

Title: Evolution of cognitive function via redeployment of brain areas

Running head: Evolution of cognitive function

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Abstract

The creative re-use of existing cognitive capacities may have played a significant role in the evolutionary development of the brain. There are obvious evolutionary advantages to such redeployment, and the data presented here confirm three important empirical predictions of this account of the development of cognition: (1) a typical brain area will be utilized by many cognitive functions in diverse task categories, (2) evolutionarily older brain areas will be deployed in more cognitive functions and (3) more recent cognitive functions will utilize more, and more widely scattered brain areas. These findings have implications not just for our understanding of the evolutionary origins of cognitive function, but also for the practice of both clinical and experimental neuroscience.

Evolution and redeployment

Part of understanding the functional organization of the brain is understanding how it evolved. The current study suggests that while the brain may have originally emerged as an organ with functionally dedicated regions, the creative re-use of these regions has played a significant role in its evolutionary development. This would parallel the evolution of other capabilities wherein existing structures, evolved for other purposes, are re-used and built upon in the course of continuing evolutionary development (“exaptation”: Gould and Vrba, 1982). There is psychological support for exaptation in cognition (Cosmides, 1989; Cruse, 2003; Glenberg and Kashak, 2002; Gould, 1991; Lakoff and Nuñez, 2000; Riegler, 2001; Wilson, 2001), and neuroanatomic evidence that the brain evolved by preserving, extending, and combining existing network components, rather than by generating complex structures *de novo* (Sporns and Kötter, 2004). However, there has been little evidence that integrates these two perspectives, bringing such an account of the evolution of cognitive function into the realm of cognitive neuroscience (although see, e.g., Barsalou 1999).

One recent hypothesis along these lines—that combines a story about the evolution of the brain based on the re-use and extension of existing elements with an exaptive account of cognitive functions—is the massive redeployment hypothesis (Anderson, 2006; Anderson, in press). The massive redeployment hypothesis suggests that cognitive evolution proceeds in a way analogous to component reuse in software engineering (Heinemann and Council, 2001), whereby existing components—originally developed to serve some specific purpose—are used for new purposes and combined to support new

capacities, without disrupting their participation in existing programs. If cognitive functions evolved in this way, then we should be able to make some specific empirical predictions regarding the resulting functional topography of the brain; here I discuss three.

First and most generally, we should expect a typical brain region to support numerous cognitive functions in diverse task categories. If this were not the case, if a typical brain region in fact served a very limited set of cognitive functions, then this would suggest instead that the brain evolved by generating new, dedicated regions for each new purpose.

Second, there should be a correlation between the phylogenetic age of a brain area and the frequency with which it is deployed in various cognitive functions. The longer an area has been around the more likely it will have proved useful to some evolving cognitive capacity, and be incorporated into the functional network of brain regions supporting the new task. Naturally this will not be true for every brain region, since a given area may have evolved to serve a very particular purpose of little use in later developments. But it should be generally the case that the older an area is, the more cognitive functions it supports.

Third and finally, there should be a correlation between the phylogenetic age of a cognitive function and its degree of localization. That is, more recent functions should generally use more, and more widely scattered brain areas than evolutionarily older

functions. Again, the reasoning is simple: the more brain areas there are when a given cognitive capacity is evolving, the more likely that one of them will already serve some purpose useful for the emerging capacity, and there is little reason to suppose that the most useful areas will be grouped together (and less reason to suppose this as evolutionary time passes, making available more functions supported by more areas).

Approach and methods

To evaluate the predictions made by the redeployment hypothesis, I performed some statistical analyses of 135 brain-imaging experiments, collected by Cabeza and Nyberg (2000). They survey 275 fMRI and PET experiments, in ten task categories. Here I focus on only four categories: attention, perception, imagery, and language. The 39 attention tasks included things like tone detection and Stroop tasks (naming colored words); the 42 perception tasks included such things as object identification and facial recognition; the 18 imagery tasks include mental rotation and landmark visualization; and the 36 language tasks included reading out loud and silently, lexical decision tasks (discriminating words from non-words), and the like.

For each task, Cabeza and Nyberg catalog the brain areas reported to be activated by that task from a list including 26 numbered Brodmann areas, plus the insula and MT, and three subcortical areas—basal ganglia, thalamus and cerebellum—for each hemisphere. Each area was divided into a lateral and medial segment, for a total of 124 brain regions. Note that the reported activations do not represent the full network of brain areas activated by a given cognitive task, but those remaining after the relevant control/comparison tasks have been subtracted out. That is, the areas identified in the

studies are understood to be those specifically responsible for the cognitive function under investigation.

In order to evaluate the three predictions, several values need to be calculated for this data set. First, we need to know how many brain areas are activated by a typical cognitive task, and whether this varies by task category. Second, we need to know how many cognitive tasks a typical brain area supports, and how these tasks are distributed across the four categories. Third, we need to measure the “scatter” of the areas participating in each task, and the variance of this value by task category. Finally, we need to correlate these values with phylogenetic age.

To calculate the first two values was primarily a matter of counting. Cabeza and Nyberg use a coding scheme for activations that forces a decision between lateral and medial activation, such that it is not possible to show both a medial and a lateral activation in a given brain area for a given task. Instead, the possible activations for each brain area are left lateral (LL), right lateral (RL), bilateral lateral (BL); left medial (LM), right medial (RM), bilateral medial (BM). Thus, for instance, they list the following activations for a task involving hearing words vs. a resting condition (Muller 1997): an LL activation in Brodmann area 47, and BL activations in areas 21 and 22. For the purposes of counting areas activated by a task, I treated bilateral activations of an area as two participants, one left and one right (medial or lateral). Thus, the language task above would have five participants, three LL participants (areas 47, 21 and 22) and two RL participants (areas 21 and 22). For the purposes of counting redeployments (areas activated by more than one task), I matched LL activations in an area to other LL activations of that area, as well as

to BL activations, and I matched RL activations in an area to other RL activations of that area, as well as to BL activations. I followed the same procedure for medial activations. I did not match bilateral activations to each other.

To calculate the diversity of activations across task categories I employed a standard measure of population diversity, *Diversity Variability* (DV). DV is calculated using the following equation, a version of standard deviation, where Cat_i is the proportion of activations in category i ; $mean$ is the mean proportion of activations in each category (always 0.25 for 4 categories), and k is the number of categories:

$$DV = \sqrt{\frac{\sum_{i=1}^k (Cat_i - mean)^2}{k}}$$

The category diversity of a given area is just (1-DV). With four categories, category diversity ranges from 0.57 (all items in one category) to 1 (equal numbers in each category). Note that for the purpose of calculating category diversity, the activation counts in each category were normalized to n=42.

Finally, to measure the distribution, or “scatter” of areas activated by a given task, I constructed an adjacency graph for the cortex (Figure 3). A graph is a set of objects called points or vertices connected by links called lines or edges. For constructing a graph of the cortex, I took the nodes to be numbered Brodmann areas (Brodmann, 1907) and the edges to indicate adjacency. Adjacency in this context means only that the Brodmann areas share a physical border in the brain.

Graph theory (Diestel, 2005) is a branch of mathematics that allows one to explore the topological properties of graphs. Graph-theoretic analyses have been used in neuroscience for such purposes as investigating neural connectivity patterns (Sporns, 2002), correcting brain images (Han, et al. 2001), and analyzing the patterns of neural activations in epilepsy (Suharitdamrong, Chaovalitwongse and Pardalos, 2006).

One of the simplest concepts in graph theory is *minimum graph distance*, which is just the fewest number of edges one must traverse to get from one node to another. Nodes that are adjacent in a graph have a graph distance of 1, nodes not adjacent to each other, but both adjacent to a third have a graph distance of 2, and so on. The minimum graph distance between every pair of nodes in the graph of the cortex was calculated using Dijkstra's algorithm (Dijkstra, 1959).

A simple extension of minimum graph distance is *average minimum graph distance*, which is the average of the minimum graph distances between every pair of nodes in some subset of nodes in a graph. Figure 1 illustrates some different graphs, and the average minimum graph distances between all the nodes in the graph.

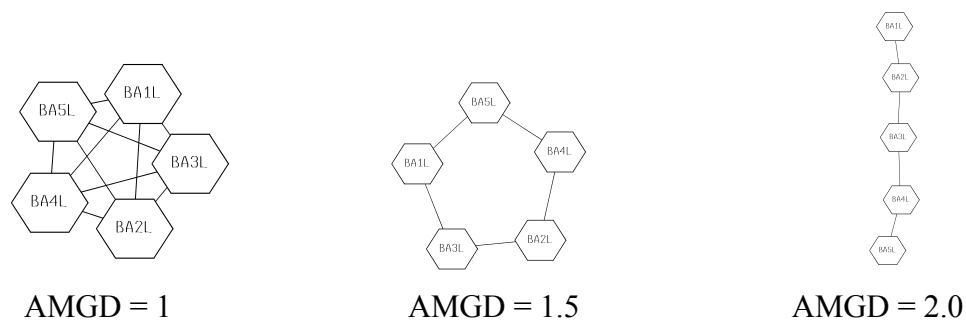


Figure 1: Illustrations of the average minimum graph distance (AMGD). The figure shows the average minimum graph distances between nodes in some simple graphs. Lines between nodes indicate adjacency.

Results

On average, each of the 135 tasks activated 5.97 regions (SD 4.80). Perceptual tasks activated 4.88 (n = 42, SD 3.55), attention 5.26 (n = 39, SD 4.23), imagery 6.39 (n = 18, SD 3.29) and language 7.81 (n = 36, SD 6.56). More importantly, the 86 brain regions that were activated by at least one task supported, on average, 9.36 different tasks (SD 8.62). Ignoring the division into medial and lateral regions gives an average of 13.00 tasks per area (SD 8.44), nearly one in ten of the tasks surveyed.

The activations were not limited to closely related tasks. Of the 86 regions activated in some task, 57 (66.3%) had activations in at least three categories; 28 of these had activations in all four categories. Only 15 regions (17.4%) had activations in just one category. Counting the number of tasks by category that activated each region, and normalizing the count of tasks in each category to n=42, shows that an average of 37.8%

(SD 21.5) of activations are in categories other than the category with the highest number of activations.

Using the measure of population diversity among categories discussed above shows that the 86 brain regions have a mean category diversity of 0.76 (SD 0.11); ignoring the medial/lateral division gives 0.81 (SD 0.09). As shown in Table 1, an average category diversity of 0.81 suggests a fairly high degree of redeployment throughout the brain.

Area	Normalized proportion of activations by category				Category diversity
	Attention	Imagery	Language	Perception	(1 – DV)
BA46R	0.55	0.24	0.00	0.21	0.80
BA18L	0.26	0.21	0.28	0.24	0.97
BA38L	0.00	0.00	1.00	0.00	0.57

Table 1: Illustrations of the category diversity of some Brodmann areas. The table shows some examples of the diversity of activations across categories for three Brodmann areas.

These results are perhaps even more striking when put in graphical form. Figure 2 represents activations of Brodmann areas in the left hemisphere, in each of the four task domains, by both color and intensity. The color represents the task domain, and the intensity indicates the number of tasks in the category that activate the area. I use the colors cyan (language), magenta (attention), yellow (perception) and black (imagery) so that these colors can be mixed using standard CMYK 4-color printing methods.

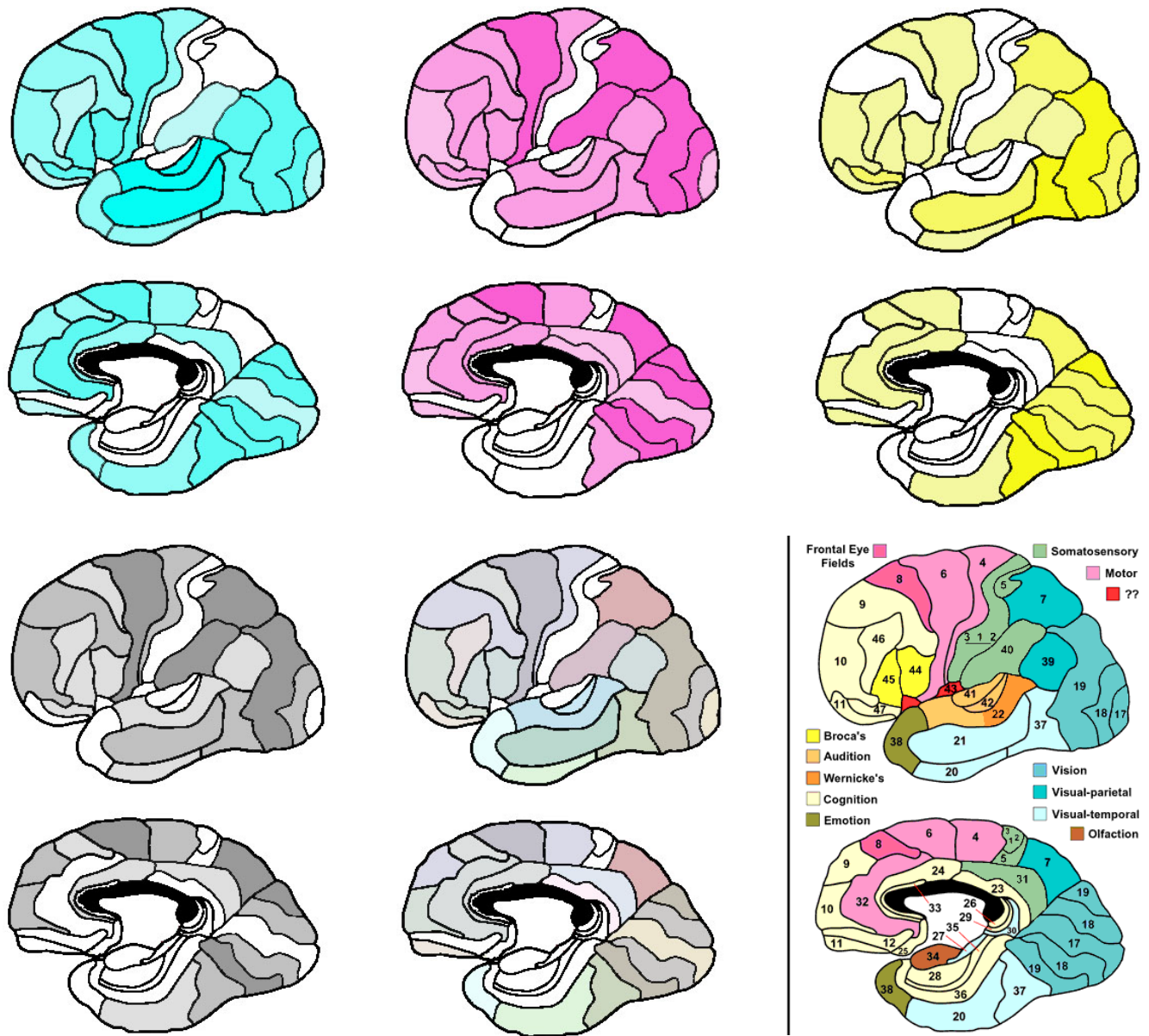


Figure 2: Color-coded activations of left cortex. The figure illustrates the activations of Brodmann areas in the left hemisphere according to color and intensity, where color represents the cognitive domain and intensity the number of tasks in the domain activating the area. In this figure, cyan represents language, magenta represents attention, yellow represents perception and black represents imagery. Overlaying the single-color images gives the 4-color image in the bottom center. This image contrasts sharply with the standard picture of localization by domain as shown in the bottom right panel.

Far from supporting the standard notion that cognitive functions are generally localizable by domain (as illustrated in the lower right panel of figure 2), the data suggest a much

more complex and subtle structure, where activity in many (most) brain areas supports multiple tasks in multiple cognitive domains. The difference between the standard picture and the functional organization suggested by the redeployment hypothesis is perhaps best illustrated by contrasting the lower middle panel with the lower right panel. Rather than large areas of mono-chromatic cortex, what we see instead is a large array of unique colors, indicating the relative contributions of each Brodmann area to supporting tasks in a given cognitive domain.

However, this does not mean that the cortex is in any way *randomly* or *holistically* organized; far from it. In fact, as is illustrated below, we can make (and support) some specific predictions about the relations between cognitive functions and brain areas based on the phylogenetic age of the function and the brain area.

But first we need to present the data on the “scatter” of brain areas supporting various cognitive functions. The average minimum graph distance between the Brodmann areas activated by each of the 135 tasks is 3.89 (SD 2.00). Broken down by task category, we get attention 3.13 (SD 2.06), perception 3.71 (SD 1.98), imagery 3.97 (SD 1.75), and language 4.82 (SD 1.76). Figure 2 represents the cortex as an adjacency graph, with an attention task (Corbetta, et al, 1993) superimposed.

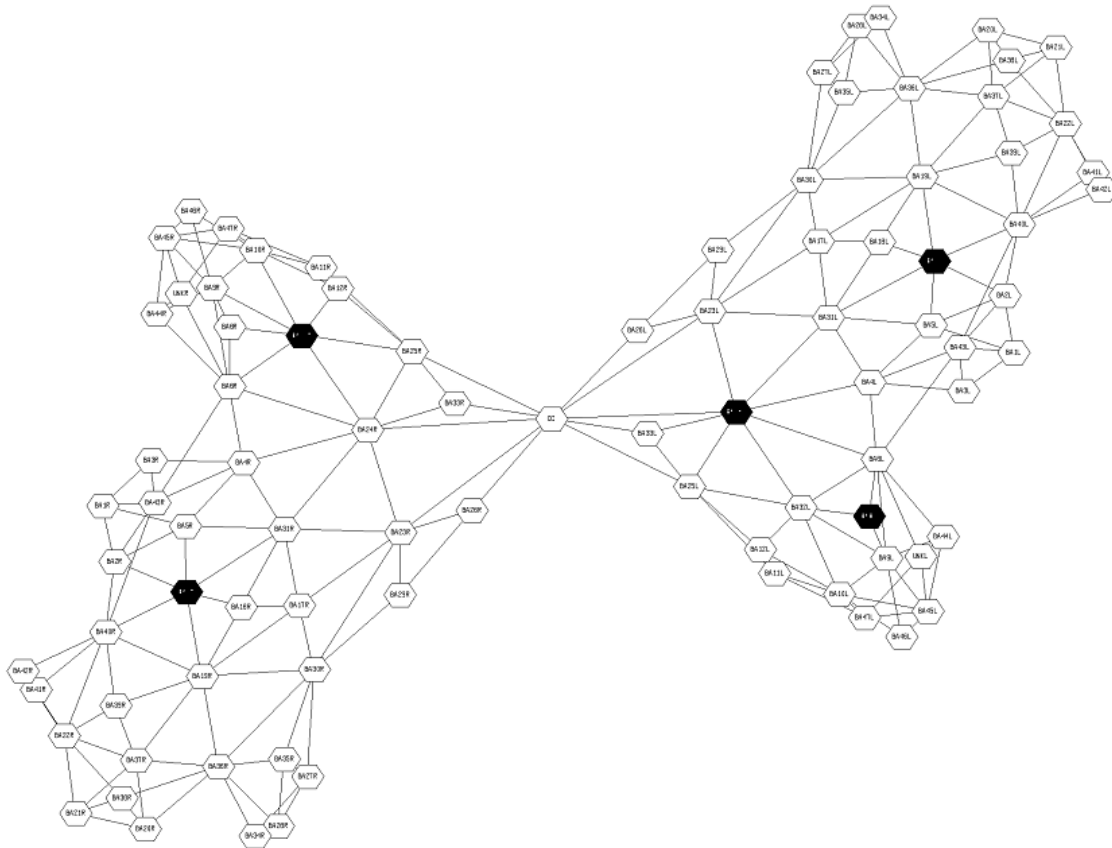


Figure 3: The cortex represented as an adjacency graph, showing the Brodmann areas as nodes, with lines between adjacent areas. The darkened nodes are those activated by an attention task reported by Corbetta (1993). That task activated left Brodmann areas 7, 8 and 24, and right Brodmann areas 7 and 32; average minimum graph distance is 4.0, close to the average for all tasks.

With this basic data in front of us, we can look at correlations between these values and phylogenetic age. As noted above, if the evolution of cognition proceeded via the extensive re-use of existing components, then evolutionarily more recent cognitive functions should activate more, and more widely scattered brain areas. Comparing language tasks with perception tasks and attention tasks gives the predicted result. For the mean number of areas activated, language is greater than perception by 2.93 (2-sample Student's-t test, double-sided $p = 0.0165$) and greater than attention by 2.55 ($p =$

0.0475). For average minimum graph distance, language is greater than perception by 1.11 ($p = 0.0121$) and greater than attention by 1.69 ($p = 0.0003$). Differences between other categories are not significant (Table 2).

Categories being compared	Difference in average number of regions activated per task	Difference in average minimum graph distance of activated regions
Language vs. Perception	2.93, $p = 0.0165^*$	1.11, $p = 0.0121^*$
Language vs. Attention	2.55, $p = 0.0475^*$	1.69, $p = 0.0003^*$
Language vs. Imagery	1.42, $p = 0.3922$	0.85, $p = 0.0998$
Perception vs. Attention	0.38, $p = 0.6618$	0.58, $p = 0.2002$
Perception vs. Imagery	1.51, $p = 0.1285$	0.26, $p = 0.6317$
Attention vs. Imagery	1.13, $p = 0.3214$	0.84, $p = 0.1402$

Table 2: Results for all category comparisons on average number of brain regions activated per task and average minimum graph distance between the activated regions. Note that only the differences between language and perception and language and attention are significant.

The last important prediction of the redeployment hypothesis to be discussed here is that evolutionarily older brain areas should be deployed in more cognitive functions. Figure 2 gives the results of plotting the number of tasks that activate a given Brodmann area versus the Y-coordinate of the area, based on the simplifying assumption that areas in the rear of the cerebral cortex (occipital lobe) are evolutionarily older than those in the front (pre-frontal cortex), *ceterus paribus*. Although the data are highly variable, as expected, there is nevertheless a significant linear correlation.

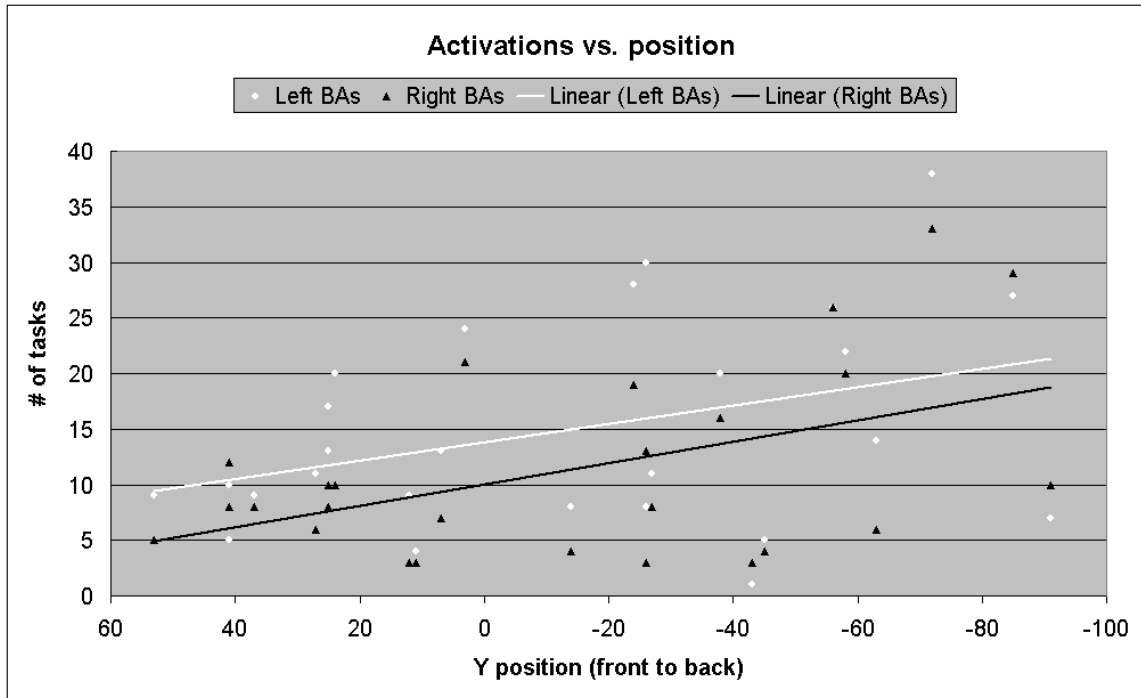


Figure 2: A plot of the number of tasks (out of 135) that activated each Brodmann area vs. the Y coordinate of the area (calculated in Talairach (Talairach and Tournoux, 1988) space using the Brede (Nielsen, 2003) database). The data shows a linear correlation, $R = -0.4121$, $p \leq 0.00244$ ($t = -3.198$, $DF = 50$).

Discussion

Together, these data suggest a picture of the evolution of cognition where redeployment plays a significant role. As predicted, we see correlations between phylogenetic age of brain areas and the frequency of their participation in cognitive function, and between the age of cognitive functions and their degree of localization. We also saw that the typical brain area is a diverse instrument, supporting cognitive tasks in multiple task categories. The massive redeployment hypothesis thus appears to be both empirically supported, and consistent with the evidence for evolution by exaptation in both psychology and neuroanatomy.

Before concluding, I would like to say a few words about the more theoretical attractions and implications of the massive redeployment hypothesis. First of all, the hypothesis offers the potential for explaining both localization of function (cognitive functions only use limited and specific parts of the brain), and diversity of purpose (a typical brain area is activated by highly diverse cognitive tasks). This may help dissolve the debate between localization and holism (Uttal, 2001), which in its typical form offers a false choice between equipotentiality (a given brain area can do many different things when it is activated) and strict localization (each brain area does one and only one thing). According to the massive redeployment hypothesis, the fact that a brain area is dedicated to some highly specific low-level task is perfectly compatible with its being used to support many different cognitive functions (Anderson, 2006; in press). In fact, if brain areas were multi- or equi-potential, and so could easily be recruited to compute substantially different functions, then it is hard to understand why older brain areas are more often recruited than younger ones, and why newer cognitive functions recruit more widely scattered brain areas. It would seem that such a pattern of redeployment would only arise if the low-level (computational) functions of brain areas were relatively fixed, such that developing a new cognitive function requires either developing new capacities *de novo*, or finding areas already performing some required role. If brain areas could instead be easily encouraged to compute many different functions, then considerations of information-processing efficiency would favor recruitment of *nearer* areas over areas already computing some desired function, but further away.

Second, redeployment may offer a clearer way of organizing the search for the neurological bases of cognitive function. In particular, it suggests that in order to determine the functional role of a given brain region it is necessary to consider its participation across multiple task categories, and not just focus on one, as has been the typical practice. Making this claim a bit more specific, when modeling a given cognitive function, and attempting to map that model onto brain areas, it will be necessary to consider not just the model of the function under primary consideration, but also the models of other functions recruiting the same brain areas, such that the sub-functional elements of each model attribute the same role to the brain areas where they overlap. Finding the functional role of a given brain area will be something like finding the right letter to go into a box on a (multidimensional) crossword puzzle, determined not just by the answer to a single clue, but by all the clues whose answers cross that box. This makes the task both harder, because it is multiply constrained, but also easier, because it offers the possibility of leveraging information from several sources to make the attribution.

Third, and closely related to the last point above, as we come to recognize the diverse cognitive functions supported by given brain regions, this should suggest more fine-grained predictions about such matters as priming and cognitive interference, as well as the likely effects (and the localization) of brain injuries. The knowledge that a given brain area is used in multiple tasks and domains opens the possibility of designing experiments leveraging these overlaps, e.g. in cross-domain priming or interference studies, or in the development of cross-domain therapies for brain-injury patients.

Finally, looking at brain organization in this way can offer a different a method to assess the relative evolutionary age of cognitive functions, and of brain areas, opening another window on our evolutionary past.

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