

DRAFT: This essay offers an informal account of neural reuse and some speculations regarding its relation to developmental homology. It is intended to facilitate discussion at the Workshop on Developmental Homology, and should not be cited or otherwise distributed.

## Neural reuse in the evolution and development of the brain

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In this paper I'll lay out some of the evidence for the importance of neural reuse—the reuse of existing (inherited and/or early-developing) neural circuitry for multiple behavioral purposes—in defining the functional structure of the brain. Given the theme of the workshop I will try to cast some of these findings using the language of homology. At the workshop, I am hoping we can reflect on some of the opportunities and potential pitfalls represented by utilizing this concept in the context of brain evolution and development.

Perhaps the best way to begin is with a brief introduction to my general perspective: I come from the embodied/embedded school of cognitive science, and so have long been especially interested in understanding the ways in which thinking is both influenced and partially constituted by emotional and physical states, bodily activity, and interactions between self, others and environment (Ackerman, Nocera & Bargh 2010; Chandler & Schwarz 2009; Chemero 2009; Kelso 1995; Lee & Schwarz 2010; Varela, Thompson & Rosch 1990). Or, to put the matter differently, I have long been interested in the understanding the nature of the cognitive system in light of research on embodiment.

Thus, when I began to investigate the neural underpinnings of cognition, I was naturally primed to place greater weight on the functional relations and interactions *between* neural structures than on the actions of individual regions. Moreover, given the evidence for the importance of action and environmental interaction to various kinds of cognitive processes, I tended to be suspicious of the modularity assumption that dominates much of cognitive science, and especially evolutionary psychology. Functionally isolated and dedicated neural modules just didn't seem to make good design sense given the importance of ongoing interactions to shaping function.

Interestingly, it is in part because embodied cognitive science (ECS) shares some fundamental assumptions with evolutionary psychology (EvoPsy) that it parts company with the dominant strain in EvoPsy on the topics of faculty psychology and modularity. A long-standing guiding principle of both ECS and EvoPsy is that cognition was built within a system primarily fitted to situated action. The central nervous system—the neocortex most definitely included—is first and foremost a control system for an organism whose main job is managing the myriad challenges posed by its environment. “Higher” cognitive faculties like language and abstract reasoning had to find their neural niche within the constraints imposed (and the opportunities offered) by the way existing neural resources were deployed for this purpose, in a way mediated and guided by whatever continuing selection pressure there is to maintain fast, effective and efficient solutions to pressing environmental challenges. Insofar as this is true, then—and this is the other guiding principle shared between EvoPsy and ECS—this phylogenetic history should have left detectable traces on both brain and behavior. Where EvoPsy and ECS part company is in their understanding of what those traces will look like, and where to find them. In particular, ECS operates on the fundamental assumption that resource constraints and efficiency

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considerations dictate that whenever possible neural, behavioral and even environmental resources should have been reused and redeployed in support of any newly emerging cognitive capacities. Cognition, that is, is largely supported by “old wheels, springs and pulleys only slightly altered” and reconfigured to serve present purposes.

A logical place to look for evidence of such a history is in the distribution of and relationships between the neural circuits supporting various cognitive functions. ECS predicts that neural circuits originally evolved for one purpose will be reused in later developing functionality. And indeed there has been a long history of experimental work demonstrating exactly this. There is, for example, ample evidence that verb retrieval tasks activate brain areas involved in motor control functions, and naming colors and animals (that is, processing nouns) activates brain regions associated with visual processing (Damasio & Tranel, 1993; Damasio et al., 1996; Martin et al., 1995; 1996; 2000; Pulvermuller, 2005). Similarly, it appears that perceiving manipulable artifacts, or even just seeing their names, activates brain regions that are also activated by grasping (Chao & Martin, 2000). And there are myriad demonstrations of interactions between language and motor control more generally, perhaps most striking the recent findings that manipulating objects can improve reading comprehension in school-age children (Glenberg et al., 2007).

Demonstrations of the use of perceptual and motor circuits in higher order cognition are not limited to language. Casasanto and Dijkstra (2010) describe bidirectional influence between motor control and autobiographical memory; Casasanto and Boroditsky (2008) suggest that our mental representations of time are built upon the foundations of our experience with space; Dagher et al. (1999) demonstrate that abstract planning can activate motor areas even when the task to be planned itself involves no motor activity; and several studies have found evidence for the involvement of hand motor circuits in number processing (Andres et al., 2007; Roux et al., 2003; Rusconi et al., 2005; Zago et al., 2001).

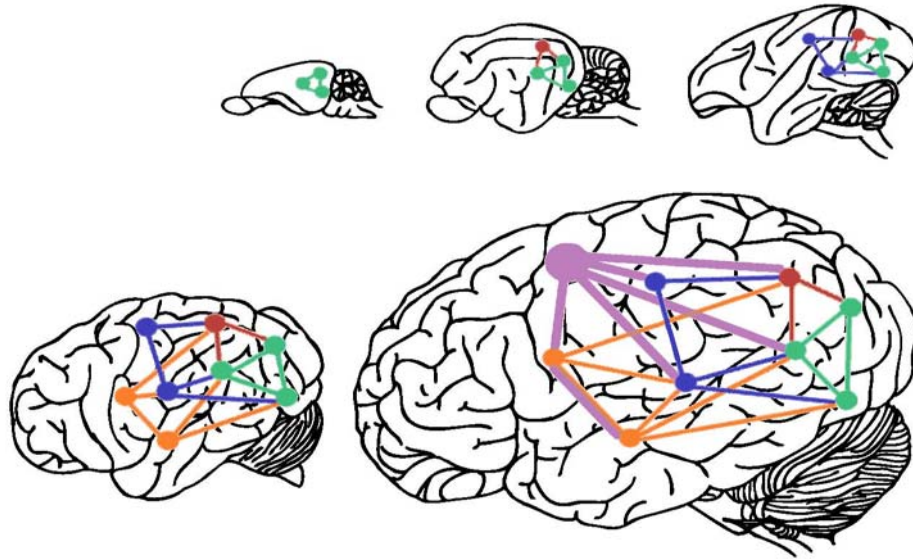
This kind of evidence certainly seems to suggest that rather than an evolutionary pathway wherein we developed specialized, dedicated neural hardware to meet each new environmental/behavioral challenge, instead much local neural structure is conserved (think of neural homologues like ocular dominance columns and orientation-preference pinwheels), but is often combined and recombined by different organisms in different ways to achieve diverse purposes.

Might there be a way to explore this possibility in a more systematic way?

Consider figure 1, which illustrates this concept abstractly (and using an incorrect lineage—my apologies, but these were the only brain pictures I was able to find on the internet!). Suppose an organism in our evolutionary lineage developed the neural circuitry (shown in green) to support a perceptual-cognitive ability such as shape discrimination. That shape circuit might be conserved in a descendant, but some of its elements (re-)combined in a novel way (red circuit) to support some different function, maybe detection of animacy. If this process repeats over evolutionary time, the end result in the case of our brains should be a functional structure wherein there is much conserved local structure, but those local structures will interact with different neural partners in different

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circumstances to support a diverse behavioral repertoire. Such a picture is rather different from the one put forth in most evolutionary psychology.



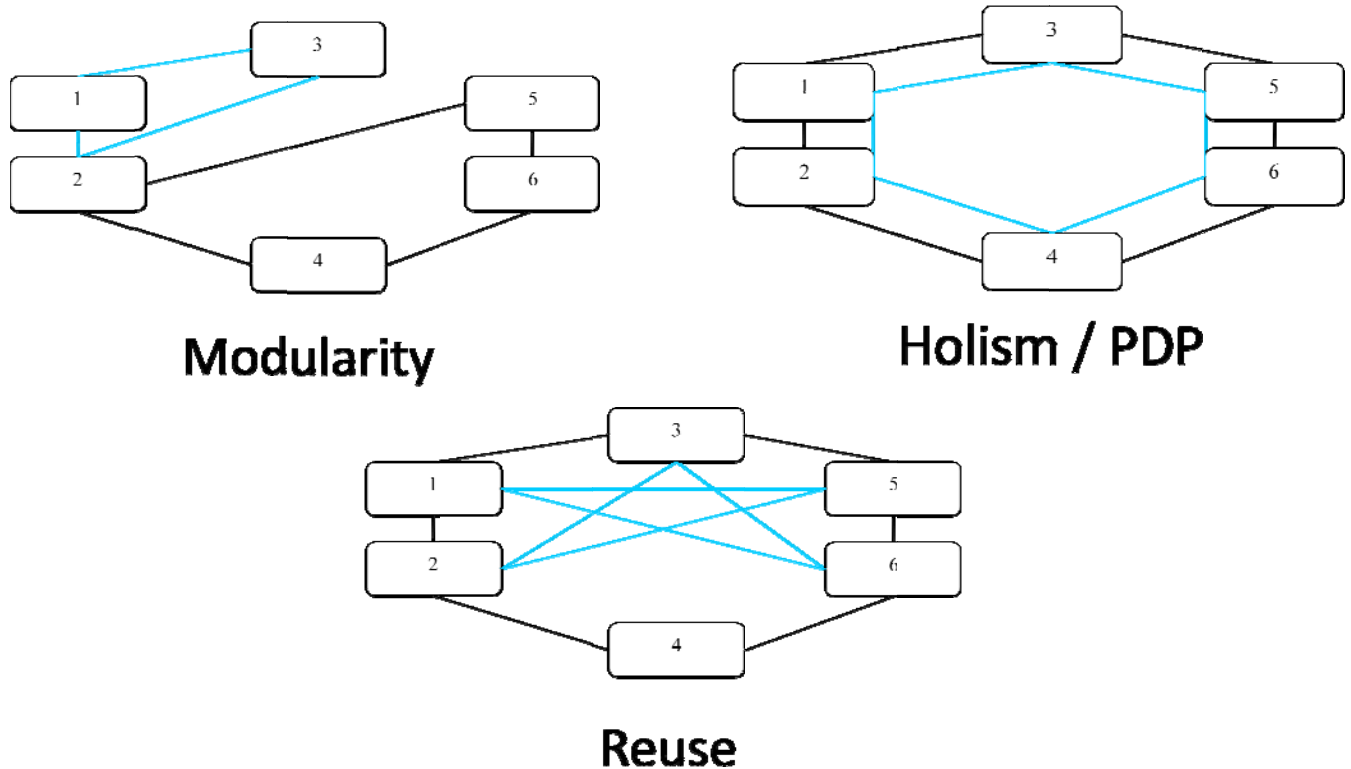
**Figure 1: Abstract ( and phylogenetically incorrect) evolutionary pathway showing conserved structure and recombination of elements**

Is there evidence that our brains are indeed like this? Imagine a simple brain consisting of six local neural circuits that could be combined in various ways to support two cognitive-behavioral tasks. Figure 2 illustrates three logical possibilities for how the local neural circuits could be functionally arranged to support the tasks in question. In a modular brain, local circuits 1, 2, and 3 would combine to support one task (blue), and 2, 4, 5, 6 would work together to support the other. Although there might be \*some\* neural and functional overlap between the modules (local circuit 2 active in supporting both tasks), the neural underpinnings of different behaviors and abilities would be largely segregated. In contrast, if the brain is more holistically organized, all the local circuits might be engaged in supporting both tasks, with the behavioral differences possibly reflected in such things as different oscillatory dynamics. Finally, it could be the case that many of the local circuits are used to support both tasks, but for each task, they cooperate in different patterns, with different partners.

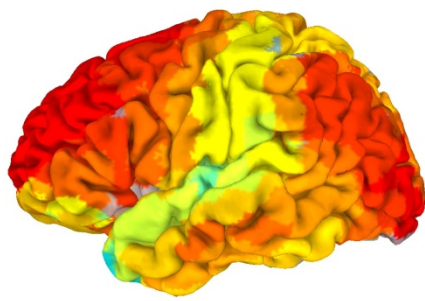
If this last possibility—which represents an especially pure form of neural reuse—obtains in the brain, then we should expect at least three things to be true of its functional structure. First, local neural circuits should be used and reused for diverse purposes in various task domains. That is, local circuits should not be classically selective. Second, we should expect the functional differences between task domains to be reflected less in differences in what neural real estate is implicated in supporting these domains than in the different patterns of interaction between many of the same elements. And third, we should expect later emerging (evolving or developing) behaviors/abilities to be supported by a

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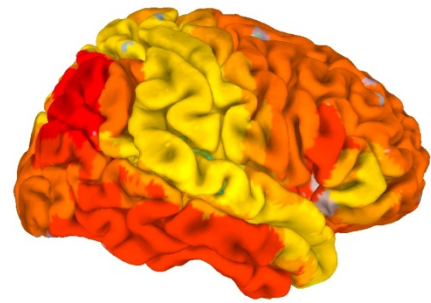
greater number of local circuits, more broadly scattered in the brain. The reason is simple: the later something emerges, the more potentially useful existing circuitry there will be, and little reason to suppose it will be grouped locally.



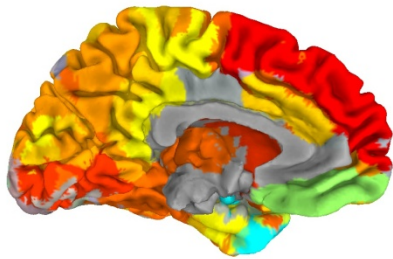
To make a potentially long story short, I have found evidence for all three of these predictions, by performing various sorts of meta-analyses of hundreds of neuroimaging studies. For instance, in one recent study (Anderson & Pessoa 2011), we examined the functional diversity of 78 standard anatomical regions of the brain (based on the Freesurfer atlas) by determining whether (and how often) each was active in 1,138 neuroimaging experiments in 11 different task domains (e.g. attention, working memory, semantics, etc.). Using a diversity scale ranging from 0 (active on only a single cognitive domain) to 1 (equally active across all 11 cognitive domains), we found that the overall average diversity of the 78 large anatomical regions was 0.70 (SD 0.12). The overall average diversity of cortical regions was 0.71 (SD 0.11) and of subcortical was 0.63 (SD 0.17). These results are represented graphically in figure 3 using a cool-to-hot scale. We also repeated the analysis after dividing the brain into 1,054 neural regions. The overall average diversity of the 574 small cortical and 21 small subcortical regions activated by 5 or more experiments was 0.52 (SD 0.13). (Those 595 regions were activated by an average of 10.67 experiments across ~5 cognitive domains.) The overall average diversity of the cortical regions was 0.52 (SD 0.13) and of the subcortical regions was 0.59 (SD 0.12). The upshot: local neural circuits are not highly selective, and typically contribute to multiple tasks across domain boundaries.



Left lateral

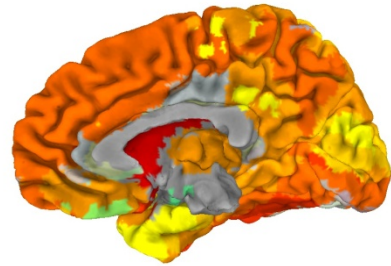


Right lateral

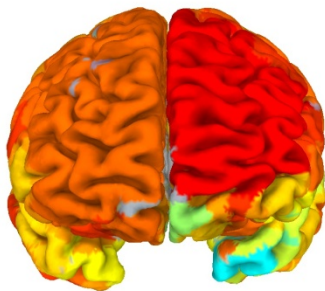


Left medial

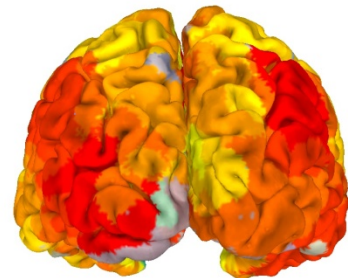
	0.89 - 0.84
	0.84 - 0.80
	0.80 - 0.75
	0.75 - 0.70
	0.70 - 0.66
	0.66 - 0.61
	0.61 - 0.56
	0.56 - 0.52
	0.52 - 0.47
	0.47 - 0.42
	0.42 - 0.37
	0.37 - 0.33
	0.33 - 0.28
	0.28 - 0.23
	0.23 - 0.19
	0.19 - 0.14
	0.14 - 0.09
	0.09 - 0.05
	0.05 - 0.00



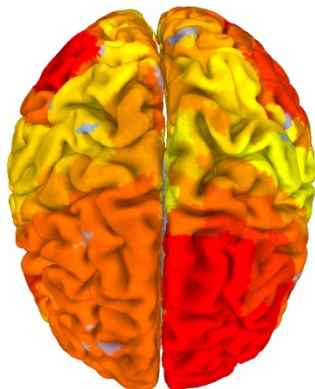
Right medial



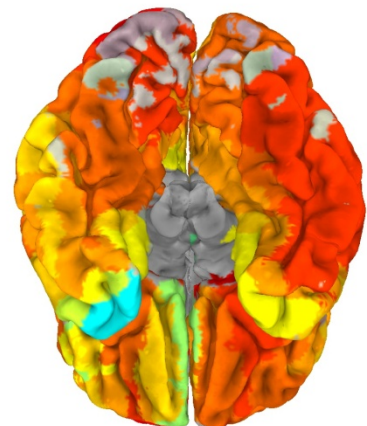
Frontal



Caudal



Dorsal



Ventral

Figure 3: Depiction of the diversity of activations for large anatomical regions. Grey indicates no information. Image prepared by Josh Kinnison and Srikanth Padmala, Indiana University.

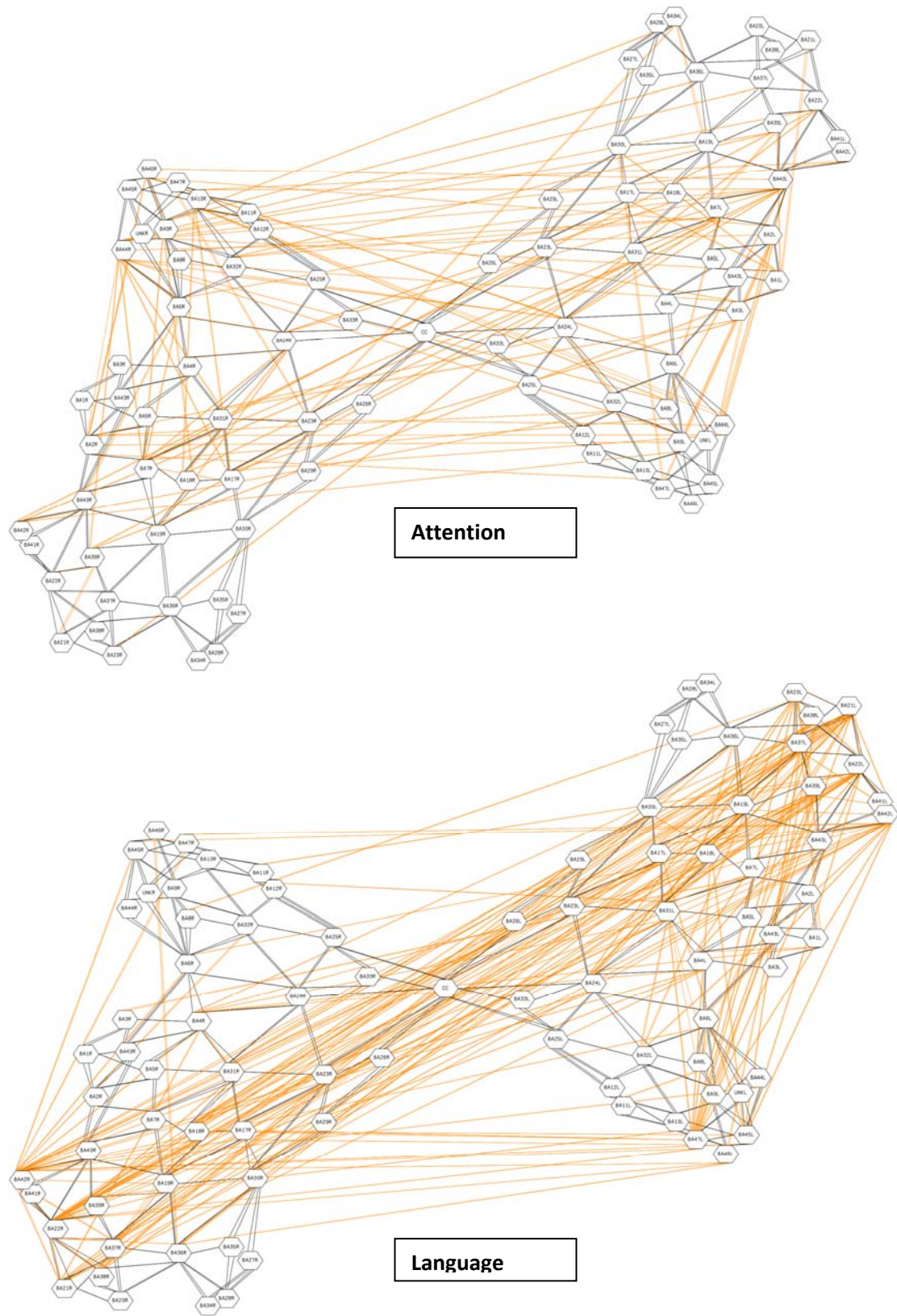


Figure 4: Showing the functional connections (orange lines) between regions (black hexagons) in two cognitive domains. Black lines indicate regions are adjacent in the brain.

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To examine the second prediction, I performed a functional connectivity analysis of 472 experiments in eight cognitive domains (Anderson, 2008—my database of imaging studies was smaller then). In a functional connectivity analysis, one looks to see how often regions of the brain co-activate under various tasks conditions. If the regions coactivate more often than would be expected given the activation profiles of the individual regions, then this indicates there is a “functional connection” between the regions. The results of such a study can be represented as a graph (see Figure 4). Looking at the data in this format, it is easy to compare how often a given region is active in more than one domain, and how often it has the same neural partners in more than one domain. The results show that while individual neural regions are active in supporting multiple tasks in different domains, they rarely share the same functional partners across domains.

Finally, as (Anderson, 2010a, 2008, 2007b) report, it appears that later developing functions like language are supported by more local circuits, more broadly distributed in the brain, than are early developing domains like visual perception and attention.

Taken together, this evidence seems to favor a reuse model over both modularity and holism. However, it is worth noting—and this is especially salient in the context of this workshop—my data do not distinguish between an evolutionary account, and a developmental one. That is, the evidence I have gathered paints a picture of the functional structure of the adult brain as emerging from a process of neural reuse, but it does not (cannot) say whether that process took place over evolutionary or developmental time, or both. I don’t think we should argue over this question in the absence of data (if we should argue about it at all—as Lickliter & Honeycutt (2003) point out, these influences are difficult if not impossible to disentangle), but rather think about the opportunities for analysis this process offers, whatever the timescale of its operation.

As I have (briefly) noted above, if this process takes place over evolutionary time, we should expect to see cross-species homologues, as structure inherited from a shared ancestor is put to different cognitive uses in different organisms (Katz, 2010). Additionally, as Moore & Moore (2010) suggest, “[b]ecause two or more psychological characteristics present at a given point in development might both (re)use neural circuits formed much earlier in development, thinking about such characteristics in terms of developmental homology could well illuminate their relationship to each other (as well as to other psychological characteristics present earlier in development that also depend on these circuits).”

That sounds right to me. To mention only one example: because finger gnosis (finger awareness) and our number sense (e.g. magnitude representation) share a local circuit (Penner-Wilger & Anderson, 2011), they are developmentally correlated, and share some interesting functional features. For instance, just as it is easier to differentiate between numbers when they differ greatly (3 vs. 4 is harder than 1 vs. 9), so it is easier to distinguish which fingers have been touched if they are further away on the hand. Moreover, such a developmental perspective potentially sheds light on order effects in learning, and on the nature and importance of critical periods—especially when (re-)understood in light of the concept of “burden” (Riedel 1978; Wagner, 1999): the more multiply integrated a circuit becomes, the more difficult to change its local character without affecting many different functions.

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Reuse, then, should place specific, detectable constraints on development that can be investigated observationally in humans, and experimentally in animals. Identifying both cross-species and developmental homologies potentially offers both conceptual and experimental leverage for advancing our understanding of the brain.

## **Bibliography**

- Ackerman, J. M., Nocera, C.C., & Bargh, J.A. (2010). Incidental haptic sensations influence social judgments. *Science*, 328, 1712-1715
- Anderson, M.L. (2010a). Neural reuse: A fundamental organizational principle of the brain. (Target article) *Behavioral and Brain Sciences*, 33(4): 245-66.
- Anderson, M.L. (2010b). Cortex in context: Reply to commentaries. *Behavioral and Brain Sciences*, 33(4): 294-313.
- Anderson, M.L. (2008). Circuit sharing and the implementation of intelligent systems. *Connection Science*, 20(4): 239-51.
- Anderson, M.L. (2007a). Massive redeployment, exaptation, and the functional integration of cognitive operations. *Synthese*, 159(3): 329-345.
- Anderson, M.L. (2007b). Evolution of cognitive function via redeployment of brain areas. *The Neuroscientist*, 13(1): 13-21.
- Anderson, M.L. (2007c). The massive redeployment hypothesis and the functional topography of the brain. *Philosophical Psychology*, 21(2): 143-174.
- Anderson, M. L. & Pessoa, L. (2011). Quantifying the diversity of neural activations in individual brain. In L. Carlson, C. Hölscher, & T. Shipley (Eds.), *Proceedings of the 33rd Annual Conference of the Cognitive Science Society* (oral presentation). Austin, TX: Cognitive Science Society.
- Andres, M., Seron, X. & Oliver, E. (2007) Contribution of hand motor circuits to counting. *Journal of Cognitive Neuroscience*, 19, 563–76.
- Cardinali, L., Frassinetti, F., Brozzoli, C., Urquizar, C., Roy, A., and Farne, A. (2008). Tool use induces morphological updating of the body schema. *Current Biology*, 19, 478-479.
- Casasanto, D. & Boroditsky, L. (2008) Time in the mind: Using space to think about time. *Cognition*, 106, 579–93.
- Casasanto, D. & Dijkstra, K. (2010) Motor action and emotional memory. *Cognition*, 115, 179-185.



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Chandler, J. & Schwarz, N. (2009). How extending your middle finger affects your perception of others: Learned movements influence concept accessibility. *Journal of Experimental Social Psychology*, 45, 123-128.

Chao L. L. & Martin A. (2000) Representation of manipulable man-made objects in the dorsal stream. *Neuroimage*, 12, 478–84.

Chemero, A. (2009). *Radical Embodied Cognitive Science*. MIT Press.

Clark, A. & Chalmers, D. (1998). The extended mind. *Analysis*, 58, 7-19.

Dagher, A., Owen, A., Boecker, H. & Brooks, D. (1999) Mapping the network for planning. *Brain*, 122, 1973–87.

Damasio, A. & Tranel, D. (1993) Nouns and verbs are retrieved with differently distributed neural systems. *Proceedings of the National Academy of Sciences, USA* 90:4957–60.

Damasio, H., Grabowski, T. J., Tranel, D., Hichwa, R. D. & Damasio, A. R. (1996) A neural basis for lexical retrieval. *Nature*, 380, 499–505.

Glenberg, A. M., Brown, M. & Levin, J. R. (2007) Enhancing comprehension in small reading groups using a manipulation strategy. *Contemporary Educational Psychology*, 32, 389–99.

Glenberg, A. & Kaschak, M. (2002). Grounding language in action, *Psychonomic Bulletin and Review*, 9, 558–565.

Katz, P. (2010). Comparative studies provide evidence for neural reuse. *Neural reuse: A fundamental organizational principle of the brain. Behavioral and Brain Sciences*, 33(4): 278-9.

Kelso, J. A. S. (1995). *Dynamic patterns: The self-organization of brain and behavior*. Cambridge, Mass.: MIT Press.

Lakoff, G. & Johnson, M. (1999). *Philosophy in the Flesh: The Embodied Mind and Its Challenge to Western Thought*. Basic Books.

Lickliter, P. & Honeycutt, H. (2003) Developmental dynamics: Toward a biologically plausible evolutionary psychology. *Psychological Bulletin*, 129(6): 819-35.

Martin, A., Haxby, J. V., Lalonde, F. M., Wiggs, C. L. & Ungerleider, L. G. (1995) Discrete cortical regions associated with knowledge of color and knowledge of action. *Science*, 270, 102–105.

Martin, A., Ungerleider, L. G. & Haxby, J. V. (2000) Category-specificity and the brain: the sensorymotor model of semantic representations of objects. In: *The new cognitive neurosciences*, 2nd edition, ed. M. S. Gazzaniga, pp. 1023–36. MIT Press.

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Martin, A., Wiggs, C. L., Ungerleider, L. G. & Haxby, J. V. (1996) Neural correlates of category-specific knowledge. *Nature*, 379, 649–52.

Moore, D. & Moore, C. (2010). Neural reuse as a source of developmental homology. *Behavioral and Brain Sciences*, 33(4): 284-5.

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? In L. Carlson, C. Hölscher, & T. Shipley (Eds.), *Proceedings of the 33rd Annual Conference of the Cognitive Science Society* (oral presentation). Austin, TX: Cognitive Science Society.

Pulvermüller, F. (2005) Brain mechanisms linking language and action. *Nature Reviews Neuroscience*, 6, 576–82.

Riedl, R. (1978) *Order in living organisms*. John Wiley & Sons, New York.

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, 716–27.

Rusconi, E., Walsh, V. & Butterworth, B. (2005) Dexterity with numbers: rTMS over left angular gyrus disrupts finger gnosis and number processing. *Neuropsychologia*, 43, 1609–24.

Wagner, G.P. (1999) A research program for testing the biological homology concept. In G. Bock and G. Cardew (eds.) *Homology* (Novartis Foundations Symposium 222), pp. 125-34. Wiley, Chichester.

Zago, L., Pesenti, M., Mellet, E., Crivello, F., Mazoyer, B. & Tzourio-Mazoyer, N. (2001) Neural correlates of simple and complex mental calculation. *NeuroImage* 13, 314–27.