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Qué PASA? The Posterior-Anterior Shift in Aging

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Abstract

A consistent finding from functional neuroimaging studies of cognitive aging is an age-related reduction in occipital activity coupled with increased frontal activity. This posterior-anterior shift in aging (PASA) has been typically attributed to functional compensation. The present functional magnetic resonance imaging sought to 1) confirm that PASA reflects the effects of aging rather than differences in task difficulty; 2) test the compensation hypothesis; and 3) investigate whether PASA generalizes to deactivations. Young and older participants were scanned during episodic retrieval and visual perceptual tasks, and age-related changes in brain activity common to both tasks were identified. The study yielded 3 main findings. First, inconsistent with a difficulty account, the PASA pattern was found across task and confidence levels when matching performance among groups. Second, supporting the compensatory hypothesis, age-related increases in frontal activity were positively correlated with performance and negatively correlated with the age-related occipital decreases. Age-related increases and correlations with parietal activity were also found. Finally, supporting the generalizability of the PASA pattern to deactivations, aging reduced deactivations in posterior midline cortex but increased deactivations in medial frontal cortex. Taken together, these findings demonstrate the validity, function, and generalizability of PASA, as well as its importance for the cognitive neuroscience of aging.

Keywords

aging; compensation; deactivation; fMRI; frontal

Introduction

The ultimate goal in the cognitive neuroscience of aging is to directly link the effects of aging on cognition to its effects on the brain (Cabeza et al. 2006). In recent years, functional neuroimaging studies using techniques such as functional magnetic resonance imaging (fMRI) have made great strides toward this goal by measuring brain activity while younger and older participants are performing different cognitive tasks (Daselaar et al. 2006). These studies have revealed 2 consistent patterns of age-related changes in brain activity across a variety of cognitive functions. One is a more bilateral pattern of frontal recruitment in older adults (for a review, see Cabeza 2002). The other is an age-related reduction in occipitotemporal activity

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coupled with an age-related increase in frontal activity. Investigating the functional significance of this second pattern, which we recently called posterior-anterior shift in aging (PASA) (Dennis and Cabeza, forthcoming), was the main goal of the present study.

PASA was first reported by Grady et al. (1994) in a positron emission tomography (PET) study that investigated perception of faces and locations. In both conditions, older adults showed weaker activity than younger adults in occipitotemporal regions but greater activity in anterior regions, including the prefrontal cortex (PFC). Grady and collaborators suggested that older adults recruited anterior regions to compensate for sensory processing deficits in occipitotemporal regions. Since 1994, PET and fMRI studies have found the PASA pattern across a variety of cognitive functions, including attention (Madden et al. 2002; Cabeza et al. 2004), visual perception (VP) (Grady et al. 1994; Madden and Hoffman 1997; Grady 2000; Levine et al. 2000; Huettel et al. 2001; Iidaka et al. 2002), visuospatial processing (Nyberg et al. 2003; Meulenbroek et al. 2004), working memory (Rypma and D'Esposito 2000; Grossman et al. 2002), episodic memory encoding (Anderson et al. 2000; Dennis et al. 2006; but see Grady et al. 1995; Morcom et al. 2003; Gutchess et al. 2005), and episodic memory retrieval (Cabeza et al. 1997; Madden et al. 1999; Grady et al. 2002; Daselaar et al. 2003; Cabeza et al. 2004). Although not all studies find age-related frontal increases (Grady et al. 1995; Iidaka et al. 2001; Milham et al. 2002; Stebbins et al. 2002), PASA is nonetheless a well-established aging phenomenon in the functional neuroimaging literature. However, there are open questions regarding its validity, function, and generalizability.

Regarding the validity of PASA, although this phenomenon is assumed to reflect the effects of aging, it may simply reflect differences in task difficulty. Given that the same cognitive tasks tend to be more demanding for older adults than for younger adults, PASA, and in particular its PFC component, could merely reflect a confound with task difficulty rather than an effect of aging per se. Supporting this difficulty account, there is abundant evidence that PFC activity in young adults tends to increase as a function of task difficulty (Grady et al. 1998; Konishi et al. 1998; Rypma and D'Esposito 2000; Braver et al. 2001). Even though the PASA pattern has been found in studies where accuracy was similar in younger and older adults (e.g., Grady et al. 1994), it is possible that older adults achieved a good level of accuracy by deploying greater cognitive resources than younger adults. Thus, in order to establish that PASA is not due to differences in task difficulty, one needs to demonstrate that PASA is not associated either with objective measures of task difficulty, such as accuracy, or with subjective measures of difficulty, such as confidence ratings. To this end, the present study investigated PASA while controlling for differences in accuracy and confidence.

Regarding the function of the PASA pattern, the compensation account is only partially supported by available functional neuroimaging evidence. This account predicts that the age-related increase in PFC activation should be positively correlated with cognitive performance and negatively correlated with the age-related decrease in occipitotemporal activity. Consistent with the first part of this prediction, several studies have linked greater PFC activity in older adults, in the form of bilateral recruitment, to better cognitive performance. For example, Reuter-Lorenz et al. (2000) found that older adults who recruited bilateral PFC regions were faster in a working memory task, and Cabeza et al. (2002) found bilateral PFC recruitment in high- but not in low-performing older adults (see also Rosen et al. 2002; Daselaar et al. 2003). However, these studies focused on lateralization changes and did not report evidence regarding the relationship between PFC and occipitotemporal activations. This evidence was reported in a study that found a negative correlation between the effects of aging on PFC and occipital activations (Cabeza et al. 2004). However, this study did not report a positive correlation between PFC activity and performance. Thus, although compensation account of PASA has been partially supported, no study has simultaneously found PFC activations in

older adults to be positively correlated with performance and negatively correlated with occipital activations. Obtaining such evidence was another goal of the present study.

Finally, regarding the generalizability of PASA, although this effect has been repeatedly observed for increases in brain activity (activations), to our knowledge, it has never been reported for decreases in brain activity (deactivations). This void in the data is important because if the PASA pattern reflects a global shift in brain function, then it should occur not only for activations but also for deactivations. Given that older adults show a shift in positive activations between posterior and anterior regions, it is reasonable to believe that there may also be a shift in deactivations along the same gradient, as older adults reallocate neural resources to perform cognitive tasks and compensate for declining neural processing in posterior brain regions. Although most functional neuroimaging studies have focused on activations, there is ample evidence that deactivations are also critical for various cognitive processes. Several functional neuroimaging studies (e.g., Mazoyer et al. 2001; Raichle et al. 2001; McKiernan et al. 2003) have identified a set of brain regions that are consistently deactivated during demanding cognitive performance. These regions typically include posterior midline regions, such as posterior cingulate and precuneus, and anterior midline regions, such as medial frontal areas. Raichle and collaborators have proposed that these regions constitute a “default network” associated with conscious rest processes, which must be suppressed for successful cognitive performance (Gusnard et al. 2001; Raichle et al. 2001). Consistent with this hypothesis, successful memory has been associated with deactivations in posterior midline cortex (Daselaar et al. 2004), and failure to deactivate this region has been associated with memory deficits in healthy aging and Alzheimer’s disease (Daselaar et al. 2003; Lustig et al. 2003; Greicius et al. 2004; Celone et al. 2006; Grady et al. 2006). The finding that healthy older adults show attenuated deactivations in posterior midline cortex suggests the intriguing possibility that they may compensate this deficit by deactivating anterior midline regions to a greater extent than younger adults. In other words, the PASA pattern may apply not only to activations but also to deactivations. To investigate this idea, the present study investigated both activations and deactivations.

The goals of the present study were to investigate the validity, function, and generalizability of PASA. Younger and older participants were scanned with event-related fMRI while performing 2 very different cognitive tasks: an “episodic retrieval” (ER) task for words studied before scanning and a VP task that involved comparing the size of 2 screen areas. Both ER and VP are associated with a network of brain regions including medial temporal lobes and PFC, posterior parietal, and occipital cortices. Given that PASA is assumed to be a general, task-independent phenomenon, we used conjunction analyses to identify age effects that occurred for both memory and perceptual tasks. In order to eliminate age-related differences due to task difficulty, we equated accuracy in younger and older adults by giving a double study presentation to older adults and by selecting pairs of younger and older adults who were perfectly matched in ER and VP accuracy. Additionally, we focused on activations that did not differ as a function of confidence. To investigate the compensation account, we focused on 2 regions of interest, PFC and occipital cortex, and calculated correlations between PFC activity and cognitive performance between PFC activity and occipital activity. Finally, to investigate the effects of aging on deactivations, we measured the effects of aging on posterior and anterior midline deactivations.

We made 3 predictions: 1) Disconfirming the difficulty account, PASA will be found in conditions in which differences in difficulty are largely eliminated. 2) Supporting the compensation account, PFC activity will be positively correlated with cognitive performance and negatively correlated with occipital activity. 3) Finally, demonstrating the generalizability of PASA to deactivations, older adults would show weaker deactivations in posterior midline regions but stronger deactivations in anterior medial regions.

Methods

Participants

Fourteen younger and fifteen older adults were paid for their participation in this study. All participants were healthy, right-handed native English speakers with no history of neurological or psychiatric episodes (See Table 1 for participant characteristics). Written informed consent was obtained from each participant, and the study met all criteria for approval from the Duke University Institutional Review Board. Younger adults were recruited from the Duke University community; older adults were community-dwelling individuals who were selected from a pool of research volunteers at Duke University. Older adults were screened for health problems and conditions that could affect blood flow (e.g., hypertension and certain medications). In order to match behavioral performance in the 2 groups, 12 younger (mean age = 22.2 years) and 12 older adults (mean age = 69.2 years) were matched by a rank order based on corrected scores of ER and VP performance during the scanning session (same couplings used for both ER and VP; see Fig. 1). The calculation of these scores is described below.

Stimuli

For the ER test, 240 five-letter words of moderate concreteness (mean = 504), frequency (mean = 39), and imageability (mean = 510) were selected from the medical research council psycholinguistic database (http://www.psy.uwa.edu.au/MRCDataBase/mrc2.html). Additionally, 80 pronounceable five-letter pseudowords were created to be used as lures in the lexical decision test used as the encoding task. For the VP task, 120 rectangles (4.5 × 6”) were divided by a jagged line into 2 areas colored orange or blue. The relative sizes of these areas were adjusted to create different versions of a perceptual stimulus, which allowed for a manipulation of difficulty and titration of subject performance across groups.

Behavioral Paradigm

Approximately 20 min prior to scanning, participants viewed an intermixed list of 120 real words and 80 pseudowords, presented at a rate of 2 s per word. Participants were asked to decide if the string was a real word (lexical decision task) and asked to remember the words for later in the study. The rationale for using a relatively shallow encoding task was to ensure a sufficient number of low-confidence recognition responses. Older adults were shown the encoding list twice in order to attenuate differences in recognition performance with younger adults. As noted above, remaining differences were completely eliminated by selecting young-old pairs matched in accuracy.

During the scanning session, participants performed 4 runs of the ER and 2 runs of the VP task. Run order was counterbalanced across participants, each run lasting 442 s. During ER runs, participants saw an equal mix of old words shown during the earlier lexical decision task and completely new words (60 total words per run). Each trial consisted of 2 phases. Participants first made an old/new judgment on the presented word (3.4 s) and were then prompted to report their confidence (1.7 s) for their answer from a scale of 1 (lowest confidence) to 4 (highest confidence). Each trial was followed by an inter-trial interval of 0-5.4 s. The VP task involved participants viewing rectangles unevenly divided into 2 colored sections, blue and orange, by a random jagged line. Participants decided which color had the greater surface area. Again, this judgment was followed by a confidence rating (timing of trial presentation and confidence ratings were the same across tasks). An advantage of the area size comparison task is that its difficulty can be easily manipulated by varying differences in area size. By doing so across several pilot studies, we were able to find a set of stimuli that yielded accuracy rates and confidence ranges similar to those of the ER task. Behavioral scores were based upon corrected performance: for the ER task hits - false alarms and for the VP task [(raw score - chance {50%})

× 2]. Because we were interested in investigating task-independent age differences, a composite behavioral score was then created by averaging across both corrected VP and ER scores.

Magnetic Resonance Imaging Scanning

Participants were scanned on a 4-T GE scanner. Coplanar functional images were acquired using an inverse spiral sequence (64 × 64 matrix, time repetition [TR] = 1700 ms, time echo [TE] = 31 ms, field of view [FOV] = 240 mm, 34 slices, 3.8-mm slice thickness, and 254 images). The anatomical magnetic resonance imaging (MRI) was acquired using a 3D T_1-weighted echo-planar sequence (256 × 256 matrix, TR = 12 ms, TE = 5 ms, FOV = 24 cm, 68 slices, 1.9-mm slice thickness, and 254 images). Scanner noise was reduced with ear plugs, and head motion was minimized with foam pads. Stimuli were presented on LCD goggles, and behavioral responses were recorded with a 4-key fiber-optic response box (Resonance Technology, Inc., Northridge, CA). When necessary, vision was corrected using MRI-compatible lenses that matched the prescription used by the participant.

fMRI Analyses

Preprocessing and data analysis were performed using Statistical Parametric Mapping software (SPM2; Wellcome Department of Cognitive Neurology, London, UK) and custom MATLAB scripts. After discarding initial volumes to allow for scanner stabilization, images were slice-time and motion corrected, spatially normalized to the Montreal Neurological Institute template, and smoothed using an 8 × 8 × 8 mm Gaussian kernel. Event-related blood oxygen level-dependent responses for each subject were analyzed using a modified general linear model (Worsley and Friston 1995) in order to model 2 trial types of interest, correct ER and VP trials. Incorrect trials, no-response trials, and responses to novel items were included in the model but not used in these analyses. Because several participants did not use the lowest confidence response, the 2 lowest and 2 highest confidence levels were collapsed into 2 levels of confidence (low [1-2] and high [3-4]) for first-level subject analyses.

Second-level random effects comparisons modeled task and confidence effects among participants who were paired on behavioral criterion described above. In order to eliminate the variance due to task type or confidence rating, SPM maps for group contrasts were masked exclusively with bidirectional (low vs. high confidence, ER vs. VP, and vice versa) contrast *t*-maps for those factors (both set to a threshold at $P < 0.01$). In addition to these conjunction maps, appropriate activation or deactivation maps, created by contrasting overall task activity with baseline (also $P < 0.01$), were also used as masks in order to identify regions of significant activations or deactivations, respectively. We report clusters of activity surviving at $P < 0.005$ (uncorrected) with a minimum cluster size of 8 voxels. Finally, in order to identify common activity across both task and confidence in young and older adults, additional conjunction analyses were performed, excluding regions which showed age differences. We report clusters surviving at $P < 0.001$ in each age group.

Regression analyses were performed on the identified regions of age-related differences in activity in order to assess the relationship between activity in the PFC and task-independent cognitive performance in behavioral tasks. Mean parameter estimates (i.e., beta values) from a spherical cluster of 10 mm around peak voxels were used to calculate correlations in older adults. In addition, extracted values were adjusted for main effects associated with both confidence and task; this was done in order to remove any variance in extracted beta values due to effects not spanned by the age-related contrast. The composite behavioral measure was correlated with parameter estimates for the activation in each cluster for each region of interest.

Results

Behavioral Data

Table 2 summarizes behavioral performance on ER and VP tasks. Mean performance did neither differ significantly between age groups in either task nor did the proportion of high- and low-confidence responses in either the ER or the VP task. This is not surprising given the double study presentation for older adults and the matching of younger and older participants according to performance (see Participants in Methods). Consistent with general age-related slowing (Salthouse 1996), older adults were slower than younger adults in both the VP task ($t_{22} = 2.64$, $P < 0.05$) and the ER task ($t_{22} = 2.43$, $P < 0.05$); however, the no response rate was less than 1% in both groups, indicating that participants had ample time to respond to the tasks.

Neuroimaging Results

Table 3 lists regions commonly activated and deactivated in both younger and older adults, excluding those regions which showed significant age differences (see below). Common activations included bilateral parietal, left, and medial prefrontal cortices (PFC). Common deactivations included bilateral inferior parietal lobules, posterior cingulate cortex, and medial rostral PFC. Regions are consistent with previous studies assessing task-independent (Cabeza et al. 2002) and default activity (Lustig et al. 2003).

Table 4 lists regions showing significant effects of aging on activations and deactivations common to both tasks and to both high- and low-confidence responses. Consistent with our first prediction, the PASA pattern was found even when potential differences in task difficulty were eliminated by controlling differences in accuracy and confidence. As illustrated by Figure 2*A, B*, compared with younger adults, older adults showed reduced activity in occipital (Brodmann areas [BA] 17, 18) and medial temporal regions but increased activity in PFC regions (BA 45). Consistent with general nature of PASA, these effects were found across 2 very different cognitive tasks.

Consistent with our second prediction, PFC activity in older adults was negatively correlated with activity in the occipital cortex ($r = -0.61$, $P < 0.05$). In other words, older adults with the least amount of occipital activity showed the greatest amount of frontal activity. Furthermore, the activity in this region of the PFC was positively correlated with ER/VP performance ($r = 0.63$, $P < 0.05$) in older adults. No significant correlations between regions or between activity and performance were found in younger adults (see Fig. 3). Taken together, these correlations provide strong support for the compensation account of PASA. Though we had no a priori hypotheses as to the correlations between behavior and occipital, parietal, and default network, these were also explored across both young and older adults. Of these, the only correlations found to be significant were those between parietal activity and cognitive performance ($r = 0.63$, $P < 0.05$) and between right posterior parietal activity and PFC activity ($r = 0.58$, $P = 0.05$) in older adults. The lack of a positive correlation between occipital activity and performance in young adults may reflect minimal variability in the activity of this region or a relatively small contribution of this region to variability in cognitive performance. At any rate, there is abundant neuroscience research supporting the assumption that occipital cortex is critical for vision and hence contributes to all cognitive tasks involving visual stimuli.

Finally, consistent with our third prediction, the PASA pattern was also found for deactivations (see Fig. 2*C, D*): whereas deactivations in posterior midline cortex (precuneus) were attenuated by aging, deactivations in anterior midline cortex (medial PFC) were increased by aging. As illustrated by Figure 2*C, D*, these age effects on deactivations were found for both tasks and were not affected by confidence. Thus, like the PASA pattern for activations, the PASA pattern for deactivations also seems to be general and unrelated to difficulty differences.

Discussion

The current study examined the validity, function, and generalizability of PASA. The results confirmed our predictions. First, supporting the validity of PASA, we found an age-related reduction in occipital activity coupled with age-related increase in PFC activity in conditions in which differences in difficulty were largely eliminated. Second, supporting the compensatory function of PASA, we found a negative correlation between the occipital reduction and the PFC increase and a positive correlation between the latter and cognitive performance in older adults. Finally, supporting the generalizability of PASA to deactivations, we found an age-related reduction in posterior midline deactivation coupled with an age-related increase in anterior midline deactivation. These 3 findings are discussed in separate sections below.

Validity of PASA: Evidence Against a Difficulty Account

Task difficulty can be a serious confounding factor in functional neuroimaging studies of cognitive aging. There is abundant evidence that brain activity changes as a function of task difficulty, and the same cognitive tasks tend to be more demanding for older than for younger adults. Thus, it could be argued that differences in activity between younger and older adults, including the PASA pattern, reflect differences in task difficulty rather than aging per se. To address this issue, we carefully matched accuracy in younger and older (see Fig. 1) and we focused on activations that were similar for high- and low-confidence responses. Even though difficulty differences were largely eliminated, we found a clear PASA pattern: occipital activity was greater in younger than in older adults, whereas PFC activity was greater in older than in younger adults. Thus, the PASA pattern in our study cannot be attributed to differences in task difficulty.

Although we eliminated differences in accuracy and confidence, older adults were significantly slower than younger adults in both tasks. However, it is unlikely that differences in reaction times (RTs) accounted for the PASA pattern. RT differences were as large between high- and low-confidence trials (ER: 1.44 s [0.48] vs. 1.95 s [0.42] and VP: 1.63 s [0.46] vs. 2.04 s [0.46]) as between younger and older adult groups (high confidence: 1.31 s [0.39] vs. 1.68 s [0.45]; low confidence: 1.81 s [0.48] vs. 2.18 s [0.46]). Thus, if the activations displayed in Figure 2 were due to differences in RTs, they should have differed not only between younger and older adults but also between high- and low-confidence trials and they did not. To further clarify whether these differences represent task-independent age-related differences in fMRI activity or are due to differences in response latency, we performed a separate analysis where RT was modeled as a covariate of interest within the second-level random effects analysis. The PASA pattern was not affected by the addition of this covariate to the analysis, and regions showing RT effects did not overlap with regions showing PASA-related activity. In sum, the present results argue against a difficulty account and support the idea that PASA is a true aging phenomenon.

Function of PASA: Evidence for the Compensation Account

If one accepts that PASA is a true aging phenomenon, a critical question to ask is what it means. In general, age-related reductions in occipital activity have been attributed to deficits in sensory processing and age-related increases in PFC activity in an attempt to compensate for these deficits (Grady et al. 1994, 2005; Madden et al. 1994; Cabeza et al. 2004). The link between occipital decreases and sensory deficits is consistent with abundant evidence that perceptual processing declines as a function of aging (for a review, see Schneider and Pichora-Fuller 2000). The fact that occipital decreases have been found across many different tasks (see Introduction) fits well with the view that sensory decline is a major factor in cognitive aging (Lindenberger and Baltes 1994). The link between PFC increases and compensatory processes

is supported by some neuroimaging evidence (e.g., Reuter-Lorenz et al. 2000; Cabeza et al. 2002; Grady et al. 2005), but the specific assumption that PFC increases compensate for occipital deficits has no direct empirical support.

In the present study, we directly examined the compensatory account by testing a clear prediction of this account: if the increase in PFC activity compensates for the decrease in occipital activity, then PFC activity should be positively correlated with performance and negatively correlated with occipital activity in older adults. As illustrated by Figure 3, our study yielded both findings. It may seem odd to consider age-related deficits in occipital activity accompanied by increases in frontal activity given that, structurally, the occipital lobe is one of the regions least affected by aging and the frontal lobe, the most (Raz 2000). However, there are several important considerations to keep in mind. Regarding age-related deficits in occipital activity, decreased activity is often found when evaluating successful task performance (Cabeza et al. 2004;Gutchess et al. 2005). These findings are consistent with several studies that show age-related dedifferentiation in sensory processing (Park et al. 2004;Gazzaley et al. 2005). Thus, it is most likely the case that age-related reductions in occipital activity in the current study reflect the inability of older adults to engage specialized neural mechanisms within this region in response to cognitive demands. Although it cannot be excluded that the negative relationship between frontal and occipital activity observed here could be driven by an inhibition of occipital activity by frontal cortex, the relationship between frontal activity and cognitive performance suggests that this frontal increase is compensatory. By matching performance and controlling for difficulty in the current study, we were able to identify brain regions showing age differences associated with equivalent performance, linking any age-related increases in activity to compensation.

Thus, results indicate that high-order cognitive processes associated with frontal functioning can come online in response to deficits in posterior brain regions. Furthermore, these frontal activations can offset the lack of posterior processing and contribute to successful cognitive performance in older adults. Though the exact function of the compensatory frontal activity has yet to be identified, several possibilities exist that could account for the observed frontal activations. In older adults, frontal regions may operate in a top-down manner directing and organizing sensory input, or they may try to reconstruct dampened signal emanating from sensory cortices. Moreover, it is very likely that there is no single age-related “compensation mechanism” across all cognitive functions but that frontal regions come online in response to degraded functioning in other regions.

As noted in the Introduction, previous research has also found age-related increases in activity in brain regions other than the frontal lobes. Age-related increases in parietal activity have been reported in several studies (Anderson et al. 2000; Grady et al. 2002, 2003; Madden et al. 2006), and in one study from our laboratory, we found them in the same participants across 3 different tasks (ER, working memory, and visual attention; Cabeza et al. 2004). It is worth noting that not all posterior brain regions in the current study showed reductions in activity as a function with aging. In accord with these previous studies, right posterior parietal regions behaved similarly to PFC regions and showed greater activity in older than in younger adults. In fact, like PFC activity, posterior parietal activity was also positively correlated with composite performance ($r = 0.63$, $P < 0.05$). Furthermore, correlations between right posterior parietal activity and PFC activity were significant ($r = 0.58$, $P < 0.05$), indicating the strong relationship between the 2 regions. Thus, these age-related increases in parietal activity seem to be reliable and task independent, indicating that parietal activity may also be compensatory. This compensatory activity may point to an age-related shift in posterior processing from ventral occipital regions to more dorsal parietal regions associated with enhanced top-down control and attentional guidance (Madden et al. 2006; Velanova et al. 2007). Given previous findings demonstrating task-independent shifts in ventral/dorsal recruitment (Cabeza et al.

2004), the present results suggest increases in neural recruitment reflecting compensation occur not only in PFC but also in parietal regions.

Generalizability of PASA: Posterior-Anterior Shift in Deactivations

The present study also found age-related changes reflecting PASA in the deactivations within regions previously described as part of a default network (Fig. 2*C*,*D*). The "default network" is comprised of a system of regions including posterior and anterior midline cortices that are often deactivated during task compared with a resting baseline. Raichle and collaborators (Raichle et al. 2001; Fair et al. 2007) proposed that these regions support processes active during conscious rest, which must be suppressed to allow for successful cognitive performance. Although this idea has been challenged (Morcom and Fletcher 2006), understanding deactivations within these regions is very important because of evidence that these deactivations are necessary for successful performance in healthy younger adults (Daselaar et al. 2004) and may reflect a reallocation of processing resources from the default network to regions involved in task performance (McKiernan et al. 2003). This view is consistent with the current findings and suggests that greater anterior medial deactivations in older adults may free up processing resources for the engagement of greater frontal activity. However, given that we did not find any direct correlations between deactivations and performance, it may be the case that a given deactivation can free up resources to be used by several other task processes, only a subset of which were common across the 2 currents and/or directly contributed to task performance.

Previous research has shown deactivations to be attenuated in several populations including Alzheimer's (Lustig et al. 2003), amnesia (Maguire et al. 2001), and schizophrenia (Fletcher et al. 1998) patients, as well as in healthy older adults (Lustig et al. 2003; Grady et al. 2006; Persson et al. 2007). The results of the present study clearly show that not all default network deactivations are attenuated in healthy older adults: whereas deactivations in the posterior midline regions (precuneus) were reduced by aging, deactivations in the anterior midline region (medial PFC) were actually enhanced by aging (Fig. 2*C*,*D*). This finding thus confirms our prediction that the PASA pattern occurs not only for activations but also for deactivations.

It is worth noting that although the observed age-related attenuation in posterior deactivations are consistent with previous studies of healthy aging (Lustig et al. 2003; Grady et al. 2006; Persson et al. 2007), the location of this deactivation is also dorsal to regions shown to activate during successful ER (e.g., Shannon and Buckner 2004; Prince et al. 2005). Conversely, the observed anterior midline deactivations differ from findings from the Lustig (2003) and Persson (2007) studies. There are several methodological variations among the studies that may account for this difference. First, both studies used semantic retrieval tasks, whereas the current study examined both ER and VP. Unlike ER (for review, see Prull et al. 2000) and visuospatial abilities (Jenkins et al. 2000), semantic retrieval is well preserved in older adults (Craik et al. 1995) and may not require the same reallocation of processing resources for successful performance. This notion is consistent with the fact that the PASA pattern has not been observed for neuroimaging studies of semantic memory (e.g., Madden et al. 2002; Persson et al. 2004). Second, both aforementioned studies used blocked designs, whereas the current findings are based on event-related data. Previous work has suggested that although there are similarities between event-related and blocked deactivations, there are still quantitative differences between the 2 (Fair et al. 2007). It is possible that the observed differences in deactivations may reflect transient versus sustained processes (Burgund et al. 2003; Visscher et al. 2003), and a recent study has shown that aging differentially effects transient and sustained processing (Dennis et al. 2006). More work is needed to investigate the potential implications for the differences between the 2 designs for neuroimaging studies of older adults. Third, the locations of the peak voxels in the previous 2 studies were classified as BA 10 and were located

more anterior to the peaks found in the present study. Although all peaks fall into locations widely considered to be part of the default network, evidence for dissociations within anterior midline is evidenced by meta-analyses that have noted a dissociation between ventral and dorsal medial frontal regions for emotional responses (Bush et al. 2000) or between anterior and posterior regions for social interaction (Frith U and Frith CD 2003). More work is necessary to better appreciate any functional dissociation within this region and to fully understand age differences in deactivations across these anterior midline regions.

Another interesting consideration is whether the PASA pattern generalizes to low-performing older adults. As the current study matched groups on performance measures, these results obviously stem from a high-performing group of aged individuals. As noted, previous studies that have separated low- and high-performing older adults only find HAROLD-related compensatory increases in the high performers, with low performers mirroring activation seen in the young comparison group (Rosen et al. 2002; Cabeza et al. 2004). Thus, it may be the case that low-performing older adults have a less pronounced pattern of PASA-related compensation. However, more work is necessary to confirm this prediction.

Conclusions

The present study shows a posterior to anterior shift in neural recruitment in aging. This age-related shift in recruitment was shown to arise independent of both task and difficulty. Moreover, results suggest that this PASA pattern acts in a compensatory manner to offset posterior-related neuroanatomical declines associated with aging. Our results also indicate that PASA is generalizable to deactivations across both task and difficulty. These findings provide important evidence of a broad pattern of change that supports cognitive performance in older adults.

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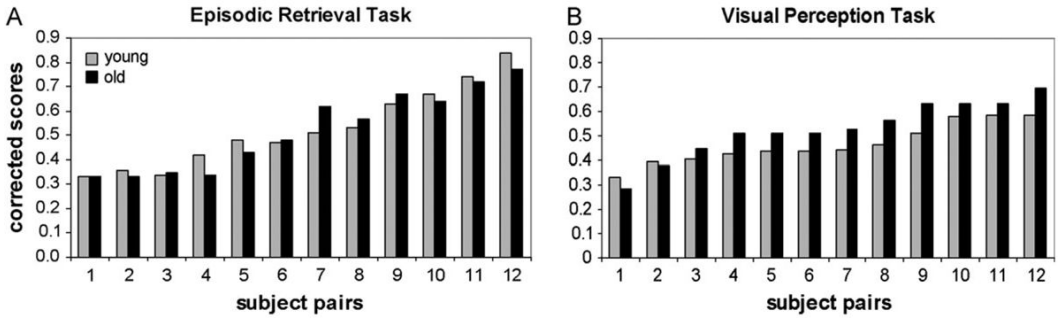

Figure 1.

Subject pairings based upon performance scores from (*A*) VP (VP: area judgment) and (*B*) ER (ER: word recognition) tasks.

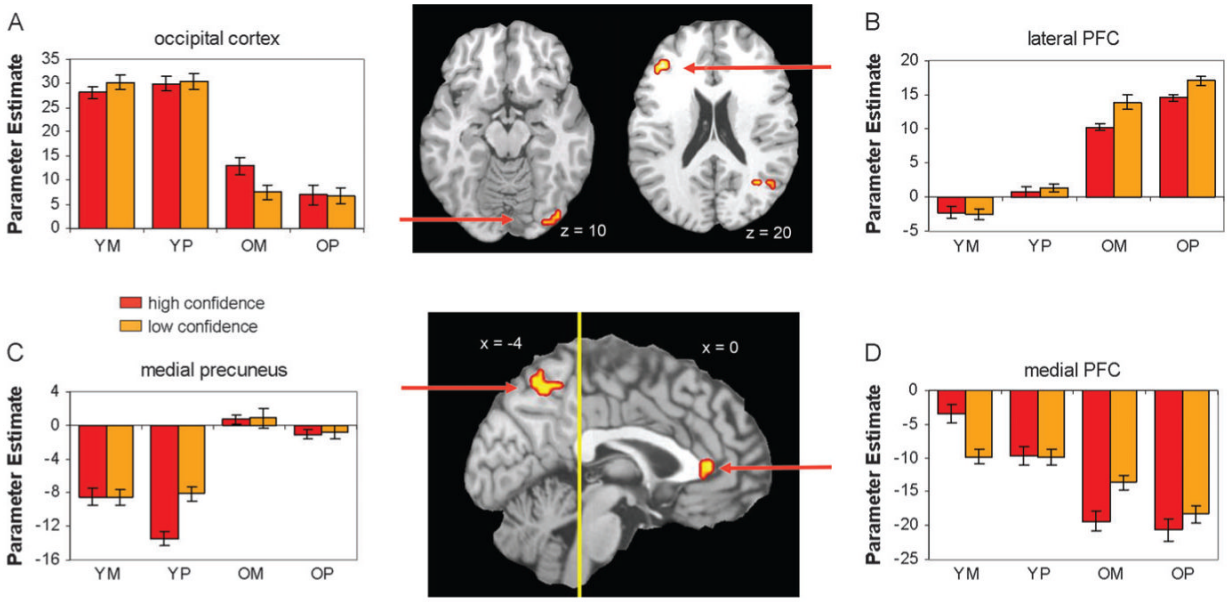

Figure 2.

The PASA pattern for activations: across 2 different tasks and 2 levels of confidence, the occipital cortex showed greater activity in younger than in older adults *A*, whereas PFC showed the opposite pattern (*B*). The PASA pattern for deactivations: across 2 different tasks and 2 levels of confidence, posterior midline cortex (precuneus, *C*) showed greater deactivations in younger than older adults, whereas the anterior midline cortex (medial PFC, *D*) showed the opposite pattern. Notes: Activation bars represent effect size for each modeled effect, and error bars represent standard error for peak activity across participants. For coordinates of peak activity within displayed regions, please see Table 4.

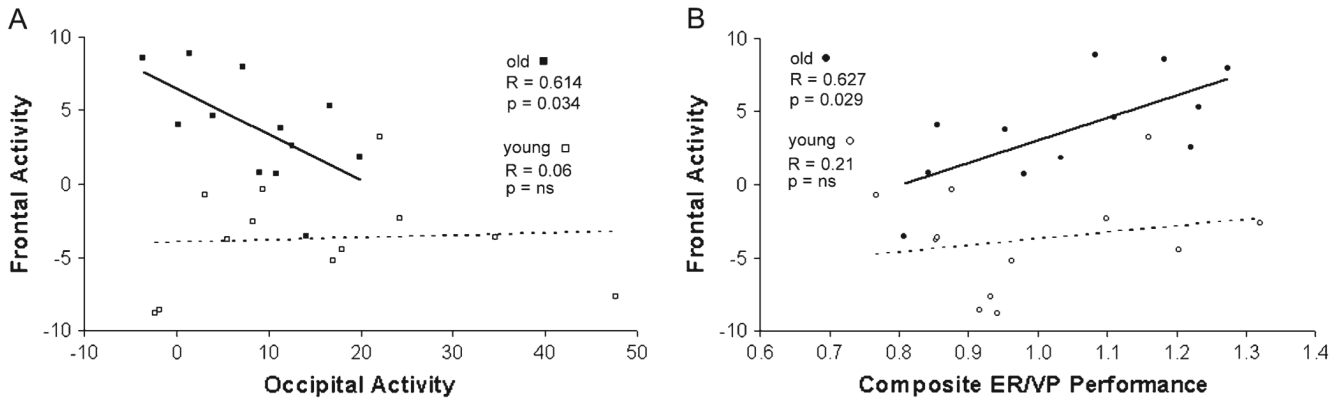

Figure 3.

(*A*) Correlation between occipital activations and frontal activations in younger and older adults. Consistent with the compensation account of PASA, older (but not younger) adults showed less occipital activity showed more frontal activity. The general pattern of these correlations also reinforces the main effects presented in Figure 2. (*B*) Correlation between frontal activity and performance in the ER and VP tasks (based on composite performance). Consistent with the compensation account of PASA, older adults who showed greater frontal recruitment showed better cognitive performance. Notes: Each data point represents one older adult, with activity collapsed across task and confidence.

Table 1

Participant characteristics and neuropsychological data

	Younger (*N* = 12), M (SD)	Older (*N* = 12), M (SD)
Age	22.2 (2.5)	69.2 (7.6)
Education (years)	n/a	18.1 (1.01)
MMSE	n/a	29.8 (0.4)
BVMT (picture memory)		
Delayed recall	11.33 (0.78)	11.58 (0.67)
BVMT (word memory)		
Delayed recall*	11.75 (0.87)	10.17 (1.90)
Digit symbol (speed)**	38.08 (1.56)	34.17 (2.66)
Shipley vocabulary**	55.67 (9.32)	70.17 (12.54)
Digit span		
Forward	10.67 (1.61)	11.42 (1.88)
Backward	9.83 (2.44)	11.25 (1.66)
Ascending	12.33 (1.30)	12.00 (1.28)

Note: M, mean; SD, standard deviation; MMSE, minimental status examination; BVMT, brief visual memory test; n/a, not applicable.

Age-related differences in performance represented:

* $P < 0.05$.

** $P < 0.01$.

Table 2
Summary of behavioral performance

	Younger, M (SD)	Older, M (SD)
ER task		
Corrected accuracy	0.53 (0.16)	0.52 (0.16)
RT	1.50 (0.25)	1.75 (0.25)*
VP task		
Corrected accuracy	0.47 (0.08)	0.53 (0.12)
RT	1.70 (0.35)	2.04 (0.28)*

Note: M, mean, SD, standard deviation.

*Age-related differences in performance represented by, $P < 0.05$.

Table 3

Age-independent effects on activations and deactivations collapsed across task and confidence

Region	H	BA	Voxels	*x*	*y*	*z*	*T*
Activations							
Cingulate cortex	M	24	100	4	8	49	9.11
Parietal cortex	L	19/7	108	-23	-76	34	8.93
	R	19/7	128	30	-68	42	8.22
Dorsolateral PFC	L	9	9	-42	0	30	6.72
Deactivations							
Inferior parietal lobule	L	39	88	-46	-68	27	6.38
	R	39/21	219	61	53	27	5.79
Posterior cingulate	R	31/23	122	11	-49	34	5.16
Rostral cortex	M	10	33	-4	49	15	4.42

Note: Regions showing significant joint probability of activity ($P < 0.001 \times 0.001 = 1 \times 10^{-6}$) between age groups across both task and confidence; clusters are described in terms of location and voxel size using Montreal Neurological Institute coordinates. *T* refers to the statistical *t* value at the peak voxel within SPM maps. H, hemisphere; M, medial; L, left; R, right.

Table 4

Effects of aging on activations and deactivations collapsed across task and confidence

Region	H	BA	Voxels	*x*	*y*	*z*	*T*
Activations							
Younger > older							
Occipital cortex	M	17/18	14	0	-95	15	3.98
Sensorimotor cortex	L	2	51	-38	-27	42	4.52
Parahippocampal cortex	L	36	8	-15	-34	-4	3.19
Older > younger							
Middle frontal gyrus	L	45	10	-42	34	19	4.19
Supramarginal gyrus	R	39	33	38	-61	23	4.09
Deactivations							
Younger > older							
Precuneus	M	19	12	-4	-57	49	3.88
Posterior insula	R	47	46	38	-11	-8	3.39
Older > younger							
Anterior cingulate cortex	L	32	13	-8	23	19	3.42
Pregenual cortex	M	32	12	0	34	11	3.2
Anterior insula	R	13	9	30	19	-8	3.55

Note: Regions showing significant ($P < 0.005$) activation related to age-specific differences across both task and confidence; clusters are described in terms of location and voxel size using Montreal Neurological Institute coordinates. *T* refers to the statistical *t* value at the peak voxel within SPM maps. H, hemisphere; M, medial; L, left; R, right.

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