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Neural Reuse in the Evolution and Development of the Brain: Evidence for Developmental Homology?

ABSTRACT: This article lays out some of the empirical 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 overall functional structure of the brain. We then discuss in some detail one particular instance of such reuse: the involvement of a local neural circuit in finger awareness, number representation, and other diverse functions. Finally, we consider whether and how the notion of a developmental homology can help us understand the relationships between the cognitive functions that develop out of shared neural supports. © 2012 Wiley Periodicals, Inc. *Dev Psychobiol* 55: 42–51, 2013.

Keywords: brain imaging; plasticity; evolution

INTRODUCTION

How are neural resources deployed to support cognitive functioning in the adult organism, and how does that architecture come about? That is, what evolutionary and developmental pathways does the brain follow in acquiring its repertoire of capacities? Consider two possible options, one that has been largely identified with the embodied/embedded school of cognitive science, and another associated with evolutionary psychology.

A long-standing guiding principle of both embodied cognitive science (ECS) and evolutionary psychology (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 (Dehaene, 2011) 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, EvoPsy has adopted a methodological focus on the challenges posed by the environment of selection (Buss, 2005), which has in turn led many researchers in this area to spotlight the efficiency of individual algorithmic and heuristic *solutions* to those problems. One result of this focus had been the development of the “adaptive toolbox” model of mind (Gigerenzer & Selten, 2002). Given the presumed pressures on these tools of mind for immediate and efficient operation, independent, modular neural implementations of these tools seem a sensible solution.

In contrast, ECS is 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,

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others and environment (Ackerman, Nocera, & Bargh, 2010; Chandler & Schwarz, 2009; Chemero, 2009; Kelso, 1995; Lee & Schwarz, 2010; Varela, Thompson, & Rosch, 1990). When considering the neural supports for cognition, this perspective naturally places greater weight on the functional relations and interactions *between* neural structures than on the actions of individual regions. Moreover, this perspective has led ECS to focus less on the efficiency of individual solutions, and more on overall efficiency in the use of bodily (and environmental and social) *resources* for cognitive ends. For ECS, resource constraints and efficiency considerations dictate that whenever possible neural, behavioral, and environmental resources should have been reused and redeployed in support of any newly emerging cognitive capacities. Functionally isolated and dedicated neural modules just do not seem to make good design sense given the importance of efficient use of available resources, and of ongoing interactions to shaping function. For ECS, cognition 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 or developed for one purpose will be reused in later emerging functionality. That is, rather than following an evolutionary/developmental pathway wherein we develop specialized, dedicated neural hardware to meet each new environmental/behavioral challenge, ECS suggests that much local neural structure is conserved but is often combined and recombined by different organisms in different ways to achieve diverse purposes.

Imagine a simple brain consisting of six local neural circuits that could be combined in various ways to

support two cognitive-behavioral tasks. Figure 1 illustrates three logical possibilities for how the local neural circuits could be functionally arranged to support the tasks in question. In a modular brain, shown in Figure 1a, local circuits 1, 2, and 3 would combine to support one task (represented using broken gray lines), and 2, 4, 5, 6 would work together to support the other (represented with black lines). 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. So for instance, in Figure 1c, local circuit 1 cooperates with local circuits 2 and 3 in the black task and with local circuits 5 and 6 in the gray task.

If such reuse (an especially pure case of which is illustrated in Fig. 1c) 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, in contrast to what is illustrated by Figure 1a, local circuits should not be classically selective in the sense of responding only to a highly restricted class of stimuli or tasks. 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 the domains than in the different patterns of interaction between many of the same elements (in contrast to the brain illustrated in Fig. 1b). And third, we should expect later emerging (evolving

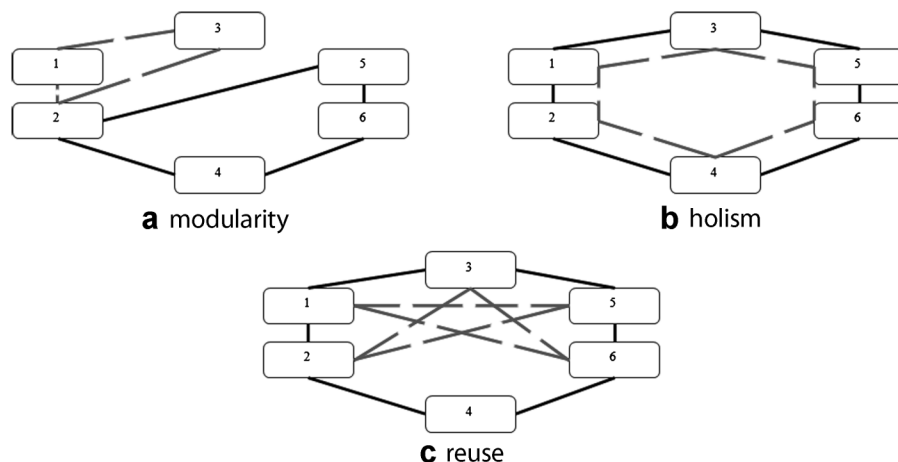


FIGURE 1 Three logical possibilities for the functional structure of the brain.

or developing) behaviors/abilities to be supported by a 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. There is in fact evidence for all three of these predictions, some of which will be recounted, below.

Taking up the first prediction, one recent study (Anderson & Pessoa, 2011) 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 experimental tasks in 11 different BrainMap task domains: action execution; action observation; action inhibition; attention; audition; vision; emotion; language semantics; reasoning; explicit (semantic) memory; and working memory (Fox et al., 2005). Using a diversity scale ranging from 0 (active in only a single cognitive domain) to 1 (equally active across all 11 cognitive domains), it was determined that the overall average diversity of the 78 large anatomical regions was .70 (*SD* .12). The overall average diversity of cortical regions was .71 (*SD* .11) and of subcortical regions was .63 (*SD* .17). Put differently, the regions were active in an average of 95 tasks spread across 9 cognitive domains. These results are represented graphically in Figure 2 using a cool-to-hot scale (gray indicates no information).

The analysis was also performed in a brain divided 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 .52 (*SD* .13). Those 595 regions were activated by an average of more than 10 experiments across 5 cognitive domains. The overall average diversity of the cortical regions was .52 (*SD* .13) and of the subcortical regions was .59 (*SD* .12). The upshot: local neural circuits are not highly selective, and typically contribute to multiple tasks across domain boundaries.

To examine the second prediction, we performed a functional coactivation analysis of 1,127 experimental tasks from the dataset (Anderson, Brumbaugh, & Suben, 2010), falling into 10 of the BrainMap task domains (Fox et al., 2005; for this study we excluded action inhibition, as it contained too few experiments for this approach). In a functional connectivity analysis, one looks to see how often regions of the brain co-activate under various tasks conditions. If the regions co-activate more often than would be expected given the activation likelihood of the individual regions—that is, if the probability of region A and region B being active in the same task is significantly ($p < .01$) higher than would be predicted from the general probability of A being active and the general probability of B being active—then this indicates there is a “functional connection” between the regions.

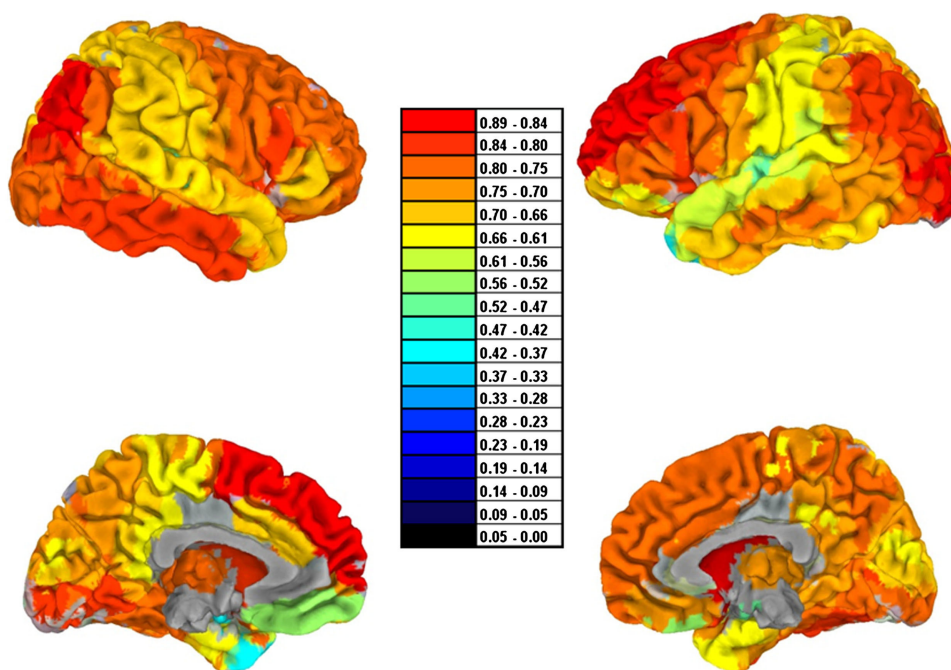


FIGURE 2 Task diversity of brain regions. Image prepared by Josh Kinnison and Srikanth Padmala, University of Maryland.

The results of such a study can be represented as a graph. A graph is simply a set of “nodes” joined by “edges,” where the nodes and edges can represent various aspects of a modeled system. For instance, in an airline route map nodes are airports and edges represent flights between them, and in a Facebook-style social network nodes are people and edges indicate “friendship.” In a brain functional network like that depicted in Figure 3, the nodes represent individual brain regions, plotted in a 3D anatomical space, and

the edges represent functional connections between them—that is, a higher-than-expected likelihood of co-activation during tasks in a given cognitive domain. 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.

Figure 3 highlights the functional partners of left precentral gyrus (the functional roles of which will be discussed further below) during semantics tasks,

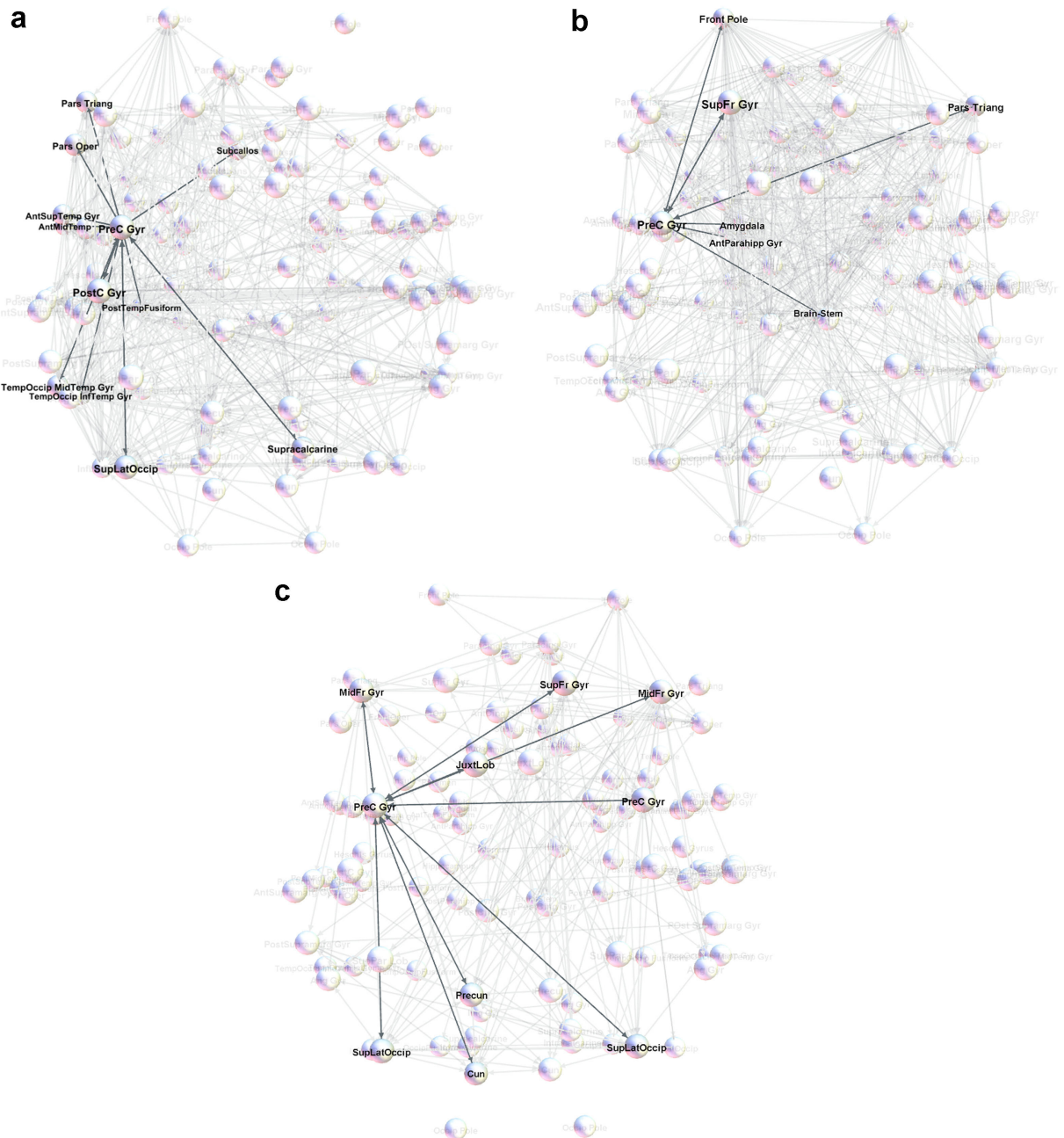


FIGURE 3 The functional partners of left precentral gyrus under three different task conditions. (a) Semantics, (b) emotion, (c) attention. Graphs rendered with Gephi <http://www.gephi.org>

emotion tasks, and attention tasks. Visually, it is clear that while this neural region is active in supporting tasks in different domains, it rarely shares the same functional partners across domains.

We can make this individual visual result quantitative and general by comparing the average node overlap with the average edge overlap in a pair-wise comparison of all the functional networks from the 10 cognitive domains analyzed. Referring back to Figure 1, we can easily generate predictions for the three possible functional architectures. If the brain is largely modular, then we should expect both low node overlap and low edge overlap. If, however, the brain is holistically organized, we should expect high node and high edge overlap. Finally, if the brain developed by reusing individual neural circuits for diverse purposes, then we should see high node overlap, but low edge overlap.

Using Dice's coefficient as our measure, $D = 2(o_{1,2})/(n_1 + n_2)$, where $o_{1,2}$ represents the number of shared components (edges or nodes) in the two networks, and n_x represents the total number of components in each network, we discover that the mean overlap for the nodes (D_N) = .60 (SD .13) while the mean overlap of the edges (D_E) = .09 (SD .07). Of course, one might worry that this result is simply an artifact of the fact that in networks there are many more possible edges than nodes, so one would expect to get this result just by chance. Thus it is important to compare these averages with the expected overlaps between *random* networks with the same number of edges and nodes as our brain networks. Doing a pair-wise comparison of random networks, Mean (D_{rN}) = .50 (SD .11) and mean (D_{rE}) = .14 (SD .07). All differences are significant $p \ll .01$ (Fig. 4). That is, the results indicate that between functional brain networks there is significantly *more* node overlap and significantly *less* edge overlap than would be expected by chance. These results replicate, with a much larger data set, those reported in Anderson (2008), and strongly suggest that low edge overlap and high node overlap between task domains is a functionally significant feature of these brain networks.

Finally, turning to the third prediction that recently emerged cognitive functions should be supported by more and more broadly scattered circuitry than tasks in older domains, Anderson (2008, 2007, 2010) reports 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 of functional organization over both modularity and holism. And given the current context it is worth

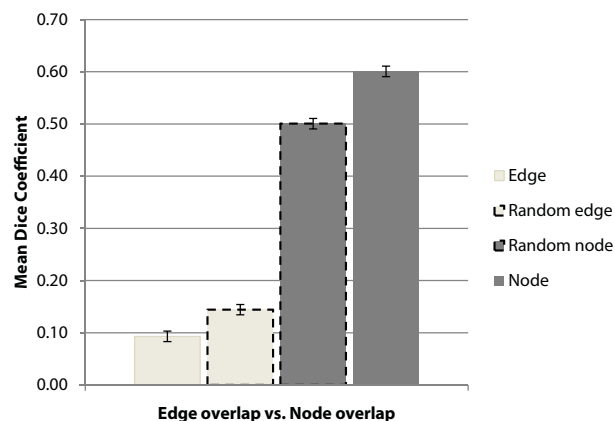


FIGURE 4 The average amount of overlap of nodes and edges in functional brain graphs as compared to random graphs.

noting that these data do not distinguish between an evolutionary account, and a developmental one. That is, the evidence paints a picture of the functional structure of the adult brain as emerging from a process of neural reuse, but it does not (cannot) differentiate the relative contributions of evolutionary and developmental pressures. It does not seem right to argue over this distinction in the absence of data (if we should argue about it at all—as Lickliter and Honeycutt (2003) point out, these influences are difficult if not impossible to disentangle). Rather, we should think about the opportunities for analysis the reuse perspective offers, whatever the timescale of its causes.

For instance, 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 and 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).”

The developmental homology perspective appears to represent a promising strategy. Here, we provide one example of how taking such a perspective can illuminate the relationship between cognitive domains and, in turn, the phenomena of interest. Finger gnosis (finger representation) and number representation are developmentally correlated (Fayol, Barrouillet, & Marinthe, 1998; Noël, 2005; Penner-Wilger et al., 2007, 2008,

2009). This relation between finger and number representation arises, at least in part, because the two tasks use overlapping neural circuits—one of the neural circuits integrated into the functional complex supporting finger gnosis is also part of the functional complex supporting the representation of number. There is strong evidence that some of the brain regions associated with finger gnosis (in the left precentral gyrus and left angular gyrus) are activated during tasks requiring the representation of number (Dehaene et al., 1996; de Jong, van Zomeren, Willemsen, & Paans, 1996; Göbel, Johansen-Berg, Behrens, & Rushworth, 2004; Jancke, Loose, Lutz, Specht, & Shah, 2000; Kuhtz-Buschbeck et al., 2003; Liu, Wang, Corbly, Zhang, & Joseph, 2006; Numminen et al., 2004; Pesenti, Thioux, Seron, & De Volder, 2000; Pinel, Piazza, LeBihan, & Dehaene, 2004; Venkatraman, Ansari, & Chee, 2005). Moreover, repetitive transcranial magnetic stimulation (rTMS; Rusconi, Walsh, & Butterworth, 2005) and direct cortical stimulation (Roux, Boetto, Sacko, Chollet, & Tremoulet, 2003) have been found to disrupt both finger gnosis and tasks requiring the representation of number. These findings are consistent with neural reuse; one of the neural circuits originally evolved or developed for finger representation has been reused in the (presumably) later-emerging function of number representation, and now serves both uses.

One tenet of reuse, for which there is strong empirical support, is that a typical brain area contributes to many uses across domains (Anderson, 2010). Thus, having identified a shared circuit involved in both finger and number representation [here we will focus on the shared circuit within the left precentral gyrus ($-42, 0, 38 \pm 6$ mm)], we next looked across domains to identify other uses that the circuit was supporting (see Penner-Wilger & Anderson, 2011 for a more complete account). This step was taken to both guide and constrain the function–structure mapping—to help discover what the circuit is *doing* in all the uses it supports. We analyzed a dataset of 2,603 functional imaging studies in over 60 task domains, reported in 823 journal articles published between 1996 and 2010. The data were compiled from the NICAM and BrainMap databases (Anderson et al., 2010; Laird, Lancaster, & Fox, 2005), with each experiment in the data set classified by cognitive domain according to the BrainMap taxonomy (Fox & Lancaster, 2002; Fox et al., 2005). All the studies involved healthy adults and used a within-subjects, whole-brain univariate design. That is, for all the studies in the data set, brain activity during an experimental task was observed over the whole brain (not just a region of interest) and then compared voxel-wise to activity observed in the same participant during a control task.

Using this data collection, we searched for experiments reporting activation inside the region of interest (ROI) in the left precentral gyrus. The results of the database search provided 65 articles reporting 80 tasks showing activation within the ROI. Of the tasks, 60 were in the domain of cognition (sub-domains: attention, language, mathematics, memory, time and theory of mind), 11 were in the domain of action (sub-domains: execution, inhibition, imagination and preparation), 7 were in the domain of perception (sub-domains: audition, somesthesia, and vision), and 2 were in the domain of emotion. Thus, consistent with reuse, the ROI was involved in varied uses across domains.

Recall that the purpose for using this cross-domain modeling methodology was to inform the function–structure mapping—what the shared circuit is *doing* during all these various tasks. In looking across the specific experimental tasks and subtractions identified by the database search, three themes emerged in addition to number representation and finger representation: generation (e.g., generate items in a given category), inhibition (e.g., incongruent Stroop condition, anti-saccade, response inhibition), and order tasks (e.g., performing memorized sequences of saccades, judging alphabetical or sequential order, n-back task—in which participants are presented with a continuous sequence of stimuli and indicate whenever the current stimulus matches the one from n steps back in the sequence). For reuse to have occurred, the service offered by the shared circuit must be something that the different uses could benefit from incorporating.

Applying this perspective to the uses found in the database search, we identified some common requirements across uses, including ordered storage of discrete representations and mapping between representational forms. Although neural activations are generally assigned functional processes specific to the domain under investigation (Cabeza & Nyberg, 2000), cross-domain structure–function mapping requires a domain-independent vocabulary. Thus, using vocabulary drawn from computation, our proposal for the structure–function pairing that could meet the functional requirements imposed by the multiple uses is an array of pointers. An array is an ordered group, and a pointer is a data structure that designates a memory location and can indicate different data types.

A concrete, familiar example of an array is an Advent calendar. Within a typical Advent calendar (the storage structure) chocolates are stored in an ordered form by date. An array can be used to store different types, not just chocolates. For example, some Advent calendars allow parents to place their own items in the storage structure (perhaps small toys or other treats). One of the authors' friends has such an Advent

calendar and instead of storing the treats within the calendar structure she instead writes notes for her children (budding readers) pointing them to a designated location where the treat is hidden (stored) in their house. This Advent calendar illustrates an array of pointers, where what is stored in the array (calendar) is the location of the data (chocolate), not the data itself.

An array of pointers meets the functional requirements imposed by the multiple uses of the ROI. It allows for storage and access of ordered elements, which are able to point to—or index—representations in memory, allowing for mapping between different representational forms. An array of pointers could be used for ordered storage of distinct representations of each finger, ordered by location, and for discrete representations of numbers, ordered by magnitude, across different representational forms (e.g., non-symbolic representations as well as numerals and number words). The proposal of a pointer structure is not unprecedented or neurologically implausible; indeed such a structure is consistent with the semantic pointer architecture, a recent elaboration of the Neural Engineering Framework (Eliasmith, in press; Eliasmith & Anderson, 2003). Thus, cross-domain modeling, compelled by evidence for reuse, can productively guide function–structure mapping.

So, given the evidence for neural reuse presented above, what is the benefit of taking a developmental homology perspective? One tenet of this perspective is that neural reuse should leave a detectable trace on behavior. That is, given that the tasks share a common physical-functional substrate that has been recombined with additional neural circuits to support performance of multiple tasks, we should expect to be able to find similar behavioral phenomena across tasks. This proves to be the case in both finger and number representation. One landmark phenomenon in number representation is the *distance effect*—it is harder to differentiate numbers that are closer together in magnitude than those that are farther apart (e.g., 3 vs. 4 is harder than 1 vs. 9; Dehaene, Dehaene-Lambertz, & Cohen, 1998). The same phenomenon is also found in finger gnosis—it is harder to differentiate fingers that are closer together physically than those that are farther apart (Benton, Hamsher, Varney, & Spreen, 1983; Gregor, House, Zigler, & Penner-Wilger, 2012). Given that this effect in finger gnosis is likely a result of the underlying physical/spatial distribution of the nerves in the hand and the way the information is represented in the brain (and is therefore likely to obtain in many sensory systems) the fact that it is also observed in an apparently abstract functional domain like magnitude comparison is all the more striking. In light of the independent evidence for the circuit sharing between part of the

finger-sense system and part of the number processing system, the persistence of a distance effect across these domains appears to reflect the influence of stable functional characteristics of the shared circuit, and thus to represent the kind of inheritance of “special qualities” that often signals a homology.

In addition, taking 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” (Riedl, 1978; Wagner, 1999): the more multiply integrated a circuit becomes, the more difficult to change its local character without affecting many different functions. Reuse, then, should place specific, detectable constraints on development that can be investigated observationally in humans, and experimentally in animals. Insofar as learning new tasks refines local circuitry and establishes additional long distance connections, these changes will be more compatible with some future learning pathways than with others. Learning task A followed by B might make learning task X difficult and Y easy, while learning task A followed by C might have the opposite effect, as a result of the different demands B and C place on the relevant neural circuitry. Certainly we see examples of the *enhancement* of later-acquired capacities as the result of apparently unrelated skills acquired earlier. For example, children who receive pitch training starting in first grade perform better in mathematics longitudinally in third grade (Gardiner, 2008). In light of such findings, however, it seems reasonable to also predict instances where the burden on a circuit *negatively* impacts learnability and performance. We know, for instance, that visual experience restricts the plasticity of visual circuits as compared with the congenitally blind (Bedny, Pascual-Leone, Dravida, & Saxe, 2011), and we would expect to see similar effects for shared circuitry.

Overall, it appears that identifying both cross-species and developmental homologies potentially offers both conceptual and experimental leverage for advancing our understanding of the brain. This being said, it also appears that some more conceptual work is called for to specify the differences between identifying a developmental homology, and simply uncovering instances of developmental *continuity*. Although the neural overlap between the finger gnosis and number representation circuits can be said to represent an instance of homology—including a shared precursor and the inheritance of “special qualities” (in the distance effect)—there are nevertheless some suggestive disanalogies here. First, there need not be a *copy* of the neural structure that is adapted to new uses; instead the very same structure comes to participate in different functional complexes. Thus, neither the physical structure

nor the developmental pathway is duplicated, and while the function is in some sense duplicated, it is a temporal rather than a physical or spatial duplication. Similarly, one of the oft-cited criteria for homologous structures is that they occupy the *same* position with the *same* connections in two different species. But in the case of neural reuse, the different uses of a given circuit are differentiated precisely by their *different* (functional) connections to other neural structures.

On the other hand, perhaps these factors need not disqualify an instance of reuse from counting as an instance of homology. Consider the case of *serial* homology, which does not always involve developmental duplication. Although many serial homologues begin as developmental duplications, there are cases of serial homologues (such as leaf hopper helmets, which are wing homologues) that have been released from selection pressures, so that their appearance is now largely determined by separate genetic factors, not resulting from gene duplication (Prud'homme et al., 2011). Thus, they do not share any common developmental resources in a particular instance of development.

Moreover, in a serial homology the physical structure need *not* occupy the same position with the same connections in different species; indeed, in some cases it cannot, in virtue of the inherit-and-duplicate aspect of serial homologues. In fact, it is precisely their violation of this rule that makes serial homologies so interesting, and such a force of evolutionary change.

So perhaps indeed a case could be made that instances of neural reuse might be fruitfully understood as a kind of *developmental serial homology*—the augmentation of overall function via temporal duplication of function. Yet there is certainly much more reflection required before such a possibility could be established. And as delving deeper into these issues would take us into a long and complicated discussion about the underlying nature of and criteria for serial homology, it is perhaps better to close instead with the thought that, however the conversation develops, it is nevertheless clear that the concept of developmental homology has the potential to focus attention on some crucial questions and phenomena, and thereby help advance our understanding of the evolutionary and developmental origins of cognition.

NOTES

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