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In favor of a 'fractionation' view of ventral parietal cortex: comment on Cabeza *et al.*

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In 'Cognitive contributions of the ventral parietal cortex: an integrative theoretical account', Cabeza *et al.* [1] examine data from manuscripts that explore (i) perceptual/motor reorienting, (ii) episodic memory retrieval, (iii) language, (iv) number processing, (v) theory of mind, and (vi) episodic memory encoding, and conclude that the activity in ventral parietal cortex (VPC) in these studies is 'largely overlapping with some differences around the edges'. As a result of this purported overlapping activity, a unifying theory (the bottom-up attention – BUA – hypothesis) is proposed.

Cabeza *et al.* state that 'a potential problem for the [BUA] hypothesis would be evidence of fMRI dissociations between anterior and posterior VPC subregions', pitting this 'overarching' BUA view against a 'fractionation' view, wherein distinct cognitive operations are found in different regions of VPC. Something akin to the 'fractionation' view, that (at least most of) the cortex is organized in terms of discrete cortical areas with different concentrations of input and outputs, different cytoarchitecture, and different functional properties, is the standard view of cortical organization (cf. [2,3]). Here, we highlight evidence of such dissociations within VPC, using the data examined in Cabeza *et al.* [1], along with other examples from the literature, and argue that considerable evidence supports a 'fractionation' view of cognitive operations.

Cabeza *et al.* claim that, 'meta-analyses do not show dissociations between [subregions of VPC]', citing [4]. In actuality, the Hutchinson *et al.* [4] meta-analysis shows that the foci extracted from studies of bottom-up attention cluster in the supramarginal gyrus, whereas foci extracted from studies of memory retrieval (specifically recollection) are located in the angular gyrus. These analyses led Hutchinson *et al.* to conclude that 'reflexive attention foci fall unambiguously anterior to retrieval effects in left ventral PPC [posterior parietal cortex]' (p. 352).

The evidence marshaled in Cabeza *et al.* for the claim that disparate tasks recruit overlapping regions in VPC is difficult to evaluate, given the depiction of these regions on separate volumes and surface renderings. To facilitate direct comparisons, we returned to the original studies highlighted in Cabeza *et al.* and plotted 1 cm spherical regions of interest around the reported peak coordinates (Figure 1). At this scale, the majority of these regions are non-overlapping. Furthermore, they are consistent with

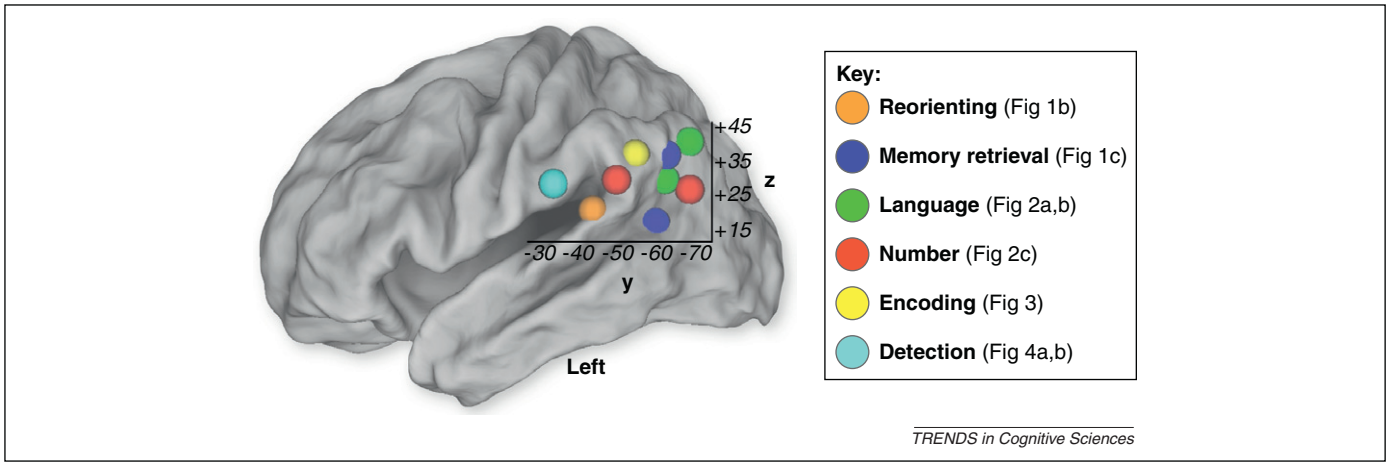

Figure 1. Data plotted from studies highlighted in Cabeza *et al.* reveal many non-overlapping peaks of activation in left ventral parietal cortex. For each of the left hemisphere maps presented in Figures 1-4 of Cabeza *et al.*, we returned to the original manuscript to obtain the peak coordinate reported there. We then simply mapped these foci (1 cm diameter spheres, 81 voxels at 2 mm^3) onto a surface rendering of the left cerebral cortex [10] (http://brainmap.wustl.edu/caret) and color-coded them based on their putative function. The scale represents the approximate y and z coordinate (MNI space).

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the distinctions from Hutchinson *et al.*: the foci plotted in Figure 1 for 'reorienting' (orange) and 'memory retrieval' (blue) are in the supramarginal and angular gyri, respectively, and are approximately 3 cm apart.

Other work supports anterior/posterior distinctions in VPC. For example, Cohen *et al.* [5] define borders between putative functional areas based on abrupt changes in global patterns of functional connectivity. Cohen *et al.* highlight an angular/supramarginal gyrus distinction as the prime example of a strong border of rapid change (see Figure 2 in [5]). Thus, the statement made by Cabeza *et al.* that 'the overarching view can also explain differences around the edges under the assumption that the strength of VPC connectivity with different brain regions differs gradually across VPC subregions' is not supported by efforts that have been made to directly test such a claim (see also [6]).

These distinctions between supramarginal and angular gyri provide strong counter-evidence against an 'overarching' view. Other data [6–9] strongly suggest that there are further divisions beyond the anterior/posterior distinction. For example, Nelson *et al.* [6] used functional connectivity mapping, functional network analyses, and differences in task-evoked fMRI activity to parcellate left lateral parietal cortex; the resulting data strongly favors a 'fractionation' view of VPC.

We welcome further discussion regarding the exact nature of fractionation in VPC and its relation to function, but we do not doubt its existence.

References

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Response to Nelson *et al.*: ventral parietal subdivisions are not incompatible with an overarching function

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Nelson, McDermott, and Petersen (NMP) [1] raised four main objections against an overarching view of ventral parietal cortex (VPC) function [2]. First, pointing to specialized subregions within visual cortex, they argued that fractionation is the 'standard view of cortical organization'. The existence of specialized subregions within a broad area, however, is a premise shared by both views [2]; the critical difference between them is that the fractionation view assumes that neighboring subregions can mediate unrelated cognitive processes, whereas the overarching view assumes that they mediate different aspects of a broad function. Contrary to NMP, the consensus in vision favors the overarching view, because aggregates of different visual cortex subregions mediate broad functional components of visual processing, such as those associated with the dorsal and ventral streams [3,4]. Likewise, subregions of lateral prefrontal cortex are assumed to mediate different aspects of a broad control function [5,6].

Second, NMP disagreed with our point that meta-analyses of fMRI activations do not show sharp dissociations between the supramarginal gyrus (SMG) and the angular gyrus (AG). A 'sharp dissociation', in our view, would entail obtaining evidence that a task frequently activates SMG but never AG, and vice versa for another task. To our knowledge, no meta-analysis has shown that SMG or AG was never activated by one of the functions we reviewed. For example, although perceptual reorienting activations are more frequent in the SMG and episodic retrieval activations in the AG [7], as we noted, perceptual reorienting activations are often found in AG, and retrieval activations in SMG. When these tasks are compared within-subjects, their activations do in fact overlap [8].

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