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Evidence for Massive Redeployment of Brain Areas in Cognitive Functions

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Abstract

This essay introduces the massive redeployment hypothesis (MRH), an account of the functional organization of the brain that centrally features the fact that brain areas are typically employed to support numerous cognitive functions. MRH offers a middle course between strict localization on the one hand, and holism on the other, in such a way as to account for the supporting data on both sides of the argument. MRH is supported by some case studies of redeployment, and an empirical review of 135 imaging experiments.

Introduction and Background

The localization-holism debate has generally been presented in terms of a choice between whether cognitive functions are typically instantiated by a few and closely grouped neural participants, or by many and widely distributed ones. Yet this is pretty clearly not the right distinguishing factor between localization and holism, for as Mundale (2002) persuasively argues, the belief that cognitive functions typically have many and widely distributed participants is perfectly compatible with localization. Instead, I would like to suggest that the following two questions offer a better contrast: (1) are brain areas that support a given function largely dedicated to—that is, are they not just *necessary* participants in, but also *exclusive* participants in—the cognitive function(s) in question?; and (2), when a brain area participates in more than one cognitive function, is it doing the same thing in each case? The believer in localization answers "yes" to both questions (although question 2 does not really arise), whereas the holist answers "no".

In contrast to both localization and holism, a redeployment hypothesis splits the difference, answering "no" to question 1, and "yes" to question 2. That is, a redeployment hypothesis claims that parts of the brain are specialized, in that they do the same thing each time they are activated. However, the thing that they do—the function they compute or transformation they effect—does not line up with any specific cognitive function. Rather, brain areas must work in concert with other areas to do anything interesting, and are generally deployed in many different functional complexes, which do many different (interesting) things.

The remainder of this essay will introduce and defend a particular redeployment hypothesis, MRH. I call it a *massive* RH (as opposed, perhaps to mild, moderate, meek, or modest) for two reasons. First, MRH predicts that non-exclusive participation will turn out to be the *norm* when it comes to the functional topography of the brain (a more moderate hypothesis might predict occasional instances of redeployment). Second, MRH predicts significant redeployment both within and between traditional cognitive domains (e.g. perception, motor control, language, memory, etc.), that is, it suggests that most brain areas are not domain specific.

Case Studies for Massive Redeployment

In this section, I will discuss three different instances involving the apparent redeployment of brain areas to support multiple functions. The case studies both provide some evidentiary support for MRH and, perhaps more importantly, illustrate how such redeployment works, and why it might have evolved.

The Organization of M1

The somatotopic organization of M1 has long been part of the standard account of the functional topography of that region. In its classic form, Penfield's homunculus specified distinct, non-overlapping regions for motor control down to the level of individual fingers and joints. It is a clear product of the localization assumption. However, over the past few decades, evidence has been mounting that the areas of M1 controlling the various body parts are in fact distributed and overlapping. Recently, Marc Schieber (2001) has reviewed this evidence, and found six factors constraining the somatotopic organization in M1:

> 1) *Convergent* output from a large M1 territory controls any particular body part, joint, or muscle. 2) *Divergent* output of many single M1 neurons reaches multiple spinal motoneuron pools. 3) *Horizontal connections* interlink the cortex throughout a major body part region. 4) *Widely distributed activity* appears in a major body part region whenever any smaller body part is moved. 5) *Partial inactivation* of a major region affects multiple smaller body parts simultaneously. 6) *Plasticity* limits the degree to which control of a specific body part can be assigned to a particular piece of cortex. (p. 2125, emphasis in original)

For the purposes of this essay, I will be focusing on findings 1, 2 and 4. Findings 3, 5 and 6, while compatible with MRH and interesting in their own right, nevertheless have implications somewhat orthogonal to the main elements of MRH I am trying to support.

The clear implication of convergence is that there are multiple, not necessarily spatially contiguous areas that

share in the motor control of a given muscle or body part. Using intracortical microstimulation (ICMS), a technique that limits the possibility that the stimulus will accidentally spread to larger areas of cortex, Asanuma and Rosen (1972) found multiple small areas controlling the same movement of, or contracting the same muscle in, a monkey's forelimb. Moreover, they found that these areas were intermixed with areas controlling other movements or muscles such that, although a gross somatotopic organizational trend could be observed (arm movements controlled by this general area, leg movements in that, face movements over here), boundaries between large areas were not necessarily clear, and the somatotopic organization did not extend to the fine-grained structure of the cortex. More recent studies have confirmed this finding, and shown further that, as the stimulation of small cortical areas is increased in intensity or duration, responses are evoked in increasing numbers of muscles or joints (an effect that cannot be adequately explained in terms of stimulation spreading or leaking to neighboring cortical areas). This brings us to the issue of divergence.

Anatomic evidence indicates that a single neuron from M1 can terminate in different spinal segments, connecting to different motoneuron pools (Shinoda, Yokota & Futami, 1981), and functional studies demonstrate that these connections can affect muscle groups across different body parts, as widely separated as finger and shoulder (McKiernan et al., 1998). In an especially striking demonstration of the possible utility of such connections Graziano et al. (2002) showed that the stimulation of individual cortical areas could evoke complex coordinated movements of a monkey's forelimb, such as reaching, grasping, or adopting a defensive posture. They found further that these areas were not somatotopically organized, but rather showed a spatial and postural organization, roughly corresponding to the locations at which the movements were directed (the endpoint of the motion in ego-centric space), and the limb posture resulting from the action.

Such evidence for convergence and divergence alone does not necessarily suggest MRH. Convergence, it might be argued, merely shows redundancy of function, while the evidence for divergence is compatible with the strict localization claim that cortical areas are functionally specialized and dedicated, so long as the functions in question are characterized in a complex way: reaching to a given spot, rather than contracting a single muscle. However, the defining claim of MRH is that the same cortical area can play a role in supporting multiple functions, however complex their characterizations. Perhaps the clearest evidence for both distribution and redeployment comes from single neuron recordings of monkeys performing individuated finger and wrist movements (Schieber & Hibbard, 1993). Schieber and Hibbard found that the general territories of M1 involved in finger control were virtually coextensive. Moreover, while each neuron was consistently related to at least one movement, there were multiple, spatially distributed neurons involved in each movement, most of which were related to multiple different finger and/or wrist movements. Imaging studies in humans confirm extensive overlap in the areas of activation in M1 corresponding not just to finger movements (Sanes et al., 1995), but also to thumb, index finger, wrist, elbow and shoulder movements (Kleinschmidt, Nitschke & Frahm, 1997).

What is attractive about the evidence from M1 is that it is such an extensively studied area. Insofar as the emerging picture of its functional organization indicates reliance on multiple, distributed and non-exclusive participants in motor control functions, then given the extent of the evidence, the hypothesis needs to be taken quite seriously. On the other side of the coin, given that the evidence is restricted to M1 and motor control, extensive redeployment might not seem all that surprising. The support for MRH coming from the study of M1, while strong, is also somewhat narrow. Thus, the next two case studies showcase some rather more radical and surprising instances of apparent redeployment. The evidence for these examples is somewhat less strong, but the implications are far broader.

Sensorimotor Coding in Working Memory

One instance of redeployment on which there has been a fair amount of work is in the apparent use of sensorimotor resources to support working memory. As the evidence has been reviewed in detail by Margaret Wilson (2001), I'll only provide a brief summary. The experiments in question typically involve the presentation of multiple items (words or letters) either visually or auditorily, with the task being to remember these items, in order. The question of interest is what kind of processing supports this ability, and there is a great deal of evidence supporting some version of the Baddeley and Hitch model of working memory, which posits that working memory has both verbal and visuospatial components, among others (Baddeley & Hitch, 1974; 1994, Baddeley, 1986; 1995). Basically, the Baddeley and Hitch model says that one strategy for remembering such lists involves (silently) saying them to one's self (producing a "phonological loop"), which engages brain areas typically used both in speech production and in audition. Another strategy for remembering words is the visual representation of their form or meaning (especially for abstract nouns). Wilson notes that this latter strategy is not particularly effective for maintaining an ordered list, and that therefore a strategy involving some version of the phonological loop is more typically employed.

A pattern of findings supports the existence of a phonological loop, a strategy that engages both inner "speaking" and inner "hearing" to support working memory. First, there is poor recall of similar sounding terms; second, there is poor recall of longer words; third, there is poor recall if the subject is made to speak during the maintenance period; and fourth, there is poor recall when the subject is exposed to irrelevant speech during the maintenance period. Moreover, imaging studies have found that such memory tasks cause activation in areas typically involved in speech production (Broca's area, left

premotor cortex, left supplementary motor cortex, and right cerebellum) and in phonological storage (left posterior parietal cortex) (Awh et al., 1996). Imaging data also tends to support the use of sensorimotor strategies in visuospatial working memory, showing activation of right hemisphere, including areas of visual and prefrontal cortex (Smith, 2000).

Although these findings will not be at all surprising to anyone who has ever tried to remember multiple things, only to be foiled by having to say, or listen to, something unrelated, the broad implications are nevertheless significant. As Wilson writes, in this case it appears that

> …sensorimotor processes are run covertly to assist with the representation and manipulation of information, in the temporary absence of task-relevant input or output. Such an arrangement would make sense, given our evolutionary heritage from creatures whose neural resources were devoted largely to perceptual and motor processes. Indeed, given that we have such resources, it would be odd if we did not exploit them whenever possible to assist in off-line cognitive processing. (pp. 44-5)

Motor Simulations in Language Understanding

Finally, the last case I would like to consider is an even more striking example of the redeployment of resources in apparently disparate functions: the action-sentence compatibility effect (Glenberg & Kaschak, 2002), which suggests the involvement of the motor system in language understanding. To demonstrate this interesting interaction between comprehension and motor control, Glenberg and Kaschak asked subjects to indicate whether a given sentence made sense or not by making a response that required a movement either toward or away from their bodies (e.g. reaching for a button). They found that response times were longer in cases where the required movement ran counter to a movement suggested by the sentence itself (e.g. where the response required a movement toward the body, and the sentence, e.g., "Close the drawer" indicated a movement away from the body, or vice-versa), and that this was true even when the "movement" indicated by the sentence was abstract, as in the transfer of information from one party to another (e.g. "You told Ann about the party."). A general explanation of this effect would be that the comprehension of the sentences involved a motor simulation of the action they describe, thus "priming" the system to move in one way, rather than another. More particularly, Glenberg and Kaschak posit that understanding language involves combining the affordances of the sentence elements, and judging the "doability" of the action corresponding to the meshed set of affordances. A doable action indicates a comprehensible sentence.

These results are intriguing and highly suggestive, yet, as Glenberg and Kaschak readily admit, there is much more work to be done.

> In summary, our results demonstrate that the understanding of imperative, double-object and dative constructions is grounded in action. Given that language almost certainly arose to facilitate

coordination of action, it is not surprising that there is an observable remnant of that history. The results also raise the intriguing possibility that much, if not all, language comprehension is similarly grounded. Although substantial work needs to be done to secure that possibility, that work may well be rewarded by an account of language and meaning firmly anchored in human experience. (p. 564)

One kind of evidence that is currently missing for this effect is neural imaging data. To help address this lacuna, I hope in the near future to run an MEG experiment featuring the Glenberg-Kaschak task. MEG evidence, especially given its temporal resolution, might help rule out the most obvious alternate explanation of the data, that it is a post-understanding simulation of the action that is interfering with the response, rather than a simulation implicated in the understanding itself. Although it is true that it is difficult to use this alternative to explain the effect in the case of abstract transfers (for there is little reason to believe that a post-understanding simulation of abstract transfers would implicate movements toward or away from the subject, even if it involved simulating the actions used in the transfer, such as speaking), MEG data might help settle the matter.

There are nevertheless other kinds of evidence available that appear to support the general finding that motor control and language understanding are intertwined with one another. For instance, patient KJ-1360, who has a lesion in left premotor cortex, shows an impairment in verb retrieval, but has otherwise normal linguistic abilities (Damasio & Tranel, 1993). Martin et al. (1995, 1996) confirm this basic finding that areas associated with motor control are involved in verb retrieval, and also show that naming colors and animals involved visual processing areas, suggesting that language use and comprehension involves the re-use of many other areas of the brain besides motor areas, and, moreover, that this redeployment is content specific, with verbs reusing motor control areas, and certain nouns like animal and color names reusing visual processing resources. That there is a large amount of redeployment of sensory processing areas in linguistic and conceptual tasks is another striking case of redeployment worth pursuing in its own right (Barsalou, 1999), but we will focus here on the relation between language use and motor areas.

One particularly interesting part of the brain in this regard is Broca's area (left Brodmann areas 44 and 45). Broca's area has long been associated with language processing, but what has recently begun to emerge is its functional complexity (Hagoort, 2005). For instance, it has been shown that Broca's area is involved in many different action-related tasks, including movement preparation (Thoenissen, Zilles, & Toni, 2002), action sequencing (Nishitani, et al., 2005), action recognition (Decety et al., 1997; Hamzei et al., 2003, Nishitani, et al., 2005), imagery of human motion (Binkofski, et al., 2000), and action imitation (Nishitani, et al., 2005). In other words, language processing involves (much) more than one region of the brain, and the regions of the brain associated with language processing are involved in many

other tasks, of which we have listed just a few. Note, however, that it does not appear to be the case that brain areas are redeployed haphazardly; rather, the contributions they make are useful in more than one situation. In the case of Broca's area, for instance, it is not surprising that an area of the brain that plays a role in action sequencing would be useful in language processing and production, since this, too, requires action sequencing. Likewise, that verb retrieval/comprehension would involve motor simulation is unsurprising, so long as we suppose that our ability to understand verbs is closely connected to our experience of acting in the world.

Returning, then, to our central theme, a main distinguishing feature of MRH is the claim that the functional complexes of the brain make heavy use of nonexclusive participants, not just within, but across classically specified domains. The three case studies above offer some evidence for this claim—and, just as importantly, help to illustrate what redeployment does for the brain, and why it makes sense as an organizational principle. But it must of course be admitted that this evidence in no way proves MRH, and certainly does not establish redeployment as the norm. Thus, in the next section we turn to a different kind of evidence that can help do just that.

Empirical Review of Imaging Experiments

The evidence for MRH is in no way restricted to the few brain areas or cognitive functions listed above. In fact, a recent review by Cabeza and Nyberg (2000) strongly suggests that rather rampant redeployment to be the norm. Cabeza and Nyberg survey 275 fMRI and PET experiments, arranging them by task category (attention, perception, imagery, language, working memory, episodic memory encoding, episodic memory retrieval, etc.). For each task, they catalog the participants in that task, from a list of 31 different brain areas (28 Brodmann, and three subcortical areas), each divided into four different parts: left lateral, right lateral, left medial and right medial. Although Cabeza and Nyberg do not do any statistical analysis of this data (their primary interest is in examining/establishing the consistency of findings across different experiments on similar tasks), the results of even a simple analysis are striking.

For simplicity and brevity, I focus here on only four of the ten categories of tasks surveyed: attention, perception, imagery, and language. The data on the other task categories is consistent with what I report here. Cabeza and Nyberg looked at 39 attention-related tasks, 42 perception-related tasks, 18 imagery-related tasks, and 36 language-related tasks, for a total of 135 tasks in these four categories. The attention tasks included things like tone detection and Stroop tasks (naming colored words); perception tasks included such things as object identification and facial recognition; the various imagery tasks include mental rotation and landmark visualization; and the language tasks included reading out loud and silently, lexical decision tasks (discriminating words from non-words), and the like.

As mentioned already above, Cabeza and Nyberg divided each brain area into 4 parts; however, their coding scheme forces a decision between lateral and medial activation, such that it is not possible to show a left medial and a left lateral activation in a given 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 et al., 1997): an LL activation in Brodmann area 47, and BL activations in areas 21 and 22.

For the purposes of counting participants in 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.

The data show that, on average, each of the 135 tasks has 5.97 participants (SD 4.80), with somewhat more than that for the language tasks and slightly less for attention and perception. More importantly, they show that each area was typically a participant in more than one task, although interestingly, there is a significant difference between medial and lateral activations in this regard. Thus, each LM area that was a participant in at least one task was, on average, a participant in 3.87 different tasks (SD 3.34); likewise, each RM area that was a participant in at least one task was, on average, a participant in 3.29 tasks (SD 1.77). In contrast (and providing incredibly striking evidence against strict localization), each LL area that was a participant in at least one task was a participant in an average of 14.29 different tasks (SD 9.20), and each RL area was a participant in 10.41 (SD 7.96). Put differently, an average LL area participated in nearly one in nine (10.6%) of the tasks studied, and the average RL area participated in one in thirteen (7.7%).

The participation of areas in multiple tasks was not restricted to only closely related tasks. In fact, of the 28 LL areas that participated in at least one task in one of the four task categories, 26 (93%) were also participants in at least one other task in a different task category. Moreover, 23 of those areas (82%) participated in tasks in at least three categories, and 15 (54%) participated in tasks in all four categories. The numbers are similar for RL activations, and while the numbers for medial activations were somewhat lower, the data overall undermine strict localization, and strongly suggest widespread redeployment throughout the cortex (see Table 1).

There *were* nine tasks of the 135 examined that activated a total of ten areas not activated by any other task. Since other tasks not examined might also activate

these areas, we cannot conclude on this basis alone that these nine tasks have exclusive participants—and, in fact, eight of these ten areas are known to be involved in tasks in categories not surveyed here. Even if the remaining two areas turn out to be exclusive to their two tasks, this still would mean that less than 1.5% of the tasks examined had exclusive participants. Only one of these two tasks had a single participant, not activated by any other task; the other had 8 other participants, none of which were exclusive.

Table 1: Number of brain regions (out of 31) with activations in exactly the number of task categories listed, out of the four categories surveyed.

Activation Type	Number of areas with activations in:			
	1 task category	2 task categories	3 task categories	4 task categories
Right Lateral	3	4	11	11
Left Lateral	2	3	8	15
Right Medial	4	4	6	0
Left Medial	6	3	4	2

Overall, the picture could hardly be clearer: nearly every brain area participates in multiple cognitive functions, and each cognitive function utilizes many participants, very few of which are exclusive. The data on brain function is decidedly not consistent with a strict localization assumption.

Note, however, that while the data appear to rule out localization, they do not argue against holism. My main motivation for rejecting holism is that it seems that one can offer an evolutionary reason for redeployment as an architectural feature of the brain *only* if brain areas do roughly the same thing for each of the functional complexes in which they participate. As new brain functions develop, one might well expect opportunistic reuse of existing functional components, but it seems that this would only be effective insofar as the existing components already did something that could easily become a useful part of a functional complex supporting the new function. Too little initial compatibility would make the incorporation of existing components into a new functional complex quite puzzling, and too much alteration in the functional structure of the existing component could cause problems with the other functions it supports. Still, until we have much better awareness of what individual brain areas contribute to cognitive functions (something that imaging data alone will not provide), it will be difficult to definitively rule out holism.

Comparison to Related Work

There has been too much work on localization to even begin to survey it in a paper of this length; more extensive discussion can be found in (Anderson, forthcoming).

Focusing just on some work that is very close in spirit to MRH, I note that my arguments for MRH are largely compatible with those in (Mundale, 2002) for a limited form of localization. However, while allowing for the possibility of multiple necessary participants in a given brain function, Mundale does not address the difference between necessary and exclusive participation, and thus she does not discuss the possibility of a form of localization in which the (localized) participants in one function also participate in other functions. Mesulam (1990, 1998) suggests a position much more similar to MRH: "many cortical nodes are likely to participate in the function of more than one network. Conceivably, top-down connections from transmodal areas could differentially recruit such a cortical node into the service of one network or another." (1998, p.1040). However, Mesulam's development and defense of this common basic idea is significantly different from that offered here (in particular, the empirical review provides more broad-based evidence for the thesis). Dan Lloyd (2000) also rejects localization, in part because of an empirical review he performed somewhat like the one I report here. However, Lloyd's review is much smaller, and does not appear to control for laterality, making its conclusions suspect. Moreover, Lloyd appears to endorse holism as the correct alternative to localization, a move I do not support. Cabeza and Nyberg, whose work was the basis of my empirical review, do notice that there is apparently a great deal of redeployment in the brain, but they decline to offer any hypotheses about the significance of this finding. Interestingly, they observe that researchers tend to interpret activations in terms of the domain within which they are working: "Area 7 activations, for instance, were usually attributed to attentional processes in attention studies, to perceptual processes in perception studies, to working memory processes in working memory studies, and so on." (Cabeza & Nyberg, 2000: 31) This tendency would serve to mask the prevalence of redeployment from those disinclined to look for it.

Conclusion

This essay introduced the massive redeployment hypothesis, an account of the functional organization of the brain that gives pride of place to the fact that brain areas are typically employed to support numerous functions, with little respect for traditional domain boundaries. Although I think that the three case studies in which there appears to be redeployment of brain areas to support very different functions, together with the empirical review that suggests such redeployment is the norm, strongly support MRH, this is not likely to be, nor is it intended as, the last word on brain organization. Still, an hypothesis can be prove useful even (or perhaps especially) in the course of being disproved and discarded, insofar as it offers a way to help (re-)organize old data and interpret new information, and may suggest novel experimental inquiries. I hope for no more than this from MRH. A much more thorough discussion of MRH, including a proposal for a specific functional architecture, is given in (Anderson, forthcoming).

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