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The space for memory in posterior parietal cortex: Re-analyses of bottom-up attention data

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ABSTRACT

The ventral (VPC) and dorsal sectors of the posterior parietal cortex are long known to mediate bottom-up and top-down attention to the external space. Because these regions also are implicated in retrieval of episodic memories, we proposed they also mediate attention to the internal (memory) space. One objection to this Attention to Memory hypothesis is that parietal regions involved in directing attention to percepts and memory are spatially adjacent but not overlapping, suggesting that different neural mechanisms are involved in each. This misalignment is most pronounced in VPC. Here, we re-examine fMRI data, and show that (1) different VPC subregions are associated with different aspects of bottom-up attention to the external space, (2) only VPC subregions showing invalid cue (but not oddball) effects overlap with those associated with episodic memory retrieval, leading us to conclude that (3) the same regions that signal unexpected percepts also signal unexpected memories. These findings are consistent with the 'overarching view' of VPC as deploying bottom-up attention during both perception and episodic memory retrieval, and suggest that the degree of anatomical convergence across the two domains depends on the correspondence between the specific bottom-up attention demands of perceptual and memory tasks.

The posterior parietal cortex has long been associated with attention. On one prominent view, its dorsal and ventral sectors have different functional properties: the dorsal parietal cortex (DPC), together with dorsal frontal regions, mediates top-down attention, which enables selection of stimuli based on internal goals, whereas the ventral parietal cortex (VPC), together with ventral frontal regions, mediates the bottom-up orienting of attention to relevant stimuli (Corbetta and Shulman, 2002; Corbetta et al., 2008; Wolfe and Horowitz, 2017). In a functional neuroimaging (fMRI) experiment using the "Posner" paradigm, DPC was indeed maximally engaged during the cue period, when participants search for a target, whereas VPC was engaged during target detection, and responded more strongly to invalidly compared to validly cued targets (Corbetta et al., 2000; Hutchinson et al., 2009 for a review). VPC is also activated when individuals detect infrequent stimuli in the environment, such as oddball stimuli, or even just (passively) encounter changes in sensory stimulation, suggesting it helps reorient attention towards relevant stimuli previously outside the focus of processing (Corbetta et al., 2008). Accordingly, patients with lesions in the right VPC may have unilateral neglect, a deficit in detecting contralesional (left) stimuli across diverse sensory modalities in the absence of sensory deficits, which makes a strong case for the involvement of posterior parietal cortex in attention. Notably, unilateral neglect can hinder the deployment of attention to internal representations as well as the external space. Bisiach and Luzzatti (1978) had two neglect patients describe Piazza del Duomo in Milan (their hometown) from memory, and they failed to report the features of the left side of the piazza from their perspective. Strikingly, the neglected features got to be mentioned once the patients were prompted to imagine the piazza from the opposite perspective, so that the features now fell on the right side of the piazza.

In the last 15 years, a conspicuous body of research has pointed to the posterior parietal cortex as an important neural correlate of episodic memory, the ability to recollect or recognize specific past experiences (Wagner et al., 2005). Episodic memory retrieval is long known to be supported by medial temporal and dorsolateral and anterior prefrontal

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regions (Spaniol et al., 2009). Recent research, however, has revealed that the posterior parietal cortex consistently shows a 'retrieval success effect', that is, greater activity for successfully recognized old items than successfully rejected new items (Ciaramelli et al., 2008; Cabeza et al., 2008). Because the posterior parietal cortex has been associated with attention – not memory – there have been many attempts to explain its involvement in episodic memory retrieval. Echoing the distinction between the roles of DPC and VPC in attention, we proposed the Attention to Memory model, according to which DPC supports the allocation of attentional resources to memory retrieval operations, for example during memory search and post-retrieval monitor (top-down attention to memory), whereas VPC mediates the change in the locus of attention following detection of relevant memories (bottom-up attention to memory; Ciaramelli et al., 2008; Cabeza et al., 2008). The most obvious example of bottom-up attention to memory is involuntary retrieval, as in the famous case of the Proustian character who (automatically) re-experienced vivid past memories upon tasting a madeleine. An example of top-down attention to memory would be searching memory voluntarily for the recipe of madeleines.

A number of studies have provided empirical support to this model. For example, in a 'Posner-like' recognition experiment (Ciaramelli et al., 2010a), DPC was active when participants anticipated a memory target based on a cue (top-down attention to memory), whereas VPC was active when memory targets were detected in the absence of cues, and more active for invalidly vs. validly cued memory targets (bottom-up attention to memory). Moreover, several meta-analyses have pointed out that DPC consistently shows greater activity for low than high confidence memory judgments, when the top-down engagement of search and monitoring operations is presumably maximal, whereas VPC is prominently active during the recognition of items accompanied by high confidence or the subjective feeling of recollection, which were capable to capture attention bottom-up (see Ciaramelli et al., 2008; Cabeza et al., 2008; Rugg and King, 2008 for reviews).

Other evidence supporting the Attention to Memory model comes from the neuropsychological study of patients with lesions to the posterior parietal cortex. If the contribution of parietal regions to episodic retrieval are due to their role in attention, one should expect the effects of parietal damage on episodic memory to resemble the neglect syndrome in some respect. For example, patients with neglect are known to be impaired in detecting stimuli spontaneously (impaired bottom-up attention) but able to direct attention voluntarily to stimuli in the neglected hemifield (preserved top-down attention). Analogously, we have noted that patients with lesions to the posterior parietal cortex, though not amnesic, show subtle memory impairments that are suggestive of a 'memory neglect'. Berryhill, Phuong, Picasso, Cabeza, and Olson (2007) found that patients with VPC lesions were impaired in recalling autobiographical memories spontaneously, but could recall their memories normally if cued by specific questions. These findings suggest that patients' memories are intact but not capable to capture attention bottom-up and enter consciousness, hence they are not reported. By contrast, the same memories can be accessed through specific questions that engage preserved top-down attention. Memory neglect findings make contact with the Piazza del Duomo experiment, because that, too, proves that the memory of the (whole) piazza was preserved, but that (left-sided) stimuli were not attended normally, perhaps because they failed to capture attention in a bottom-up fashion. In later experiments, indeed, we found that patients with VPC lesions were poor at recalling the landmarks on a map of downtown Toronto, but could place the same landmarks on the map upon request (Ciaramelli et al., 2010a), again pointing to a disproportionate deficit in spontaneous (as opposed to prompted) spatial memory retrieval, mirroring the autobiographical memory domain. Of course, the left/right dimension is relevant when describing a spatial array, such as a piazza, but not when narrating a memory, which makes the Piazza del Duomo and autobiographical memory findings not fully comparable. In this respect, more relevant is the novel evidence that patients with neglect are impaired in projecting themselves back into the past (Anelli et al., 2018), which is represented on the left side of an imaginary mental time line (Bonato et al., 2012), and in categorizing events that took place before ('left of') compared to after ('right of') a central, reference event (Bonato et al., 2016), which encourages us to inquire further into the relation between spatial attention and episodic memory retrieval.

Other studies have challenged the Attention to Memory model on a number of points. One is the different localization of posterior parietal cortex activity while orienting attention to the internal (memories) vs. external space (percepts) (Hutchinson et al., 2009; Sestieri et al., 2017). The misalignment is particularly apparent in VPC, and for this reason in this paper we will focus on this sector of the posterior parietal cortex. First of all, VPC activations related to bottom-up attention to memory tend to be stronger in the left hemisphere, whereas those related to bottom-up attention to the external space tend to be stronger in the right hemisphere. It must be noted that episodic retrieval studies tend to use meaningful, verbal stimuli, whereas attention studies tend to use meaningless, perceptual stimuli, and, therefore, it is possible that lateralization differences reflect differences in stimuli. Second, a meta-analysis of fMRI studies pointed out that, even with respect to the left VPC foci, those associated with bottom-up attention to the external space cluster anteriorly, around the supramarginal gyrus (mean coordinates: $x = -44$, $y = -45$, $z = 36$), whereas those associated with bottom-up attention to memory (mean coordinates: $x = -42$, $y = -56$, $z = 36$), and retrieval success effects in general (mean coordinates: $x = -41$, $y = -56$, $z = 41$), are situated more posteriorly, closer to the angular gyrus (Hutchinson et al., 2009). Because they did not overlap completely, the authors concluded that retrieval effects in posterior parietal cortex likely reflect functionally distinct mechanisms from attention, 'though attention must play a role in aspects of retrieval' (Hutchinson et al., 2009, p. 343). Here one could ask which aspect of retrieval, and which type of attention. The authors addressed the former. In an fMRI study probing different aspects of episodic memory retrieval, Hutchinson et al. (2012) detected multiple response profiles in the posterior parietal cortex, of which some were deemed reflective of attention to memory, but others were not. Within VPC, activity in the temporo-parietal junction tracked bottom-up attention to memory, whereas activity in the angular gyrus was argued to reflect instead the operation of an 'outcome buffer' for recollected information (see Rugg and King, 2018). It was concluded that a binary account based on top-down and bottom-up attention does not capture the multiple episodic memory responses exhibited by the posterior parietal cortex.

We do not think that the lack of general overlap in parietal regions mediating attention to the external space vs. memory, as the one shown by Hutchinson et al. (2009), necessarily disqualifies an attentional account of the role of the posterior parietal cortex in episodic retrieval. Our primary reason is that just as posterior parietal cortex subregions show different response profiles during episodic memory retrieval, they display a similar heterogeneity in attention to external stimuli that goes beyond the coarse distinction between bottom-up (VPC) and top-down attention (DPC) (Corbetta et al., 2008).

Consider VPC. In Table 1 we redisplay the foci of bottom-up attention reported by Hutchinson et al. (2009), this time not collapsing across all studies investigating bottom-up attention, but separating them according to whether they pertained to the detection of oddball targets or of invalidly cued targets, two attentional tasks that differentially engage different aspects of bottom-up attention (e.g., target detection, reorienting of attention). We found that oddball effects clustered in the supramarginal gyrus ($VPC_{Oddball}$; median coordinates: $x = -53$, $y = -40$, $z = 33$), whereas invalid cue effects clustered in a more posterior region of VPC closer to the angular gyrus ($VPC_{Invalid}$; median coordinates: $x = -34$, $y = -52$, $z = 40$),

Table 1
Coordinates of bottom-up attention to invalidly cued or oddball sensory targets (from Hutchinson et al., 2009).

	x	Y	z
Invalid cueing effects			
Indovina and Macaluso (2007)	−30	−55	41
	−32	−53	38
	−12	−60	45
Kincade et al. (2005)	−57	−43	31
Macaluso and Patria (2007)	−30	−47	38
Vossel et al. (2006)	−42	−51	44
	−36	−45	44
Macaluso et al. (2002)	−58	−52	28
Median coordinate	*−34*	*−52*	*40*
Oddball effects			
Bledowski et al. (2004)	−51	−29	35
	−47	−40	46
Braver et al. (2001)	−53	−27	24
Clark et al. (2000)	−61	−45	21
Kiehl et al. (2001)	−38	−48	60
	−56	−41	30
Linden et al. (1999)	−55	−34	33
	−58	−40	27
	−55	−37	33
	−46	−39	46
Marois et al. (2000)	−21	−63	51
	−54	−34	23
Mayer et al. (2006)	−42	−46	45
	−31	−50	37
Menon et al. (1997)	−60	−32	30
	−56	−48	32
Strange and Dolan (2007)	−48	−54	33
Median coordinates	*−53*	*−40*	*33*

Note. All coordinates are reported in Talaraich space.

with a significant difference in the *y* coordinates of $VPC_{Oddball}$ and $VPC_{Invalid}$ foci ($t_{1,23} = 2.54$, $p = 0.02$; see Fig. 1). Thus, within VPC, different regions are associated with specific components of bottom-up attention (see also Cabeza et al., 2012). Accordingly, transcranial magnetic stimulation evidence indicates that the angular - but not the supramarginal - gyrus is critical for reorienting attention after invalid cueing (e.g., Chambers et al., 2004).

Interestingly, $VPC_{Invalid}$ is quite close to VPC regions showing episodic retrieval success effects (median coordinates: x = −41, y = −61, z = 42; Cabeza et al., 2008), and somewhat in between the median coordinates for bottom-up (median coordinates: x = −50, y = - 57, z = 38; Ciaramelli et al., 2008) and top-down attention to memory effects (median coordinates: x = −36, y = - 57, z = 42; Ciaramelli et al., 2008) (Fig. 1). One possibility, therefore, is that VPC regions implicated in episodic memory do not generally overlap with all those mediating bottom-up attention (as shown by Hutchinson et al., 2009), but do overlap with those mediating the specific subcomponents of bottom-up attention that are more crucially engaged by episodic memory retrieval, such as bottom-up reorienting of attention. Clearly, different components of bottom-up attention, including reorienting of attention, are expected to be differentially engaged during episodic retrieval depending on the memory task at hand. For example, in an fMRI experiment (Ciaramelli et al., 2010a), we had individuals study word pairs and then distinguish studied words from new words either in the absence of cues, after a valid cue (i.e., the word with which they were paired at study), or after an invalid cue (i.e., a word studied in the context of another pair), in which case bottom-up reorienting of attention should be engaged the most. If, as we think, VPC subregions mediating this specific reorienting component of bottom-up attention to the external space would also be deployed to internal (memory) contents, then we expect that $VPC_{Invalid}$ - but not necessarily $VPC_{Oddball}$ - should respond more to invalidly than to validly cued memory targets.

To test this prediction, we created 9 mm spherical regions of interest (ROIs) centered on $VPC_{Invalid}$ and $VPC_{Oddball}$, and extracted the mean percent signal change from these ROIs for validly cued old items, invalidly cued old items, uncued old items, and uncued new items in Ciaramelli et al. (2010a) (see Fig. 2). We ran an ANOVA on percent signal changes with ROI and Item type as factors, and found a significant effect of ROI ($F_{1,13} = 17.36$; $p = 0.001$) and a significant effect of Item

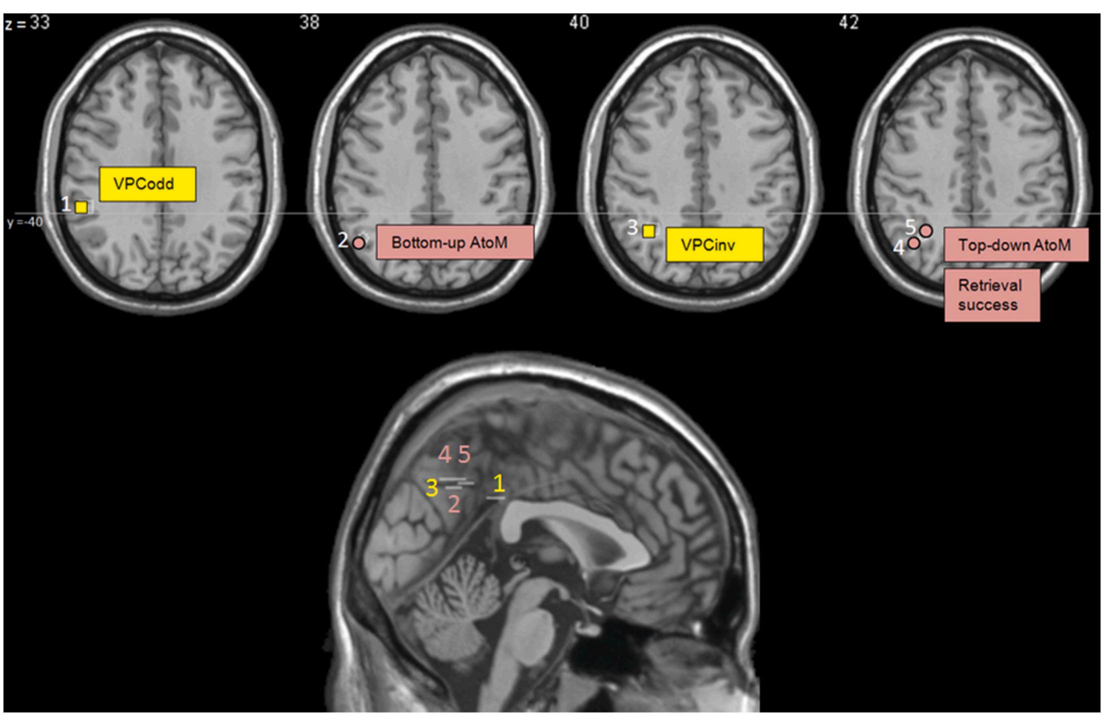

Fig. 1. Bottom-up attention and memory in left posterior parietal cortex. Centers of mass for attentional activations related to oddball effects (VPC_{odd}; x = −53, y = −40, z = 33) and invalid cueing effects (VPC_{inv}; x = −34, y = −52, z = 40). VPC_{inv} is more anterior than VPC_{odd} and close to the centers of mass of episodic memory effects, including retrieval success (x = −41, y = −61, z = 42; Cabeza et al., 2008), bottom-up attention to memory (AtoM) (x = −50, y = −57, z = 38; Ciaramelli et al., 2008) and top-down attention to memory (x = −36, y = −57, z = 42; Ciaramelli et al., 2008).

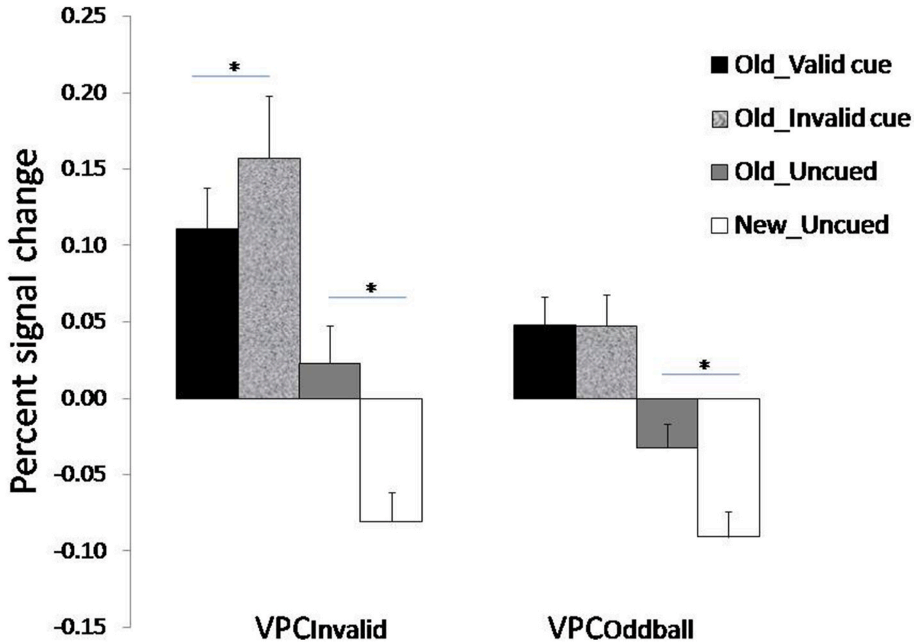

Fig. 2. Memory properties of bottom-up attention regions. Mean percent signal change of VPC regions associated with the detection of invalidly cued ($VPC_{Invalid}$) and oddball sensory stimuli ($VPC_{Oddball}$) during recognition of validly cued, invalidly cued, and uncued old words and new words. Error bars indicate the standard error of the mean, and asterisks indicate significant differences ($p < 0.05$).

type ($F_{3,39} = 19.06$; $p = 0.001$), qualified by a significant ROI X Item type interaction ($F_{3,39} = 3.89$; $p = 0.015$). Post hoc Newmann-Keuls comparisons showed that both ROIs showed more activity for (uncued) old compared to new items (retrieval success effect; $p < 0.02$ in both cases). In line with our hypothesis, whereas the $VPC_{Invalid}$ ROI was more active during the recognition of invalidly vs. validly cued memory targets ($p = 0.03$), the $VPC_{Oddball}$ ROI responded similarly to the two classes of items ($p = 0.98$) (Fig. 2).

Consistent with an 'overarching view' of the role of VPC in bottom-up attention (Cabeza et al., 2012), our results show that different VPC subregions are associated with different components of bottom-up attention to the external space, and differentially sensitive to episodic memory retrieval depending on the specific demands posed by episodic memory on bottom-up attention. On this view, one should expect the anatomic overlap between regions associated with bottom-up attention to the external vs. internal (memory) space not to be general (Hutchinson et al., 2009), but strictly dependent on the correspondence between the components of bottom-up attention needed to detect percepts and memories. Future studies will be needed to clarify whether the posterior parietal cortex is fractionated along attention and memory properties, or, as we continue to claim, in line with the Attention to Memory model, that common attentional (and possibly other) processes are engaged for perception and episodic memory retrieval.

Declaration of competing interest

The authors declare no potential sources of conflict of interest.

CRediT authorship contribution statement

Elisa Ciaramelli: Conceptualization, Formal analysis, Writing - original draft, Writing - review & editing. **Morris Moscovitch:** Conceptualization, Writing - review & editing.

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