

Target article: "Neural re-use as a fundamental organizational principle of the brain" by Michael L. Anderson.

Title:

Redeployed Functions Versus Spreading Activation: A Potential Confound

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Abstract:

Anderson's meta-analysis of fMRI data is subject to a potential confound. Areas identified as active may make no functional contribution to the task being studied, or may indicate regions involved in the coordination of functional networks rather than information processing per se. I suggest a way in which fMRI adaptation studies might provide a useful test between these alternatives.

That there is a many-to-one mapping between cognitive functions and brain areas should now be beyond dispute. The tricky part is figuring out what to say about it. Anderson's massive redeployment hypothesis is a plausible position in the debate. Good engineers often find new uses for old tricks; we should expect nature to be no less clever.

A crucial piece of evidence for the massive redeployment hypothesis is Anderson's impressive meta-analyses of fMRI experiments (Anderson, 2007a, 2007b). These show that phylogenetically older areas tend to be more active, across a variety of tasks, than phylogenetically newer ones. Crucially, Anderson assumes that the areas identified as active make a functional contribution to the experimental tasks being studied. That is often assumed in fMRI experiments, and so may seem unproblematic. This assumption is subject to a potential confound, however, and one that becomes especially troublesome when doing large scale meta-analyses.

The BOLD response on which fMRI depends is a measure of physiological change. *Which* physiological change fMRI tracks is a matter of considerable debate. There is increasing evidence that the BOLD response better tracks regional increases in synaptic activity, rather than increased output of action potentials (Logothetis et al., 2001; Viswanathan and Freeman, 2007; Nair, 2005 §2.2 reviews). Crucially, this

means that observed BOLD activity may represent a mix of both excitatory and inhibitory inputs. A region which receives subthreshold excitatory input, or one which is both excited and inhibited enough to suppress further activation, may nevertheless show a measurable---even strong---BOLD response (Logothetis, 2008). These 'active' regions would make no *functional* contribution to the experimental task, though.

Hence the potential confound. The fact that phylogenetically older areas are more often active may be explained by redeployment. It may also be explained by assuming that older areas simply receive more input than newer ones. This potential confound may be manageable in individual fMRI experiments. Meta-analyses increase statistical power, however, making even small effects more likely to be noticed. Further, meta-analyses necessarily lack the fine-grained detail that might normally allow these functional byproducts to be explained away.

This is not a merely academic worry. To give one example: Mahon and Caramazza recently reviewed the fMRI evidence for the sensorimotor account of conceptual grounding (including many of the studies reviewed by Anderson in §4). They conclude that the evidence is consistent with a view on which the semantic analysis of a sentence activates motor areas as an inevitable consequence of spreading activation within a complex neural system (Mahon and Caramazza, 2008). Thus, while the motor system may often be activated during semantic analysis tasks, this activation need not represent a functional contribution to semantic analysis itself. It would instead be the natural consequence of a system in which the typical *consumers* of representations were primed for action, but inhibited (or simply under-excited) if their further, functionally specific, contribution was unnecessary. Note that a reliance on subtraction-based imaging does not obviate this problem: distinct semantic terms may well prime distinct motor regions.

Spreading activation and massive redeployment are not mutually exclusive hypotheses. Indeed, it seems to me that the redeployment model should accept some version of the former. If the brain does consist of pluripotent regions that flexibly combine into functional networks, problems of coordination---and especially the necessity of inhibiting preponent but contextually inappropriate dispositions---become paramount. Further, phylogenetically newer areas evolved in the context of organisms which already had well-functioning brains. We should expect newer areas to project heavily to older areas, both because the information they provide might be relevant to these older adaptive repertoires and because those older functions will need to be coordinated in light of newer capacities.

The crucial question, then, is how we might get experimental evidence that favors redeployment over the alternatives. Anderson suggests several plausible possibilities for testing his hypothesis. I'd suggest a further possibility: the use of fMRI adaptation. This technique exploits the fact that recently active neurons tend to show a decreased response to further stimulation; a decreased BOLD response across experimental conditions thus provides evidence that a region is making the same contribution to both tasks. Adaptation would allow one to distinguish areas which are truly

redeployed from those which have simply parcellated into functionally specific areas that are smaller than the resolution of fMRI (an open evolutionary possibility; Streidter, 2005 Ch7 reviews). Further, adaptation would allow us to distinguish areas that are truly re-used from areas that are involved in the coordination of complex networks.

Crinion et al. used this technique to distinguish the contribution of various cortical and subcortical areas in language processing (Crinion et al., 2006). Proficient bilingual speakers showed both within- and cross-language priming in the left anterior temporal lobe, suggesting a shared substrate for semantic information (and thus supporting a form of re-use). Activation in the left caudate, in contrast, did not show a priming effect. This supports a hypothesized role for the caudate in language *control*: plausibly, the caudate helps inhibit contextually inappropriate responses, a real problem when distinct languages partially share the same substrate. fMRI adaptation might thus allow us to disentangle the contribution of frequently-activated areas in a variety of tasks, and so provide a further test of Anderson's intriguing hypothesis.

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