginal gyrus. Firstly, ROI time series analysis showed deactivations across all conditions for left AG, and all, except for easy/hard single and easy complex dual addition, for right AG. This is in line with the previous finding that right AG deactivation is less compared to left. Secondly, the level of activation, compared to baseline, was lower for hard compared to easy conditions in both right and left AG across all single and dual conditions, except for right AG during simple dual easy/hard conditions (the difference was not significant). This supports the previous finding that easy addition (arithmetic fact retrieval) relies more on AG compared to hard addition. In addition we found that the activations in left and right AG significantly correlated across all conditions. Left AG participation in a verbal mode of number processing does not explain this strong correlation, given that perisylvian language network is left lateralized for most right-handed individuals. We propose that AG participates in a finger-based representation of numbers, for example a mapping between digits and fingers (Di Luca, et al., 2006), which would require bilateral participation of AG given the fingers present in both hands. Finally, the functional localizer that compares the activation for complex tapping to simple tapping revealed bilateral angular gyrus activation. Although this activation was

71

significant only at the 0.01 level (as opposed to 0.001 for all other contrasts) it provides evidence for the relevance of AG in accessing finger representations sequentially.

Comparison of activations for hard addition to easy addition revealed significant bilateral superior parietal, supplementary motor (less for right), and precentral (less for right, extending anteriorly into the middle frontal gyrus) area activations. This result is consistent with findings in Zago et al.'s study (2001), where the activation of the frontoparietal network involving left premotor and intraparietal sulcus were interpreted as evidence for a finger-based representation of numbers. The bilateral superior parietal activation might indicate use of visuo-spatial and mental imagery strategies for hard addition questions in addition to the finger representation network. Superior parietal lobe is known to be functional in visuo-spatial processing in relation to motor movement, and receives input from hand related sensory areas. Lesions in this area were shown to result with difficulties in simulating hand related movements, for example imagining to grasp or to reach to an object, as well as executing actions (Sirigu et al., 1996). The middle frontal gyrus activation in hard addition can be attributed to the additional working-memory demands, due to calculation with multi-digit numbers.

Dual-Task Dynamics

If number processing relies on a frontoparietal network that is originally for finger related sensorimotor processes. What happens when an individual is asked to do both arithmetic and move fingers at the same time? The dual-task conditions were introduced to answer this question. In addition, we intended to study the effects of finger tapping complexity. The idea here was that while simple tapping requires access to finger representations, and activation of motor networks, complex finger tapping puts additional

72

demands in working memory resources, to remember the sequence, and executive functions to mediate sequence processing.

The dual-single contrasts for both simple and complex tapping conditions did not reveal any activations except for a cluster in the left motor area. This activation was obviously due to the finger tapping movement of the right hand during the dual conditions. On the other hand single-dual contrasts showed extensive activations of middle-frontal, parietal, and occipital areas. This shows that the frontoparietal network in addition to visual areas were deactivated during the dual conditions compared to single conditions. The *underadditivity* of single task activations in dual-task performance was previously shown in numerous studies. Underadditivity refers to the condition where the activation for a dual-task condition is significantly less than the sum of single-task activations. In studies where the two single tasks activate overlapping corticical regions (for example Rees, et al., 1997; Vandenberghe, et al., 1997), the activation associated with a particular task decreases in dual-conditions, due to the shared use of the same area with the second task and activate distinct areas (Klingberg & Roland, 1997). The 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. Alternatively these two explanations might overlap, given that limitations on attentional resources might be due to a limit on brain activation (Just, et al., 2001). In a dual-task study, where the focus was on working memory demands on prefrontal areas, Goldberg et al. (1998) found that the activation in prefrontal areas were less in the dual-task condition, compared to the single-task conditions. Our observations here are compatible with the previously established underadditivity effect.

In our analysis of how sequential finger tapping demands during dual-task conditions interact with task difficulty, we found that task difficulty modulates the activity in the left supramarginal gyrus differently for single addition compared to complex tapping dual addition. During single addition the SMG activity increased with difficulty, whereas during dual complex addition SMG showed less activity for hard addition compared to easy. SMG lies anterior to angular gyrus and previously was found to be functional in mental imagery of finger movements (Kuhtz Buschbeck et al., 2003), planning of hand related actions (Tunik, Lo, & Adamovich, 2008), pantomiming tool use (Choi et al., 2001) and working memory in addition to various arithmetic processing tasks (Menon et al., 2000; Zago & Tzourio-Mazoyer, 2002). There are also cases where patients with left SMG lesions suffer from finger agnosia and acalculia. These evidence signal that SMG might be participating in a finger-based representation of numbers. The higher activation of SMG during hard addition, compared to easy, might be due to both increased working memory demands due to multi-digit processing in addition and increased access to finger-based number representations. Complex finger tapping requires activation of finger representations in a non-automatic way, unlike simple tapping. This might lead to higher access to SMG causing an increased shared demand on SMG during complex dual addition task. This is not observed for the simple dual addition conditions. While the SMG activation is the lowest during simple dual addition conditions, the hard conditions still shows higher SMG activation compared to easy. It is possible that simple finger tapping does not demand resources from SMG as much as complex tapping during the dual-task performance. Therefore decreasing the activation in left SMG to a minimum during simple dual addition might be a strategy to use the resources at maximum efficiency. While the

brain gets into a mode of efficiency during dual-task performance, when two processes demand overlapping resources in a region the activity in that region might increase compared to a second dual-task situation where there is demand from only one of the processes. Dual complex hard addition possibly puts the highest demand on SMG given the higher processing needs from both hard addition and complex tapping. Given that the brain responds to higher dual-task demand by decreasing activation, the decrease in activation during hard complex dual addition compared to easy might be attributed to the underaddivity affect.

Our comparison of left SMG and AG signal change across all conditions/subjects did not reveal any significant correlations. This shows that the activation in SMG and left/right AG does not relate in the same way across individuals. One possible reason for this might be use of different strategies for calculation. For example, left SMG might be more activated when a finger-based arithmetic strategy is used compared to a more visuospatial one. In addition, this finding shows that, in spite of being neighboring regions, left SMG and AG are functionally separate units in arithmetic processing. This idea is further supported by the fact that, during addition, the SMG shows positive activation compared to baseline, while AG, particularly left, shows deactivation across conditions. This is particularly important given that AG and SMG were not attributed different functional roles in previous studies of arithmetic cognition.

Conclusion

Based on a previous study where we found that finger tapping interfered with addition more than a control task, we hypothesized that addition and sequential finger tapping use shared neural resources. In this study we investigated how sequential finger

tapping interacts with easy (arithmetic fact retrieval) and hard (calculation) addition. A functional localizer was identified, based on a comparison of complex (non-anatomical order) finger tapping compared to simple (anatomical order), which revealed bilateral angular gyrus activation. Unlike most of the previous studies where comparisons between task conditions were made, we used a resting state to compare activations across conditions. This allowed us to observe that angular gyrus bilaterally deactivates during both single and dual addition tasks and the level of deactivation increases with the difficulty of questions, which confirms previous reports on AG being a part of the default network. Comparison of brain activations of single hard to single easy condition revealed a frontoparietal network that overlaps with finger sensorimotor areas in addition to frontal areas affiliated with working memory and executive functioning. The dual-task performance showed that a large frontoparietal network, in addition to visual areas, are deactivated during dual-task conditions. This finding was compatible with the previously found underaddivity effect during task conditions. We found that left supramarginal gyrus (SMG) was particularly sensitive to dual-task demands, possibly because of its role both in mental representation of fingers as well as number processing. The left SMG activation was consistently positive across all conditions compared to the resting state, unlike the neighboring AG. This, in addition to a lack of significant correlations of signal change between left SGM and both right and left AG, supported the idea that AG and SGM act as separate functional units. This was unlike the strong positive correlation between right and left AG across all conditions, showing that the two areas function in parallel, possibly serving for a finger-based representation of numbers.

Chapter 4 -The Effects of Finger Counting Strategy, Music Experience, and Gender on Addition

Abstract

The embodiment of number processing is a hotly debated topic. The hand/finger sensorimotor system appears to play a particularly important role in number processing. However, the nature of the relationship between finger/hand and number processing is not well understood. In the current study we investigated the relationship between both bodily and cognitive measures and mathematical performance. The bodily measures included the degree of right handedness, finger tapping ability, and finger counting habits in addition to musical instrument playing experience. Cognitive measures included working memory (WM) capacity and spatial ability. The results showed that sequential finger tapping ability, finger counting habits and musical experience significantly interact with number skill indicators, such as addition performance and WM capacity.

Introduction

We know a great deal about how mathematical ability relates to cognitive measures like spatial ability; however, we know very little about how it relates to bodily measures like finger tapping ability or finger counting strategies. From an embodied perspective mathematical cognition is grounded in bodily processes (Lakoff & Nunez, 2000). To clarify our perspective, we refer to embodiment as providing "a deep understanding of what human ideas are, and how they are organized in vast (mostly unconscious) conceptual systems grounded in physical, lived reality" (Nunez, Edwards, & Filipe-Matos, 1999). Because within this perspective conceptual representations are grounded in the sensorimotor system, bodily skills, particularly those related to fingers, may have an impact on mathematical performance.

The goal of this study was to investigate the hypothesis that finger processing skills are related to arithmetic. This was done by examining the effects of finger-counting habits, finger tapping ability, handedness, and musical instrument playing experience, as well as WM (working memory) capacity, spatial ability and gender on arithmetic performance. The arithmetic operation examined was addition. To our knowledge this is the first study to empirically investigate the influence of bodily measures on mathematics.

There are a number of studies focusing on the effects of musical ability (Vaughn, 2000), spatial ability (Bishop, 1980; Casey, Nuttall, Pezaris, & Benbow, 1995; Casey, Pezaris, & Nuttall, 1992) and gender differences (Hyde, Fennema, & Lamon, 1990) on mathematical cognition. There have also been a host of studies examining the relationship between WM and mathematics (Bull & Scerif, 2001; K. M. Wilson & Swanson, 2001).

While few studies have investigated the relationship between fingers and numbers, there is some research to support a relationship from the behavioral (Noel, 2005; Penner-Wilger, et al., 2007), neuropsychological (Gerstmann, 1940; Roux, et al., 2003), and neuroimaging (Rusconi, et al., 2005) research areas. In addition it was shown that finger counting habits might influence the way numbers are represented and processed (Fias & Fischer, 2005; Fischer, 2008; Pesenti, et al., 2000; Zago, et al., 2001). For example, Fischer (2008) examined 445 individuals and found that two-thirds started counting with their left hand regardless of handedness and that finger counting habits correlate with the relationship between space and numbers.

The current literature makes it difficult to determine the complex relationships between the cognitive and bodily processes involved in mathematical thinking. In this study we investigated the relations among an array of both cognitive and bodily processes to mathematical cognition. Based on embodied accounts of the grounding of mathematical processes in the sensorimotor system we investigated how finger processing relates to mathematics.

Methods

Participants

163 adults (age 18-35, M=20.54, 97 females) from the Indiana University community participated. Participants were right handed, native English speakers with no reported neuropsychological conditions. All gave written, informed consent approved by the Indiana University institutional review board.

Procedure

The data was obtained from nine versions of a dual-task experiment. This experiment explored the relationship between arithmetic and finger movement (Soylu & Newman, *submitted*). During the dual condition participants performed a finger tapping task while adding. Participants responded to addition trials with their left hand and tapped with their right. While aspects of the task varied across the nine experiments (e.g., finger tapping complexity, and whether there was an easy addition condition), the common condition was the single hard addition. This hard addition condition involved adding 2 two digit numbers between 11 and 99, excluding multiplies of 5. Data related to handedness (Edinburgh inventory, Oldfield, 1971), finger counting strategy, music experience, sequential finger tapping (SFT) ability, WM (forward and backward digit span) and visuo-spatial ability (Vandenberg mental rotation, Vandenberg & Kuse, 1978) were also obtained. Finger counting strategy was obtained by presenting a left and right hand picture and asking participants how they count from 1 to 10, indicating whether they were left or right-hand starters.

A task was designed to measure SFT ability. A finger tapping sequence was shown on a computer screen. Participants then tapped the sequence, using the number pad on the keyboard, as fast and as accurately as possible 10 times. Each sequence involved four fingers of the right hand (all but the little finger). A total of 5 sequences were shown. Two sequences involved the anatomical order of the fingers (from ring finger to thumb and vice versa). Three sequences were complex and did not follow the anatomical order. Two composite scores, ranging from 0 to 1, were calculated: the first represented the

performance across all sequences (SFT score), and the second for the complex sequences only (cSFT score).

Participants completed the psychometric tests and surveys followed by the dual-task experiment. Out of 163 participants, 86 completed the mental-rotation (MR) task, 157 were asked about previous musical instruments experience, and 86 completed the SFT task. All 163 subjects completed the digit span tasks, handedness inventory and reported their finger counting strategy.

Data Analysis

For the addition reaction time (RT) measures, all trials with RT values outside the M ±2 SD range were not included in the analysis. The range was calculated separately for each participant. A combination of correlational analysis and between group t-tests was performed. We first compared performance differences between left and right-hand finger counting starters. We also divided participants into groups based on their music experience and gender. Finally, we examined the correlation between the obtained measures.

Results

Effect of Finger Counting Strategy

79 participants were left-starters and 84 were right-starters. Addition RT showed a significant effect of finger counting strategy with the right-starters having faster RT than the left starters (see Table 1). Error rate, finger tapping ability, forward and backward digit-span, visuo-spatial ability and degree of right handedness were not found to be significantly different between groups (see Table 1).

Table 1. *Differences between Left- and Right-starters*

finger/ starter	RT		Error		SFT		cSFT		FDS		BDS		MRT		Handedness	
	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD
Right	4.69	1.54	0.90	0.13	0.60	0.17	0.66	0.18	6.65	1.20	5.29	1.38	20.83	9.31	73.77	16.49
Left	5.30	1.86	0.92	0.10	0.58	0.17	0.71	0.13	6.42	1.17	5.09	0.88	18.53	10.29	70.41	21.22
p(1t)	0.03*		0.11		0.31-		0.10		0.12-		0.15-		0.14		0.13	

Effects of Musical Experience

Participants were divided into two groups. Only 151 participants were asked about music experience. 91 had experience while 60 did not. Analysis revealed an effect for only the cSFT measure with the participants with music experience performing better than those without. There were similar trends observed for BDS and handedness (see Table 2).

Table 2. *Differences between musicians and non-musicians*

	RT		Error		SFT		cSFT		FDS		BDS		MRT		Handedness	
	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD
Music	4.71	1.57	0.93	0.09	0.62	0.19	0.73	0.18	6.63	1.14	5.40	1.04	18.46	10.58	75.00	20.84
No music	5.11	1.87	0.91	0.12	0.57	0.15	0.64	0.14	6.40	1.20	5.08	1.27	19.01	9.19	70.05	17.78
p(1t)	0.13		0.13		0.12		0.01*		0.13		0.06		0.41		0.06	

Effects of Gender

66 participants were male and 97 female. Analysis showed significant effects of SFT, MR ability, and handedness (see Table 3). On average, female participants had higher sequential finger tapping scores and degree of right-handedness. Male participants had higher MR scores, compatible with previous research on gender differences.

Table 3. *Differences between females and males*

Gender	RT		Error		SFT		cSFT		FDS		BDS		MRT		Handedness	
	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD
Female	5.04	1.72	0.91	0.12	0.62	0.16	0.70	0.14	6.49	1.27	5.21	1.16	17.40	10.39	75.07	18.97
Male	4.95	1.75	0.92	0.11	0.55	0.18	0.64	0.20	6.63	1.05	5.17	1.19	21.85	8.95	68.08	18.20
P	0.39		0.23		0.04*		0.06		0.25		0.41		0.02*		0.01*	

Correlations among Measures

Correlation analysis was also performed. The results revealed that there were significant correlations between FDS and SFT scores (r=0.312, p=0.008), FDS and MR ability (r=0.320, p=0.008), and RT and MR ability (r=-0.294, p=0.011), which is compatible with the previously established relation between spatial and math ability (Bishop, 1980). MR was shown to be stronger predictor of math ability with males as compared to females: the RT and MR correlation was higher for males (r=-0.479, p=0.0024) compared to females (r=-0.104, p=0.545).

Discussion

The primary aim of the current study was to obtain a better understanding of what variables may be contributing to mathematics performance. Here we examined a number of measures including cognitive and motor ability. We also examined the effect of how individuals count with their fingers to test the question of embodiment. The results, while preliminary, are fascinating in that they may open up new ways of investigating the interaction between sensorimotor and cognitive processes in mathematics.

Finger Counting Hand Preference

The most intriguing finding here is that how individuals use their fingers to count has a significant impact on cognition. Right-starters outperformed left-starters in the addition task. There are some discrepancies in the literature regarding the prominence of right-starters. For example, a strong right-to-left hand-digit mapping preference was found for right-handed French children and adults (Sato & Lalain, 2008) and for Italian adults (Di Luca, et al., 2006; Sato, et al., 2007). However, in a study of 445 British adults two-

thirds were left-starters regardless of their handedness (Fischer, 2008). Further work is necessary to determine whether left- or right-starters is more common.

There are a number of studies that seem to suggest a relationship between handedness and cognitive ability (Casey, Diana, & Goris, 1992; Nettle, 2003; O'Boyle & Benbow, 1990). Much of the data shows a consistent and reliable relationship between handedness and intellectual ability. Orton (1937) proposed that reading disabilities and speech problems may be a function of a lack of consistent cerebral asymmetry. Also, Corballis, Hattie and Fletcher (2008) found that individuals identified as ambidextrous perform more poorly than left- or right-handers on tests measuring arithmetic, memory, and reasoning. A large-scale study involving 12,770 British children showed matching results. Significant deficits in verbal, non-verbal, and mathematical ability and reading comprehension were found in individuals with equal hand skill, which is an indicator of hemispheric indecision; lack of asymmetry (Crow, Crow, Done, & Leask, 1998). These results are in line with those of Corballis et al. (2008) who found a relationship between performance on arithmetic and memory tasks, and handedness. The results presented here suggest a strong relationship between finger counting hand preference and WM and addition performance.

However, while the right-starters had higher handedness scores, there was no significant difference between our left- and right-starters on our measure of handedness. One problem in this research area is how handedness is defined. In many studies examining the relationship between handedness and intelligence hand writing preference was used. Annett (2004, 2009) has investigated how handedness is assessed. For example, there are right-handers who prefer their right hand to write but their left hand to throw.

This suggests that the questions on the handedness questionnaire as well as how they are scored are non-trivial and can have significant consequences. While the Edinburgh handedness inventory does not show significant differences between our left- and right-starters, there may very well be hand preference differences for hand skills other than counting. Therefore, the lower arithmetic performance of left starters might be due to the relatively lower level of hemispheric asymmetry, given the incongruence between their right handedness and finger counting habit.

Music Experience

Several previous studies have shown a relationship between musical and mathematical ability (Vaughn, 2000). Recent research on the relation between music training and educational achievement for high-school students showed that orchestra and band students' performance in the Education Longitudinal Study math section and SAT was higher compared to choir students (Elpus, 2011). Instrument playing and choir practice share many common aspects of musical training, for example following notes and rhythm processing; however, the one major difference is sequential finger movement. Therefore, the results might be due to the contribution of the sequential finger movement aspect of instrument playing improving both sequence processing skills as well as the distinct representation of fingers.

However, while there was a trend in the expected direction, we did not find any significant differences in addition performance or WM between musicians and non-musicians. One possible explanation for this failure to observe significant results is that our subjects were young individuals who have grown up using computers and who are adept texters, making them all proficient with keyboarding, which involves sequential

movement of fingers. The keyboarding experience, which all participants had, may have weakened our effect of instrument playing here. It should also be noted that many of the previous studies that demonstrate a relationship between music and math use young children (see Vaughn, 2000 for a review). In this way the non-music group would have considerably less keyboard experience possibly making the difference in sequence processing between the groups larger.

Gender Differences

Previous mathematic research has consistently shown gender differences (Hyde, Fennema, & Lamon, 1990). In addition to differences in mathematical ability gender differences in handedness (Papadatou-Pastou, Martin, Munafò, & Jones, 2008) and spatial ability (Linn & Petersen, 1985; Masters & Sanders, 1993) have also been observed. There are a variety of models to explain this phenomenon focusing on genetic, hormonal, and brain dynamics (see Papadatou-Pastou, Martin, Munafò, & Jones, 2008). Although only right handed subjects were recruited in this study, it is notable that there was a significant difference between the right handedness levels, with males showing greater tendency toward left-handedness compared to females.

Gender-related differences in spatial ability has been extensively and reliably reported, first in Maccoby and Jacklin's (1974) work followed by other studies showing that males obtain higher spatial test scores compared to females (Halpern, 2000; Harris, 1981; Hyde, 1981). A meta-analysis showed that the magnitude of gender differences depends on the nature of the spatial-task (Linn & Petersen, 1985; Masters & Sanders, 1993). The largest differences tend to be in mental-rotation task performance (Stumpf, 1993). Our results are in line with this finding.

In addition we found that while there was a significant correlation between addition performance and MR scores for male participants, the correlation was not significant for female participants. In a previous study Casey et al. (1995) investigated the MR and SAT-M relation across genders as well as within two achievement and three age groups. The results showed that while MR was a significant predictor of SAT results for females regardless of age and ability, this relation was mediated by ability in males - there was no significant correlation in the high-ability male group. Our results contradict these results. Gender differences on the relation between spatial-ability and mathematical performance is an open topic. In an earlier study it was shown that MR scores is a significant predictor of math ability, as measured by SAT-M scores, for both genders (Burnett, Lane, & Dratt, 1979). However, in this study all participants were a high-ability group mainly majoring in science and engineering. In a meta-analysis Linn and Petersen (1985) suggested that the relation between spatial and math ability might be modulated by achievement levels and backgrounds of participants. Based on this we separated both female and male participant data into high and low groups based on RT. Among the four groups; male high ($r=0.063$, $p=0.86$), male low ($r=-0.435$, $p=0.02$), female high ($r=0.170$, $p=0.60$), female low ($r=-0.094$, $p=0.66$), the correlation between RT and MRT was significant only for the low performance male group. This result can be explained due to a ceiling effect for the male and female high performance groups. Given that the math task is addition, it may be that female participants make relatively less use of visuospatial strategies here, which might explain the result for the low female group.

Previous studies have shown higher female performance for rhythmic tapping (Wolff & Hurwitz, 1976) and higher male performance for tapping as fast as one can with

one finger (Dodrill, 1979; Ruff & Parker, 1993). In our study female participants performed significantly better in the sequential finger tapping task. Gender differences in sequential tapping is a new finding. Based on our previous finding that instrument players had higher complex sequence tapping scores, the gender difference might at least partially be attributed to the fact that 45 percent of female and 33 percent of male participants had musical instrument playing experience. We compared male and female participants separately based on their instrument playing experiences. Among the group who had no instrument playing experience, female participants had higher SFT scores (M=0.59) compared to males (M=0.56), but the difference was not significant (p=0.25). The SFT score difference between female (M=0.65) and male (M=0.53) participants was also not significant (p=0.16) in the group of instrument players, suggesting that there may be a statistical power issue. While the results suggest that female participants were better in sequential finger tapping, further investigation, by controlling for previous musical instrument playing experience, is necessary.

Other Findings

Compatible with the previously suggested relation between spatial and math ability (see Bishop, 1980), in a recent study, Markey (2010) found that problems with visual-spatial reasoning is an underlying cause of math disability in students who struggle with geometry in particular, and math in general. Therefore, the negative correlation between spatial ability and addition RT observed here was expected and is compatible with previous findings.

A significant correlation between SFT and FDS scores was also observed. One explanation for this correlation is that SFT relies on short-memory processes - to maintain

the sequence information in memory. Because of the process overlap between these tasks, participants with higher memory capacity may be expected to more easily perform the SFT task. An alternative explanation is that because independent movement of fingers relies on distinct finger representations, the ability to activate distinct finger presentations might correlate with the ability to represent distinct numbers, supporting a finger-based representation of numbers theory (Anderson & Penner-Wilger, 2007; Penner-Wilger, et al., 2007). Finally, a correlation between spatial ability and WM was found previously (Miyake, Friedman, Rettinger, Shah, & Hegarty, 2001) and the significant correlation between MRT and FDS scores may suggest the use of visuospatial strategies (e.g., visuospatial sketchpad) in numeric memory processing.

Conclusion

The current study focused on the contribution of bodily and cognitive measures to mathematics ability. The results show that handedness, finger-counting habits, spatial and musical abilities interact with math ability. The findings contribute to a body of work that can be used to develop tools both to diagnose problems and predict future performance of students based on a number of indicators. In addition, we propose a link between bodily skills and mathematical ability, which contribute to the understanding the embodied groundings of mathematical thinking.

Chapter 5 - Mathematical Cognition as Embodied Simulation

Abstract

Based on behavioral, neuroimaging and neuropsychological data, I argue that a key to understanding mathematical cognition is the sharing of neural resources between sensorimotor and mathematical processes. Mathematical cognition is embodied in the sense that it is grounded in simulations of sensorimotor processes through the use of neural resources that are also active in bodily perception and action. There are two approaches to the study of embodied mathematical cognition: (1) behavioral, neuroimaging and neuropsychological investigations providing empirical evidence, and (2) the study of conceptual metaphors, focusing on how inferences from physical domains are used to understand abstract mathematical ideas. The first approach suffers from not providing a unified explanation, while the second approach is criticized for not having empirical validation. I discuss the possible implications of approaching mathematical cognition as embodied simulation in relating disparate findings to provide a more connected picture of how mathematics emerges from the embodied mind.

Introduction

Embodied cognition is a theoretical stance that argues that cognitive processes are grounded in the body's interaction with the world. Different approaches in embodied cognition propose varying levels for bodily involvement in higher cognition. Clark (1999) has distinguished between simple versus radical embodiment. Simple embodiment focuses on how the body and environment places constraints on a theory of inner organization and processing. Radical embodiment, however, asserts that all cognitive processes are grounded in the sensorimotor system, proposing a profound change in the "subject matter and theoretical framework of cognitive science" (p. 348). The fundamental difference between these two approaches is that simple embodiment still relies on internal representations, especially in explaining higher level thinking, whereas radical embodiment entirely rejects the idea of an internal realm and provides a *representation free* account of cognitive phenomena. I use the term *simulation theories of cognition* to refer to theories positing that all cognitive processes are simulations of sensorimotor processes. Note that the term *simulation theories* is also used to refer to a theory of mind asserting that humans understand other people's mental states by adopting their perspective (Davies & Stone, 1995), which is different than the usage here.

Simulation theories posit a decoupling of sensorimotor functions from their original physical inputs and outputs. For example, consider the case of counting on one's fingers. In its initial form, counting can be done through explicit motor behavior where an observer can see the fingers moving. However, the motor movement of fingers can become gradually more subtle, where at some point it might merely seem like twitching to the observer. We can push the activity inward even further allowing the use of motor

91

programs without any overt behavior. At this point finger counting is a motor simulation. This situation exemplifies how a motor function, without overt behavior, can be the underlying neural mechanism for off-line thinking in the very simple case of counting (M. Wilson, 2002).

Previous theories focused on how conceptual content is represented in the sensorimotor system. Gallese& Lakoff (2005) proposed that embodied simulations are the source of both structural and semantic content in conceptual knowledge. Embodied simulations take place in multimodal sensorimotor networks. Unlike the conventional idea of distinct sensory and motor areas communicating through association areas, multimodality refers to the integration of sensory modalities with one another and also with motor modalities. Barsalou (1999) argued that during perceptual experience association areas in the brain capture bottom-up sensory-motor patterns. Later, during the use of perceptual symbols association areas facilitate some of the same sensory-motor areas in a top down manner. Through experience, memories of the same component are stored in a schematic manner. The memories implement simulators of the perceptual experiences they represent. Simulators can be perceptual, proprioceptive, or introspective. Abstract concepts are grounded in the combinatorial and recursive integration of simulators.

Mathematics is often characterized as a challenge to embodiment (Nunez, 2008). Although it is relatively difficult to apply the idea of embodied simulations to explain mathematical cognition due to abstract nature of mathematics, there is accumulating evidence for how basic mathematical processes are grounded in the sensorimotor system. In this paper I review different studies on mathematical cognition and discuss some of the

challenges in interpreting findings to create a meaningful image of how mathematics can emerge from the embodied mind.

Embodiment of Mathematical Thinking

Research on the embodiment of mathematics is still in its infancy. Mathematical cognition is a big puzzle with many pieces, each piece requiring us to draw knowledge from a different field. Currently, there are two trends in studying embodiment of mathematical cognition: First, empirical investigations of basic number processing skills, for example number recognition and comparison, through behavioral, neuroimaging and neuropsychological studies. The second trend, most typically exemplified by Lakoff and Johnson's book on embodied mathematics (Lakoff & Nunez, 2000), is the study of conceptual metaphors in mathematics to explain how mathematical concepts are grounded in bodily processes. Both trends have strengths and shortcomings. Empirical studies provide accumulating disparate evidence on embodiment of number processing; however they do not provide a unified, big picture of how number processing is grounded in the sensorimotor system. Nevertheless, general theories explaining how number processing takes place in the brain exists. One, arguably the most well-known, theory is the triple-code model (Dehaene, et al., 2003), which provides a relatively disembodied account of number processing.

The second trend is explanation of mathematical cognition based on conceptual metaphors (Lakoff & Nunez, 2000). The role of conceptual metaphors in language and thinking was first studied by Lakoff and Johnson (1980). Sfard (1994) incorporated ideas from cognitive linguistics, on the use of metaphors in language and thinking (Lakoff & Johnson, 1980) to explain how we rely on daily physical inferences to make sense of

mathematical concepts. Lakoff and Nunez (2000) extended this program by inquiring how metaphors are used in diverse domains of mathematics, for example algebra, logic, sets and even trigonometry. The main argument in this approach is that we use inferences from our bodily interactions to understand mathematical concepts. A conceptual metaphor links a physical source domain to a target abstract domain. This approach is criticized for lacking empirical verification and for overextending the claims of embodiment to higher domains of mathematics without sufficient support (Goldin, 2001).

I believe that there is a need for bridging these two trends to have a unified explanation of numerical cognition that is supported by empirical findings. Approaching mathematical cognition as embodied simulations might have the potential to do that.

Empirical Evidence

There are four major sources of evidence supporting the relation between bodily processes and mathematical cognition. First, studies on neural correlates of hand movements and action understanding of hand gestures point to an overlapping circuitry in the prefrontal and intraparietal regions with number processing (Binkofski, et al., 1999; Chong, et al., 2008; Corina & Knapp, 2006; Peltier et al., 2007; Sakata & Taira, 1998). In addition, a separate body of neuroimaging research points to a relation between neural correlates of hand/finger movement control and number processing (Andres, et al., 2007). Secondly, studies conducted with repetitive Transcranial Magnetic Stimulation (rTMS) show excitability of hand muscles during different number processing tasks (Andres, et al., 2007; Sato, et al., 2007). Third, behavioral studies on math learning provide evidence for better math learning when instruction is supported with hand gestures, b) higher problem solving performance when non-communicative hand gestures are allowed,

94

compared to when hands are restricted, and c) non-communicative hand gestures during problem solving provide clues for misconceptions in conceptual understanding of arithmetic and algebra (Goldin-Meadow, 1997, 1999, 2006; Goldin-Meadow, Nusbaum, Kelly, & Wagner, 2001; Goldin-Meadow & Singer, 2003; Goldin-Meadow & Wagner, 2005). The fourth major support comes from neuropsychological conditions, particularly Gerstmann syndrome (Gerstmann, 1940), which is discussed later in this paper.

Conceptual Metaphors and First Person Accounts

The use of conceptual metaphors is characterized by the use of a physical, source domain to understand an abstract, target domain. First person accounts of mathematical experience provide additional insight into how metaphorical thinking is involved in mathematical processes. In a letter to mathematician Jacques Hadamard, Einstein once wrote:

> Thoughts do not come in any verbal formulation. Words and language, whether written or spoken, do not seem to play any part in my thought processes. The psychological entities that serve as building blocks for my thought are certain signs or images, more or less clear, that I can reproduce and recombine at will…The above mentioned elements are, in my case, of visual and some of muscular type. Conventional words or other signs have to be sought for laboriously only in a secondary stage, when the mentioned associative play is sufficiently established and can be reproduced at will (Hadamard, 1945, pp. 142,143)

Sfard (1994) questioned mathematicians about how they process mathematical concepts. In particular, she investigated if they process mathematical concepts in a way that is similar to physical objects. When Sfard asked how it feels to have a deep understanding of a mathematical idea, three mathematicians responded by saying, "identify a structure [one is] able to grasp somehow," "to see an image," and "to play with some unclear images of things." One mathematician reported, "In those regions where I

feel an expert … the concepts, the [mathematical] objects turned tangible for me" (Sfard, 1994, p. 48). Another mathematician stated:

> To understand a new concept I must create an appropriate metaphor. A personification. Or a spatial metaphor. A metaphor of structure. Only then can I answer questions, solve problems. I may even be able then to perform some manipulations on the concept. Only when I have the metaphor. Without the metaphor I just can't do it. (Sfard, 1994, p. 48)

The same mathematician also reported that the structure he uses has to have some spatial elements no matter how abstract the mathematical idea is. In the same study, mathematicians pointed to personification as another strategy for understanding mathematical concepts. Similarly, Hadamard (1945) reported mathematicians' tendency to treat mathematical concepts as human faces.

In a discussion of understanding and meaning in mathematical thinking, Sfard (1994) distinguished between objectivist and embodied theories of meaning. She characterized objectivist claims about knowledge as propositional and disembodied. Following the steps of Lakoff and Johnson (1980), Sfard defines a metaphor as a relation between a bodily and a conceptual domain. Metaphors facilitate our use of inferences from physical and bodily experiences to understand abstract concepts and relations. Lakoff and Johnson (1980) introduce *embodied schemata* to explain how metaphors work. Embodied schemata is "the vehicle which carries our experimentally constructed knowledge" (Sfard, 1994, p. 46). They are the " . . . structures of an activity by which we organize our experience in ways that we can comprehend. They are a primary means by which we construct or constitute order and are not mere passive receptacles into which experience is poured" (Lakoff & Johnson, 1980, pp. 29-30). According to Sfard, embodied schemata are non-propositional. They are " . . . image-like and embodied, embodied in the sense that

96

they should be viewed as analog reflections of bodily experience rather than as factual statements we may wish to check for validity. The non-propositional nature of embodied schemata makes it difficult, sometimes impossible, to describe them in words." In this sense, embodied schemata are preverbal constructs that are dynamic, ever-changing and shaped by our physical and social experiences. However, the nature of embodied schemata, how they are shaped in the sensorimotor system and how abstract thinking emerges from these preverbal constructs is still not clear. Although an embodied schema is a preverbal construct shaped in the sensorimotor system, we still talk about it like a cognitive construct since we cannot explain how it relates to the simple bodily functions and sensorimotor interactions.

Interpretation of mathematical thinking as embodied simulations requires a conceptual shift. Mathematical thinking is reconceptualized as simulated sensorimotor activity. This activity takes place in a temporal and spatial stage involving all modalities. As mathematician Alain Connes puts it: "The evolution of our perception of mathematical reality causes a new sense to develop, which gives us access to a reality that is neither visual nor auditory, but something else together" (Dehaene, 1997, p. 149). The key to understanding the multimodal sensorimotor foundations of mathematical might be through adopting an embodied perspective in designing studies and interpreting data.

An Embodied Approach to Interpreting Neuroimaging Data

Imaging studies, as well as neuropsychological cases, point to the importance of a network of areas consisting of prefrontal and parietal regions, particularly the angular gyrus and IPS (Intraparietal Sulcus). In this section I will revisit previous interpretations on the functional contribution of the angular gyrus and IPS to number processing and

propose an alternative embodied approach to provide a more connected explanation that is also compatible with behavioral and neuropsychological findings. The idea here is to provide an example for how the embodied simulations framework can be applied to the interpretation of neuroimaging data in the mathematical cognition domain.

Angular Gyrus

The angular gyrus is located in the inferior parietal cortex. It is situated at a very central location in the cortex, neighboring multimodal sensory regions. It was once characterized as the "association area of association areas" together with the supramarginal gyrus (Geschwind, 1965). Angular gyrus activation, particularly left, was found in various number processing tasks, for example, exact addition (Dehaene, et al., 1999), multiplication (Lee, 2000) and number recognition (Pesenti, et al., 2000). Although it is established that the angular gyrus is an essential part of the number processing network, its role is still not well understood. According to the well-known, triple-code model, being part of the perisylvian language network, the angular gyrus is involved in the verbal processing of numbers (Dehaene, et al., 2003). Nevertheless accumulating behavioral, neuroimaging and neuropsychological data tell us a different story about the involvement of the angular gyrus.

A relation between the angular gyrus and number processing was first formulated when, in 1924, Josef Gerstmann diagnosed a condition, now named Gerstmann's Syndrome, with four co-occurring symptoms: finger agnosia (loss in finger sense), acalculia (inability to do simple calculations), left-right disorientation, and agraphia (inability to write). Gerstmann found that the condition was most commonly due to a lesion in the left angular gyrus (Gerstmann, 1940). He believed that the main symptom

was finger agnosia, a specific type of body schema impairment (autopagnosia) affecting the mental representation of hands and fingers. He proposed that the loss of finger sense combined with the left-right disorientation caused acalculia, - the inability to carry out simple mathematical calculations (Butterworth, 1999b, p. 219). There have been a number of studies reporting data to support Gerstmann's theory. For example, a study examining patients with tumors in and around the angular gyrus found that these patients had impairments in writing, calculating, and finger recognition (Roux, Boetto, Sacko, Chollet, &Tremoulet, 2003). Also, in a rTMS study of healthy subjects it was found that disruption of the left angular gyrus impaired access to the finger schema and number processing (Rusconi, Walsh, & Butterworth, 2005).

These studies support the idea that involvement of angular gyrus in number processing is due to a functional relation between number processing and finger representations. There is also supportive behavioral data for this argument. A series of behavioral studies have consistently shown that finger gnosia (finger sense) in younger children is a predictor of numerical abilities (Noel, 2005; Penner-Wilger, et al., 2007). In addition, in our lab we found that finger tapping differentially interferes with finger tapping, showing use of shared resources between addition and finger processing (Soylu & Newman, 2011).

IPS (Intraparietal Sulcus) and the SNARC Effect

IPS is another region that has been consistently found active in a variety of number processing tasks, for example number comparison (Pinel, et al., 2004) and simple addition (Pesenti, et al., 2000). In the triple-code model it was proposed that the IPS, particularly its horizontal segment, is responsible from quantity processing independent from the

number notation, and that its function is analogous to one of a "mental number line" (Dehaene, et al., 2003). The mental number line argument is also supported by the SNARC (spatial-numerical association of response codes) effect, which refers to the finding that in a parity judgment test right button responses are faster for large numbers and left button responses are faster for small numbers. This supports the idea that the comparison of numerical quantities takes place on a mental number line extending from left to right. (Dehaene, et al., 1993).

However, there is evidence challenging the idea of a mental number line for quantity processing. Fischer (2008) explored whether finger-counting habits contribute to the SNARC effect and found that subjects who are left-starters show a SNARC effect significantly more than right-starters. In another study subjects were asked to identify Arabic digits by pressing one of 10 keys with all 10 fingers. The configuration of response buttons varied both in terms of the global direction of the hand-digit mapping and the direction of the finger-digit mapping within each hand, from small to large digits or vice versa. The results showed that subjects performed better when there was a congruency between the reported finger-counting strategy of the subject and the mapping of the response buttons (Di Luca, et al., 2006).

Based on the presented evidence it is possible that the angular gyrus contributes to a finger-based representation of numbers, while IPS contributes to a multimodal representation of numerical quantity. The "mental number line" analogy can still be useful in explaining the function of IPS, while taking into account that the direction and structure of this number line is grounded in bodily dynamics, for example handedness and finger

counting habits. In addition the analogy can be modified in a way that we not only talk about a number line but also hands tracing it during its use.

We need further neuroimaging studies investigating the relation between bodily and basic mathematical processes to clarify the question about the exact roles of angular gyrus and IPS, as well as pre-frontal regions in number processing.

Adopting an Evolutionary Perspective

Since one of the main ideas behind embodiment is the exploitation of simple perceptual and motor neural resources for higher cognitive functions, adopting an evolutionary perspective can help not only in understanding how these functions emerged during evolution, but also in explaining how they are currently situated in the sensorimotor system. This is also true for mathematics. An evolutionary perspective provides a bigger and more connected picture as to why a distributed network of brain areas is functional in number processing.

One recent theory of the evolution of higher cognition is Anderson's "massive redeployment theory" (2007). Anderson argues that higher cognition is possible through redeployment of existing neural systems for new functions. By reviewing 135 neuroimaging studies in different domains he provided empirical validation for three predictions: 1) A single brain region is used for many cognitive functions, 2) evolutionarily older brain areas are affiliated with more cognitive functions, and 3) newer cognitive functions utilize more distributed brain areas. Let's revisit the case of angular gyrus from this perspective. We have already covered how interpretation of angular gyrus activation as verbal processing (Dehaene, et al., 2003) makes it difficult to explain a range of neuropsychological (such as Gerstmann's Syndrome), neuroimaging and behavioral

findings. What we currently know about the evolution of language can help us in understanding the role of the angular gyrus. Arbib (2002, 2005) proposed that human languages followed an evolutionary trajectory including such stages as: the simple grasping movement, understanding actions of another individual, imitation, a manual based communication, and verbal communication, finally yielding to complex human languages. Considering the argument that hand/finger related sensorimotor areas were redeployed for language during evolution, we can expect that verbal processing also use neural resources related to the perception and execution of hand movements. Studies of verb meaning provide support for the proposed relation between the sensorimotor system and language processing. Buccino et al. (2005) showed that action-related sentences modulate relevant parts of the motor system, especially the mirror neuron system. A simulation theory is proposed as one possible explanation for this phenomenon: " . . . the understanding of action-related sentences implies an internal simulation of the actions expressed in the sentences, mediated by the activation of the same motor representation that are involved in their execution" (Buccino, et al., 2005, p. 361). This partially supports the idea that angular gyrus activation in verbal processing might be due to the use of finger processing resources, which is shared by number processing. Although we do not have empirical data to support this claim, the idea here is to show how adopting an evolutionary perspective has the potential to provide alternative explanations that are more consistent with disparate findings on number processing. In this sense, the interpretation of data requires consideration of not only the nature of the task, but also its evolutionary past.

Criticisms & Alternative Views

The idea of the embodiment of mathematics is not free of criticism. The embodied account of mathematics was particularly criticized by mathematicians who believe that "brain based" mathematics necessarily refuses a "transcendent mathematics." Transcendent mathematics refers to the idea that mathematics is universal. From this perspective mathematical embodiment negates mathematical realism; that is propositions about embodiment and transcendence mathematics are mutually exclusive. The view that mathematics cannot be a product of the embodied mind since it is transcendent is characterized as "Romance of Mathematics" by Lakoff and Nunez (2000).

However, according to an alternative view the "… fact that human mathematics is based in human cognitive capacities does not mean that these capacities cannot provide recognition of transcendent mathematical truth" (Voorhees, 2004, p. 87). I believe that how we perform mathematics and what mathematics is should be studied separately, since the answer to the former question does not inform the latter one. The confusion of these two fundamental questions can blur the study of embodied mathematics by attracting invalid criticism.

A different perspective, which shows that the discussion about the transcendence of mathematics is more philosophical rather than empirical in nature, was proposed by Gödel. He argued that mathematical concepts are as "real" as physical objects: "It seems to me that the assumption of [mathematical] objects is quite as legitimate as the assumption of physical [ones] and there is quite as much reason to believe in their existence" (Longo, 2007, p. 207). However, the mathematical realism of Gödel is not conclusive. He points out that questions that relate to the ontology of physical objects are

103

the same as the ontology of mathematical concepts: "the objective existence of the objects of mathematical intuition … is an exact replica of the question of the objective existence of the outside world" (Longo, 2007, p. 209). Overall, I believe that studies on mathematical cognition inform how we do mathematics and not what mathematics is.

Conclusion

Mathematics, being one of the most abstract domains of human knowledge, is a challenge to embodiment. There are two types of approaches to the study of mathematical embodiment: 1) empirical investigation of how bodily processes interact with mathematical processes, and 2) the study of how people use conceptual metaphors to make sense of mathematical concepts. While the former approach provides empirical validation for claims, it does not provide a unified theory of how mathematics is grounded in the sensorimotor systems. The second approach, focusing on the role of conceptual metaphors in mathematical thinking, provides a general theory, but attracts serious criticisms due to lack of empirical validation. I propose that approaching mathematical cognition as embodied simulation can make it possible to interpret seemingly disparate findings to provide a more comprehensive explanation for how people do math.

I have also reflected on the implications of adopting an embodied and evolutionary perspective in interpreting neuroimaging data. I proposed that a study of the neural underpinnings of mathematical cognition should aim at explaining how the processes studied are grounded in the complex interactions of sensorimotor networks from an evolutionary perspective. Study of the neural underpinnings of mathematical thinking is more about understanding how a complex network of sensorimotor circuitry interact to

bring forth mathematical ideas rather than identifying rigidly modularized areas that are only specific to mathematical thinking.

Chapter 6 - Conclusion

Studies presented here focused on different aspects of the relation between number processing and the hand/finger sensorimotor system. The most prominent finding of the first study was that finger tapping interferes more with addition compared to the control, sentence comprehension task, indicating a large resource overlap. This is the first performance-based evidence for shared use of resources between the sensorimotor system and arithmetic processes. While behavioral indicators implied shared use of neural resources, only through a neuroimaging study could we know what was happening in the brain during the finger tapping and addition interaction.

In the second study the neural dynamics of the interaction between finger sensorimotor system and arithmetic processing was investigated. Being one of the few studies where activation for each addition condition was compared to a fixation baseline (as opposed to a task condition), we found that left angular gyrus (AG) consistently deactivated across all conditions. The level of deactivation increased with difficulty. In addition, we found that the supramarginal gyrus (SMG) showed an entirely different pattern of activation compared to AG, indicating different functional contributions to arithmetic. AG was more active during the easy addition compared to hard addition. This pattern was stronger for the left AG. On the contrary, SMG was more active during hard addition, except when complex sequential finger tapping took place concurrently. We proposed that this is because AG contributes to finger representation of small numbers whereas SMG is recruited to mediate both visuospatial and finger-based modes of number representation when processing larger numbers.

The first two studies showed a relation between addition and finger tapping, however they did not show that the finger/number relation apply to a wide range of numerical and finger related processes. If numbers are represented on a finger related circuit, then are there other finger related measures that relate to numerical processes? Due to use of a shared circuit it is possible that number and finger-related skills/attributes follow similar developmental trajectories. If this is true then people who are good at numerical skills might also be good at performing finger related actions. Given that we are most skillful with our fingers in our dominant hands, does handedness modulate the finger/number relation? Are there gender differences? The third study aimed at answering these questions.

The third study examined the relationship between both bodily and cognitive measures and mathematical performance. The relation between finger-counting habits and math ability, right starters showing higher performance than left starters, and the correlation between tapping ability and digit-span are new findings, both of which support a finger-based representation of numbers. In addition, gender differences in sequential finger tapping, female participants performing better than males, was reported.

The empirical findings in the first three studies provided evidence for embodiment of number processing. At this point it was important to situate embodiment of numerical processes within the embodied cognition research program and discuss philosophical ramifications.

The fourth study was a theoretical reflection on an embodied approach to mathematical cognition. I argued that approaching mathematical cognition as simulation

of low level sensorimotor processes makes it possible to relate disparate findings on math cognition and to provide a unified explanation.

The empirical findings presented here make a case for the embodiment of arithmetic. The theoretical approach proposed wraps the empirical findings and situates number processing within a larger framework of embodiment of higher cognition centered around the idea of embodied simulations.

The idea that number processing is grounded in the sensorimotor systems has implications in various fields. While some of these implications are directly related to the findings presented here some of them generally concern the idea of mathematical embodiment.

Implications

Although the focus in this dissertation is not the developmental dynamics of the finger and number processing relation, the results have implications for cognitive development. It was shown that arithmetic processing takes place in a sensorimotor circuit. Sharing of neural resources might also imply that these two systems follow similar developmental trajectories. If mathematics and other domains of higher thinking are grounded in the sensorimotor system, then children's early sensorimotor development might influence their later mathematics learning skills. In this sense improvement of the base level skill, such as finger tapping, might mediate the learning of the higher level skill, arithmetic in this case. Activities that facilitate finger movements in complex ways (playing musical instruments, playing with toys etc.) might yield to improvements in mathematical abilities in later years. There is already supporting evidence for children who are better at distinguishing fingers (having better finger sense) early on becoming

more successful in math in later school years (Fayol, Barrouillet, & Marinthe, 1998; Noel, 2005). However there are no previous experimental studies that have focused on the possible merits of early finger sensorimotor experiences in arithmetic learning. Experimental longitudinal studies comparing children who get abundant finger-related motor experiences with children who do not, in terms of their elementary level mathematical abilities would answer these questions.

Previous studies have shown a relation between musical and mathematical abilities (Vaughn, 2000). For example, in a study by Zafranas (2004) it was found that piano keyboard training resulted in significant improvement on the hand movement and arithmetic subtests of the Kaufman Assessment Battery for Children. Music involves many distinct cognitive processes and it is not clear which of these processes overlap with mathematics. Sequence processing and sequential movement of fingers is an important aspect of instrument playing. Although there is some evidence for instrument playing correlating with mathematical skills, whether or not there is a casual relation and if there is, which aspects of instrument playing contribute to mathematical skills are not known. In a recent study it was shown that, at the high school level, orchestra and band students' performance in the Education Longitudinal Study math section and SAT was higher compared to choir students (Elpus, 2011). The difference between band and choir students can be explained through the finger movement aspect of instrument playing, given that the other aspects of musical experience are shared by the two groups. Nevertheless, this study does not report data from a controlled experiment, therefore it is hard to know if there are other factors that influence the results. Investigating which aspects of musical experience interact with mathematical cognition would be an important future direction.

The finger-mathematics relation also has implications in use of physical manipulatives in mathematics education. If mathematical thinking occurs on a sensorimotor circuit, and if we use inferences from physical interactions to understand mathematical concepts, then providing the learners with relevant physical interactions can be crucial. This proposition would explain the effectiveness of physical manipulatives in learning math. It might also imply a disadvantage of computer-based learning interventions for younger learners due to the limitations with physical experiences in this type of learning. Nevertheless, new modes of human-computer interaction that focus on embodied ways of interaction (Millard & Soylu, 2009) might remedy this problem.

The findings in this study contribute to our understanding of why limited lesions in the angular and, to a lesser extent, supramarginal gyrus lead to Gerstmann's Syndrome (Gerstmann, 1940). It is widely accepted that this syndrome indicates pathology of the dominant parietal cortex, particularly the left angular gyrus (Roux, et al., 2003). Nevertheless, it is still not clear why the dysfunction of the angular gyrus results with the disruption of seemingly disparate systems, finger sense and arithmetic abilities, in addition to right/left orientation and ability to write. Our results support the idea that the angular and supramarginal gyri both participate in finger and number processing. A finger-based representation of numbers might explain why acalculia and finger agnosia occur concurrently in the case of a left angular gyrus lesion.

Finally, the correlations between finger counting habits and arithmetic ability, as well as finger tapping ability and numerical working memory has implications for predicting student, both adult and younger student, success. Within a large scale study data on measures such as finger tapping, handedness, finger counting habits, spatial ability

and digit-span can be collected to see if these measures have predictive power on mathematical ability. Finding such relations would be very helpful in diagnosing possible problems in student performance to take preventative measures.

Reflections and Future Studies

The findings presented in this dissertation are far from providing a complete explanation about the contribution of fingers in numerical thinking. They rather contribute to a new path for the study of embodiment of mathematics with a focus on the finger and number processing relation. While the experiments described were being designed there were many different ways to investigate the finger number relation, each alternative way focusing on a different aspect. Due to practical limitations I could not realize every experiment design I thought would provide a contribution. However, these ideas are worthy of mentioning to allow me and other researchers to formulate future studies.

Are Fingers Special?

The behavioral experiment results in Chapter 2 showed that addition uses more overlapping resources with finger tapping compared to sentence comprehension. This finding yields to two questions: (1) are fingers special, or would any motor task interfere more with addition? And, (2) does this mean that sentence comprehension is disembodied? Probably not given that there are previous studies showing involvement of sensorimotor systems in various aspects of language comprehension (see for example, Buccino et al., 2005). However, it is possible that while sentence comprehension also uses a sensorimotor network, this network does not overlap with finger related areas as much as it does for addition. A future study that addresses this point by testing the interference of a different motor movement, for example lip movements, that potentially interferes more

111

with sentence comprehension compared to addition would establish a double disassociation.

Other Numerical Tasks

If numbers are represented on a finger-based circuit than we would expect to see the type of finger tapping interference we observed for addition on any numerical task. In alternative designs finger tapping interference on parity judgment or number comparison could be compared to another control task. Sentence comprehension is probably not a good control for these tasks given that most parity and comparison tasks take less than a second. A word judgment task might be a good alternative for the control task. Overall, testing the interference of tapping on various numerical tasks would allow one to investigate which aspects of number processing share more resources with finger movements.

Congenitally Missing Limbs

It is not clear whether the finger and number relationship is due to a developmental/cultural association or is inherent in the organization of the brain. One possible way to investigate this question would be to study people who congenitally miss fingers. A simple neuroimaging study investigating the neural correlates of simple arithmetic in this population might reveal a different pattern of activation compared to a normal population, which might support the association theory. Nevertheless even if fingers and number processing are inherently related, the patterns of activation might still differ compared to a normal population, because the finger-related sensorimotor areas might be repurposed for other functions due to brain plasticity.

References

Algom, D., Dekel, A., & Pansky, A. (1996). The perception of number from the separability of the stimulus: The Stroop effect revisited. *Memory and Cognition, 24*, 557-572.

Allman, B., Keniston, L., & Meredith, M. (2009). Not just for bimodal neurons anymore: The contribution of unimodal neurons to cortical multisensory processing. *Brain Topography, 21*(3), 157-167.

Anderson, M. L. (2006). *Evidence for massive redeployment of brain areas in cognitive function.* Proceedings of the 28th Annual Conference of the Cognitive Science Society, Vancouver, Canada: Cognitive Science Society.

Anderson, M. L. (2007). Evolution of cognitive function via redeployment of brain areas. *The Neuroscientist, 13*(1), 13.

Anderson, M. L., & Penner-Wilger, M. (2007). *Do redeployed finger representations underlie math ability*. Proceedings of the 29th Annual Conference of the Cognitive Science Society, Nashville, Tennessee: Cognitive Science Society.

Andres, M., Ostry, D., Nicol, F., & Paus, T. (2008). Time course of number magnitude interference during grasping. *Cortex, 44*(4), 414-419.

Andres, M., Seron, X., & Olivier, E. (2007). Contribution of hand motor circuits to counting. *Journal of Cognitive Neuroscience, 19*(4), 563-576.

Annett, M. (2004). Hand preference observed in large healthy samples: Classification, norms and interpretations of increased non right handedness by the right shift theory. *British Journal of Psychology, 95*(3), 339-353.

Annett, M. (2009). Patterns of hand preference for pairs of actions and the classification of handedness. *British Journal of Psychology, 100*(3), 491-500.

Arbib, M. A. (2002). The mirror system, imitation, and the evolution of language. In K. Dautenhahn (Ed.), *Imitation in animals and artifacts* (pp. 229-280).

Arbib, M. A. (2005). From monkey-like action recognition to human language: An evolutionary framework for neurolinguistics. *Behavioral and Brain Sciences, 28*(02), 105-124.

Badets, A., Andres, M., Di Luca, S., & Pesenti, M. (2007). Number magnitude potentiates action judgements. *Experimental Brain Research, 180*(3), 525-534.

Barnes, M., Smith-Chant, B., & Landry, S. (2005). Number processing in neurodevelopmental disorders. Spina bifida myelomeningocele. *Handbook of mathematical cognition*, 299-313.

Barsalou, L. W. (1999). Perceptual symbol systems. *Behavioral and Brain Sciences, 22*(04), 577-660.

Binkofski, F., Buccino, G., Posse, S., Seitz, R. J., Rizzolatti, G., & Freund, H. J. (1999). A fronto-parietal circuit for object manipulation in man: evidence from an fMRI-study. *European Journal of Neuroscience, 11*(9), 3276-3286.

Bishop, A. J. (1980). Spatial abilities and mathematics education-A review. *Educational Studies in Mathematics, 11*(3), 257-269.

Brozzoli, C., Ishihara, M., Gobel, S. M., Salemme, R., Rossetti, Y., & Farne, A. (2008). Touch perception reveals the dominance of spatial over digital representation of numbers. *Proceedings of the National Academy of Sciences, 105*(14), 5644.

Buccino, G., Riggio, L., Melli, G., Binkofski, F., Gallese, V., & Rizzolatti, G. (2005). Listening to action-related sentences modulates the activity of the motor system: A combined TMS and behavioral study. *Cognitive Brain Research, 24*(3), 355-363.

Buhusi, C. V., & Meck, W. H. (2005). What makes us tick? Functional and neural mechanisms of interval timing. *Nature Reviews Neuroscience, 6*(10), 755-765.

Bull, R., & Scerif, G. (2001). Executive functioning as a predictor of children's mathematics ability: Inhibition, switching, and working memory. *Developmental neuropsychology, 19*(3), 273-293.

Burnett, S. A., Lane, D. M., & Dratt, L. M. (1979). Spatial visualization and sex differences in quantitative ability. *Intelligence, 3*(4), 345-354.

Butterworth, B. (1999a). A head for figures. *Science (New York, NY), 284*(5416), 928.

Butterworth, B. (1999b). *What counts: How every brain is hardwired for math*: The Free Press.

Butterworth, B. (2005). The development of arithmetical abilities. *Journal of Child Psychology and Psychiatry, 46*(1), 3-18.

Cappelletti, M., Barth, H., Fregni, F., Spelke, E., & Pascual-Leone, A. (2007). rTMS over the intraparietal sulcus disrupts numerosity processing. *Experimental Brain Research, 179*(4), 631-642.

Casey, M. B., Diana, C., & Goris, Y. (1992). Family handedness as a predictor of mental rotation ability among minority girls in a math-science training program. *Brain and Cognition, 18*(1), 88-96.

Casey, M. B., Nuttall, R., Pezaris, E., & Benbow, C. P. (1995). The influence of spatial ability on gender differences in mathematics college entrance test scores across diverse samples. *Developmental Psychology, 31*(4), 697.

Casey, M. B., Pezaris, E., & Nuttall, R. L. (1992). Spatial ability as a predictor of math achievement: The importance of sex and handedness patterns. *Neuropsychologia, 30*(1), 35-45.

Choi, S., Na, D. L., Kang, E., Lee, K., Lee, S., & Na, D. (2001). Functional magnetic resonance imaging during pantomiming tool-use gestures. *Experimental Brain Research, 139*(3), 311-317.

Chong, T., Cunnington, R., Williams, M., Kanwisher, N., & Mattingley, J. (2008). fMRI adaptation reveals mirror neurons in human inferior parietal cortex. *Current biology, 18*(20), 1576-1580.

Clark, A. (1999). An embodied cognitive science? *Trends In Cognitive Sciences, 3*(9), 345-351.

Cohen Kadosh, R., Kadosh, K., & Henik, A. (2008). When brightness counts: The neuronal correlate of numerical-luminance interference. *Cerebral Cortex, 18*(2), 337.

Cohen Kadosh, R., Lammertyn, J., & Izard, V. (2008). Are numbers special? An overview of chronometric, neuroimaging, developmental and comparative studies of magnitude representation. *Progress in Neurobiology, 84*(2), 132-147.

Corballis, M. C., Hattie, J., & Fletcher, R. (2008). Handedness and intellectual achievement: An even-handed look. *Neuropsychologia, 46*(1), 374-378.

Corina, D. P., & Knapp, H. (2006). Special issue: Review sign language processing and the mirror neuron system. *Cortex, 42*, 529-539.

Crow, T., Crow, L., Done, D., & Leask, S. (1998). Relative hand skill predicts academic ability: global deficits at the point of hemispheric indecision. *Neuropsychologia, 36*(12), 1275-1282.

Crozier, S., Sirigu, A., Lehéricy, S., van de Moortele, P., Pillon, B., Grafman, J., et al. (1999). Distinct prefrontal activations in processing sequence at the sentence and script level: An fMRI study. *Neuropsychologia, 37*(13), 1469-1476.

D'Esposito, M., Detre, J. A., Alsop, D. C., Shin, R. K., Atlas, S., & Grossman, M. (1995). The neural basis of the central executive system of working memory. *Nature, 378*(6554), 279-281.

Davies, M., & Stone, T. (1995). *Mental simulation: evaluations and applications*: Blackwell.

Dehaene, S. (1992). Varieties of numerical abilities. *Cognition, 44*(1-2), 1-42.

Dehaene, S. (1997). *The Number Sense: How the Mind Creates Mathematics*: Oxford University Press, USA.

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

Dehaene, S., & Cohen, L. (1995). Towards an anatomical and functional model of number processing. *Mathematical Cognition, 1*(1), 83-120.

Dehaene, S., & Cohen, L. (1997). Cerebral pathways for calculation: Double dissociation between rote verbal and quantitative knowledge of arithmetic. *Cortex, 33*, 219-250.

Dehaene, S., Dehaene-Lambertz, G., & Cohen, L. (1998). Abstract representations of numbers in the animal and human brain. *Trends in Neurosciences, 21*(8), 355-361.

Dehaene, S., Piazza, M., Pinel, P., & Cohen, L. (2003). Three parietal circuits for number processing. *Handbook of mathematical cognition*, 433-453.

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

Detweiler, M., & Schneider, W. (1991). Modeling the acquisition of dual-task skill in a connectionist/control architecture. In D. L. Damos (Ed.), *Multiple-task performance* (pp. 69-100). London: Taylor and Francis.

Di Luca, S., Grana, A., Semenza, C., Seron, X., & Pesenti, M. (2006). Finger-digit compatibility in Arabic numeral processing. *Quarterly Journal of Experimental Psychology, 59*(9), 1648-1663.

Dodrill, C. B. (1979). Sex differences on the Halstead Reitan neuropsychological battery and on other neuropsychological measures. *Journal of Clinical Psychology, 35*(2), 236-241.

Elpus, K. (2011). Justifying Music Education: Econometric Analyses of Issues in Music Education Policy. Unpublished Doctoral Dissertation: Northwestern University.

Evans, A. C., Collins, D. L., Mills, S., Brown, E., Kelly, R., & Peters, T. (1993). *3D statistical neuroanatomical models from 305 MRI volumes*.

Fayol, M., Barrouillet, P., & Marinthe, C. (1998). Predicting arithmetical achievement from neuro-psychological performance: A longitudinal study. *Cognition, 68*(2), B63-B70.

Fias, W., & Fischer, M. (2005). Spatial representation of numbers. *Handbook of mathematical cognition*, 43-54.

Fischer, M. (2008). Finger counting habits modulate spatial-numerical associations. *Cortex, 44*(4), 386-392.

Fodor, J. A. (1983). *The modularity of mind* (Vol. 341): MIT press Cambridge, MA.

Friedman, A., Polson, M. C., Dafoe, C. G., & Gaskill, S. J. (1982). Dividing attention within and between hemispheres: Testing a multiple resources approach to limited-capacity information processing. *Journal of Experimental Psychology: Human Perception and Performance, 8*(5), 625.

Friston, K., & Penny, W. (2003). Posterior probability maps and SPMs. *Neuroimage, 19*(3), 1240-1249.

Fulbright, R., Manson, S., Skudlarski, P., Lacadie, C., & Gore, J. (2003). Quantity determination and the distance effect with letters, numbers, and shapes: a functional MR imaging study of number processing. *American journal of neuroradiology, 24*(2), 193.

Gallese, V., & Lakoff, G. (2005). The brain's concepts: the role of the sensory-motor system in conceptual knowledge. *Cognitive Neuropsychology, 1*(1), 1-1.

Gerstmann, J. (1940). Syndrome of finger agnosia, disorientation for right and left, agraphia and acalculia. *Archives of Neurology and Psychiatry, 44*, 398-408.

Geschwind, N. (1965). Disconnexion syndromes in animals and man. *Brain, 88*(3), 585.

Gobel, S., Walsh, V., & Rushworth, M. F. S. (2001). The mental number line and the human angular gyrus. *Neuroimage, 14*(6), 1278-1289.

Goldberg, T. E., Berman, K. F., Fleming, K., Ostrem, J., Van Horn, J. D., Esposito, G., et al. (1998). Uncoupling Cognitive Workload and Prefrontal Cortical Physiology: A PET rCBF Study. *Neuroimage, 7*(4), 296-303.

Goldin-Meadow, S. (1997). When Gestures and Words Speak Differently. *Current Directions in Psychological Science, 6*(5), 138-143.

Goldin-Meadow, S. (1999). The role of gesture in communication and thinking. *Trends In Cognitive Sciences, 3*(11), 419-429.

Goldin-Meadow, S. (2006). Talking and Thinking With Our Hands. *Current Directions in Psychological Science, 15*(1), 34-39.

Goldin-Meadow, S., Nusbaum, H., Kelly, S. D., & Wagner, S. (2001). Explaining Math: Gesturing Lightens the Load. *Psychological Science, 12*(6), 516-522.

Goldin-Meadow, S., & Singer, M. A. (2003). From children's hands to adults' ears: Gesture's role in the learning process. *Developmental Psychology, 39*(3), 509-520.

Goldin-Meadow, S., & Wagner, S. M. (2005). How our hands help us learn. *Trends In Cognitive Sciences, 9*(5), 234-241.

Goldin, G. A. (2001). Counting on the metaphorical. *Nature, 413*(6851), 18-19.

Grabner, R., Ansari, D., Koschutnig, K., Reishofer, G., Ebner, F., & Neuper, C. (2009). To retrieve or to calculate? Left angular gyrus mediates the retrieval of arithmetic facts during problem solving. *Neuropsychologia, 47*(2), 604-608.

Greicius, M. D., & Menon, V. (2004). Default-mode activity during a passive sensory task: uncoupled from deactivation but impacting activation. *Journal of Cognitive Neuroscience, 16*(9), 1484-1492.

Hadamard, J. (1945). *An essay on the psychology of invention in the mathematical field*: Princeton University Press.

Halpern, D. F. (2000). *Sex differences in cognitive abilities* (3rd ed.). Mahwah, NJ: L. Erlbaum Associates

Harris, L. (1981). Sex-related variations in spatial skill. *Spatial representation and behavior across the life span*, 83-125.

Herath, P., Klingberg, T., Young, J., Amunts, K., & Roland, P. (2001). Neural correlates of dual-task interference can be dissociated from those of divided attention: an fMRI study. *Cerebral Cortex, 11*(9), 796.

Houdé, O., & Tzourio-Mazoyer, N. (2003). Neural foundations of logical and mathematical cognition. *Nature Reviews Neuroscience, 4*(6), 507-514.

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.

Hyde, J. S. (1981). How large are cognitive gender differences? A meta-analysis using! w² and d. *American Pyschologist, 36*(8), 892-901.

Hyde, J. S., Fennema, E., & Lamon, S. J. (1990). Gender differences in mathematics performance: A meta-analysis. *Psychological Bulletin, 107*(2), 139.

Jaeggi, S. M., Seewer, R., Nirkko, A. C., Eckstein, D., Schroth, G., Groner, R., et al. (2003). Does excessive memory load attenuate activation in the prefrontal cortex? Load-dependent processing in single and dual-tasks: functional magnetic resonance imaging study. *Neuroimage, 19*(2), 210-225.

Jonides, J., Smith, E. E., Koeppe, R. A., Awh, E., Minoshima, S., & Mintun, M. A. (1993). Spatial working memory in humans as revealed by PET. *Nature, 363*, 623-625.

Just, M. A., Carpenter, P. A., Keller, T. A., Emery, L., Zajac, H., & Thulborn, K. R. (2001). Interdependence of nonoverlapping cortical systems in dual cognitive tasks. *Neuroimage, 14*(2), 417-426.

Keefe, K. (1985). Motor and cognitive interference effects on unimanual tapping rates. *Brain and Cognition, 4*(2), 165-170.

Kemmerer, D., & Gonzalez-Castillo, J. (2008). The Two-Level Theory of verb meaning: An approach to integrating the semantics of action with the mirror neuron system. *Brain and Language*.

Kinsbourne, M. (1981). Single channel theory. *Human skills*, 65-89.

Kinsbourne, M., & Cook, J. (1971). Generalized and lateralized effects of concurrent verbalization on a unimanual skill. *The Quarterly Journal of Experimental Psychology, 23*(3), 341-345.

Kinsbourne, M., & Hicks, R. E. (1978). Functional cerebral space: A model for overflow, transfer and interference effects in human performance. *Attention and performance*, 345-362.

Klingberg, T. (1998). Concurrent performance of two working memory tasks: potential mechanisms of interference. *Cerebral Cortex, 8*(7), 593.

Klingberg, T., & Roland, P. E. (1997). Interference between two concurrent tasks is associated with activation of overlapping fields in the cortex. *Cognitive Brain Research, 6*(1), 1-8.

122

Kuhtz Buschbeck, J., Mahnkopf, C., Holzknecht, C., Siebner, H., Ulmer, S., & Jansen, O. (2003). Effector independent representations of simple and complex imagined finger movements: a combined fMRI and TMS study. *European Journal of Neuroscience, 18*(12), 3375-3387.

Lakoff, G., & Johnson, M. (1980). *Metaphors we live by*: Chicago London.

Lakoff, G., & Nunez, R. E. (2000). *Where Mathematics Comes from: How the Embodied Mind Brings Mathematics Into Being*: Basic Books.

Lee, K. (2000). Cortical areas differentially involved in multiplication and subtraction: A functional magnetic resonance imaging study and correlation with a case of selective acalculia. *Annals of Neurology, 48*(4), 657-661.

Linn, M. C., & Petersen, A. C. (1985). Emergence and characterization of sex differences in spatial ability: A meta-analysis. *Child Development, 56*(6), 1479-1498.

Logan, G. D. (1980). Attention and automaticity in Stroop and priming tasks: Theory and data* 1. *Cognitive Psychology, 12*(4), 523-553.

Longo, G. (2007). Mathematical Concepts and Physical Objects. *Rediscovering Phenomenology: Phenomenological Essays on Mathematical Beings, Physical Reality, Perception and Consciousness*, 195.

Maccoby, E. E., & Jacklin, C. N. (1974). Myth, reality and shades of gray: What we know and don't know about sex differences. *Psychology Today, 8*(7), 109-112.

Markey, S. M. (2010). *The relationship between visual-spatial reasoning ability and math and geometry problem-solving*. AMERICAN INTERNATIONAL COLLEGE.

Martory, M. D., Mayer, E., Pegna, A. J., Annoni, J. M., Landis, T., & Khateb, A. (2003). Pure global acalculia following a left subangular lesion. *Neurocase: case studies in neuropsychology, neuropsychiatry, and behavioural neurology, 9*(4), 319.

Masters, M. S., & Sanders, B. (1993). Is the gender difference in mental rotation disappearing? *Behavior Genetics, 23*(4), 337-341.

Maturana, H. R., & Varela, F. J. (1987). *The Tree of Knowledge: The Biological Roots of Human Understanding*: New Science Library: Distributed in the United State by Random House, Boston.

Mayer, E., Martory, M., Pegna, A., Landis, T., Delavelle, J., & Annoni, J. (1999). A pure case of Gerstmann syndrome with a subangular lesion. *Brain, 122*(6), 1107.

Menon, V., Rivera, S., White, C., Eliez, S., Glover, G., & Reiss, A. (2000). Functional optimization of arithmetic processing in perfect performers. *Cognitive Brain Research, 9*(3), 343-345.

Millard, M., & Soylu, F. (2009). An Embodied Approach for Engaged Interaction in Ubiquitous Computing. In *13th International Conference on Human-Computer Interaction* (Vol. 5612, pp. 472). San Diego, CA, USA: Springer.

Miyake, A., Friedman, N. P., Rettinger, D. A., Shah, P., & Hegarty, M. (2001). How are visuospatial working memory, executive functioning, and spatial abilities related? A latent-variable analysis. *Journal of Experimental Psychology: General, 130*(4), 621.

Navon, D. (1985). Attention division or attention sharing. *Attention and performance XI, 133*, 146.

Nettle, D. (2003). Hand laterality and cognitive ability: A multiple regression approach. *Brain and Cognition, 52*(3), 390-398.

Newell, A., & Simon, H. A. (1976). Computer science as empirical inquiry: Symbols and search. *Communications of the ACM, 19*(3), 113-126.

Newman, S. D., Keller, T. A., & Just, M. A. (2007). Volitional Control of Attention and Brain Activation in Dual-task Performance. *Human Brain Mapping, 28*, 109-117.

Noel, M. (2005). Finger gnosia: a predictor of numerical abilities in children? *Child Neuropsychology, 11*(5), 413-430.

Nunez, R. E. (2008). M athematics, the U ltimate C hallenge to E mbodiment: T ruth and the G rounding of A xiomatic S ystems.

Nunez, R. E., Edwards, L. D., & Filipe-Matos, J. (1999). Embodied cognition as grounding for situatedness and context in mathematics education. *Educational Studies in Mathematics, 39*(1), 45-65.

O'Boyle, M. W., & Benbow, C. P. (1990). Handedness and its relationship to ability and talent.

Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia, 9*(1), 97-113.

Orton, S. T. (1937). Reading, writing and speech problems in children.

Papadatou-Pastou, M., Martin, M., Munafò, M. R., & Jones, G. V. (2008). Sex differences in left-handedness: A meta-analysis of 144 studies. *Psychological Bulletin, 134*(5), 677.

Pascual-Leone, A., & Hamilton, R. (2001). The metamodal organization of the brain. *Vision: From Neurons to Cognition, C. Casanova, and M. Ptito, eds.(New York: Elsevier)*, 427-445.

Pashler, H. (1994). Dual-task interference in simple tasks: Data and theory. *Psychological Bulletin, 116*, 220-220.

Pashler, H., Carrier, M., & Hoffman, J. (1993). Saccadic eye movements and dual-task interference. *The Quarterly Journal of Experimental Psychology Section A, 46*(1), 51-82.

Peltier, S., Stilla, R., Mariola, E., LaConte, S., Hu, X., & Sathian, K. (2007). Activity and effective connectivity of parietal and occipital cortical regions during haptic shape perception. *Neuropsychologia, 45*(3), 476-483.

Penner-Wilger, M., & Anderson, M. L. (2008). *An alternative view of the relation between finger gnosis and math ability: Redeployment of finger representations for the representation of number.* Proceedings of the 30th Annual Conference of the Cognitive Science Society, Washington D.C: Cognitive Science Society.

Penner-Wilger, M., & Anderson, M. L. (2011). *The relation between finger gnosis and mathematical ability: Can we attribute function to cortical structure with cross-domain modeling?* Proceedings of the 33th Annual Conference of the Cognitive Science Society, Boston, MA: Cognitive Science Society.

Penner-Wilger, M., Fast, L., LeFevre, J., Smith-Chant, B., Skwarchuk, S., Kamawar, D., et al. (2007). *The foundations of numeracy: Subitizing, finger gnosia, and fine-motor ability.* Proceedings of the 29thth Annual Conference of the Cognitive Science Society, Nashivelle, TN: Cognitive Science Society.

Pesenti, M., Thioux, M., Seron, X., & Volder, A. D. (2000). Neuroanatomical substrates of Arabic number processing, numerical comparison, and simple addition: A PET study. *Journal of Cognitive Neuroscience, 12*(3), 461-479.

Petrides, M., Alivisatos, B., Meyer, E., & Evans, A. C. (1993). Functional activation of the human frontal cortex during the performance of working memory tasks. *Proceedings of the National Academy of Sciences, 90*, 878-882.

Piaget, J. (1954). The construction of reality in the child (M. Cook, Trans.). *New York: Ballantine.(Original work published 1937)*.

Pinel, P., Piazza, M., Le Bihan, D., & Dehaene, S. (2004). Distributed and overlapping cerebral representations of number, size, and luminance during comparative judgments. *Neuron, 41*(6), 983-993.

Pulvermüller, F. (2003). Sequence detectors as a basis of grammar in the brain. *Theory in Biosciences, 122*(1), 87-103.

Rees, G., Frith, C. D., & Lavie, N. (1997). Modulating irrelevant motion perception by varying attentional load in an unrelated task. *Science, 278*(5343), 1616.

Rickard, T., Romero, S., Basso, G., Wharton, C., Flitman, S., & Grafman, J. (2000). The calculating brain: an fMRI study. *Neuropsychologia, 38*(3), 325-335.

Roland, P. E., & Zilles, K. (1998). Structural divisions and functional fields in the human cerebral cortex. *Brain research reviews, 26*(2-3), 87-105.

Roux, F. E., Boetto, S., Sacko, O., Chollet, F., & Tremoulet, M. (2003). Writing, calculating, and finger recognition in the region of the angular gyrus: a cortical stimulation study of Gerstmann syndrome. *Journal of neurosurgery, 99*(4), 716-727.

Ruff, R. M., & Parker, S. B. (1993). Gender-and age-specific changes in motor speed and eye-hand coordination in adults: Normative values for the Finger Tapping and Grooved Pegboard tests. *Perceptual and motor skills*.

Rusconi, E., Walsh, V., & Butterworth, B. (2005). Dexterity with numbers: rTMS over left angular gyrus disrupts finger gnosis and number processing. *Neuropsychologia, 43*(11), 1609-1624.

Sakai, K., Ramnani, N., & Passingham, R. (2002). Learning of sequences of finger movements and timing: frontal lobe and action-oriented representation. *Journal of neurophysiology, 88*(4), 2035.

Sakata, H., & Taira, M. (1998). Parietal control of hand action. *Findings and current opinion in cognitive neuroscience, 4*, 263.

Sato, M., Cattaneo, L., Rizzolatti, G., & Gallese, V. (2007). Numbers within our hands: Modulation of corticospinal excitability of hand muscles during numerical judgment. *Journal of Cognitive Neuroscience, 19*(4), 684-693.

Sato, M., & Lalain, M. (2008). On the relationship between handedness and hand-digit mapping in finger counting. *Cortex; a journal devoted to the study of the nervous system and behavior, 44*(4), 393-399.

Schwarz, W., & Keus, I. (2004). Moving the eyes along the mental number line: Comparing SNARC effects with manual and saccadic responses. *Perception and Psychophysics, 66*(4), 651-664.

Seghier, M. L., Fagan, E., & Price, C. J. (2010). Functional Subdivisions in the Left Angular Gyrus Where the Semantic System Meets and Diverges from the Default Network. *The Journal of Neuroscience, 30*(50), 16809.

Sestieri, C., Corbetta, M., Romani, G. L., & Shulman, G. L. (2011). Episodic Memory Retrieval, Parietal Cortex, and the Default Mode Network: Functional and Topographic Analyses. *The Journal of Neuroscience, 31*(12), 4407.

Sfard, A. (1994). Reification as the Birth of Metaphor. *For the learning of mathematics, 14*(1), 44-55.

Sirigu, A., Duhamel, J. R., Cohen, L., Pillon, B., Dubois, B., & Agid, Y. (1996). The mental representation of hand movements after parietal cortex damage. *Science, 273*(5281), 1564.

Slobin, D. I. (1966). Grammatical transformations and sentence comprehension in childhood and adulthood. *Journal of verbal learning and verbal behavior*, 5, 219-227.

Soylu, F., & Newman, S. D. (2011). *Is arithmetic embodied? Differential interference of sequential finger tapping on addition during a dual-task paradigm.* Proceedings of the 33th Annual Conference of the Cognitive Science Society, Boston, MA: Cognitive Science Society.

Stein, B. E., & Stanford, T. R. (2008). Multisensory integration: current issues from the perspective of the single neuron. *Nature Reviews Neuroscience, 9*(4), 255-266.

Stroop, J. (1935). Studies of interference in serial verbal reactions. *Journal of Experimental Psychology, 18*, 643-662.

Stumpf, H. (1993). Performance factors and gender-related differences in spatial ability: Another assessment. *Memory & cognition, 21*(6), 828-836.

Telford, C. W. (1931). The refractory phase of voluntary and associative responses. *Journal of Experimental Psychology, 14*(1), 1.

Tunik, E., Lo, O. Y., & Adamovich, S. V. (2008). Transcranial Magnetic Stimulation to the Frontal Operculum and Supramarginal Gyrus Disrupts Planning of Outcome-Based Hand-Object Interactions. *The Journal of Neuroscience, 28*(53), 14422.

Vandenberghe, R., Duncan, J., Dupont, P., Ward, R., Poline, J. B., Bormans, G., et al. (1997). Attention to one or two features in left or right visual field: a positron emission tomography study. *The Journal of Neuroscience, 17*(10), 3739.

Vaughn, K. (2000). Music and mathematics: Modest support for the oft-claimed relationship. *Journal of Aesthetic Education, 34*(3/4), 149-166.

Voorhees, B. (2004). Embodied Mathematics. *Journal of Consciousness Studies, 11*, 83-88.

Welford, A. (1952). The psychological refractory period and the timing of high speed performance—a review and a theory. *British Journal of Psychology, 43*(1), 2-19.

Wilson, K. M., & Swanson, H. L. (2001). Are mathematics disabilities due to a domain-general or a domain-specific working memory deficit? *Journal of Learning Disabilities, 34*(3), 237.

Wilson, M. (2002). Six views of embodied cognition. *Psychonomic Bulletin & Review, 9*(4), 625-636.

Wolff, P. H., & Hurwitz, I. (1976). Sex differences in finger tapping: A developmental study. *Neuropsychologia, 14*(1), 35-41.

Wu, S. S., Chang, T. T., Majid, A., Caspers, S., Eickhoff, S. B., & Menon, V. (2009). Functional heterogeneity of inferior parietal cortex during mathematical cognition assessed with cytoarchitectonic probability maps. *Cerebral Cortex*.

Zago, L., Pesenti, M., Mellet, E., Crivello, F., Mazoyer, B., & Tzourio-Mazoyer, N. (2001). Neural correlates of simple and complex mental calculation. *Neuroimage, 13*(2), 314-327.

Zago, L., & Tzourio-Mazoyer, N. (2002). Distinguishing visuospatial working memory and complex mental calculation areas within the parietal lobes. *Neuroscience letters, 331*(1), 45-49.

Zebian, S. (2005). Linkages between number concepts, spatial thinking, and directionality of writing: The SNARC effect and the reverse SNARC effect in English and Arabic monoliterates, biliterates, and illiterate Arabic speakers. *Journal of Cognition and Culture, 5, 1*(2), 165-190.

FIRAT SOYLU

3878 S. Bushmill Dr., Bloomington, IN 47403 • (573) 280 6410
fsoylu@indiana.edu • http://mypage.iu.edu/~fsoylu

EDUCATION

2011	*Indiana University, Bloomington, IN* **Ph.D. Dual Major: Instructional Systems Technology and Cognitive Science (ABD)**
2009	*Indiana University, Bloomington, IN* **M.Sc.: Instructional Systems Technology**
2004	*Middle East Technical University, Ankara, Turkey* **Cognitive Science Program**: Completed 18 graduate credits (transferred to Indiana University)
2003	*Middle East Technical University, Ankara, Turkey* **B.Sc.: Computer Education and Instructional Technology**

WORK EXPERIENCE

2011 -	*Northwestern University, Evanston, IL* **Postdoctoral Fellow** - Center for Connect Learning and Computer Based Modeling & Learning Sciences Program
2009 - 2011	*Indiana University, Bloomington, IN* **Graduate Student** - Dr. Sharlene Newman's Cognitive Neuroimaging Lab
2010 - 2011	*Indiana University, Bloomington, IN* **Teaching / Research Assistant -** Learning Sciences Program
2008 - 2010	*Indiana University, Bloomington, IN* **Graduate Assistant** - Office of Instructional Consulting
2004 - 2008	*Indiana University, Bloomington, IN* **Associate Instructor -** Instructional Systems Technology Department
2007	*Cisco Networking Academy, Bloomington, IN* **Activity Developer**
2003 - 2004	***Middle East Technical University, Ankara, Turkey*** **Teaching Assistant** - Cognitive Science Program / Informatics Institute
2002	*ODEVA Internet Technologies, Ankara, Turkey* **Linux Systems Administrator - Industry**
2001-2002	*Samtek Innovative Technology Center, Ankara, Turkey* **Linux Systems Administrator - Industry**

JOURNAL PAPERS, CONFERENCE PROCEEDINGS & BOOK CHAPTERS

Hickey, D.T. & Soylu, F. (in press). Wikifolios, Reflections, and Exams for Online Engagement, Understanding, and Achievement. In *Quick Hits: Teaching with Technology*. Indiana University Press.

Ayar, M. C., Yalvac, B., & **Soylu, F**. (accepted). Teaching Engineering with Wikis. *International Journal of Engineering Education.*

Soylu, F. & Newman, S. D. (2011). *Is Arithmetic Embodied? Differential Interference of Sequential Finger Tapping on Addition during a Dual Task Paradigm*. In L. Carlson, C. Hölscher, & T. Shipley (Eds.), Proceedings of the 33rd Annual Conference of the Cognitive Science Society. Austin, TX: Cognitive Science Society.

Soylu, F. (2011). *Mathematical Cognition as Embodied Simulation*. In L. Carlson, C. Hölscher, & T. Shipley (Eds.), Proceedings of the 33rd Annual Conference of the Cognitive Science Society. Austin, TX: Cognitive Science Society.

Yalvac, B., **Soylu, F.,** & Arikan, A., (2011). Embodied cognition and education. *ETHOS: Dialogues in Philosophy and Social Science.*

Millard, M. & **Soylu, F**., (2009). *An embodied approach for engaged interaction in ubiquitous computing.* In A. Jacko (Ed.), Proceedings of the 13th International Conference on Human-Computer Interaction, San Diego, CA: July, 2009.

Soylu, F. (2009). Academics' views and uses of Wikipedia. *Gnovis [Georgetown University's Peer-Reviewed Journal of Communication, Culture and Technology].http://gnovisjournal.org/journal/academics-views-and-uses-wikipedia*

Soylu, F. (2009). Designing online learning communities: Lessons from Ekşisözlük. *European Journal of Open Distance and E-Learning*(1).

CONFERENCE PRESENTATIONS

Soylu, F. & Newman, S. (2011). *Finger Based Representation of Numbers: Correlation Between Finger Tapping Ability and Digit Span*. Abstract for the 33th Annual Conference of the Cognitive Science Society, Boston, MA: July, 2011

Hickey, D.T., McWilliams, J., Bishop, S., & **Soylu, F**. (2011). Participatory Assessment for Engagement, Understanding, and Achievement in Online Learning Contexts. Paper presented at AERA Annual Meeting, New Orleans, LA: April, 2011.

Soylu, F., Soylu, M. and Davis, H. (2010), *Relating embodied cognition and phenomenology to art experience*. Paper presentation at the National Art Education Association Conference, Baltimore, MD: April, 2010.

Soylu, F. & Millard, M. (2009). *Use of embodied learning approaches in teaching technology*. Paper presented at Association for Educational Communications and Technology (AECT) meeting, Louisville, KY: October, 2009.

Millard, M., Hallett, K., van Leusen, P., & **Soylu, F**. (2009). *Online student course evaluation systems: Effective strategies and best practices*. Poster presentation at Association for Educational Communications and Technology (AECT) meeting, Louisville, KY: October, 2009.

Soylu, F. & Yalvac, B. (2009). *What does embodied cognition have to offer for science education?* Paper presented at European Science Education Research Association (ESERA) Conference, Istanbul: August, 2009.

Soylu, F. (2008). *Academics' views on and uses of Wikipedia*. Paper presented at 10th

International Conference on Education, Athens: May, 2008.

Soylu, F. (2008). *Application of design principles of Eksisozluk to online learning communities*. Paper presented at Harvard Graduate School of Education Student Research Conference, Cambridge, MA: March, 2008.

Soylu, F. (2008). *Academics' views on and uses of Wikipedia*. Paper presented at Harvard Graduate School of Education Student Research Conference, Cambridge, MA: March, 2008.

TEACHING EXPERIENCE

Indiana University, Bloomington, IN

2011	**Teaching Assistant -** P574 "Learning in New Media" (Online)
2010	**Teaching Assistant -** P540 "Learning and Cognition" (Online)
2010 - 2011	**Teaching Assistant -** P574 "Assessment in Education" (Online)
2007 - 2008	**Instructor** - R341 "Multimedia in Instructional Technology"
2008	**Instructor** - W450 "Internship in Instructional Computing"
2006 - 2007	**Instructor** - W201 "Beginning Technology Skills"
2006	**Teaching Assistant** - R521 "Instructional Design and Development"
2005	**Instructor** - W220 "Technical Issues in Educational Computing"

Middle East Technical University, Ankara

2003-2004	**Teaching Assistant** - IS100 "Introduction to Information Technologies"

TECHNICAL SKILLS

Programming/Scripting: Python, C++
Data Analysis / Management: SPSS**,** Matlab**,** Excel, SPM for fMRI data analysis
Operating Systems: Linux, Unix, Mac OSX, Windows

HONORS, AWARDS & FELLOWSHIPS

2010	Cognitive Science Summer Research Fellowship, Indiana University, Bloomington
2010	The University Graduate School Grant-in-Aid of Doctoral Research Fellowship, Indiana University, Bloomington
2010	Achasa Beechler Dissertation Award, Indiana University, Bloomington
2010	Graduate and Professional Student Organization (GPSO) Research Award, Indiana University, Bloomington
2009	IST A.V. Summer Fellowship, Indiana University, Bloomington
2009	Achasa Beechler Dissertation Proposal Award, Indiana University, Bloomington
2004	Research Council of Norway Foreign Exchange Fellowship
2000-2002	Turkish Education Association Undergraduate Scholarship
1998-2002	Turkish Ministry of Education Undergraduate Scholarship

CITIZENSHIP & PERMANENT RESIDENCY

- Citizenship: Turkey
- Permanent Residency: USA