

The Relation between Finger Gnosis and Mathematical Ability: Can we Attribute Function to Cortical Structure with Cross-Domain Modeling?

Marcie Penner-Wilger (Marcie.Penner-Wilger@fandm.edu)

Department of Psychology, Franklin & Marshall College, Lancaster, PA 17604 USA

Michael L. Anderson (michael.anderson@fandm.edu)

Department of Psychology, Franklin & Marshall College, Lancaster, PA 17604 USA

Institute for Advanced Computer Studies, University of Maryland, College Park, MD 20742 USA

Abstract

This paper details and applies a novel method for assigning function to local cortical structure. Imaging results from multiple cognitive domains were used to investigate what a shared neural substrate could be contributing to two apparently different domains: finger and number representation. We identified a region within the left precentral gyrus contributing to both tasks; identified, across several cognitive domains, other cognitive uses to which the ROI may have been put; and looked across these cognitive uses to ascertain the functional contribution of the ROI. The result of this process is a proposed local working—an array of pointers—that can be tested empirically and will allow for further elaboration of the redeployment view of the relation between finger and number representations. This work is significant for understanding the relationship between finger gnosis and math, and for introducing cross-domain modeling as a new empirical method.

Keywords: number representation; finger representation; neural substrate; exaptation; function-structure mapping; localization; cross-domain modeling.

The Redeployment View

Finger gnosis or “finger sense” (indexed by the ability to distinguish which fingers have been lightly touched without visual feedback) is related to math ability (Fayol, Barrouillet, & Marinthe, 1998; Noël, 2005; Penner-Wilger et al., 2007). In Penner-Wilger and Anderson (2008) we elaborated a novel hypothesis regarding the observed predictive relation between finger gnosis and mathematical ability. In brief, we suggested that these two cognitive capacities have overlapping neural substrates, as the result of the re-use (“redesign”) of part of the finger gnosis circuit for the purpose of representing number. On this *redesign view*, the neural circuitry shared between finger gnosis and number representation forms one part of the functional complex necessary for number representation. Along with the neural circuit shared with finger gnosis, additional neural circuits (with additional abstract functional capacities) are expected to combine in support of the capacity for number representation.

The crucial question that a shared neural circuit raises is: What is the shared circuit *doing* for the different functional complexes of which it is a part? What is the working of this circuit that allows it to support tasks in such apparently different cognitive domains?

In the framework we adopt here, *workings* represent low-level operations that are performed by small,

anatomically distinct brain areas (Bergeron, 2008). As such, workings are neither consciously available nor describable with higher-level psychological vocabulary. Therefore, in contrast to the current practice in cognitive neuroscience, workings should be described using domain-independent vocabulary. Here, we adopt a vocabulary drawn from information processing theory, although certainly other possibilities (e.g. dynamic systems theory) may turn out to be more appropriate to the task (Anderson, 2007a).

According to the Massive Redeployment Hypothesis (MRH; Anderson, 2010, 2007a,b) multiple workings, in concert, compose higher-level cognitive *uses*, and a typical brain area will contribute to many cognitive uses, across domains, but perform the same working across uses (Anderson, 2010). MRH straddles the middle ground between localization and holism in that, although parts of the brain are specialized (i.e., they always perform the same working), this specialization is at the lower-order level of cognitive workings (e.g., computations or transformations) rather than that of higher order cognitive uses. Anderson (2007a, p. 339) uses the analogy of “finding the right letter to go into a box on a (multidimensional) crossword puzzle” to describe the task of determining a shared cognitive working. Thus, knowing the many cognitive uses that a brain area supports will help to determine what that brain area does. Both Anderson (2010, 2007a,b) and Bergeron (2008) advocate for the determination of shared cognitive workings within and across domains as a method to advance our understanding of high-level cognition and to achieve the interdisciplinary goals of cognitive science.

The methodology of looking across domain boundaries to determine the working of a brain area is not common in cognitive neuroscience; activations are generally attributed to processes specific to the domain under investigation (Cabeza & Nyberg, 2000). Cabeza and Nyberg conclude, in a review of 275 imaging studies, “it would be useful to systematically compare functional neuroimaging data in different cognitive domains and to develop general theories that account for the involvement of brain regions in a variety of cognitive tasks” (Cabeza & Nyberg, 2000, p. 31). One such working was proposed by Hubbard et al. (2005): a computational transformation for spatial updating implemented within the parietal sulcus. This cognitive working is also thought to play a role in another cognitive use: shifting attention along the mental number line. It is hypothesized that the SNARC effect—

the finding that smaller numbers are responded to faster with the left hand and larger numbers with the right hand—arises as a result of this shared working.

Tettamanti and Weniger (2006) examined activation of Broca's area in a variety of cross-domain tasks with the purpose of determining the shared working. Though generally held to be a language area, responsible for phonological processing and language production, Broca's area is also activated in non-linguistic domains such as object manipulation, action perception, and music (Tettamanti & Weniger, 2006). The authors examined the existing imaging data, across domains, and concluded that the cognitive working of Broca's area "may be to process hierarchical structures in a wide range of functional domains" (p. 491). Such investigations illustrate how looking across domain boundaries for shared workings can help generate more specific proposals for those workings, as well as potentially contribute to a better understanding of the nature of high-level cognitive domains and their relations.

In Penner-Wilger and Anderson (2008), one possible shared working between finger and number representation was suggested—a register. A register is a representational form comprised of an ordered series of elements that can be independently activated. Different patterns of activation across the register reflect different representational content. The suggestion of a register, however, was based solely on the two domains of interest: finger and number. In the current paper, imaging results from multiple domains are used to more systematically investigate the shared working. The steps in this process were to (1) identify the brain area of interest; (2) identify, across domains, other cognitive uses that the area of interest supports; and (3) look across tasks and domains to ascertain the shared working of the area of interest. The final result of this process was a proposed shared working that can be tested empirically (e.g., via interference studies), and should generate a better, more accurate, and more fruitful description of our representation of number and its relation to other domains.

Identifying the Brain Region of Interest

The brain region of interest is taken from the PET study of Zago et al. (2001), who reported activation in the left precentral gyrus at the coordinates for finger representation during adults' performance of both single-digit and multi-digit multiplication. This same area within the left precentral gyrus was also activated during single-digit multiplication (Dehaene et al., 1996), single-digit addition (de Jong et al., 1996; Pesenti et al., 2000), number comparison (Dehaene et al., 1996; Pinel, Piazza, LeBihan & Dehaene, 2004), and symbolic and non-symbolic exact and approximate addition with dots (Venkatraman, Ansari & Chee, 2005). Thus, the selected ROI is activated across a range of numerical formats and tasks.

Zago et al. had four conditions: rest, read, retrieve, and compute. The read condition involved reading pairs of Arabic digits, which were composed of zeros and ones. The retrieve condition involved solving single-digit multiplication problems from 2×2 to 5×6 . The compute

condition involved solving two-digit by two-digit multiplication problems with a product less than 1000. Stimuli were presented visually and participants responded verbally.

The most relevant subtraction for the present purposes is the conjunction of compute and retrieve conditions minus the read condition, as number representations are accessed for both single and multi-digit arithmetic. The conjunction analysis isolates the common neural activation for the two arithmetic tasks over and above activation associated with the control (i.e., read) condition. The area of interest is significantly activated in all three comparisons. Thus, the ROI for investigation of the shared working between finger and number representation is taken to be within the left precentral gyrus centered on coordinates (-42, 0, 38) \pm 6 mm.

Identifying, Across Domains, Other Cognitive Uses that the Region of Interest Supports

Identification, across domains, of other cognitive uses that the ROI supports was accomplished using (1) existing neuroscience results of shared brain areas in number and finger representation from Step 1, and (2) the Action-Grounded Cognition Lab's (www.agcognition.org) database of post-subtraction activations for 2164 studies from 692 journal articles (Anderson, Brumbaugh, & Suben, 2010). All studies in the database were conducted with healthy adult participants. Areas of activation recorded in the database reflect greater neural activation in the noted region for a given condition compared to a baseline or other comparison as noted (i.e. post-subtraction activations as reported in the original papers).

The output of the database search included the following information for experiments reporting post-subtraction activation with a center inside the ROI within the left precentral gyrus: publication citation, domain (i.e., action, cognition, emotion, interoception, perception, etc.) and sub-domain (e.g., attention, language, memory, etc.) based on the BrainMap database classification system (Laird, Lancaster, & Fox, 2005), imaging method, Talairach coordinates and Brodmann area of each recorded activation, relative placement within the Brodmann area, and the subtraction used to generate the results (Anderson, Brumbaugh, & Suben, 2010). Finding that our region of interest was activated in tasks across domain boundaries would provide further support for MRH. Investigation of the output of the database search at the levels of domain, sub-domain, and the relevant tasks and subtractions used was necessary to guide and constrain identification of a proposed shared working.

Results. The results of the database search provided 65 studies and 80 subtractions showing post-subtraction activation within the region of interest in the left precentral gyrus. Of the subtractions, 11 were in the domain of action, 60 in cognition, 2 in emotion, and 7 in perception. Within the domain of action, four were in the sub-domain of execution, five in inhibition, and one in each of imagination and preparation. Within the domain of cognition, 20 were in the sub-domain of attention (including four in visual attention), 16 in language (one in

orthography, two in phonology, nine in semantics, and four in speech), 2 in mathematics, and 20 in memory (seven in explicit memory and ten in working memory) and one in each of time and theory of mind. Within the domain of perception, two were in audition, one in somesthesia, and four in vision. Thus, consistent with Anderson's (2010) MRH, the region of interest was involved in varied cognitive uses across domains.

Looking Across Cognitive Uses to Ascertain the Shared Working of the Region of Interest

Given the variety of domains, sub-domains, tasks, and subtractions that showed activation in our ROI within the left precentral gyrus, the challenge was to glean the underlying shared working. The output of such an endeavor should be a low-level cognitive working, described in domain-neutral vocabulary, which the different cognitive uses could plausibly benefit from incorporating.

The region of interest was activated in expected tasks including number comparison (Gobel et al., 2004; Liu et al., 2006) and mental representation of fingers (Kuhtz-Bushbeck et al., 2003; Jancke et al., 2000; Numminen et al., 2004), confirming that this area is involved in both cognitive uses. In examining the variety of cognitive uses that share common activation in the ROI, three additional themes emerged: generation (e.g., generate items in a given category), inhibition (e.g., incongruent Stroop condition, anti-saccade, response inhibition), and order (e.g., n-back task, performing memorized sequences of saccades, judging alphabetical or sequential order). Further examination of tasks within each theme was undertaken as a means to both guide and constrain the proposed shared working.

In nine papers (10 subtractions), generation tasks showed activation in the ROI. Increased activation was found when participants covertly generated words within a given category, compared to rest (Frankenstein, Richter, McIntyre, & Remy, 2001; Tremblay & Gracco, 2006) or compared to listing numbers (Pihlajamaki et al., 2000). Increased activation was found for generation of related verbs when participants were shown nouns, relative to fixation or rest (Drobyshevsky, Baumann & Schneider, 2006; Hamzei et al., 2001) and also found when participants produced verbs, compared to nouns, in the context of short phrases or sentences (Shapiro, Moo, & Caramazza, 2006). Increased activation was found for the generation of neutral words relative to emotional words (Cato et al., 2004). Thus, word generation is one cognitive use associated with our shared working of interest. Word generation requires, among other things, representation of the category of items to be generated, mapping between category and items, and some means of keeping track of items already generated.

In thirteen papers (16 subtractions), inhibition tasks showed activation in the ROI. Increased activation was found in task switching conditions compared to task repetition (Cools, Clark, & Robbins, 2004; Dove et al., 2000). Increased activation was also found in task switching, where the meaning of the cue switched,

compared to cue switching, where two cues indicated the same action (Brass & von Cramon, 2004) or to direct mapping between cue and task (Dassonville et al., 2001). Increased activation was found for the incongruent compared to neutral condition in Stroop paradigms (Liu et al., 2006; Norris et al., 2002). Increased activation was also found for antisaccades compared to controlled saccades or fixation—in the antisaccade task participants are required to direct their gaze to a mirror-symmetrical location in the opposite visual field of the target, requiring response inhibition (Chikazoe et al., 2007; Connolly et al., 2000) as well as for anti-pointing (Connolly et al., 2000). Thus, task switching/response inhibition is one cognitive use associated with our shared working of interest. Task switching requires, among other things, representation of the response sets (tasks) and some means of mapping cues to response sets.

In six papers (10 subtractions), order tasks showed activation in the ROI. Executing saccades to a sequence of memorized locations, compared to rest (Heide et al., 2001; Petit et al., 1996), correct hits in deciding whether the first and last letter of a word were in alphabetical order compared to misses (Henson et al., 2005), in an order-memory task following presentation of five letters compared to an item-memory task (Marshuetz et al., 2000), and in spatial and non-spatial n-back tests, where participants are asked to recall items presented n-items previously, compared to indicating which object changed luminance or recalling items presented 0-back (Owen et al., 1998; Ragland et al., 2002). Thus, storage and recall of order information is one cognitive use associated with our shared working of interest. Order tasks require, among other things, some means of representing information in an ordered form.

In summary, the cognitive uses for our ROI include: finger representation, number representation, category representation, task representation, and order representation. Note we are not claiming that this ROI is the *only* region that performs these various tasks, for instance that it plays some unique, unduplicated role in task switching. Rather, these are the various conditions under which we have observed increased activation in our ROI. Given the brain area of interest here, and the cognitive uses the area supports, our goal is to look across uses to see if it is possible to identify a shared working—some cognitive resource it provides that would account for its contribution to all these various tasks.

Proposal for a Shared Working

Given the shared uses from the database search, the specifications for a shared working are: that it allows for ordered storage of discrete representations and for mapping between representational forms. Does our initial proposal of a register (Penner-Wilger & Anderson, 2008) meet these updated requirements? A register does provide ordered storage (the reason for our initial proposal). A register, however, does not provide a means for mapping. One possibility is that our ROI performs storage and another shared region performs mapping, in which case a register would be a plausible shared working. Another

possibility is that our selected ROI did not pick out a small, anatomically-distinct brain area and, therefore, is large enough to encompass two or more workings, one of which could again plausibly be a register. The third possibility is that our ROI did successfully pick out a small, anatomically-distinct brain area that performs one working, but that this working is more complex than our original proposal and performs both the storage and the mapping. This final possibility is addressed for the duration of the paper.

One computational unit that could implement both the ordered storage and mapping requirements is an array of pointers. An array is an ordered group, meeting the requirements for ordered storage. A pointer is a data structure that designates a memory location and can indicate different data types. The added functionality in this proposed working comes not from the array, as our proposed register could easily have instead been described as an array, but from what the array contains. An array of pointers allows for storage and access of ordered elements, which are able to point to—or index—representations or locations in memory, allowing for mapping between different representational forms. Thus, an array of pointers would allow for the ordered storage of different types of information and would facilitate the mapping between representations.

In finger representation, an array of pointers could hold distinct ordered representations for each finger. In number representation, an array of pointers could hold representations of discrete numbers (not limited to values ≤ 10), ordered by magnitude, across different representational forms: non-symbolic and number words, numerals, etc. This structure could support number comparison, but also numerical estimation—as estimation involves translating between alternative representations. Imaging evidence shows the ROI is activated for both tasks. In generation tasks, an array of pointers could store category items and map from categories to items. In task switching, the array could point to the different task demands and map cues to response sets. In order tasks, as in number and finger representation, the array could store ordered information (e.g., alphabet, sequence of movements, etc.). Thus, each cognitive use could benefit from a shared working in the form of an array of pointers.

In summary, the results of the cross-domain investigation lead to further specification of the proposed shared working, from a register (Penner-Wilger & Anderson, 2008) to an array of pointers. The function of pointers is similar to one of the physical functions of the fingers. It would thus not be implausible to suppose that this basic function of the fingers was supported by a brain mechanism wherein representational content is determined by the object being indexed, rather than the state of the indicator per se. An array of pointers—one part of the functional complex supporting finger gnosis—would be a candidate for redeployment in any later-developing complex with functional elements able to take advantage of a component with this abstract functional structure. We suggest that the number representation complex did just that.

We should pause here to admit that if one were modeling the finger gnosis complex in isolation it is unlikely that an array of pointers implementation for one of its components would leap out as the obvious choice. One of the important general implications of MRH is that one should not model functional complexes in isolation, but should consider what other complexes may also be using the same neural substrates. The effect of this change in methodology is often to suggest novel decompositions (and candidate implementations) of cognitive functions. And yet this general suggestion of a pointer structure is not unpreceded or neurally implausible. In fact, such a structure is consistent with the semantic pointer architecture, a recent elaboration of the Neural Engineering Framework (Eliasmith & Anderson, 2003). According to this theory, some neural networks implement *semantic pointers*, composable neural representations with partial semantic content that play an important role in integrating information for higher-order cognition.

How can the same working, in this case an array of pointers, be used to support diverse types of representations across uses? For our proposed working, the representational power is associated both with the properties of the array, including (1) which ordered elements in the array are bound (i.e. pointing to or indexing something) and which are not (i.e., are free), and (2) the representational flexibility inherent in the structure of the array, as well as with the properties of the pointers, including (3) what the pointers are indexing (i.e., bound to). The full content of the representation depends on all three properties. Across different uses, tasks, and contexts, the same working can be used to represent vastly different content by altering any one of these properties of the array or pointers. This distinction is more broadly captured by the distinction between the representation itself and the representation consumer (Millikan, 1984). Depending on how the representation consumer is tuned, it might be sensitive to: whether there are bound elements, how many bound elements there are, the particular ordering of the bound elements (and there is great flexibility here, depending on how the order is exploited for content), the individual index content of the pointers, the overall unordered content, the overall ordered content.

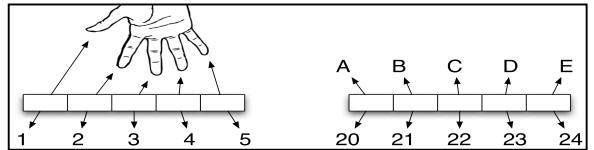


Figure 1: Illustration of array of pointers structure

The same working, an array of pointers, could support different forms of numerical representation (e.g., Arabic digits, number words, etc.). Doing so would require binding of the indexed content of the pointers to different locations. Other properties of the array, however, could remain constant. This rebinding would incur costs associated with switching the indexed location as well as reading the new value. As shown in Figure 1, this same

working could also support diverse representations such as fingers, items in a category, response sets, or an ordered list of spatial locations. Switching between item classes would again require binding of the indexed content of the pointers to different locations, but would also likely involve differences in the other properties of the array such as the number of elements in the array and number of bound elements. Precise modeling of the various steps involved in different sorts of task/representation switching will allow for specific reaction-time predictions in each case (e.g. which kinds of switching will take more, and which less time; and also how the time needed will change with variations in the number of items being tracked). We are exploring such properties, having built and currently testing a model of number representation using the novel candidate implementation described here in artificial spiking neurons based on the Neural Engineering Framework (Eliasmith & Anderson, 2003).

Conclusion

In conclusion, the relation between finger gnosis and math ability may be the result of redeployment of a neural substrate that supports both finger gnosis and the representation of number, along with a variety of other uses. Our current findings, based on the outlined cross-domain structure-function mapping methodology, suggest that the shared resource may be implementing an array of pointers. This shared working suggests a novel decomposition (and candidate implementation) of number representation. We hope that the methodology of investigating overlapping functional complexes rather than modeling in isolation will be a fruitful addition to the field of cognitive science, serving as a provisional model for a new, more integrative approach to functional localization.

References

Anderson, M.L. (2010). Neural reuse: A fundamental organizational principle of the brain. (Target article) *Behavioral and Brain Sciences*, 33(4): 245-66.

Anderson, M. L. (2007a). Massive redeployment, exaptation, and the functional integration of cognitive operations. *Synthese*, 159, 329-345.

Anderson, M. L. (2007b). Evolution of cognitive function via redeployment of brain areas. *The Neuroscientist*, 13, 13-21.

Anderson, M.L., Brumbaugh, J. & Suben, A. (2010). Investigating functional cooperation in the human brain using simple graph-theoretic methods. In W. Chaovallitwongse, P. Pardalos and P. Xanthopoulos, eds. (Eds.), *Computational Neuroscience*. Springer.

Bergeron, V. (2008). *Cognitive architecture and the brain: beyond domain-specific functional specification*. Unpublished doctoral dissertation, University of British Columbia, Vancouver, British Columbia, Canada.

Brass, M. & von Cramon, D. Y. (2004). Decomposing components of task preparation with functional magnetic resonance imaging. *Journal of Cognitive Neuroscience*, 16, 609-620.

Cabeza, R. & Nyberg, L. (2000). Imaging cognition II: An empirical review of 275 PET and fMRI studies. *Journal of Cognitive Neuroscience*, 12, 1 – 47.

Cato, M. A., Crosson, B., Gökçay, D., Soltsik, D., Wierenga, C., Gopinath, K., Himes, N., Belanger, H., Bauer, R.M., Fischler, I.S., Gonzalez-Rothi, L., & Briggs, R.W. (2004). Processing words with emotional connotation: an fMRI study of time course and laterality in rostral frontal and retrosplenial cortices. *Journal of Cognitive Neuroscience*, 16, 167-177.

Chikazoe, J., Konishi, S., Asari, T., Jimura, K., & Miyashita, Y. (2007). Activation of right inferior frontal gyrus during response inhibition across response modalities. *Journal of Cognitive Neuroscience*, 19, 69-80.

Connolly, J. D., Goodale, M. A., DeSouza, J. F., Menon, R. S., & Vilis, T. (2000). A comparison of frontoparietal fMRI activation during anti-saccades and anti-pointing. *Journal of Neurophysiology*, 64, 1645-1655.

Cools, R., Clark, L., & Robbins, T. W. (2004). Differential responses in human striatum and prefrontal cortex to changes in object and rule relevance. *Journal of Neuroscience*, 24, 1129-1135.

Dassonville, P., Lewis, S. M., Zhu, X. H., Ugurbil, K., Kim, S. G., & Ashe, J. (2001). The effect of stimulus-response compatibility on cortical motor activation. *NeuroImage*, 13, 1-14.

Dehaene, S., Tzourio, N., Frak, V., Raynaud, L., Cohen, L., Mehler, J., & Mazoyer, B. (1996). Cerebral activations during number multiplication and comparison: A PET study. *Neuropsychologia*, 34, 1097-1106.

de Jong, B. M., van Zomeren, A. H., Willemsen, A. T. M., & Paans, A. M. J. (1996). Brain activity related to serial cognitive performance resembles circuitry of higher order motor control. *Experimental Brain Research*, 109, 136 – 140.

Dove, A., Pollmann, S., Schubert, T., Wiggins, C. J., & von Cramon, D. (2000). Prefrontal cortex activation in task switching: An event-related fMRI study. *Cognitive Brain Research*, 9, 103-109.

Drobyshevsky, A., Baumann, S. B., & Schneider, W. (2006). A rapid fMRI task battery for mapping of visual, motor, cognitive, and emotional function. *NeuroImage*, 31, 732-744.

Eliasmith, C., & Anderson, C. H. (2003). *Neural engineering: Computation, representation, and dynamics in neurobiological systems*. Cambridge, MA: MIT Press.

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

Frankenstein, U. N., Richter, W., McIntyre, M. C., & Remy, F. (2001). Distraction modulates anterior cingulate gyrus activations during the cold pressor test. *NeuroImage*, 14, 827-836.

Göbel, S.M., Johansen-Berg, H., Behrens, T., & Rushworth, M. F. S. (2004). Response-selection-related

parietal activation during number comparison. *Journal of Cognitive Neuroscience*, 16, 1536-1551.

Hamzei, F., Rijntjes, M., Dettmers, C., Glauche, V., Weiller, C., & Buchel, C. (2003). The human action recognition system and its relationship to Broca's area: An fMRI study. *NeuroImage*, 19, 637-644.

Hanakawa, T., Honda, M., Sawamoto, N., Okada, T., Yonekura, Y., Fukuyama, H., & Shibasaki, H. (2002). The role of rostral Brodmann area 6 in mental-operation tasks: An integrative neuroimaging approach. *Cerebral Cortex*, 12, 1157-70.

Heide, W., Binkofski, F., Seitz, R. J., Posse, S., Nitschke, M. F., Freund, H. J., & Kompf, D. (2001). Activation of frontoparietal cortices during memorized triple-step sequences of saccadic eye movements: An fMRI study. *European Journal of Neuroscience*, 13, 1177-1189.

Henson, R.N.A., Hornberger, M., & Rugg, M.D. (2005). Further dissociating the process involved in recognition memory: An fMRI study. *Journal of Cognitive Neuroscience*, 17, 1058-1073.

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

Jancke, L., Loose, R., Lutz, K., Specht, K., & Shah, N. J. (2000). Cortical activations during paced finger-tapping applying visual and auditory pacing stimuli. *Cognitive Brain Research*, 10, 51-66.

Kuhtz-Buschbeck, J. P., Mahnkopf, C., Holzknecht, C., Siebner, H. R., 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, 3375-3387.

Laird, A.R., Lancaster, J.L., & Fox, P.T. (2005). BrainMap: The social evolution of a functional neuroimaging database. *Neuroinformatics* 3, 65-78.

Liu, X., Wang, H., Corbly, C. R., , Zhang, J., & Joseph, J. E. (2006). The involvement of the inferior parietal cortex in the numerical stroop effect and the distance effect in a two-digit number comparison task. *Journal of Cognitive Neuroscience*, 18, 1518-1530.

Marshuetz, C., Smith, E.E., Jonides, J., DeGutis, J., & Chenevert, T.L. (2000). Order information in working memory: fMRI Evidence for parietal and orefrontal mechanisms. *Journal of Cognitive Neuroscience*, 12: Supplement 2, 130-144.

Millikan, R. (1984). *The language of thought and other biological categories*. Cambridge, MA: MIT Press.

Noël, M.-P. (2005). Finger gnosis: A predictor of numerical abilities in children? *Child Neuropsychology*, 11, 413-430.

Norris, D. G., Zysset, S., Mildner, T., & Wiggins, C. J. (2002). An investigation of the value of spin-echo-based fMRI using a Stroop color-word matching task and EPI at 3 T. *NeuroImage*, 15, 719-726.

Numminen, J., Schurmann, M., Hiltunen, J., Joensuu, R., Jousmaki, V., Koskinen, S. K., Salmelin, R., & Hari, R. (2004). Cortical activation during a spatiotemporal tactile comparison task. *NeuroImage*, 22, 815-821.

Owen, A. M., Stern, C. E., Look, R. B., Tracey, I., Rosen, B. R., & Petrides, M. (1998). Functional organization of spatial and nonspatial working memory processing within the human lateral frontal cortex. *Proceedings of the National Academy of Sciences*.

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. In B.C. Love, K. McRae & V.M. Sloutsky (Eds.), *Proceedings of the 30th Annual Cognitive Science Society* (pp. 1647-1652). Austin, TX: Cognitive Science Society.

Penner-Wilger, M., Fast, L., LeFevre, J., Smith-Chant, B. L., Skwarchuk, S., Kamawar, D., & Bisanz, J. (2007). The foundations of numeracy: Subitizing, finger gnosis, and fine-motor ability. In D. S. McNamara & J. G. Trafton (Eds.), *Proceedings of the 29th Annual Cognitive Science Society* (pp. 1385-1390). Austin, TX: Cognitive Science Society.

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

Petit, L., Orssaud, C., Tzourio-Mazoyer, N., Crivello, F., Berthoz, A., & Mazoyer, B. (1996). Functional anatomy of a prelearned sequence of horizontal saccades in humans. *Journal of Neuroscience*, 16, 3714-3726.

Pihlajamaki, M., Tanila, H., Hanninen, T., Kononen, M., Laakso, M., Partanen, K., Soininen, H., & Aronen, H. J. (2000). Verbal fluency activates the left medial temporal lobe: A functional magnetic resonance imaging study. *Annals of Neurology*, 47, 470-476.

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

Ragland, J. D., Turetsky, B. I., Gur, R. C., Gunning-Dixon, F., Turner, T., Schroeder, L., Chan, R., & Gur, R. E. (2002). Working memory for complex figures: An fMRI comparison of letter and fractal n-back tasks. *Neuropsychology*, 16, 370-379.

Shapiro, K. A., Moo, L. R., & Caramazza, A. (2006). Cortical signatures of noun and verb production. *Proceedings of the National Academy of Sciences*, 103, 1644-1649.

Tettamanti, M. & & Weniger, D. (2006). Broca's area: a supramodal hierarchical processor? *Cortex*, 42, 491 – 494.

Tremblay, P., & Gracco, V. L. (2006). Contribution of the frontal lobe to externally and internally specified verbal responses: fMRI evidence. *NeuroImage*, 33, 947-957.

Venkatraman, V., Ansari, D., & Chee, M.W.L. (2005). Neural correlates of symbolic and non-symbolic arithmetic, *Neuropsychologia*, 43, 744-53.

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