Domain-Generality of Parietal Attentional Processes and their Implications for Old Age

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Abstract

The posterior parietal cortex (PPC) has been reliably implicated in visuospatial attention, such that the dorsal regions (dPPC) are associated with voluntary ‘top-down’ attention, whereas the ventral regions (vPPC) are associated with automatic ‘bottom-up’ attentional processes. The Attention-to-Memory model (AtoM: Ciaramelli, Grady, & Moscovitch, 2008) has suggested that it also plays a similar role in memory retrieval, suggesting that the PPC mediates a domain-general attentional process. Furthermore, domain-generality of attentional processes may account for differences in perception and memory function accompanying old age. This study examined domain-generality by determining the shared variance in performance of tasks thought to recruit top-down and bottom-up attentional processes mediated across both domains. Results clearly suggested generality across domains in top-down processing; and in bottom-up processing, depending on its operationalization. Ageing was characterized by an absence of shared variance across domains and slower reaction times during bottom-up attentional reorienting only in perception.
Acknowledgments

*They say it takes a village to raise a child. I think it applies to graduate students, too...*

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1 Introduction

1.1 Episodic memory and the posterior parietal cortex

Since the seminal work of Scoville and Milner (1957), who observed profound amnesia following bilateral hippocampal ablation in patient H.M., episodic memory has been intrinsically associated with the hippocampus and the surrounding medial temporal lobes (MTL). A hippocampally-driven account of episodic memory has continued to garner strong support in the rodent and nonhuman primate (Eichenbaum, 2007; Eichenbaum, Sauvage, Fortin, Komorowski, & Lipton, 2012), human patient (Moscovitch et al., 2005), and functional neuroimaging literatures (Ranganath, 2010a; Rugg et al., 2012). As with any attempt to localize brain function, however, one must recognize that the hippocampus cannot mediate a complex cognitive process such as episodic memory on its own. It is instead the dynamic interactions between a specific region, such as the hippocampus, and other distributed brain regions that allow for specific neural computations to produce complex cognition (Bressler & Menon, 2010; Cabeza & Moscovitch, 2013). Structural and functional connections with prefrontal cortices (PFC), for example, have become theoretical mainstays when considering the large-scale networks involved in episodic memory processes (Andrews-Hanna, Reidler, Sepulcre, Poulin, & Buckner, 2010; Cabeza & Moscovitch, 2013; Huijbers et al., 2012; Miller & D’Esposito, 2012; Moscovitch, 2008; Preston & Eichenbaum, 2013; Ranganath, 2010b; Rugg & Vilberg, 2013). Moscovitch (2008) described the hippocampus as a domain-specific module (i.e., processes a specific domain of cognition: explicit mnemonic information¹) that obligatorily encodes each relevant memory trace, and its web of associations with conscious experience, randomly and independently of one another, as if they are “beads in a jar” (p. 65, para. 7). The PFC then organizes, monitors, and facilitates the retrieval of a coherent memory, or “string(s) … the beads into different necklaces to be worn as befits the occasion” (p. 65, para. 7). More recent developments in understanding interactions in this episodic memory network have suggested yet another important component: the lateral posterior parietal cortices (PPC) (for reviews, see Cabeza, 2008; Cabeza, Ciaramelli,

¹ The hippocampus may be domain-specific, but there is considerable debate as to what that domain is. For some other accounts of hippocampal function, see: Lee, Yeung, & Barense (2012); Maguire & Mullaly (2013); Schacter et al. (2012); Tulving (2002).
Moscovitch, 2012a; Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Ciaramelli, Grady, & Moscovitch, 2008; Nelson, McDermott, Wig, Schlaggar, & Petersen, 2013; Vilberg & Rugg, 2008; Wagner, Shannon, Kahn & Buckner, 2005).

Before reviewing the functional relationship between the PPC and episodic memory processes, it is important first to characterize its anatomy and connectivity within the brain. The PPC is a large swath of cortex in the parietal lobes, posterior to the post-central sulcus (see Figure 1). It is located in lateral posterior parietal cortices, distinct from the medial regions (e.g., precuneus) that have been also associated with episodic memory retrieval (for a review, see Cavanna & Trimble, 2006). The PPC can be subdivided horizontally along the intraparietal sulcus (IPS), creating dorsal (i.e., BA 7, superior parietal lobule) and ventral regions (i.e., BA 39, supramarginal gyrus; BA 40, angular gyrus). In terms of connectivity, the PPC shows robust structural projections between regions of the prefrontal cortex, medial parietal and medial temporal lobes (Pandya & Seltzer, 1982; Petrides & Pandya, 1984; Schmahmann et al., 2007; Selemon & Goldman-Rakic, 1985, 1988). Similarly, functional associations as measured using BOLD functional magnetic resonance imaging (fMRI) have been observed between the PPC, hippocampus, and PFC regions while participants are at rest (Vincent et al., 2006; Vincent, Kahn, Snyder, Raichle, & Buckner, 2008) and during episodic memory performance (Burianová, Ciaramelli, Grady, & Moscovitch, 2012; Hayama, Vilberg, & Rugg, 2012; Huijbers et al., 2012; Miller & D’Esposito, 2012; Yonelinas, Otten, Shaw & Rugg, 2005). Therefore, based on the nature of structural and functional connectivity between the PPC and the brain regions traditionally associated with episodic memory, the PPC is in a viable neural context to contribute to episodic memory processes.

The first indications that the PPC was involved in mnemonic processing came from electroencephalographic (EEG) studies examining event-related potentials (ERPs) (for reviews, see Rugg, 1995; Rugg & Curran, 2007). Using recognition memory paradigms, a left-lateralized and positive-going ERP (i.e., P600) was consistently observed over the parietal cortices when contrasting waveforms associated with correctly identified old items (i.e., hits) against correctly identified new items (i.e., correct rejections). Even contrasts based on depth of encoding (Rugg et al., 1998), comparing deeply against shallowly encoded hits, would produce this effect – now known as the parietal ‘old/new’ effect. Based on the reliability of this finding, it became clear
that the PPC was responding preferentially to old information, and was thus engaged during mnemonic processing. Subsequent studies using fMRI and positron emission tomography (PET) have also confirmed reliable recruitment of the PPC during episodic memory performance (Cabeza & Nyberg, 2000; Wagner et al., 2005). For example, meta-analyses of episodic recollection, a process considered to be strongly hippocampally-driven (Rugg et al., 2012), have demonstrated strong PPC activity (Simons et al., 2008; Skinner & Fernandes, 2007). One analysis demonstrated even more reliable activity in the PPC than traditional MTL regions (Simons et al., 2008, Figure 1).

However, the functional role of the PPC in episodic memory remained unclear. A particularly enigmatic finding was the absence of an observable memory deficit following lesions to the PPC (Berryhill, 2012). According to traditional neuropsychological work, damage to the PPC was not associated with memory deficits but with deficits in attentional processes, resulting in syndromes such as hemineglect (for a review, see Mesulam, 1981). Though it remains the case that lesions to the PPC do not leave the patient amnesic, recent work has shown more subtle changes in episodic memory performance following damage to the PPC (for a review, see Berryhill, 2012). A study examining autobiographical memory of two patients with bilateral PPC damage reported that the patients were able to freely recall personal memories, but the memories were broadly lacking detail relative to healthy controls (Berryhill, Phuong, Picasso, Cabeza, & Olson, 2007). When these patients were probed for such details by the experimenter, their memory performance was no longer impaired. Similarly, patients with PPC lesions have an impaired subjective recollective experience, or a reduction in the perceived richness of their memories, where they are able to access episodic details but tend to provide low subjective confidence ratings (Simons, Peers, Mazuz, Berryhill, & Olson, 2010).

Due to its robust connectivity within an ‘episodic memory network’ (Rugg & Vilberg, 2013), reliable engagement during episodic memory tasks (Wagner et al., 2005), and the subtle changes in episodic memory performance accompanying damage to this region (Berryhill, 2012), it appears clear that the PPC is contributing to episodic memory processing. Though this may be evident, its specific functional role is still debated. Wagner, Shannon, Kahn & Buckner (2005) provided the first integrative attempt at exploring possible theoretical accounts of the computations engaged by the PPC. Stemming from their initial work, many further elaborated
hypotheses explaining PPC function have emerged, such as: formation of memory strength signals (Wagner et al., 2005), maintaining/representing multimodal episodic information (Vilberg & Rugg, 2008), and orienting internal attention toward mnemonic information (Cabeza, 2008; Ciaramelli, Grady, & Moscovitch, 2008; Jaeger et al., 2013). One model that fits particularly well with our current understanding of episodic memory and brain organization, the Attention-to-Memory (AtoM) model, will provide the framework for the present study. The AtoM model proposes that the role of the PPC in episodic memory is an extension of its traditional role in attentional orienting in visuospatial perception, reflecting a fundamentally similar attentional process across both domains. Before the model is discussed, the role of the PPC in visuospatial attention will be reviewed.

1.2 Attention-to-Perception

The AtoM model was initially proposed by Ciaramelli, Grady, & Moscovitch (2008) (see also, Cabeza, 2008) and interpreted the involvement of the PPC in mnemonic processing through its traditional role in the allocation of visuospatial attention (for reviews, see Behrmann, Geng, & Shomenstein, 2004; Corbetta & Shulman, 2002; Corbetta, Patel, & Shulman, 2008; Shomstein, 2012; Vossel, Geng, & Fink, 2013). In terms of visuospatial attention, the PPC is considered critical during the engagement of both top-down and bottom-up attentional processes (for a review of these attentional processes, see Yantis, 2000). Top-down, or goal-driven, attention refers to the ability to use acquired predictive information to bias incoming information. For example, consider the typical Posner spatial cueing task (Posner, 1980), where a target will appear on the right or left side of the screen. Before the target appears, a predictive cue is presented (e.g., a central arrow) which indicates where the target is likely to appear – the ability to use this information to strategically bias attention towards the cued side is referred to as top-down. Top-down influences over attentional control do not function independently, but must interact with the properties of the attended stimulus itself (Desimone & Duncan, 1995). Bottom-up, or stimulus-driven, attention refers to the relatively automatic allocation of attention towards a salient or behaviourally relevant target. Using the same example, detecting the target without any predictive information (e.g., a meaningless cue) would engage bottom-up attention. Also, bottom-up attention is associated with attentional reorienting from an inappropriate top-down attentional focus to attend to a salient target (e.g., a cue indicated the target would appear on the
left, but instead, it appeared on the right). Recognizing the mismatch between the cue and target is purported to be an automatic bottom-up process, which drives the reorientation of attentional focus towards the appropriate target (Corbetta & Shulman, 2002).

Using such a Posner spatial cueing task, Corbetta, Kincade, Ollinger, McAvoy, & Shulman (2000) determined that top-down and bottom-up visuospatial attention preferentially engaged distinct subregions of the PPC. While in the scanner, participants attended to a screen where a target would appear on either the left or right side, and was preceded by a predictive central arrow. BOLD activations during the cue period (i.e., while the predictive cue was present) and the target period (i.e., when the target was presented) were compared. Activity during the cue period, which would presumably reflect top-down attention, primarily engaged regions of the right dorsal PPC (dPPC) such as the intraparietal sulcus. Conversely, activity during the target period, especially following invalid cueing, engaged relatively ventral PPC (vPPC) regions, such as the inferior parietal lobule (IPL), temporoparietal junction (TPJ), and superior temporal gyrus. Furthermore, patients showing damage relatively localized to the dPPC and vPPC have been similarly reported to show preferential deficits in top-down and bottom-up visuospatial attention, respectively (Shomstein, Lee, & Behrmann, 2010). Though recent work has demonstrated that this dichotomy may not be as strict as previously believed (e.g., dPPC engaged during bottom-up and top-down attention), the general distinction of top-down attention preferentially engaging the dPPC and bottom-up engaging the vPPC has proven consistent (for reviews, see Corbetta, Patel, & Shulman, 2008; Vandenberghe, Molenberghs, & Gillebert, 2012; Vossel, Geng, & Fink, 2013).

### 1.3 Attention-to-Memory

Considering its role in the allocation of visuospatial attention, attentional processes provide a strong framework for interpreting the involvement of the PPC in episodic memory. Ciaramelli et al. (2008) provided a review of retrieval processes in the memory literature that show rather surprising neural correspondence with top-down/bottom-up attentional systems involving the PPC. Beyond overall retrieval success broadly engaging the PPC, recollection and familiarity processes were preferentially associated with the ventral and dorsal regions, respectively. One possible explanation could be that highly salient mnemonic information may be more likely to engage direct retrieval/capture (i.e., bottom-up attention), while items with reduced salience
would instead require greater post-retrieval processing (i.e., top-down attention). As such, recollection is thought to have a direct retrieval component (Dewhurst, Holmes, Brandt, & Dean, 2006; Sheldon & Moscovitch, 2010; cf. Yonelinas, 2002), associated with greater conscious retrieval of contextual details, possibly reflecting bottom-up attention capture of salient mnemonic information (Ciaramelli et al., 2008). Familiarity has been considered as a relatively indirect, effortful retrieval process (Dewhurst, Holmes, Brandt, & Dean, 2006; Sheldon & Moscovitch, 2010; cf. Yonelinas, 2002) associated with recall lacking contextual details, thus relying more heavily on top-down search processes in lieu of capture (Ciaramelli et al., 2008). These findings extended into the memory literature beyond simply recollection and familiarity. For example, the increased salience of mnemonic information in general, as reflected by deep encoding and high memory confidence were associated with activation of the vPPC (i.e., left IPL), while shallow encoding and low confidence were associated with the dPPC (i.e., right SPL). Attentional processes may interact with mnemonic information, such that the vPPC may be associated with the bottom-up capture of salient mnemonic information, and the dPPC with top-down search for non-salient mnemonic information.

A subsequent study by Ciaramelli, Grady, Levine, Ween, & Moscovitch (2010) provided an empirical test of an attention-to-memory hypothesis. In the scanner, participants studied word pairs and performed a cued-recognition test, based on a traditional Posner spatial cueing design. Participants were presented with a predictive cue (i.e., a studied word, non-studied word, or a meaningless cue) and were asked to make a recognition judgment of a subsequently presented target word (i.e., a studied word which was usually the paired associate of the cue, or a non-studied word). Activity associated with a studied cue (i.e., the top-down attentional bias of search toward a paired associate in memory) preferentially engaged the dPPC. Bottom-up attention to memory, as measured when a studied target was detected without cueing information (i.e., meaningless cue and studied target) or after inappropriate cueing (i.e., studied cue and studied target, but from a different pair), was associated with the vPPC. A further examination of this paradigm using patients with lesions in either the vPPC or dPPC also supported such a top-down and bottom-up distinction (Ciaramelli et al., 2010). Patients with lesions of the dPPC did not benefit from predictive cue information relative to normal controls. By comparison, patients with lesions of the vPPC had more difficulty detecting a target after being invalidly cued than did normal controls.
1.4 A domain-general attentional account of PPC function

The focus of attention in the Corbetta & Shulman (2002) studies was externally oriented targets presented on screen. Episodic memory retrieval similarly requires attention, but instead, directed internally towards the mnemonic item of interest (Wagner et al., 2005). Equally, top-down and bottom-up attentional processes in memory and perception generally have been shown to follow the same functional topography in the posterior parietal cortex, where the dPPC is associated with top-down attention and the vPPC is associated with bottom-up attention (Cabeza, 2008; Cabeza, Ciaramelli, & Moscovitch, 2012a; Ciaramelli et al., 2008, 2010; Nee & Jonides, 2009; Uncapher, Hutchinson, & Wagner, 2011; cf. Hutchison et al, 2009). The question remains, however, whether the attentional processes recruited across memory and perception are in fact the same, but simply operating on different inputs. To test this hypothesis, top-down and bottom-up attention in both a perceptual and memory task must be examined, importantly, within the same sample. A study by Cabeza et al. (2011) provided initial support for this claim (cf., Sestieri, Shulman, & Corbetta, 2010). Participants performed a cued-recall task that entailed studying lists of word pairs where each pair would partially overlap with three other pairs to form a four-word chain (e.g., dog-cat, cat-tiger, tiger-stripe). Importantly, the non-contiguous words in these chains and words across different chains did not have strong semantic associations with one another (e.g., dog-tiger), allowing recall to be primarily episodic rather than semantic. Then, during the cued-recall test phase, participants would be presented with a word from one of these chains and would then have to recall the remaining four words, pressing a button upon recalling the last word (e.g., studied word pairs: dog-cat, penguin-tuxedo, tiger-stripe, sour-taste, cat-tiger; cue word: dog; recall: dog, cat, tiger, stripe). Participants also performed a perception task where, instead of attending to a mnemonic chain, they had to attend to serially presented strings of letters and press a button only upon seeing a vowel. BOLD activity measured during the orienting phase (i.e., primarily sampling cue-related activity), when participants attended to strings of items presented either externally (perception) or internally (memory), overlapped in the dPPC (i.e., bilateral IPS) in both tasks. Similarly, activity measured during the detection phase (i.e., primarily sampling response-related activity) showed overlap in the vPPC (i.e., bilateral TPJ). Though activity did largely overlap, the spread of activity in perception tended to be more superior than memory in the IPS, and also more anterior in the TPJ (Cabeza et al., 2011). However, due to the considerable overlap, it was reasonable to conclude that the PPC
could indeed support a domain-general attentional process that can be oriented internally or externally, while the general computations remain the same.

This proposal, however, has been contested, as some researchers argue that the perception and memory activations are fundamentally distinct. Previous meta-analytic work comparing memory and perception-related activation in the PPC support such a distinction, finding that activity for perception is typically more superior in the dPPC and anterior in the vPPC relative to memory-related activity (Hutchinson, Uncapher, & Wagner, 2009; Nelson, McDermott, & Petersen, 2012). Though this may be true, the underlying reason why this disparity exists remains unresolved. As discussed by Cabeza et al. (2012a), there are two relevant theoretical views of cortical organization that speak to this issue. A ‘fractionation’ view is heavily reliant on recent anatomical studies demonstrating that the PPC can be subdivided into distinct components, using techniques such as automated cytoarchitectonics (Caspers et al., 2006, 2008; Scheperjans et al., 2008), diffusion MRI (Mars et al., 2011; Ruschel et al., 2013), task-related functional connectivity (Bzdok et al., 2013), and resting-state boundary mapping (Nelson et al., 2010; Uddin et al., 2010) (for a brief review, see Nelson, McDermott, Wig, Schlaggar, & Petersen, 2013). Considering the PPC is anatomically heterogeneous, ‘fractionation’ suggests that it is misguided to apply a global top-down/bottom-up distinction that overlaps memory and perception, as the existence of PPC subregions suggests they are likely to mediate discrete cognitive functions. Alternatively, an ‘overarching’ view posits that brain organization is parsimonious, and thus, it is more likely that the vPPC and dPPC engage in a global function (i.e., bottom-up and top-down attentional processes, respectively) with the different subregions supporting minor variations in computations based on particular task-demands. As such, extraneous differences between perceptual and memory tasks themselves (e.g., stimuli, response methods, etc.) may largely explain the disparities found in neural activation. This issue also pertains to the Cabeza et al. (2011) study, where the memory and perceptual tasks, though both verbal, were considerably different.

To resolve this issue, it would be necessary to implement a design that employs tasks that differ only at the level of cued attention and required judgement (e.g., perceptual or mnemonic), such that the extraneous properties of the tasks themselves are identical, and then compare the respective performance and topography of neural activity. An ‘overarching’ view, such as
proposed by the AtoM model, would predict that the activation patterns in memory and perception would be much more similar than different under these circumstances – providing concrete evidence for a domain-general attentional process to which the PPC is critical. Beyond spatial overlap, it would also be predicted that the top-down and bottom-up related neural activity would be highly predictive of their across-domain counterpart (e.g., top-down memory and perception) considering they rely upon the same attentional process. A ‘fractionation’ view would predict that the general pattern of differential activity would remain unchanged, therefore suggesting that distinct subregions of the PPC are involved in mediating perceptual and mnemonic processing independently. Also, no shared variance in neural activity would be predicted across domain, because the processes themselves would be domain-specific. Furthermore, the domain-generality of PPC attentional processes could be further assessed using other techniques, such as comparisons across groups. For example, if a certain group has a characteristic change in attentional processing in one domain (e.g., visuospatial attention) – whether neural or behavioural – this change in attentional processing should also be apparent in other domains as well (e.g., memory). It is important to acknowledge, however, neither a purely ‘overarching’ or ‘fractionation’-based view of functional organization in the human brain is likely to prove accurate. It is more likely that both views are appropriate to some degree. Therefore, what remains to be determined is which of the two provides a relatively better characterization of functional organization in the PPC? Interestingly, an ideal testing ground to examine this hypothesis would be in older adults.

1.5 The context of old age

Visuospatial attentional processes are known to change with age (for a review, see Kramer & Madden, 2008; Kramer, Scialfà, Petersen, & Irwin, 2001). In terms of visuospatial orienting, older adults have been reported to show greater sensitivity to cueing effects than younger adults (Langley, Friesen, Saville, & Ciernia, 2011; Lincourt, Folk, & Hoyer, 1997; Nissen & Corkin, 1985) (cf. Folk & Hoyer, 1992), and a subset of these studies have reported the effect being driven by an increase in the cost of invalid cueing (Greenwood & Parasuraman, 1994; Greenwood, Parasuraman, & Haxby, 1993). In a study by Greenwood and Parasuraman (1994), cognitively healthy participants aged 17 – 85 years performed a Posner spatial cueing paradigm, where a letter appeared on the left or right side of the screen preceded by a predictive cue. Two
versions of the task were administered: one was a simple detection task and the other required a vowel/consonant discrimination of the target, where reaction time (RT) was measured. A significant increase in the combined effects of cueing (i.e., the difference in RT between invalid and validly cued trials) became apparent with increasing age, specifically in the discrimination task. Higher combined cueing effects, as per their definition, represent an increased slowing due to the invalid relative to valid cues in older adults. Considering these conditions differ from one another only in terms of whether the cue validly (or invalidly) engages spatial attention, an increased combined cueing effect may reflect an age-related change in bottom-up attention, specifically in the cost of reorienting from an invalid cue. To further confirm this, the data were parsed relative to a neutral cueing condition (benefits = neutral cue RT minus valid cue RT; costs = invalid cue RT minus neutral cue RT), which were then compared across the two oldest subgroups (65-74 year olds vs. 75-84 year olds), where age effects were predicted to be most robust. Although it has been argued that comparisons against a neutral cue may not properly represent cueing costs and benefits (Jonides & Mack, 1984), the results remained consistent with the previous analysis. Benefits in RT, or the effect of valid cueing, did not differ between these two age groups. However, RT costs, or the effect of invalid cueing, were significantly greater for the 75-84 year olds. Therefore, ageing is generally associated with an increase in the effects of attentional cueing, though reports examining its specific composition claim this may possibly represent a deficit in the ability to disengage or reorient from invalid cues in old age (Greenwood, Parasuraman, & Haxby, 1993; Greenwood & Parasuraman, 1994).

Ageing appears to be associated with a characteristic change in visuospatial attention (i.e., increased cost of invalid cueing), and the AtoM model posits that a domain-general attentional process is mediated by the PPC, such that a similar attentional process may also operate on mnemonic information. Thus, it would be expected that a similar age-related increase in combined cueing effects in RT would be observed in a cued memory task. Unless the ageing process itself changes the relationship between attention-to-perception and attention-to-memory, this should provide a straightforward test of this hypothesis.

Beyond simply providing a suitable context to examine the relationship between parietal attentional processes in visuospatial perception and episodic memory, the processes themselves are especially relevant to the cognitive neuroscience of ageing. Older adults are known to show
reduced performance on many aspects of episodic memory relative to younger adults, such as the formation of associations between items (Old & Naveh-Benjamin, 2008), retrieving contextual information (Spencer & Raz, 1995) and relevant episodic details (Levine, Svoboda, Hay, Winocur, & Moscovitch, 2002); while instead relying on semantic gist-based retrieval strategies (Tun, Wingfield, Rosen, & Blanchard, 1998). In a recent fMRI meta-analysis of episodic retrieval studies conducted by Rajah, Maillet, & Grady (in press), when performance was matched across younger and older adults, a clear increase in recruitment of the PPC, especially the IPS and angular gyrus, accompanied old age. Though direct measures of attention were not collected, it may be speculated that this pattern reflects a compensatory mechanism, where older adults must recruit additional PPC attentional processes to bolster episodic memory performance to match younger adults.

Furthermore, ageing is associated with increased distractibility (i.e., attentional capture and processing of irrelevant distractors) during memory tasks (for a review, see Healey, Campbell, & Hasher, 2008), which has again been associated with changes in brain networks involving the PPC (Campbell, Grady, Ng, & Hasher, 2012; Stevens, Hasher, Chiew, & Grady, 2008). Such age-related changes in episodic memory may not be distinct from visuospatial attention processes, considering the evidence also supporting maintained, or even increased, visual attentional capture in old age (for review, see Kramer et al., 2001). For example, Juola, Koshino, Warner, McMickell, and Petersen (2000) administered a spatial cueing paradigm to younger and older adults, in which a target appeared in one of four locations and was preceded by an initial central, and then peripheral, cue. Each age group was divided into two groups, one of whom was told that the peripheral cues were not predictive of the target location but the central cues were, while the other group was told that both the peripheral and central cues were predictive. Unlike younger adults, the older adults were slowed by invalid peripheral cues, even when they were warned they were not predictive and should have been ignored. Therefore, older adult were less able to moderate attentional capture of visuospatial distractors relative to younger adults (Juola et al., 2000; Kramer et al., 2001). Interestingly, when transcranial magnetic stimulation (TMS) was applied to disrupt activity in the superior parietal lobule of the dPPC, the effect of distractibility during visual search increased significantly (Kanai, Dong, Bahrami, & Rees, 2011). Though this was not examined in older adults, this finding clearly demonstrates the role of the PPC in moderating the attentional capture of distractors in visual perception (Corbetta et al., 2008).
Ageing appears to be associated with changes in PPC-mediated attentional processes across perception and memory. In visuospatial attention, ageing is often associated with a deficit in bottom-up attentional reorienting (Greenwood & Parasuraman, 1994; Parasuraman et al., 1993), alongside maintained top-down attention (Greenwood & Parasuraman, 1994; Madden, Whiting, Cabeza, & Huettel, 2004; Parasuraman et al., 1993; Whiting, Madden, Pierce, & Allen, 2005) and bottom-up attentional capture (Juola et al., 2000; Kramer et al., 2001). It is not often, however, that findings from ageing research in the memory literature are framed in terms of top-down and bottom-up attention. Some evidence can be found in the recollection and familiarity literature. Ageing is largely characterized by a deficit in recollection while familiarity is maintained (Levine et al., 2002; Spencer & Raz, 1995). As recollection and familiarity can be framed in terms of bottom-up and top-down processes, respectively (Ciaramelli et al., 2008; Dewhurst, Holmes, Brandt & Dean, 2006; Sheldon & Moscovitch, 2010; cf. Yonelinas, 2002), this literature would also suggest that old age is associated with a particular impairment of bottom-up attention. Furthermore, in the separate literature on distraction in memory tasks, older adults tend to be more distractible than younger adults (Healey, Campbell, & Hasher, 2008). This deficit has been conceptualized as an age-related decline in the ability to delete, or disengage from, irrelevant information within a working memory store (for review, see Hasher, Lustig, & Zacks, 2007). More recent work examining ageing and distractibility in memory has provided support at the neural level, where older adults were less able to disengage from irrelevant information (in terms of BOLD activity as measured by fMRI) when compared to younger adults (Clapp, Rubens, Sabharwal & Gazzaley, 2011).

In sum, it is apparent that ageing affects episodic memory and visuospatial attention processes associated with the PPC. Similar effects of age, such as a decrease in bottom-up attentional reorienting, are apparent across both domains. The emergence of these similar trends across memory and perception may result from age-related changes in a domain-general attentional process involving the PPC; however, further evidence is necessary to determine whether or not this is plausible.

1.6 Current study

The functional role of the PPC in cognitive processes, such as episodic memory and visuospatial attention, remains uncertain. Although the PPC may be anatomically heterogeneous, the
involvement of the PPC in both of these functions, at its core, may be due to a general attentional process operating across mnemonic and perceptual domains (Ciaramelli et al., 2008; Cabeza et al., 2012a). It may equally be possible that these attentional processes are distinct across domains, and in fact, the PPC activations themselves may be distinct when examined with greater anatomical precision (Nelson et al., 2010, 2013). Furthermore, the changes in such attentional processes, and their neural underpinnings, may be a contributing factor to the typical memory decline associated with healthy ageing. The current study attempts to develop and examine a behavioural paradigm to provide an initial test of these hypotheses. The assumption that any behavioural study must make to assess these neurally-grounded questions is that the relationship between reaction times associated with PPC-related cognitive processes (i.e., attention-to-memory and perception) provides, at least preliminary, insight into their relationship in terms of neural organization. With this assumption, and its caveats (e.g., other factors that may moderate the behavioural relationship, besides neural domain-generality) in mind, the reasoning behind the current study will be discussed.

Using the AtoM framework, Ciaramelli et al. (2010) were able to depict a dorsal-ventral distinction in the PPC that corresponded with top-down and bottom-up attention in episodic memory retrieval. In the current study, a similar cued recognition memory task was administered alongside a novel perceptual version of the same paradigm. These two tasks differed only in the nature of the attentional cue (i.e., mnemonic or perceptual) and decision required (i.e., mnemonic or non-mnemonic), such that the extraneous properties of the tasks themselves were identical. By using similar attentional cueing paradigms across memory and perception, we were able to examine the relationship between the behavioural manifestations (i.e., accuracy and reaction time) of attentional processes typically engaging the PPC. If these PPC attentional orienting processes were domain-general, one would expect that general top-down and/or bottom-up attention processes could flexibly operate on perceptual or mnemonic information. Therefore, domain-generality should predict that effects of top-down (or bottom-up) attention in memory and perception would share variance considering they reflect the same underlying process. However, if these processes were not domain-general, but rather specific, there should be less reason that they should share variance significantly across domains. The paradigm was also extended to both younger and older adults. By incorporating both age groups, we were able to explore the general trends associated with ageing in attentional processes across memory and
visuospatial perception, and whether they were consistent with a domain-general account of PPC attentional processes. Domain-generality would predict that the effects of ageing in visuospatial attention (i.e., a deficit in bottom-up reorienting) should be similarly observed in attentional processes applied to mnemonic information, while this result should not hold if attentional processes were distinct across domains. Finally, considering top-down and bottom-up attention are associated with different regions of the PPC, age-differences in behavioural measures of these attentional processes will serve to guide predictions for age-related changes in the recruitment of the PPC in both memory and perception.

2 Methods

2.1 Participants

Twenty younger ($M = 19.8$ years; range: 18 – 24 years; $n_{\text{female}} = 14$) and twenty older adults ($M = 72.1$ years; range: 66 – 77 years; $n_{\text{female}} = 15$) were recruited for participation in the current study. All participants had no history of neurological or psychiatric illness, and had both normal or corrected-to-normal vision and hearing. Younger adults were recruited through both the Psychology Undergraduate Research Pool and ads that were posted throughout the university campus, and all received either course credits or monetary compensation for participation. Recruitment of older adults was conducted through the University of Toronto’s Adult Volunteer Pool, and all received monetary compensation for participation. This study was conducted in full accordance with all guidelines set by the ethics review committee of the University of Toronto’s Psychology Department.

2.2 Procedure

Participants were administered the following tasks in a fixed order: a background questionnaire, Mini-Mental State Exam, Shipley Institute of Living – Vocabulary subtest, AtoM memory task, and the AtoM perception task. A fixed order was used to ensure that the memory task was performed prior to the perception task, so that the verbal stimuli from the perception task could not interfere with the learning of word pairs during the memory task. The AtoM tasks were both developed on E-Prime v.2 (Psychology Software Tools, Pittsburgh, PA) and administered on a
desktop computer with an E-Prime compatible serial response box (Psychology Software Tools, Pittsburgh, PA; Model 200A). The whole experiment took approximately 2 hours.

2.3 General cognitive functioning

General cognitive functioning was assessed using the Mini-Mental State Examination (MMSE; Folstein & McHugh, 1975). The MMSE is a well-validated and brief screening measure for cognitive impairment. It consists of questions probing aspects of cognition such as: general orientation, short-term memory, attention, language, and ability to follow complex commands. The MMSE was administered to all participants to ensure that both groups were cognitively healthy. All participants scored in the normal range, with scores of at least 27 out of a possible 30.

2.4 Vocabulary

Vocabulary was assessed using the vocabulary subtest from the Shipley Institute of Living Scale (SILS-V; Shipley, 1940). An untimed test of verbal intelligence, the SILS-V required participants to select one of four words closest in meaning to a target word. Forty trials were administered from which accuracy was calculated.

2.5 Attention-to-Memory procedure

The influence of attention on memory was measured using a ‘Posner-like’ paired associates paradigm similar to that of Ciaramelli et al. (2010), with only minor variations (see Figure 2a.). To create the stimuli, eight hundred and fifty-five words were drawn from The English Lexicon Project pool (Balota et al., 2007: http://elexicon.wustl.edu/). Words were all between four to eight letter concrete nouns and of relatively high frequency (> 30 occurrences per million) and high lexical decision accuracy (> .94). Next, each word was categorized as “natural”, “manmade”, or “unsure” by 5 independent raters. Only words that were considered unanimously across all raters as “natural” or “manmade” were used. The remaining 600 words (300 natural and 300 manmade) were used as stimuli for both tasks in the current study ($M_{\text{length}} = 6.26$, $M_{\text{lexical decision accuracy}} = .98$, $M_{\text{frequency}} = 7923.99$).
For each participant, a random list of 384 words was drawn from the pool. The task was divided into eight runs with 48 unique words used per run. Each run contained a study and a cued-recognition phase. For each run, 42 of the 48 words were randomly selected to form the studied paired associates presented during the study, while the remaining 6 words acted as non-studied distractors used during cued-recognition. During the study phase, participants studied 21 word pairs. Each pair was presented in the centre of the screen for four seconds, during which they were asked to form a sentence associating both words. This technique was adopted from Ciaramelli et al. (2010) and acted to prompt each participant to engage in a similar encoding strategy. Also, the word on the left was in red font and the word on the right was in black, facilitating discrimination between cue and target in the subsequent recognition phase. Next, a central fixation cross was presented for 500 ms, followed by the next word pair. Once each of the 21 pairs had been studied, a cued-recognition phase would begin. The cued-recognition phase consisted of 21 trials, beginning with a 500 ms fixation and then followed by a cue, presented for 1900 ms. The cue stimulus was either a 1) studied word (i.e., the word presented on the left of a studied pair), or 2) a meaningless stimulus (i.e., @@@@@). The cue was then followed by a 100 ms delay, followed by the target. The target stimulus was either 1) a studied word (i.e., the word presented on the right of a studied pair), or 2) a non-studied word. Unlike the Ciaramelli et al. (2010) design, the target appeared randomly on either the left or right side of the screen, approximately 10 degrees from fixation (the participant being approximately 75 cm from the screen). This allowed for the memory and the new perceptual task to be directly comparable – an important premise of the current study. In response to the target, participants were required to make an old-new recognition judgment by pressing one of two buttons (oriented vertically) on a response box, which was counterbalanced across subjects. Critically, participants were told to try to remember the paired associate of the cued word and that the consideration of the cue word was generally helpful in making the subsequent old-new decision (2:1 ratio of valid to invalidly cued trials per run). After each run, participants had a one-minute break before continuing. There were 168 trials in total. Before performing the test trials, participants performed a practice experiment with two runs of 7 trials each, using a list of word pairs not included in the actual experiment.

As in Ciaramelli et al. (2010), specific combinations of cue and target types were used to measure top-down and bottom-up attentional effects in memory. The possible cue-target
combinations were: Intact (i.e., a studied cue and its appropriate paired word as a target; 48 trials), Recombined (i.e., a studied cue and a word from a different studied pair as a target; 24 trials), NoOld (i.e., a meaningless cue and a studied word as a target; 48 trials), OldNew (i.e., a studied cue and a non-studied target word; 24 trials), and NoNew (i.e., a meaningless cue and a non-studied target word; 24 trials). A reaction time (RT) measure of top-down attention was calculated by comparing the difference in RT between NoOld and Intact conditions, as these two conditions only differ by the use of a valid cue – i.e., the engagement of top-down attentional guidance in memory search. The consequent formula was: $RT_{NoOld} - RT_{Intact}$. Bottom-up attention, unlike top-down, can be considered as two separate components: reorienting and detection. Reorienting, reflecting the disengage function defined by Posner (1980) or the ‘circuit-breaker’ function defined by Corbetta & Shulman (2002), refers to when top-down attentional guidance is inappropriately engaged and is consequently cancelled by bottom-up orientation towards the appropriate target. Therefore, a measure of invalid cueing, as achieved by comparing the Recombined and Intact conditions (i.e., $RT_{Recomb} - RT_{Intact}$), operationalized this component as they only differed in terms of whether the cue was valid or invalid. Detection simply refers to the engagement of bottom-up attention towards a relevant (i.e., studied) target without the assistance of any predictive cueing information and was assessed using RT measures from the NoOld condition.

2.6 Attention-to-Perception procedure

The influence of attention in a perceptual context was measured using a paradigm that followed a similar procedure to the memory task, using stimuli from the same pool, but stripped of the memory component (see Figure 2b.). Again, the task was divided into eight runs, but using only 21 randomly selected words per run. The words used in the perception task were a subset of those studied in the memory task for each individual. This was to ensure that the stimuli across both tasks were identical, and differences across tasks were restricted to the target of cued attention (i.e., visuospatial or mnemonic) and the nature of the decision (i.e., non-mnemonic or mnemonic). Runs in the perception task did not have a study phase (i.e., no study pairs or memory component), but retained an otherwise identical procedure, including the 21-trial cued-test phase. Each trial began with a 500 ms fixation, followed by a 1900 ms cue. The cue stimulus was either 1) “LEFT”, 2) “RIGHT”, or 3) a meaningless stimulus (i.e., @@@@@). The cue was
followed by 100 ms delay, and then by the target. The target appeared on either the left or right side of the screen (~10 degrees of visual angle to left or right of central fixation). In response to the target, participants were required to make a ‘natural/manmade’ judgement by pressing one of two keys on a response box, which was counterbalanced across subjects. Again, critically, participants were told to covertly attend to the cued side of the screen and that consideration of the cue word was generally helpful in making the subsequent natural-manmade decision (2:1 ratio of valid to invalidly cued trials per run). After each run, participants had a one-minute break before continuing. Again, there were 168 trials in total. Before performing the test trials, participants performed a practice experiment with two runs of 7 trials each, using a list of words not included in the actual experiment.

As in the memory task, specific combinations of cue and target types were used to measure top-down and bottom-up attentional effects in perception. The possible cue-target combinations were: Valid (e.g., cue: LEFT, target on the left side of screen; 64 trials), Invalid (e.g., cue: LEFT, target on the right side of screen; 32 trials), and Neutral (i.e., meaningless cue, target equally likely on either side; 72 trials). Top-down attention, or goal-oriented guidance evoked by predictive cueing, was determined from the relative difference between neutrally and validly cued trials (i.e., $RT_{Neutral} - RT_{Valid}$). Bottom-up reorienting, the disengagement of inappropriate top-down guidance, was assessed by comparing invalid and valid conditions (i.e., $RT_{Invalid} - RT_{Valid}$). Bottom-up detection, the engagement of attention without any predictive assistance, was assessed by RT measures from the neutral condition alone.

Reaction times were used primarily in calculating the attention scores employed in this study across both tasks, although accuracy can also provide a valid measure of attention. Both accuracy and RT data were collected, but as will become apparent, behavioural performance under certain cueing conditions better reflected the cognitive process of interest when attentional difference scores were operationalized using RT measures, while in others accuracy proved more valid.
2.7 Analyses

2.7.1 Data-processing

In order to remove the influence of the exponential tails of the RT distributions, all RT data, from accurate trials only, were winsorized by 10% within participant and condition using the R statistical package (R Project for Statistical Computing, http://www.r-project.org). Winsorization is a procedure where a certain percentage of the extreme values at both tails of the distribution are removed, leaving new less extreme values at the tails, which are then used to replace all of the removed data. This approach reduces the influence of extreme values without losing data by trimming trials, and is becoming more commonly used in experimental psychology (Healey, Campbell, Hasher, & Osher, 2010; Healey, Ngo, & Hasher, in press; Nee & Jonides, 2009; Van Dyke & McElree, 2011). All statistical analyses were conducted either using R through the RStudio run environment (RStudio, Boston, MA) or SPSS 22 (SPSS IBM, New York, NY).

2.7.2 Tests of domain-generality

To examine whether attentional processes across memory and perception are domain-general, two separate tests were conducted. If attention is, in fact, domain-general, it would follow that any age-related change in attentional processing shown to affect one domain should also similarly affect the other domain. A decline in bottom-up attentional reorienting, or a greater difference in RT between invalid and valid cueing, has been an implication of ageing on attentional orienting in visual perception tasks (Greenwood & Parasuraman, 1994; Greenwood, Parasuraman, & Haxby, 1993). Furthermore, top-down attentional processes, such as the benefit of valid cueing, do not typically show any decline with age (Greenwood & Parasuraman, 1994; Greenwood, Parasuraman, & Haxby, 1993; Madden, Whiting, Cabeza, & Huettel, 2004; Parasuraman et al., 1993; Whiting, Madden, Pierce, & Allen, 2005). Assuming the attentional computations generalize across domains, such that the computations themselves are the same but operating on perceptual or mnemonic information, and that they are sensitive to ageing, one would also expect a similar pattern of age-related changes in cueing effects in performance of the memory task. This question was tested using linear regression, where task-specific measures of top-down (i.e., in perception = RT_{Neutral} – RT_{Valid}; memory = RT_{NoOld} – RT_{Intact}) and bottom-up attentional reorienting (i.e., in perception = RT_{Invalid} – RT_{Valid}; RT_{Invalid} – RT_{Valid}) were each
entered as the criterion variables in a separate regressions, while age was input as the predictor. The existence of a domain-general attentional process would suggest that age would affect attention-to-memory similarly to attention-to-perception, such that it would be a significant predictor in bottom-up attention measures across both tasks but not in measures of top-down. Therefore, characterizing the effect of ageing across top-down and bottom-up attentional processes in memory and perception may provide some insight into the domain-generality of these PPC-mediated attentional processes.

The second analysis provides a subsequent and more direct test of domain-generality. Again, if these attentional orienting processes were domain-general, one would expect that top-down and/or bottom-up attention would be general processes that could flexibly operate on perceptual or mnemonic information. Therefore, this question lends itself to linear multiple regression models. For example, to test if top-down attention in memory (as measured by RT difference score) is generalizable across tasks, it was entered as the criterion in a multiple regression, where top-down and bottom-up attention in perception were regressors (for actual models, see Tables 5-7). Considering domain-generality supposes top-down attention across tasks would reflect similar computations operating on different information, it would follow that top-down attention in memory would share variance with top-down attention in perception, and more so than with bottom-up attention in perception. To test this hypothesis, this analysis was conducted for both top-down and bottom-up attention scores across both tasks. Furthermore, bottom-up attention in these analyses represents reorienting and not detection. Since bottom-up detection did not have a formula representing its effect relative to another condition, and considering its use in the calculation of top-down scores (i.e., high collinearity), it was not included in any analyses contrasting attention scores. These analyses were run separately across younger and older adults to determine whether similar patterns existed across both age groups.

3 Results & Discussion

3.1 Background measures

The means and standard deviations for all background measures are reported in Table 1. Independent sample t-tests were conducted to explore any differences between groups in years of education, MMSE, and SILS-V scores. No significant differences between groups were observed
in education, $t(38) = -1.325, p = .193$, or MMSE, $t(38) = .809, p = .423$. A significant difference between groups, however, was found in SILS-V, $t(38) = -5.788, p < .001$. This supports a large literature demonstrating that ageing is often associated with improved or maintained vocabulary and verbal intelligence (for a meta-analysis, see Verhaeghen, 2003). Furthermore, age and education in years were shown to have a significant Pearson correlation with SILS-V scores, where $r_{\text{age}} = .691, p < .001$ and $r_{\text{education}} = .355, p = .025$. No other background measures were significantly correlated.

### 3.2 Attention-to-Memory and Perception

The means and standard deviations for accuracy and RT, separated by condition and group, are reported in Table 2 and in Table 3. For the memory task to be comparable to perception, only the conditions with an old target were used (i.e., Intact, Recombined, and NoOld), which were then re-labelled to match their corresponding conditions in the perception task (i.e., valid, invalid, and neutral, respectively). A task x condition x group mixed-design ANOVA was conducted on the accuracy and RT data separately to characterize any general trends in the data and to confirm that the cueing manipulation indeed affected performance. Task (memory and perception) and condition (valid, invalid, and neutral cueing) were treated as within-subject, while group (YA and OA) was a between-subject variable. For a graph of the mean accuracy per condition in the memory and perception tasks, see Figure 3a and b. For RT, see Figure 4a and b.

#### 3.2.1 Overall accuracy

Accuracy was calculated as the proportion of correct trials from the total number of trials. A 3-way mixed ANOVA on mean accuracy revealed a significant main effect of task [$F(1, 38) = 20.515, p < .0001, \eta^2 = .323$] and condition [$F(2, 76) = 16.504, p < .0001, \eta^2 = .301$]. These main effects were modified by significant interactions between task x condition [$F(2, 76) = 13.791, p < .0001, \eta^2 = .256$] and task x group [$F(1, 38) = 4.944, p = .0314, \eta^2 = .079$]. Firstly, to unpack the task x condition interaction, data were collapsed over group and followed by one-way ANOVAs comparing level of accuracy for each cueing condition across the memory and perception tasks separately. For memory, a significant effect of condition was observed [$F(2, 78) = 18.91, p < .0001, \eta^2 = .327$]. This was further unpacked using Bonferroni corrected pairwise t-tests, revealing all conditions were significantly different from one another [
valid:invalid, \( t(39) = -5.663, p < .0001 \); valid:neutral, \( t(39) = -3.790, p = .0015 \); invalid:neutral, \( t(39) = 2.684, p = .0319 \). For perception, no significant effect of condition was observed \([ F(2, 78) = .061, p = .94, \eta^2 \approx 0 \]. Therefore, the validity of cueing was associated with changes in accuracy in the memory task but not the perception task, such that valid trials were most accurate, followed by neutral, and then invalid (see Figure 3a). This was expected, as a directional cue should not necessarily have a direct impact on the accuracy of a ‘natural/manmade’ decision, but instead should affect RT. Cueing in a paired-associates recognition paradigm, however, should support the retrieval of the cued memory target.

Secondly, to unpack the task \times group interaction, data were collapsed over condition, and followed by independent samples t-tests assessing group differences in accuracy across the memory and perception tasks separately. No significant group effect was found in memory \([ t(118) = .582, p = .562 \]; however, a significant group effect was observed in perception \([ t(118) = -5.135, p < .0001 \]. This effect was driven by the higher accuracy scores in the OA group \((M_{\text{young}} = .900, SD_{\text{young}} = .078; M_{\text{old}} = .958, SD_{\text{old}} = .038). Greater accuracy scores in the perception task for OA is likely reflecting their higher vocabulary scores, considering accuracy was based on a semantic judgement (i.e., a natural/manmade judgement). Although age-related decreases in accuracy on the memory task were expected, none were observed; therefore, accuracy was recalculated as number of hits (i.e., correctly recognized old targets) – false alarms (i.e., incorrectly recognized new targets). Again, no significant group effect was observed, as their mean difference scores were nearly identical \((M_{\text{young}} = 79, SD_{\text{young}} = 14.30; M_{\text{old}} = 80, SD_{\text{old}} = 9.82). Such a lack of age-differences in memory accuracy may be a product of the chosen paradigm – cued recognition. Age effects are typically more apparent when retrieval processes are not bolstered by environmental support (i.e., free recall) (for review, see Hasher, Tonev, Lustig, & Zacks, 2001). Cued recognition, according to this logic, is likely less sensitive to detecting age-effects than free recall, for example, considering retrieval is supported both by the presentation of a predictive cue and the target.

In summary, the general trends in accuracy largely followed our expectations, such that cueing condition affected memory accuracy but not perception, and age differences were found in accuracy for the perception task. Age differences were not found in the memory task, but due to
the nature of the task, the availability of environmental support for retrieval processes may have dampened any such effect.

3.2.2 Overall reaction time

A 3-way mixed ANOVA on mean RT revealed a significant main effect of condition \[ F(2, 76) = 52.84, p < .0001, \eta^2 = .569 \] and interactions between task x condition \[ F(2, 76) = 14.77, p < .0001, \eta^2 = .273 \] and task x group \[ F(1, 38) = 10.50, p = .00248, \eta^2 = .216 \]. Firstly, to unpack the task x condition interaction, data were collapsed over group and followed by one-way ANOVAs comparing RTs across condition in the memory and perception tasks separately. For memory, a significant effect of condition was observed \[ F(2, 78) = 37.9, p < .0001, \eta^2 = .493 \], which was further unpacked using Bonferroni corrected pairwise t-tests. Significant differences were found between valid and invalid \[ t(39) = - 6.414, p < .0001 \], and between valid and neutral \[ t(39) = - 8.958, p < .0001 \], but not between invalid and neutral conditions \[ t(39) = - 1.333, p = .560 \]. Similarly, a significant effect of condition was observed in perception \[ F(2, 78) = 20.32, p < .0001, \eta^2 = .343 \], which revealed significant differences between all conditions \[ \text{valid:invalid, } t(39) = - 5.329, p < .0001; \text{valid:neutral, } t(39) = - 3.620, p = .0025; \text{invalid:neutral, } t(39) = 3.642, p = .0025 \]. Therefore, the memory and perception tasks both appear to show similar RT patterns across younger and older adults, and both showed that valid cueing produced significantly faster RTs than neutral and invalid cues. However, invalid cueing did not differ from the neutral cue condition in the memory task.

A possible explanation for the lack of a difference between invalid and neutral cueing in memory, and a robust difference in perception, could be due to comparably weak associations between the cue and target in the memory task. In the perception task, an invalidly cued trial is very distinct because one’s attention is clearly engaged towards the incorrect side of the screen. This is due to the evident mismatch between the spatial location of one’s attentional focus and the target on the opposite side of the screen. In the memory task, participants memorized 21 word pairs per run and then underwent a cued recognition test. Invalidly cued trials in the memory task may not have evinced a comparable mismatch signal, because the association between word pairs would not typically be very strong, considering the number of studied pairs and the short encoding time (i.e., 4 seconds). However, it is unclear why a significant effect of condition was observed in memory accuracy, in spite of this concern.
Secondly, to unpack the task x group interaction, these data were collapsed over condition, and followed by independent samples t-tests comparing group differences in RT across the memory and perception tasks separately. For memory, a significant effect of group was observed \[ t(118) = -4.309, p < .0001 \] due to the slow RTs in the OA (\( M_{\text{young}} = 1044.560, SD_{\text{young}} = 288.084 \); \( M_{\text{old}} = 1289.744, SD_{\text{old}} = 333.620 \)). No significant effect of group was found in perception \[ t(118) = .212, p = .832 \]. Therefore, an age difference in overall speed was found in the memory, but not the perception task. Overall-slower processing speed is typically characteristic of cognitive ageing (for review, see Salthouse, 1996), but perhaps any such effects in the perception task may have been tempered by an interaction between the higher vocabulary scores in OAs and the task’s reliance on a semantic judgement.

In summary, the general trends in the RT data demonstrated the task was able to engage attentional cueing, as evidenced by the significant difference between invalid and valid cueing across both memory and perception. However, a difference in strength between cue-target associations across the tasks may explain task-dependent disparities between neutral and invalid cueing RTs. Typical age-related slowing was observed in the memory task, but not perception – possibly reflecting the higher vocabulary scores in OAs acting as a buffer against any group differences.

### 3.2.3 Domain-generality

The primary goal of the current study was to examine whether the attentional processes associated with visuospatial and mnemonic cueing tasks, purportedly engaging the PPC, are general across both domains or specific to memory or perception. Statistical assessment of this hypothesis was comprised of two separate sets of analyses 1) examining if characteristic age-related changes in visuospatial cueing (i.e., increased effect of invalid cueing – or bottom-up attentional reorienting) predicted in perception would also generalize to memory RTs, and 2) whether top-down and bottom-up attention difference scores (for calculation of scores, see Methods: Attention-to-memory and Attention-to-perception) would share variance significantly across domains in each age group. The Pearson correlations between attention scores across group and tasks are reported in Table 4.
For the first test, the bottom-up attentional reorienting (BUA) effect was calculated by taking the difference between the average RT for invalid and validly cued trials per subject (Greenwood et al., 1993; 1994), for the perception and memory tasks separately. The top-down attention (TDA) effect was operationalized as the difference between the average neutral and validly cued RTs, again for both tasks separately. To observe the general pattern of scores across groups and tasks, the mean difference scores for BUA are plotted in Figure 5, and TDA, in Figure 6. These four measures served as criterion variables in separate in linear regressions, where age was the predictor variable. As four tests were conducted, the Bonferroni corrected significance level for these regression models was set to \( p = .0125 \) (i.e., alpha/# of tests = .05/4 = .0125) to reduce inflation in family-wise error. As expected, age was a marginally significant predictor of BUA-perception \([\beta = .367, t(39) = 2.434, p = .020]\) and did not reach significance in predicting TDA-perception \([\beta = .111, t(39) = .688, p = .496]\). Considering the \( \beta \) coefficient in the regression of BUA-perception was positive, it reflects that increasing age was significantly associated with slowing due to invalid cueing in the perceptual task, as previously reported in the literature (Greenwood et al., 1993; 1994). When memory was examined, however, age was no longer a significant predictor of BUA \([\beta = -.043, t(39) = -.268, p = .790]\) or TDA \([\beta = -.190, t(39) = -1.190, p = .241]\).

In summary, ageing showed no association with performance in measures of TDA across tasks. Old age was associated with an increase in the invalid cueing effect (i.e., BUA) in perception, yet it did not carry over into memory (see Figure 5.). Contrary to our hypothesis, this initial test did not support domain-generality, as the effects of ageing on attentional cueing were not comparable across tasks. To be relatively certain that domain-generality does not characterize attentional cueing, alternate possibilities need to be assessed. One possibility may be that the ageing process itself changes the nature of the relationship between attention-to-perception and attention-to-memory. If domain-generality, for example, decreased with age, perhaps due to an increase in behavioural variance (Garret, Kovacevik, McIntosh, & Grady, 2010; Lövdén, Li, Shing, & Lindenberger, 2007; MacDonald, Li, & Bäckmann, 2009), it could provide an alternate explanation for the previous results. Furthermore, the previous test relied on detecting the ageing effect known to visuospatial perception in memory performance, and perhaps the age effect, though similar in nature, may not prove as robust in the memory task. Instead, directly examining how the variance in TDA and BUA processes are shared across tasks, as in the
subsequent set of analyses, may provide a better assessment of the shared variance across domains.

The second test of domain-generality consisted of four multiple regressions, one for each type of attention (i.e., top-down; TDA, and bottom-up; BUA), per task (i.e., memory and perception). The measure of attention used here were the same RT difference scores from the previous set of analyses (for calculation of scores, see Methods: Attention-to-memory and Attention-to-perception). Unlike the previous test examining the effects of ageing across attentional process in memory and perception, this test provides a direct assessment of the shared variance between these processes across tasks, without relying on detecting the effects of ageing. The regressors input in the model were TDA and BUA from the opposite domain of the criterion, for example, when TDA-memory was input as a criterion, TDA and BUA-perception served as regressors (see Tables 5-7 for each model). By including TDA and BUA of the other domain in the model, it allowed for a direct test of shared variance across domains. As four tests were conducted, the Bonferroni corrected significance level for these regression models was set to \( p = .0125 \) (i.e., alpha/# of tests = .05/4 = .0125). Furthermore, due to the absence of evidence supporting domain-generality from the previous test, younger and older adults were analyzed separately and the patterns of results were compared. The results for younger adults were examined first, followed by the older adults.

### 3.2.4 Domain-generality in younger adults

With BUA-memory as the criterion (regressors: BUA-perception and TDA-perception; Table 5a.), the model did not reach significance \( R^2 = .137, F(2, 19) = 1.353, p = .285 \). Domain-generality would suggest that BUA-memory would be best predicted by BUA-perception, however, this was not found. Similarly, with BUA-perception as the criterion (regressors: BUA-memory and TDA-memory; Table 5b.), the model also did not reach significance \( R^2 = .069, F(2, 19) = 1.886, p = .123 \). Therefore, these analyses did not support a characterization of BUA processes as domain-general. This is made clear in Figure 7b, where the relationship between BUA memory and perception are presented in a scatterplot. Considering the trend line is fairly flat, no significant relationship is apparent between these two processes.
Interestingly, when TDA-memory was entered as the criterion (regressors: BUA-perception and TDA-perception; Table 5c.), the model was significant \[ R^2 = .431, F(2, 19) = 6.433, p = .008 \]. Within the model, TDA-perception was the most significant regressor \[ \beta = .674, t(19) = 3.406, p = .003 \]. BUA-perception was also significant \[ \beta = -.463, t(19) = -2.339, p = .032 \], but to a considerably lesser degree. This was consistent with an account of domain-generality, as TDA-memory was best predicted by TDA-perception, speaking to a possible general top-down attentional mechanism operating similarly on perceptual and mnemonic information. When the final model was tested using TDA-perception as the criterion (regressors: BUA-memory and TDA-memory; Table 5d.), the model also trended towards significance \[ R^2 = .249, F(2, 19) = 2.815, p = .088 \]. Unlike the previous non-significant BUA models, however, the regressors in this model also showed a pattern of significance in line with domain-generality. The only regressor that approached significance was TDA-memory \[ \beta = .533, t(19) = 1.783, p = .092 \]. Though the overall model did not reach significance, this pattern was in accordance with a domain-general account of top-down attentional processes (see Figure 7a.).

According to the second test of domain-generality, top-down attention appears to have a considerable positive relationship across memory and perception in younger adults, yet bottom-up attention does not appear to share variance across domains. From this, two possibilities emerge. Bottom-up attention may, in fact, be domain-specific (e.g., Hutchinson et al., 2009; Nelson, McDermott, Petersen, 2012), unlike top-down attention. It is also possible, however, that the process of bottom-up reorienting in memory was not appropriately captured by RT difference scores and thus the relationship across domains failed to emerge. The latter explanation can be further substantiated considering the invalid cueing condition in memory did not differ from neutral cueing, in terms of RT. The absence of this difference in the memory task alone, as it was present in the perception task, may indicate that the invalid cueing condition in memory should not be interpreted in terms of RT (see Results: Overall reaction time). Invalid cueing, however, did affect memory accuracy, where the invalid condition was associated with the lowest accuracy (see Results: Overall accuracy). This suggests that memory accuracy may, in fact, provide a better measure of bottom-up attentional reorienting that RT in the memory task.

To determine whether this was the case, BUA-memory, as defined in terms of both accuracy (i.e., \( ACC_{\text{Invalid}} - ACC_{\text{Valid}} \)) and RT (i.e., \( RT_{\text{Invalid}} - RT_{\text{Valid}} \)), were correlated with BUA-perception.
as defined by RT (i.e., RT_{Invalid} − RT_{Valid}). BUA-perception showed a significant correlation with BUA-memory as measured by accuracy \( (r = -0.454, p = .045) \) rather than RT \( (r = -0.032, p = .893) \).

Unlike when comparing two RT scores, such a negative relationship was expected, considering a reduction in the effect of invalid cueing in terms of accuracy would reflect an increase in the proportion correct, while in RT it would reflect a decrease in response time. This significant correlation provided the rationale to run a subsequent test post-hoc, using previous analyses again while defining BUA-memory in terms of accuracy. With BUA-memory as the criterion (regressors: BUA-perception and TDA-perception; Table 7a.), the model did not reach significance \[ R^2 = .218, F(2, 19) = 2.370, p = .124 \], but interestingly, the regressors showed a pattern consistent with domain generality, where BUA-perception proved significant \[ \beta = -0.499, t(19) = -2.152, p = .046 \] and TDA-perception did not \[ \beta = .120, t(19) = .518, p = .611 \].

Similarly, with BUA-perception as the criterion (regressors: BUA-memory and TDA-memory; Table 7b.), the model trended towards significance \[ R^2 = .259, F(2, 19) = 2.978, p = .078 \], and again the regressors supported domain generality, where BUA-memory proved significant \[ \beta = -0.467, t(19) = -2.232, p = .039 \] and TDA-memory did not \[ \beta = -0.232, t(19) = -1.111, p = .282 \].

In line with the previous set of analyses, including TDA-memory and TDA-perception as criterions continued to support domain-generality in terms of the pattern of significance amongst the regressors themselves (see Table 7c. and d.), although the model for TDA-perception only trended towards significance \[ R^2 = .249, F(2, 19) = 2.823, p = .087 \].

In summary, top-down attention appears to have a considerable positive relationship across memory and perception, as does bottom-up attention, but only when the latter is defined in terms of accuracy (see Figure 8.). Although this choice was made post-hoc, domain-generality of attentional processes appears to be supported in younger adults, as predicted by the AtoM hypothesis (Cabeza et al., 2012a; Ciaramelli et al., 2008, 2010).

### 3.2.5 Domain-generality in older adults

As in younger adults, the RT difference scores from the older adults were submitted to an identical set of multiple regressions to test domain-generality. Again, as four tests were conducted, the Bonferroni corrected significance level for these regression models was set to \( p = .0125 \) (i.e., alpha/# of tests = .05/4 = .0125). Surprisingly, none of the models approached significance in the older adults \( (all \ ps > .2; \ for\ regression\ models,\ see\ Table\ 6a-d;\ also,\ see\ Fig\ 8)\).
One possibility for this finding could be that the performance of older adults was overall more variable (Garret, Kovacevik, McIntosh, & Grady, 2010; Lövdén, Li, Shing, & Lindenberger, 2007; MacDonald, Li, & Bäckmann, 2009), and perhaps an increase in unexplained variance in the older data overshadowed any patterns of shared variance. The coefficient of variation (i.e., mean score divided standard deviation) was determined per participant, separately for each cueing condition per task. These scores were then averaged within age group and submit to uncorrected t-tests, comparing the coefficient of variation scores across age groups. Even with such a sensitive test, the only difference that approached significance was valid cueing in perception [ $t(39) = 2.004, p = .052$ ] (all other $p$s > .1), where the reverse was observed, such that older adults had lower variability than the young (MYA = .227, SDYA = .067; MOA = .193, SDOA = .036). Therefore, an overall increase in unexplained variability did not explain the results in support of domain-specificity of attentional processes amongst older adults.

The previous analyses did not support domain-generality, particularly in TDA. It is possible, however, that BUA may still be domain-general, though it was not detected due to the inappropriate use of RT instead of accuracy scores in its calculation. To determine whether this was the case, BUA-memory scores, as defined by accuracy (i.e., ACCInvalid − ACCValid) and RT (i.e., RTInvalid − RTValid), were correlated with BUA-perception as defined by RT (i.e., RTInvalid − RTValid). BUA-perception was not significantly correlated with BUA-memory as measured by accuracy ($r = .373, p = .105$) or RT ($r = -.348, p = .132$). Therefore, the lack of evidence supporting domain-generality of BUA processes in older adults was not simply due to an inappropriate measure of BUA-memory.

In summary, the analyses of domain generality were not as straightforward as initially expected. In younger adults, evidence for domain-generality was observed in TDA, in line with our predictions, showing a robust trend towards sharing variance across domains (i.e., TDA in perception and memory), more so than across attentional processes (i.e., BUA). Support for domain-generality in BUA was less clear, as it was not evidenced in terms of RT, but a consistent trend emerged when BUA-memory was defined in terms of accuracy. Finally, older adults appeared not to show any evidence for domain-generality, but instead, specificity of processes across domains. Therefore, the previous analyses provide considerable support for
domain-general attentional processes in younger adults; however, behavioural evidence suggests that this relationship deteriorates into old age.

4 General Discussion

The functional contribution of the PPC to cognitive processes, such as episodic memory and visuospatial attention, remains a disputed topic in the cognitive neuroscience of memory. Despite the anatomical heterogeneity of the PPC, its engagement across both of these cognitive functions may reflect, as purported by an ‘overarching’ view of functional organization, the recruitment of a domain-general attentional process operating on mnemonic and perceptual information alike (Cabeza, 2008; Cabeza et al., 2012a; Ciaramelli et al., 2008). Another possibility is, as suggested by a ‘fractionation’ view, the PPC may be a processing hub with multiple distinct functional components that work independently of one another. Thus, attentional processes recruited in episodic memory and visuospatial attention may not only be cognitively distinct, but also mediated by distinct functional components within the PPC (Nelson et al., 2010, 2012, 2013).

The present study examined the proposed cognitive processes associated with the PPC (i.e., top-down and bottom-up attention; Corbetta et al., 2002, 2008; Ciaramelli et al., 2008, 2010), to characterize the associations between these attentional processes across memory and perception at a cognitive behavioural level. Assuming the nature of the behavioural manifestation (i.e., RT) of these cognitive processes reflects the organization of their underlying neural computations, we can address whether domain-generality (i.e., an ‘overarching’ view) or domain-specificity (i.e., a ‘fractionation’ view) provides a better account of the cognitive processes associated with the PPC.

4.1 Attention, domain-generality & the PPC

According to the findings of this study, whether domain-generality or specificity better characterizes attentional processes in visuospatial perception and episodic memory depends primarily on the type of attention being considered. Top-down attention (TDA) showed the pattern predicted by domain-generality in younger adults across, where TDA shared variance across domains more so than with bottom-up attention (BUA) (e.g., TDA-perception shared more variance with TDA-memory than with BUA-memory; see Results: Domain-generality). These results suggest that the cognitive process of TDA, as operationalized by the current study,
appears to operate similarly in both memory and perception. It is possible, therefore, that the neural computations associated with TDA may be in fact be similar across memory and perception, yet simply applied to different inputs (i.e., mnemonic or perceptual information, respectively). However, the possibility that an extraneous variable may be moderating the relationship between the behavioural manifestations of TDA, other than the hypothesized neural domain-generality, must be acknowledged. Future exploration of this paradigm incorporating neuroimaging would be required to further clarify the validity of this prediction. Nonetheless, at a behavioural level, it appears as if the cognitive processes associated with TDA are of a similar nature across memory and perception, in support of a domain-generality argument. This pattern was less clear in BUA. When RT was considered, this attentional process did not appear to share variance significantly across domains, contrary to a domain-general account of attentional processes, and instead provided support for domain-specific BUA processes across memory and perception (see Figure 7b.). When BUA-memory was defined in terms of accuracy, a trend towards domain-generality emerged (see Figure 8.).

This discrepancy may, as argued previously, emerge from an issue with comparing memory and perception using the same reaction time metrics. These processes are considerably different in nature, as reflected by the experimental measures often used to capture them: as studies of memory tend to use accuracy, while those looking at perceptual tasks often employ reaction time. Furthermore, specific to this study, invalid cueing in the memory task appears different relative to neutral cueing than the perception task when operationalized using RT – possibly indicating the nature of invalid cueing is not appropriately captured using RT in the memory task. Thus, consistent with our predictions (Cabeza, 2008; Cabeza et al., 2012a; Ciaramelli et al., 2008), when BUA-memory was measured appropriately using accuracy, trends towards domain-generality across BUA processes in perception and memory were observed. To determine whether this effect is robust, and not an artefact from conducting multiple tests, these findings must be replicated in a new sample of younger adults.

The test of domain-generality in younger adults, although provides support for the notion of similar attentional processes operating across memory and perception, demonstrates that the effects for BUA are more delicate. Considering the nature of TDA and BUA, some reasonable explanations are available post-hoc. TDA, as discussed by Ciaramelli et al. (2008)
Introduction: Attention-to-memory), is an indirect process by definition. It does not reflect direct processing of the stimulus, but instead modulates such processing based on overarching goals or attentional sets. Therefore, even if the stimuli (i.e., inputs) themselves are different across two similar indirect processes, there will still likely be overlap in processing at a more downstream level (e.g., biasing of attention). More direct processes, however, would share less overlap in terms of overarching goals, and may, by nature, share less variance across domains than indirect processes. Stimulus-driven, or BUA, is one such direct process. Therefore, domain-generality may simply be more likely to be found in TDA compared to BUA.

An alternate explanation may be due to potential differences in associative strength between cue and target across the tasks themselves (see Results: Domain-generality). The association between cue and target in the perceptual task is very strong, such that if a participant is incorrectly spatially cued, it is very apparent that the target appeared on the opposite hemisphere relative to where they were attending. In the memory task, the association between cue and target is comparatively weak, because it was only developed based on the 4 seconds of encoding during study, amongst the 21 competing associations also learned within a run. This difference in strength between invalid cue conditions across tasks may have consequently perpetuated into the calculations of BUA score (i.e., $RT_{\text{Invalid}} - RT_{\text{Valid}}$), and therefore reduced the potential variance shared across tasks. Perhaps increasing the associative strength (e.g., highly imageable words; Madan, Glaholt, & Caplan, 2010) between paired-associates in the memory task would reveal greater overlap in BUA across tasks, although some initial pilot data in younger adults does not appear to support this claim. Interestingly, however, considering TDA is primarily associated with the dPPC and BUA with the vPPC, evidence at the neural level can also support the notion of domain-generality in the dPPC and domain-specificity in the vPPC.

Nelson et al. (2010) performed a parcellation analysis of the left lateral PPC based on resting-state functional connectivity boundary mapping. Using this technique, they were able to define subregions based on sharp changes in the whole-brain functional connectivity observed across the PPC. Beyond isolating these PPC subregions at rest, they also showed retrieval success effects with unique BOLD time courses during task, speaking to relatively independent contributions to cognitive functioning. According to their parcellation, the dPPC was composed of two separate functional components, an anterior SPL-frontal eye field (FEF) component and a
posterior lateral IPS-dorsolateral prefrontal cortex (dPFC) component. The vPPC was divided into four, the most prominent of which were an anterior SMG-insula (INS) component and a posterior AG-medial prefrontal (mPFC) component. The extra-PPC regions listed above are the primary targets of each PPC subregion based on the measures of resting functional connectivity. Furthermore, each of these regions has been previously reported as nodes within robust large-scale functional brain networks. Thus, by considering which networks reliably recruit these extra-PPC targets, we can similarly predict which networks are more likely to be associated with specific subregions of the PPC. The two primary targets of the separate dPPC components (i.e., the FEF and dPFC) are considered to be reliable nodes of a single large-scale network, the dorsal attention network (Corbetta & Shulman, 2002; Fox et al., 2005, 2006; Spreng, Sepulchre, Turner, Stevens, & Schacter, 2013), purported to be preferentially engaged during TDA processes (Corbetta & Shulman, 2002; Corbetta, Patel, & Shulman, 2008; Ozaki, 2011). The primary targets of the two vPPC components (i.e., the INS and mPFC), however, are often associated with two separate large-scale networks, the salience network (Bressler & Menon, 2010) and the default-mode network (Fair et al., 2008; Fox et al., 2005; Spreng et al., 2013), respectively. These large-scale networks are often associated with different aspects of cognitive functioning as well. The salience network is often engaged during monitoring of external or internally-oriented information for differences in salience (Bressler & Menon, 2010). The default-mode network, on the other hand, is often engaged during self-referential cognition, autobiographical memory, and relatively internally-oriented cognitive functions (Andrews-Hanna et al., 2010; Spreng & Grady, 2010; Mars et al., 2012). The anterior-posterior distinction between the connectivity of these two vPPC components is also reminiscent of their functional dissociation according to meta-analytic studies (Hutchinson et al., 2009; Kubit & Jack, 2013), where the more anterior SMG tends to be associated with perceptual reorienting and the relatively posterior AG with reorienting in memory or social cognition (e.g., theory of mind). Although differences in functional activity between memory and perception have been observed in the dPPC as well, they tend to be more dorsal for perception and ventral for memory (Hutchinson et al., 2009), which does not correspond to the anterior-posterior distinction observed through anatomical parcellations (Nelson et al., 2010).

The functional organization of the PPC appears to suggest the domain-generality for computations associated with the dPPC, but instead, domain-specificity in the vPPC. As the
dPPC and vPPC are presumed to preferentially mediate TDA and BUA processes, respectively, it provides a neural framework to support the behavioural results observed in the current study. However, this claim must be tested directly, and one possibility would be to adapt the current behavioural paradigm for use in the scanner. The pattern of activity in the PPC could be contrasted between valid cueing and invalid cueing across the matched memory and perception tasks, in addition to a classic non-verbal Posner spatial cueing paradigm (Posner, 1980). The inclusion of both a perceptual task that is matched in terms of presentation (i.e., the perception task from the present study) and another that is not (i.e., classic Posner spatial cueing paradigm), posited to both recruit the same visuospatial attentional processes, should allow for a direct assessment of the effect of extraneous differences in tasks themselves and their contribution to the reported distinct patterns of PPC recruitment across memory and perception. If activity shows considerably more overlap across the matched memory and perception task, relative to the non-verbal Posner spatial cueing, then this can provide direct support for the domain-generality account as purported by AtoM hypothesis and an ‘overarching’ view of PPC organization. In sum, this would clearly demonstrate that the paradigms used in both conditions must be equated before comparisons across domains can be determined accurately, and these extraneous differences in task materials and procedures used to assess memory and perception largely contribute to distinctive topography of PPC activity across domains (Cabeza et al., 2012a; Cabeza, Ciaramelli, & Moscovitch, 2012b). If, however, the pattern of activity in the PPC evoked during the memory task does not show any preferential overlap with the matched perception task, again relative to the non-verbal Posner cueing task, then extraneous differences in the paradigms themselves likely cannot explain the domain-specificity across memory and perception in the PPC, as suggested by the ‘fractionist’ models (Hutchinson et al., 2009; Nelson et al., 2010, 2012, 2013).

Furthermore, studies examining domain-generality and functionality of the PPC should not be constrained to memory and perceptual domains alone. There have been consistent reports of PPC recruitment, often specific to the AG in the vPPC, during social cognitive processes (Carter & Huettel, 2013; Kubit & Jack, 2013). Further consideration of potential mechanisms able to operate across both cognitive and social cognitive domains, such as attentional processes (Corbetta, Patel, & Shulman, 2008), will be critical to furthering our understanding of the PPC in cognition more generally (Carter & Huettel, 2013; Nelson et al., 2013).
4.2 Domain-generality in the PPC & old age

An interesting finding of the current study was that support for domain-generality emerged in younger adults, but was non-existent in the older group (see Figure 9a. and b.). It was not predicted that increased age would lead to decrease in shared variance across attention in memory and perception. This is in direct contrast with the traditional cognitive ageing phenomenon of dedifferentiation. Ageing is typically associated with a reduction in the distinctiveness of information processes and representations, whether neural or behavioural, such that processes/representations found to be distinct in YA are found to have more overlap in OA (de Frias, Lövden, Lindenberger, & Nilsson, 2007; Goh, 2011; Lindenberger & Baltes, 1994; Lindenberger, Scherer, & Baltes, 2001). For example, Lindenberger & Baltes (1994) administered a battery of tests assessing sensory functioning (i.e., visual auditory acuity measures) and intelligence (i.e., including memory, processing speed, knowledge, and fluency measures) to older adult (70 – 103 years) participants. Sensory measures shared 91.3% of the variance associated with age-related changes in measures of intelligence. Further studies have demonstrated that simply reducing sensory acuity in middle-aged adults does not approximate the overlap between sensory and cognitive processing in older adults (Lindenberger, Scherer, & Baltes, 2001), likely speaking to a neural-based explanation beyond differences in perceptual input. Recent studies have shown, in fact, age-related dedifferentiation at the brain level, where neural representation of distinct categories of visually presented stimuli showed more overlap in OA relative to YA (Park et al., 2012; Voss et al., 2008; for review, see Joh, 2011). Therefore, it is unclear why the opposite pattern was observed in the present study, such that old age was associated with less overlap between TDA in memory and perception.

It is also possible, however, to recognize the effect of dedifferentiation when examining the combined cueing effects across task. In examining Figure 5 we can see that younger adults show a different pattern of BUA (i.e., invalid cueing) across memory and perception, while older adults tend to show more similar effects. Unlike the tests of domain generality in this study, which examine the shared variance across TDA and BUA separately, this effect would appear to suggest increased domain-generality (i.e., less differentiation in combined cueing effects between memory and perception) in old age. Although this may be true, typical behavioural approaches examining dedifferentiation tend to use multiple regressions and variance modelling
approaches, specifically examining the shared variance across tasks (e.g., Baltes & Lindenberger, 1997; Lindenberger & Baltes, 1994) rather than a comparison of the general pattern of results. Nonetheless, to ensure the reliability of these findings, replications are necessary before further speculating about this effect.

Another possibility could be that the behavioural manifestation of attentional processes may not be the most appropriate at assessing shared variance across domains in older adults. Older adults often show increased variability in behavioural performance (Garret, Kovacevik, McIntosh, & Grady, 2010; Lövdén, Li, Shing, & Lindenberger, 2007; MacDonald, Li, & Bäckmann, 2009), and although this was not the case in this study (see Results: Domain generality in older adults), it may indicate that behavioural measures may be too unreliable to assess patterns of shared variance across cognitive domains in older adults. If increased domain-specificity in attention with age does prove to be reliable, it would be interesting to examine its neural basis. Perhaps, if a similar approach to that applied by Nelson et al. (2010) was examined in OA, a fundamentally different parcellation of the PPC (especially the dPPC) could emerge, supporting the change in overlap across TDA across both memory and perceptual domains.

4.3 Age-related changes in attention & the PPC

The regression analyses comparing the effect of ageing on attentional difference scores across tasks revealed slowed RT for BUA in perception, specifically representing when attention needs to be disengaged after invalid cueing and subsequently reoriented towards the target (see Figure 5.). This was operationalized as the difference in RT between invalid and valid cueing (e.g., $RT_{\text{Invalid}} - RT_{\text{Valid}}$). It is unclear whether the same trend would have been more clearly observed in memory if the associative strength between the cue and target were increased (see Discussion: Attention, domain-generality, & the PPC). Nonetheless, this finding, at least in perception, has been reported in the literature with older adults in the same age range as the present study (Greenwood et al., 1993), but more robust effects were reported in those above the age of 75 (Greenwood et al., 1994) and patients with mild Alzheimer’s dementia (Parasuraman et al., 1992).

It is possible that the MMSE, known for its specificity in screening for dementia rather than sensitivity in detecting mild cognitive impairment (Hoops et al., 2009), did not capture subtle
cognitive deficits in the OA tested in the current study, and thus explaining the correspondence in results between healthy OA in our study and the older/patient groups from previous studies. The OA recruited in the current study, however, were rather high functioning and highly educated. In a heterogeneous sample of highly educated patients with diagnosed dementia or mild cognitive impairment and healthy controls, a cut-off score of 28 had a relatively high sensitivity and specificity in detecting cognitive impairment (i.e., .78) (O’Bryant et al., 2008). In the current study, OA had MMSE scores that ranged between 28 – 30, making it unlikely that an explanation of pathological cognitive impairment alone could have differentially impaired our OA group. Again, although replication is necessary, it is possible that BUA in terms of the disengagement and reorienting of attention may be impaired in healthy ageing.

Although ageing does appear to be associated with increased cueing effects (Langley, Friesen, Saville, & Ciernia, 2011; Lincourt, Folk, & Hoyer, 1997; Nissen & Corkin, 1985) (cf. Folk & Hoyer, 1992), and an age-related deficit specific to disengagement or reorienting of spatial attention has been reported (Greenwood et al., 1993; 1994) – it does not appear to be a prominent claim in the literature on cognitive ageing in healthy older adults. Although domain-generality of attentional processes was not apparent in the older adult data from the current study, a parallel pattern of results has long been reported in studies of ageing and working memory, in which OA tend to have difficulties deleting, or disengaging from, irrelevant information within a working memory store (for review, see Hasher, Lustig, & Zacks, 2007). May, Hasher, & Kane (1999) had young and old participants perform a working memory span task in which participants had to read a certain number of sentences, and after each sentence had been read, they were asked to repeat the last word from each sentence. Typically, span tasks such as these begin with trials with fewer items (e.g., two sentences) and progressively increase (e.g., five sentences), but in this study both an increasing and decreasing order was administered. As expected by previous research suggesting ageing was associated with a reduced working memory span, OA performed worse than YA in the increasing condition, but no age-differences were found in the decreasing condition. The authors argued that OA do not have a reduced working memory capacity, considering they perform equally during the decreasing condition where the largest span is tested first. Instead, they are unable to disengage from the mnemonic information of previous trials, such that during the increasing condition, they build up interference from the earlier shorter trials and are thus unable to complete the longer subsequent trials (May et al., 1999). More recent
work has provided support for an age-related deficit in attentional disengagement in working memory even at the neural level (Clapp, Rubens, Sabharwal, & Gazzaley, 2011).

It is possible, perhaps, that top-down and bottom-up attentional processes are domain-general in older adults, but are only observable at the neural level. Behaviourally, older adults show increased variability in performance, but the opposite trend is apparent in neural activity (for review, see Garrett et al., 2013; Grady, 2012). With less variability in neural activity, perhaps examining the spatial overlap in neural processes associated with attentional orienting across domains may provide a better context to test our hypothesis in older adults.

Furthermore, if domain-generality does exist in older adults, perhaps ageing affects the same attentional mechanism, producing an age-related deficit in BUA disengagement or across the domains of memory and perception. From this proposition, a couple predictions emerge regarding regions of the PPC particularly subject to age-related decline. The AtoM model (Ciaramelli et al., 2008, 2010) and its perceptual precursors (Corbetta & Shulman, 2002), would likely predict impaired function in the vPPC. BOLD activity following invalid spatial cueing, a critical aspect of BUA reorienting, has been consistently reported to engage the relatively ventral PPC (vPPC) regions such as the inferior parietal lobule (IPL), temporoparietal junction (TPJ), and superior temporal gyrus (Corbetta & Shulman, 2002; Corbetta et al., 2008). Furthermore, patient work has also provided support for the impairment of BUA processes following damage relatively localized to regions of the vPPC (Ciaramelli et al., 2010; Shomstein, Lee, & Behrmann, 2010; for review, see Cabeza et al., 2012a). However, recent work suggests that assuming a pure association between BUA and the vPPC may be misguided. Considerable evidence exists demonstrating attentional reorientation also recruits the dPPC (for review, see Vossel et al., 2013), and the process of reorientation itself undoubtedly relies on TDA (i.e., top-down attention towards an inappropriate target – from which attention must then be reoriented) (Yantis, 2000). A recent study by Chica, Bartolomeo, & Valero-Cabré (2011) used TMS during both an exogenous (automatic capture of attention – BUA) and endogenous (self-initiated orienting – TDA) spatial cueing task. They reported significant changes in behavioural performance following TMS of the TPJ only in the exogenous condition, yet stimulation of the IPS affected both exogenous and endogenous conditions. This provides evidence supporting the IPS in both TDA and BUA, while more ventral regions like the TPJ show exclusive relationship
with BUA processes. As attentional reorienting in particular requires the interaction between TDA and BUA (Corbetta et al., 2008), the IPS may be a likely candidate for having a computational contribution to this process. A recent proposal based primarily on lesion work, suggests that the IPS (posterior segment, specifically) may be involved in attentional enhancement of the contralateral hemisphere (Vandenberghe, Molenberghs, & Gillebert, 2012). This function is a fundamental component of attentional reorienting in the visuospatial domain, and thus may be expected to show impaired function in healthy old age. Nonetheless, direct examination of attentional orienting paradigms in young and old adults, as used in the current study, in combination with fMRI is required to provide an empirical test of this hypothesis.

4.4 Conclusion

In sum, the present study provides an initial behavioural examination of the relationship between attentional processes in matched memory and perception paradigms. As these attentional processes consistently recruit the PPC across both domains, perhaps the PPC is associated with the engagement of a domain-general attentional process that simply operates across different inputs, whether mnemonic or perceptual. This was supported, at least in TDA, for young adults where significant proportion of the overall variance from these attentional measures was shared across tasks. BUA, however, only showed this pattern when the measure of BUA was calculated using accuracy instead of RT. The relationship between the behavioural manifestation of TDA in memory and perception suggests that the neural correlate of TDA in the PPC (i.e., dPPC) may be associated with a domain-general goal-oriented attentional function. The fragile nature of the effect in BUA makes any inferences regarding the neural organization of the vPPC (i.e., associated with BUA) less clear. Furthermore, these attentional processes were suggested to change with old age. Older adults did not show domain-generality effect across attentional processes, and furthermore, demonstrated impaired BUA reorienting, specific to perception. It is unclear whether the relationship between the behavioural manifestations of cognitive processes, as examined here, will reflect their neural organization in the PPC, however, behavioural findings may serve to guide predictions for future neuroimaging studies directly exploring the functional role of the PPC in cognition and it how it may contribute to cognitive ageing.
References


Selemon, L., & Goldman-Rakic, P. (1988). Common cortical and subcortical targets of the dorsolateral prefrontal and posterior parietal cortices in the rhesus monkey: evidence for a


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Figure 1. The posterior parietal cortex (PPC), divided into the dorsal (rose-colour; dPPC) and ventral subregions (teal-colour; vPPC). The dPPC is comprised of the superior parietal lobule (SPL) and the intraparietal sulcus (IPS), or Brodmann area 7. The vPPC is comprised of (anterior to posterior) the supramarginal gyrus (SMG), the temporoparietal junction (TPJ), and the angular gyrus (AG). Figure was from Cabeza, Ciaramelli, Olson, & Moscovitch (2008), © (2008) Macmillan Publishers Limited.
Figure 2a. Procedure for the memory task. Possible cue-target combinations are listed below. Blue represents when top-down attention is engaged towards a mnemonic target and purple similarly represents bottom-up attention. For comparison with the perception task: Intact = Valid, Recomb = Invalid, and NoOld = Neutral.
Figure 2b. Procedure for the perception task. Possible cue-target combinations are listed below. Blue represents when top-down attention is engaged towards a perceptual target and purple similarly represents bottom-up attention.
Figure 3a. Mean memory accuracy scores by group and condition.

Figure 3b. Mean perception accuracy scores by group and condition.
Figure 4a. Mean memory reaction times by group and condition.

Figure 4b. Mean perception reaction times by group and condition.
Figure 5. Mean attention scores by task and group for BUA. RT difference scores represent the relative difference between invalid and valid cueing (i.e., $RT_{\text{invalid}} - RT_{\text{valid}}$). Age was a significant predictor of BUA in Perception, but not Memory.
**Figure 6.** Mean attention scores by task and group for TDA. RT difference scores represent the relative difference between valid and neutral cueing (i.e., $RT_{Neutral} - RT_{Valid}$). Age was not a significant predictor of TDA in Perception or Memory.
Figure 7a. Scatterplot of top-down attention scores in perception and memory in younger adults. RT difference scores represent the difference between valid and neutral cueing (i.e., $RT_{\text{Neutral}} - RT_{\text{Valid}}$). There appears to be a significant positive relationship between TDA across tasks in the younger group.

Figure 7b. Scatterplot of bottom-up attention scores in perception and memory in younger adults. RT difference scores represent the difference between invalid and valid cueing (i.e., $RT_{\text{Invalid}} - RT_{\text{Valid}}$). There appears to be no positive relationship between BUA processes across tasks in the younger group.
Figure 8. Scatterplot of bottom-up attention scores in perception and memory in younger adults. ACC difference scores in BUA-memory represent the difference between invalid and valid cueing (i.e., $\text{ACC}_{\text{Invalid}} - \text{ACC}_{\text{Valid}}$), while RT difference scores represent the difference between invalid and valid cueing (i.e., $\text{RT}_{\text{Invalid}} - \text{RT}_{\text{Valid}}$). When accuracy is considered appears to be a significant negative relationship between BUA processes across tasks in the younger group.
Figure 9a. Scatterplot of top-down attention scores in perception and memory in older adults. RT difference scores represent the difference between valid and neutral cueing (i.e., $RT_{\text{Neutral}} - RT_{\text{Valid}}$). There appears to be no relationship between TDA across tasks in the older group.

Figure 9b. Scatterplot of bottom-up attention scores in perception and memory in older adults. RT difference scores represent the difference between invalid and valid cueing (i.e., $RT_{\text{Invalid}} - RT_{\text{Valid}}$). Though it appears as if there was a negative relationship between BUA processes across tasks in the older group, nothing emerged significant in the statistical models.
### Tables

*Table 1. Background measures.*

<table>
<thead>
<tr>
<th>Background Measures</th>
<th>YA (n = 20)</th>
<th>OA (n = 20)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$M$</td>
<td>$SD$</td>
</tr>
<tr>
<td>Age (in years)</td>
<td>19.83</td>
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<td>MMSE</td>
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<td>0.83</td>
</tr>
<tr>
<td>SILS-V</td>
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<td>Education (in years)</td>
<td>14.30</td>
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Table 2. Mean accuracy scores.

<table>
<thead>
<tr>
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<th>SD</th>
<th>OA M</th>
<th>SD</th>
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<tbody>
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<td>0.116</td>
<td>0.901</td>
<td>0.091</td>
</tr>
<tr>
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<td>Recomb</td>
<td>0.804</td>
<td>0.161</td>
<td>0.813</td>
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<tr>
<td></td>
<td>NoOld</td>
<td>0.861</td>
<td>0.134</td>
<td>0.832</td>
<td>0.136</td>
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<td></td>
<td>NoNew</td>
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<td>0.931</td>
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<td>OldNew</td>
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<td>0.091</td>
<td>0.919</td>
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<td>Valid</td>
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<td>0.073</td>
<td>0.953</td>
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<tr>
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<td>Invalid</td>
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<td>0.083</td>
<td>0.952</td>
<td>0.057</td>
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<td>Neutral</td>
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<td>0.969</td>
<td>0.025</td>
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Table 3. Mean reaction time scores.

<table>
<thead>
<tr>
<th>Task</th>
<th>Condition</th>
<th>YA M</th>
<th>YA SD</th>
<th>OA M</th>
<th>OA SD</th>
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<tr>
<td>Memory</td>
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<td>282.502</td>
<td>1176.899</td>
<td>306.816</td>
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<tr>
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<tr>
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<td>1126.583</td>
<td>184.014</td>
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Table 4. Pearson correlations between attention scores within each age group.

<table>
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<tr>
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<th>Variables</th>
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<th>3</th>
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<td>-.032</td>
<td>-.206</td>
<td>-.454*</td>
</tr>
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<td>.382*</td>
<td>.</td>
<td>.329</td>
<td>.498*</td>
<td>-.070</td>
</tr>
<tr>
<td>(n = 20)</td>
<td>BUA-Mem</td>
<td>-.032</td>
<td>.329</td>
<td>.</td>
<td>.711**</td>
<td>.113</td>
</tr>
<tr>
<td></td>
<td>TDA-Mem</td>
<td>-.206</td>
<td>.498*</td>
<td>.711**</td>
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<td>-.056</td>
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<tr>
<td></td>
<td>BUA-Mem(ACC)</td>
<td>-.454*</td>
<td>-.070</td>
<td>.113</td>
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<td>.</td>
</tr>
<tr>
<td>OA</td>
<td>BUA-Per</td>
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<td>.483*</td>
<td>-.348</td>
<td>.058</td>
<td>.373</td>
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<tr>
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<td>TDA-Per</td>
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<td>-.356</td>
<td>-.050</td>
<td>.056</td>
</tr>
<tr>
<td>(n = 20)</td>
<td>BUA-Mem</td>
<td>-.348</td>
<td>-.356</td>
<td>.</td>
<td>.209</td>
<td>-.244</td>
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<tr>
<td></td>
<td>TDA-Mem</td>
<td>.058</td>
<td>-.050</td>
<td>.209</td>
<td>.</td>
<td>.295</td>
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<tr>
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<td>BUA-Mem(ACC)</td>
<td>.373</td>
<td>.056</td>
<td>-.244</td>
<td>.295</td>
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** p < .01    * p < .05    “ p < .10
Table 5a. Multiple regression for domain-generality test in younger adults: Bottom-up attention in memory.

<table>
<thead>
<tr>
<th>Model</th>
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<th>$\beta$</th>
<th>$t$</th>
<th>$p$</th>
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<tr>
<td>TDA-Per</td>
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<td>1.639</td>
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<tr>
<td>BUA-Per</td>
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<td>0.359</td>
<td>-0.184</td>
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<td></td>
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Table 5b. Multiple regression for domain-generality test in younger adults: Bottom-up attention in perception.

<table>
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<th>$t$</th>
<th>$p$</th>
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<td>0.246</td>
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<tr>
<td>BUA-Mem</td>
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<td>0.226</td>
<td>0.231</td>
<td>0.694</td>
<td>0.497</td>
</tr>
<tr>
<td>Criterion:</td>
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Table 5c. Multiple regression for domain-generality test in younger adults: Top-down attention in memory.

<table>
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<td>-0.463</td>
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Criterion: TDA-Mem

Table 5d. Multiple regression for domain-generality test in younger adults: Top-down attention in perception.

<table>
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<th>Model</th>
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<td>-0.167</td>
<td>0.870</td>
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</table>

Criterion: TDA-Per
Table 6a. Multiple regression for domain-generality test in older adults: Bottom-up attention in memory.

<table>
<thead>
<tr>
<th>Model</th>
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<th>p</th>
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<td>0.376</td>
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Criterion: BUA-Mem

Table 6b. Multiple regression for domain-generality test in older adults: Bottom-up attention in perception.

<table>
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<tr>
<th>Model</th>
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<th>p</th>
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<tr>
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<td>0.120</td>
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</table>

Criterion: BUA-Per
Table 6c. Multiple regression for domain-generality test in older adults: Top-down attention in memory.

<table>
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<tr>
<th>Model</th>
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Criterion: TDA-Mem

Table 6d. Multiple regression for domain-generality test in older adults: Top-down attention in perception.

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<tr>
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</tr>
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</table>

Criterion: TDA-Per
Table 7a. Multiple regression for domain-generality test in younger adults: Bottom-up attention in memory.

<table>
<thead>
<tr>
<th>Model</th>
<th>B</th>
<th>SE</th>
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<th>p</th>
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<td>TDA-Per</td>
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<td>0.000</td>
<td>0.120</td>
<td>0.518</td>
<td>0.611</td>
</tr>
<tr>
<td>BUA-Per</td>
<td>-0.001</td>
<td>0.000</td>
<td>-0.499</td>
<td>-2.152</td>
<td>0.046</td>
</tr>
</tbody>
</table>

Criterion: BUA-Mem(ACC)

Table 7b. Multiple regression for domain-generality test in younger adults: Bottom-up attention in perception.

<table>
<thead>
<tr>
<th>Model</th>
<th>B</th>
<th>SE</th>
<th>β</th>
<th>t</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>51.468</td>
<td>45.979</td>
<td>1.119</td>
<td>0.279</td>
<td></td>
</tr>
<tr>
<td>TDA-Mem</td>
<td>-0.172</td>
<td>0.155</td>
<td>-0.232</td>
<td>-1.111</td>
<td>0.282</td>
</tr>
<tr>
<td>BUA-Mem(ACC)</td>
<td>-428.290</td>
<td>191.871</td>
<td>-0.467</td>
<td>-2.232</td>
<td>0.039</td>
</tr>
</tbody>
</table>

Criterion: BUA-Per
Table 7c. Multiple regression for domain-generality test in younger adults: Top-down attention in memory.

<table>
<thead>
<tr>
<th>Model</th>
<th>B</th>
<th>SE</th>
<th>β</th>
<th>t</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>219.105</td>
<td>31.072</td>
<td>7.052</td>
<td>0.000</td>
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</tr>
<tr>
<td>TDA-Per</td>
<td>1.399</td>
<td>0.411</td>
<td>0.674</td>
<td>3.406</td>
<td>0.003</td>
</tr>
<tr>
<td>BUA-Per</td>
<td>-0.626</td>
<td>0.267</td>
<td>-0.463</td>
<td>-2.339</td>
<td>0.032</td>
</tr>
</tbody>
</table>

Criterion: TDA-Mem

Table 7d. Multiple regression for domain-generality test in younger adults: Top-down attention in perception.

<table>
<thead>
<tr>
<th>Model</th>
<th>B</th>
<th>SE</th>
<th>β</th>
<th>t</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>-23.945</td>
<td>30.143</td>
<td>-0.794</td>
<td>0.438</td>
<td></td>
</tr>
<tr>
<td>TDA-Mem</td>
<td>0.239</td>
<td>0.101</td>
<td>0.495</td>
<td>2.353</td>
<td>0.031</td>
</tr>
<tr>
<td>BUA-Mem(ACC)</td>
<td>-25.339</td>
<td>125.789</td>
<td>-0.042</td>
<td>-0.201</td>
<td>0.843</td>
</tr>
</tbody>
</table>

Criterion: TDA-Per