The massive redeployment hypothesis and the functional topography of the brain

Michael L. Anderson
Institute for Advanced Computer Studies
University of Maryland
College Park, MD 20742

Abstract

This essay introduces the massive redeployment hypothesis, an account of the functional organization of the brain that centrally features the fact that brain areas are typically employed to support numerous functions. The massive redeployment hypothesis is supported by three case studies of redeployment, and compared and contrasted with other theories of the localization of function.

1. Introduction

The brain, it needs hardly be said, has many functions. Even focusing on the so-called cortical functions—and thus leaving out the largely unconscious, automatic, "lower" functions like homeostatic regulation, balance, and the like—leaves quite a large number of things for the brain to do, from moving one's fingers (say, to turn the pages of this essay), to reading and understanding these sentences (because of which the pages will soon need turning). Naturally, there is a great deal of interest in how the brain does these things, and that has generally involved interest in *where* the brain does them. This interest in the functional topography of the brain is at least as old as Gall's phrenology (Gall, 1798), and has undergone a recent resurgence, due in large measure to advances in various imaging technologies. The main purpose of the current essay is to outline an idea regarding what we should generally expect the functional topography of the brain to be, an idea I call the massive redeployment hypothesis.

In the sections that follow, I will first discuss what I take to be the current, orthodox position on the functional topography of the brain. This will serve as a contrast to the

massive redeployment hypothesis (henceforth MRH), also explained in section 2. Next I will discuss evidence for MRH, in the form of three examples of the re-deployment of brain areas in different functions. Finally, I will briefly discuss some of the implications of, and possible objections to, MRH.

2. Brain function and brain areas.

Roughly speaking, a brain function is a brain process of cognitive or psychological interest (e.g. that supports or causes some cognitive effect like intentionally moving one's fingers, recognizing a face, or remembering a list of words) that can be specified in terms of inputs, outputs, and the (often mysterious) transformation of the former into the later. In this I am following Fodor (2000) in the pragmatic definition of a (cognitive) function as whatever appears in one of the boxes in a psychologist's diagram of cognitive processing. The project of functional topography, simply put, is to map these boxes onto brain areas. In imaging studies, this generally involves getting subjects to engage in some cognitive task, and seeing what "lights up", that is, finding brain areas, the activation of which is reliably and uniquely correlated to the cognitive activity in question, once noise and background processing are subtracted out.

So far, so good. What the brain topographer wants to know is which brain areas participate in which functions. Let us say a brain area *participates* in a function if activity or processing in that area supports the transformation of inputs to outputs that define the function. A given function may (and typically does) have more than one participant; among these, there may be those the failure of which would cause the failure

of the function; let us call these the *necessary* participants.[1] In addition, there may be areas that participate in only one function; let us call these the *exclusive* participants. Finally, let us call the collection of participants in a certain function a *functional complex*.

Now, let us assume, for the sake of the discussion, that the brain topographer is interested only in the necessary participants in brain function. And let us assume further that every function has at least one exclusive participant (something I think is possibly true, but need not be). It does not follow from these assumptions that all, or even that most, of the necessary participants in a function are exclusive participants. Yet this is clearly the predominant working assumption of brain topography; let's call this the *strict localization hypothesis*. Now, it is certainly true that working brain scientists are often quite cautious when stating their conclusions (consider the following, multiply hedged passage from Grasby et. al. (1993): "The brain areas identified in these comparisons define a number of the neuroanatomical components of a distributed system for signal processing and storage relevant to auditory—verbal memory function."), yet the impression that they are in fact committed to the strict localization hypothesis is encouraged by the many available brain maps—such as might be found in any text of cognitive neuroscience—showing the functional breakdown of the brain in terms of neat, contiguous, non-overlapping brain areas.[2] Indeed, even when there are controversies regarding the function of a given area—as for instance in the ongoing controversy about how to explain the fact that the so-called "fusiform face area" (Allison, 1994; Haxby, *et. al.* 1994; Kanwisher, *et. al.* 1997; McCarthy, *et. al.* 1997) seems to be involved in processing stimuli other than faces (Gauthier, *et. al.* 2000; Tarr & Gauthier, 2000)—the

arguments are typically directed not toward identifying the multiplicity of functions in which the area(s) of interest participate, but rather toward properly defining *the* unique function in which a given area participates.

Moreover, even if few scientists would accept the strict localization hypothesis when it is put starkly before them, their methodology is at least somewhat biased toward producing data consistent with it. What I mean is this: a typical design for an imaging experiment involves subjects who perform a number of trials of an assigned task, along with control trials that generally involve the subject engaging in a different but closely related task (but may also consist of resting periods). The experimenters image the brain during all these periods, and the data analysis involves comparing—within subjects, between subjects, or both—on-task activations with control activations, and *subtracting out* what is common; the images that result are *difference* images. I intend no broad attack on this method,[3] nor will I suggest that the results garnered from its use are in any way invalid. The brain areas that are shown to be active in the on-task trials are indeed participants, and in most cases *necessary* participants, in the function in question. What I *do* claim, however, is that this method will typically uncover the participants in a task that are *both* necessary *and* exclusive, and that necessary but *non*-exclusive participants will often be, or are at least at risk of being, subtracted out (and the more closely related the experimental and control task, the higher the risk is likely to be).[4]

Why this is so is easy to see. Imagine that the following table represents the average[5] level of activity in five brain areas, in the task and control conditions.

Brain area / Activation	A	B	C	D	E
Task	5	6	2	1	0
Control	2	6	5	1	0
Difference	3	0	-3	0	0

Table 1: Imaginary brain area activations for task and control conditions

A brain image created using the subtraction method (based on the difference line in Table 1) would strongly suggest that area A was the brain area responsible for the main experimental task (and perhaps that area C was involved in the control task, or inhibited by the experimental task). But note the high activation in area B for both task and control. There are a number of possible explanations for this: for instance, that area B has generally high activation having nothing to do with either the task or the control; that area B has high activation because it participates in the processing of the *inputs* for both the task and control; or that area B is a necessary (but non-exclusive) participant in both the experimental *and* the control task. In the first two cases, it would be both legitimate and desirable to subtract out the activation of area B; but in the third case the effect of subtraction is the loss of valuable information, and potentially misleading support for strict localization.

Still, arguing about who would, and who would not, endorse the strict localization hypothesis is something of a distraction from the main point of the essay, which is to introduce and support an alternative hypothesis: MRH. Put simply, MRH says that

necessary, non-exclusive participation is the norm when it comes to the functional topography of the brain. It is easy to see that this is a *logical* possibility, but what does the science tell us? In the next section, I will discuss three different studies that appear to favor MRH over strict localization.

3. 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.

3.1 The organization of M1

The first case study I would like to discuss involves the organization of the primary motor cortex, or M1. One of the brain maps with which nearly everyone is familiar is the motor homunculus (see fig. 1).

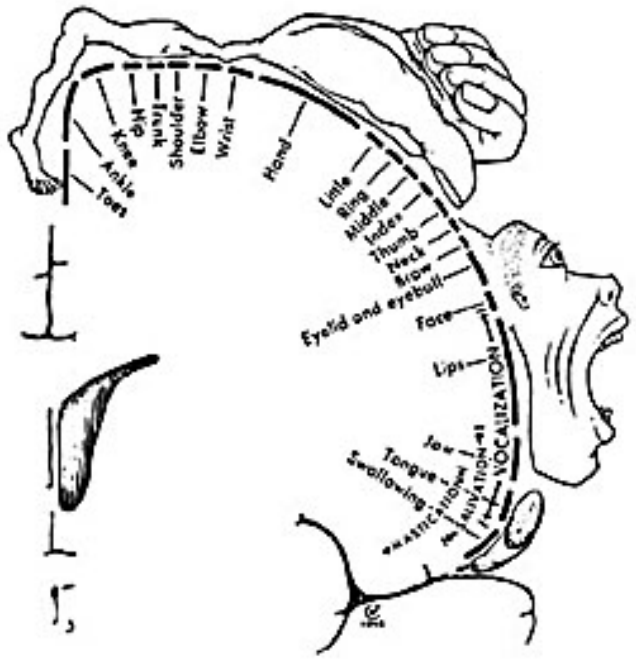

Figure 1: *"Motor homunculus" from Penfield and Rasmussen (1950).*

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 strict localization hypothesis.[6] 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 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 *et al*., 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. I present evidence for this specific claim below, but before doing so, it is worthwhile to address a concern that may well occur to the reader at this point. It might be thought that I am understating the case in saying that evidence like that presented in (Graziano *et al*., 2002) is *compatible* with strict localization; rather it seems to positively cry out for such interpretation. After all, stimulation of each of the cortical sites studied did exactly one thing, which was to move the monkey's arm to a spatially well-defined posture. I have two responses to this claim. The first involves a clarification of the scope of MRH: the hypothesis does *not* amount to the claim that *no* part of the brain is organized according to strict localization; the part of the cortex studied by Graziano *et al*. may turn out to be one of those areas. However, MRH predicts that strict localization will not turn out to be the norm of functional organization. This brings us to the second response, which is to point out that the electrical stimulation of brain areas is a *highly* unnatural event. It does not follow from the fact that the stimulation of an area provokes a given movement that

this movement is evoked in the course of an organism's natural behavior by the selective activation of that same brain area. To demonstrate this latter claim would require observing brain activation during behavior elicited under the control of the organism, and the evidence gathered this way suggests a more complex picture, involving both distributed activation in the control of individual movements, and redeployment of single areas for the control of different movements.

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 *et al*., 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.

3.2 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)

3.3 The use of 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. "John 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 Glenburg-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.

The 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, but it must of course be admitted that this evidence in to way *establishes* MRH—at best, it puts

MRH in the running for further consideration and testing. This, however, is all that can be wanted from any hypothesis.

4. Implications, objections, and replies

In this section I will address some of the implications of MRH, thereby further clarifying the position, by answering some of the questions most likely to occur to the reader.

4.1 Are you denying modularity or localization?

No, although I must add the usual caveat that it depends what one *means* by modularity or localization. MRH is a version of the localization hypothesis, at least insofar as localization does not require all localized participants in a brain function to be exclusive participants in that function. Since I am obviously denying the *strict* localization hypothesis, I also deny any version of modularity that requires it. What I am proposing is an hypothesis regarding the functional organization of the brain that posits overlapping functional complexes; that is, I expect the entities that implement different brain functions to share functional elements ("participants"). Any version of modularity on which modules could be such functional complexes (or organized groups of functional complexes) could thereby be compatible with MRH.[7]

One aspect of the modularity hypothesis that, in its strong from, sits uneasily with MRH is the claim that modules are *domain specific*. I have reviewed evidence that motor areas are participants in language-related and memory-related tasks. Prinz (2005) notes further that focal brain lesions can produce deficits across multiple domains, and that genetic

language disorders often manifest non-linguistic problems. Thus it appears that, although functional complexes might be domain specific as organized, they are not thereby composed of domain-specific parts. Although the strong interpretations of localization and domain specificity are not strictly speaking *necessary* to the modularity hypothesis, Prinz argues that insofar as we have to weaken our interpretation of its various tenets, we should discard the hypothesis, and focus on functional decomposition more broadly construed. This may well be the right position, but I'll not pursue the matter further here.

4.2 Can't there be parts of the brain that conform to the strict localization hypothesis?

There can be, and probably are, brain areas that are best understood in terms of strict localization of function. But I am betting that not all of them will be; indeed, I am proposing that re-deployment is the norm. A further prediction of MRH would be that evolutionarily younger areas of the brain would make greater use of re-deployment, there being a greater range of pre-existing functions that might be "borrowed" (see further discussion in section 4.3). These are empirical questions, and will eventually be settled by the data.

4.3 Didn't scientist/philosopher X say this already?

There are a large number of discussions and critiques of the localization hypothesis, and I do not claim to have gone much beyond existing literature in my specific critique of that hypothesis (although I do believe my particular formulation of the strict localization hypothesis is original, and this, along with the distinction between necessary and exclusive participation in brain functions, might perhaps prove useful whatever the

ultimate fate of MRH). I have already mentioned Dan Lloyd's work in this regard, and noted that we share the same concern about the typical methodology of imaging studies. My chief difference with Lloyd (and I believe that this can also be said about my differences with Uttal (Uttal, 2001)), is in the *alternative* to the strict localization hypothesis I propose. That is, I am neither a holist, nor am I betting on highly distributed, connectionist-style processing in the brain. Rather, I expect that it will be possible to identify small, localized and specialized components that are deployed in (perhaps many) different functional complexes. Thus, I reject Uttal's prediction that it will not prove possible to decompose brain functions into component operations, localized in different brain regions (in this I follow Bechtel, (2002)). I also question Dan Lloyd's theory of sparsely distributed networks, whereby "[a] region may be recruited to join a subnetwork to compute one function, and later recruited to a different subnet to compute a different function." I believe in the re-deployment of regions, but not that they do different things for each of the functional complexes (subnetworks) in which they participate. In fact, I think that if the regions are doing roughly the *same* thing for each of the functional complexes in which they participate, then this opens the possibility of an evolutionary reason for re-deployment as an architectural feature of the brain. As new brain functions develop, one might well expect opportunistic re-use of existing functional components,[8] 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. The use of a phonological loop to support working memory offers a nice illustration of the redeployment of existing components to support a novel task, in such a way that little modification of that original function is required (it might be, for instance, that covert or silent rehearsal was a later adaptation of existing function, developed to support memory).

Nevertheless, a note of caution is in order here: it *could* be that Lloyd's claim is not that the *region* computes a different function in each of the subnetworks of which it is a part, but rather that the *subnetwork* computes a different function, utilizing the resources of the region (which does the same thing in each sub-network).[9] If *this* is his position, then our views appear to be largely compatible. However, insofar as Lloyd is committed to a connectionist architecture, it is not at all clear how it would be possible for him to make this claim. In a given connectionist network, is not generally possible to specify *what* a given part is doing, never mind claim that it is doing the *same* thing when the part is included in different networks. A network generally processes as a whole. Still, I must acknowledge the possibility that our views are more similar than I am allowing here.

Someone else theorizing in the same ballpark as MRH is Jesse Prinz, who centrally features evidence that brain regions are used in multiple functions in his critique of modularity (Prinz, 2005). I thus expect he would be sympathetic to the account offered here, but (Prinz, 2005) does not develop such an account.

Likewise, my arguments for a form of localization are largely compatible with those in (Mundale, 2002). There, Mundale argues that the localization hypothesis allows for the possibility that brain functions utilize multiple participants in complex combinations—and, furthermore, she implies that this is what localization has meant all along. However, while allowing for the possibility of multiple necessary participants in a given brain function, her argument 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. I do not know whether she would agree that MRH is compatible with (or is one form of) localization, as I am happy to allow (see section 4.1, above).

4.4 Why didn't you discuss topic Y?

There are a large number of topics, the discussion of which could conceivably have enhanced this essay. Here is a partial list: the various conceptions and critiques of functional localization;[10] the organization of other well-studied brain regions;[11] evolutionary accounts of cognition;[12] embodied cognition.[13] However, it was my hope to keep this essay focused on the relatively narrow task of introducing MRH, and offering some evidence in support of it. In maintaining this focus I have had to sacrifice some breadth. If there remains some obvious flaw in the hypothesis, excepting the ever-present flaw that more (detail, nuance, supportive evidence, etc.) is always possible, and if said flaw could be mitigated by a discussion of topic Y, then certainly I am interested to hear about it. One topic that I hope to address in more detail in future work is the

specific implications of MRH for the modularity hypothesis (massive or otherwise).[14] This is something that deserves an essay of its own.

5. 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. Although I think that the three case studies discussed, in which there appears to be redeployment of brain areas to support different functions, 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.

Acknowledgements

Thanks are due to the participants of the workshop for early career researchers, sponsored by the McDonnell Project in Philosophy and the Neurosciences, and especially to John Bickle, Valerie Gray Hardcastle, Ben Hardy, David Kaplan, Anthony Landreth, and Bill Seeley. Without the discussions we had, I probably would not have thought to write this essay.

Notes

[1] There is a complication here that is worth noting, but does not require solving: redundancy in some brain areas, and cooperation among others, may mean that actually specifying the necessary participants would be logically complex; for instance, it could be that what is necessary is *either* area A *or* areas (B & C) together, or some such. But for our purposes, we will not need to spell out any such relations; it is enough

to agree that there is indeed some set of necessary participants for each brain function, however difficult to specify their firm and identity. Note further that the necessary participants do not exhaust the necessary *conditions*—nor even the necessary brain processing—for the success of the function. In the case of understanding a sentence, for instance, there is a great deal of processing necessary to prepare the inputs to the comprehension function (if such there be), the failure of which would prevent the success of the comprehension function. Because we are focusing on the processes supporting the post-input *transformation*, these sorts of issues are not material.

[2] And, of course, for every cautious statement can be found a corresponding less cautious one. Consider the following, cited by (Lloyd, 2000): "These data localize the vigilance aspects of normal human attention to sensory stimuli.. ."(Pardo *et al*. 1991); "The implications of these results are discussed, and it is argued that they are consistent with localization of a lexicon for spoken word recognition in the middle part of the left superior and middle temporal gyri, and a lexicon for written word recognition in the posterior part of the left middle temporal gyrus." (Howard *et al.* 1992).

[3] Although it is worth noting that there are other sorts of analytical methods available, for instance multi-variate methods including multiple regression, discriminant analysis, and principle component analysis, all of which are designed to reveal the multiple contributors to a given effect or outcome. It is likely that imaging experiments would be designed somewhat differently from the usual "blocked" designs, were the data to be analyzed using multi-variate methods.

[4] Dan Lloyd has made a similar charge, although he apparently favors replacing the strict localization hypothesis with a more highly distributed, connectionist-based approach, a move I do not favor. (Lloyd, 2000).

[5] Activation results are typically averaged over many trials, thereby filtering out noise.

[6] This is a potentially interesting case study of the effect of prior assumptions in science, because both (Penfield and Rasmussen, 1950) and (Woolsey *et al*. 1952) admit that the pictures they offered did not reflect the complexity of the data, and the degree to which their evidence indicated a great deal of overlap of the areas controlling different body parts. It took a certain amount of interpretive effort to make their findings consistent with strict localization—for instance, focusing only on the *primary* movement evoked by the electro-stimulation, and discounting some movements as the effect of spreading activation from the primary target site. This is *not* to say that these interpretive moves were unreasonable or illegitimate. See (Schieber, 2001) for some of the interesting details.

[7] Another possibility is a version of modularity on which modules were identified with the participants in functional complexes. But this would make for some very low-level, uninteresting modules, and so is not likely to be an attractive option for the modularity theorist.

[8] This is one reason there is—or we should expect there will turn out to be—so much redeployment of sensorimotor resources, as these are some of the oldest. For some discussion of this issue, and its relevance to embodied cognition, see (Anderson, in press).

[9] The text is somewhat equivocal with respect to these possibilities. Here is a fuller quotation: "Third, there could be sparsely distributed networks. Here anatomically defined brain regions are multifunctional. A region may be recruited to join a subnetwork to compute one function, and later recruited to a different subnet to compute a different function. Thus, subnetworks would overlap in their anatomy. This form of distribution is sparse, however, insofar as particular brain regions are not omnifunctional. That is, each function is computed by a subset of regions, rather than the whole brain. The engaged subnetworks overlap, but the adaptability of each region is limited to a fixed list of functions." (Lloyd, 2000).

[10] On this see, e.g. Mundale (2002), Bechtel and Richardson (1993), and Zola-Morgan (1995).

[11] See, for instance, Bechtel (2001), Dagher et al. (1999).

[12] See Barkow, Cosmides & Tooby (1992), Sperber (1996).

[13] See Clark (1997; 1998), Wilson (2002), Anderson (2003). For a brief account of the relation between embodied cognition and the redeployment hypothesis, see Anderson (in press).

[14] There are many, many works on modularity. Here are a few: Carruthers (2003; 2005; 2006), Fodor (1983; 2000), Pinker (2005), Prinz (2005), Sperber (2002).

References

Allison, T., Ginter, H., McCarthy, G., Nobre, A. C., Puce, A., Luby, M. and Spencer, D.D. (1994). Face recognition in human extrastriate cortex. *J. Neurophysiol.* 71, 821-825.

Anderson, M. L. (2003). Embodied cognition: A field guide. *Artificial Intelligence*, 149 (1): 91-103.

Anderson, M.L. (in press). How to study the mind: An introduction to embodied cognition. In: F.Santoianni and C. Sabatano, eds. *Brain Development in Learning Environments: Embodied and Perceptual Advancements*.

Asanuma, H. and Rosen, I. (1972). Topographical organization of cortical efferent zones projecting to distal forelimb muscles in the monkey. *Experimental Brain Research*, 14: 143-56.

Awh, E., Jonides, J., Smith, E.E., Schumacher, E.H., Koeppe, R.A., and Katz, S. (1996). Dissociation of storage and rehearsal in verbal working memory: Evidence from positron emission tomography. *Psychological Science*, 7: 25-31.

Baddeley, A.D. (1986). *Working Memory*. Oxford: Oxford University Press.

Baddeley, A.D. (1995). Working memory. In: M.S. Gazzaniga, ed. *The cognitive neurosciences*. Cambridge, MA: The MIT Press. 755-64.

Baddeley, A.D. and Hitch, G. (1974). Working memory. In; G.H. Bower, ed. *The Psychology of Learning and Motivation*. Hillsdale, NJ: Earlbaum. 647-67.

Baddeley, A.D. and Hitch, G. (1994). Developments in the concept of working memory. *Neuropsychology*, 8: 485-93.

Barkow, J., Cosmides, L., and Tooby, J. (1992). *The Adapted Mind: Evolutionary Psychology and the Generation of Culture.* New York: Oxford University Press.

Bechtel, W. (2001). Decomposing and localizing vision: An examplar for cognitive neuroscience. In: W. Bechtel, P. Mandik, J. Mundale, and R.S. Stuffelbeam, eds. *Philosophy and the Neurosciences: A Reader*. Basil Blackwell, Oxford, pp. 225-49.

Bechtel, W. (2002). Decomposing the mind-brain: A long-term pursuit. *Brain and Mind*, 3: 229-242.

Bechtel, W. and Richardson, R.C. (1993). *Discovering Complexity: Decomposition and Localization as Scientific Research Strategies*. Princeton University Press, Princeton, N.J.

Carruthers, P. (2003). Moderately massive modularity. In A. O'Hear (ed.), *Mind and Persons*. Cambridge.

Carruthers, P. (2005). The case for massively modular models of mind. In R.Stainton (ed.), *Contemporary Debates in Cognitive Science*. Blackwell.

Carruthers, P. (2006). Simple heuristics meet massive modularity. In P.Carruthers, S.Laurence and S.Stich (eds.), *The Innate Mind: Culture and Cognition*. Oxford University Press.

Clark, A. (1997). *Being There: Putting Brain, Body, and World Together Again*. Cambridge, MA: MIT Press.

Clark, A. (1998). Embodied, situated, and distributed cognition. In W. Bechtel and G. Graham (eds.), *A Companion to Cognitive Science*. Malden, MA: Blackwell Publishers.

Dagher, A., Owen, A., Boecker, H., and Brooks, D. (1999). Mapping the network for planning. *Brain* 122: 1973-1987.

Fodor, J. (1983). *The Modularity of Mind*. Bradford Books, Cambridge, MA.

Fodor, J. (2000). *The Mind Doesn't Work That Way*. The MIT Press, Cambridge, MA.

Gall, F. J. (1798). Letter from Dr. F. J. Gall, to Joseph Fr[eiherr] von Retzer, upon the Functions of the Brain, in Man and Animals. *Der neue Teutsche Merkur*, 3: 311-332.

Gauthier, I., Skudlarski P., Gore, J.C. and Anderson, A.W. (2000). Expertise for cars and birds recruits brain areas involved in face recognition. *Nature Neuroscience* 3: 191-197.

Glenburg, A. and Kaschak, M. (2002). Grounding language in action. *Psychonomic Bulletin and Review* 9: 558-565.

Grasby P.M., Frith C.D., Friston K.J., Bench C., Frackowiak R.S. and Dolan R.J. (1993). Functional mapping of brain areas implicated in auditory—verbal memory function. *Brain*, 116: 1, 1-20.

Graziano, M.S.A., Taylor, C.S.R., Moore, T., and Cooke, D.F. (2002). The cortical control of movement revisited. *Neuron*, 36: 1-20.

Haxby, J.V., Horwitz, B., Ungerleider, L.G., Maisog, J.M., Pietrini, P., and Grady, C.L. (1994). The functional organization of human extrastriate cortex: A PET-RCBF study of selective attention to faces and locations. *J. Neurosci.* 14, 6336-6353.

Howard, D., Patterson, K., Wise, R., Brown, W., Friston, K., Weiller, C., & Frackowiak, R. (1992). The cortical localization of the lexicons. *Brain*, 115: 1769-1782.

Kanwisher, N., McDermott, J. & Chun, M.M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *J. Neurosci*. 17, 4302-4311.

Kleinschmidt, A., Nitschke, M.F., and Frahm, J. (1997). Somatotopy in the human motor cortex hand area: A high-resolution functional MRI study. *European Journal of Neuroscience*, 9: 2178-86.

Lloyd, D. (2000). Terra cognita: From functional neuroimaging to the map of the mind. *Brain and Mind*, 1: 1-24.

McCarthy, G., Puce, A., Gore, J. C. & Allison, T. (1997). Face-specific processing in the human fusiform gyrus. *J. Cogn. Neurosci*. 9, 605-610.

McKiernana, B.J., Marcario, J.K., Karrier, J.H., and Chenery, P.D. (1998). Corticomotoneuronal postspike effects in shoulder, elbow, wrist, digit, and intrinsic hand muscles during a reach and prehension task. *Journal of Neurophysiology*, 21: 1132-39.

Pardo, J., Raichle, M., & Fox, P. (1991). Localization of a human system for sustained attention by positron emission tomography. *Nature*, 349: 61-63.

Penfield, W. and Rasmussen, T. (1950). *The Cerebral Cortex of Man*. New York: MacMillan.

Pinker, S. (2005). So how *does* the mind work? *Mind and Language*, 20 (1): 1-24.

Prinz, J. (2005). Is the mind really modular? In: R. Stainton, ed. *Contemporary Debates in Cognitive Science*. Blackwell, New York.

Sanes, J.N., Donoghue, J.P., Thangaraj, V., Edelman, R.R. and Warach, S. (1995). Shared neural substrates controlling hand movements in human motor cortex. *Science*, 268: 1775-77.

Schieber, M.H. (2001). Constraints on somatotopic organization in the primary motor cortex. *Journal of Neurophysiology*, 86: 2125-43.

Schieber, M.H. and Hibbard, L.S. (1993). How somatotopic is the motor cortex hand area? *Science*, 261: 489-92.

Shinoda, Y., Yokota, J., and Futami, T. (1981). Divergent projection of individual corticospinal axons to motoneurons of multiple miscles in the monkey. *Neuroscience Letters*, 96: 7-12.

Smith, E.E. (2000). Neural bases of working memory. *Current Directions in Psychological Science*, 9: 45-9.

Sperber, D. (1996). *Explaining Culture: A Naturalistic Approach.* London: Blackwell.

Sperber, D. (2002). In defense of massive modularity. In E. Dupoux, ed. *Language, Brain and Cognitive Development*. The MIT Press: Cambridge, MA.

Tarr, M.J. and Gauthier, I. (2000). FFA: a flexible fusiform area for subordinate-level visual processing automatized by expertise. *Nature Neuroscience* 3, 764-769.

Wilson, M. (2001). The case for sensorimotor coding in working memory. *Psychonomic Bulletin and Review* 8: 44-57.

Wilson, M. (2002). Six views of embodied cognition. *Psychonomic Bulletin and Review* 9 (4): 625-36.

Woolsey, C.N., Settlage, P.H., Meyer, D.R., Sencer, W., Hamuty, T.P., and Travis, A.M. (1952). Patterns of localization in precentral and "supplementary" motor areas and their relation to the concept of a premotor area. *Res Pub Assoc Res Nerv Ment Dis*, 30: 238-264.

Zola-Morgan, S. (1995). Localization of brain function: The legacy of Franz Joseph Gall (1758-1828). *Annual Review of Neuroscience*, 18: 359-83.