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Changing channels: An fMRI study of aging and cross-modal attention shifts

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Abstract

Age-related deficits in visual selective attention suggest that the efficiency of inhibitory processes is particularly affected by aging. To investigate whether processing inefficiencies observed in visual attention are similar in auditory attention and when shifting attention across modalities, we conducted an fMRI study with healthy young and older adults using a task that required sustained auditory and visual selective attention and cross-modal attention shifts. Older adults in this study performed as well as the younger adults, but showed age-related differences in BOLD responses. The most striking of these differences were bilateral frontal and parietal regions of significantly increased activation in older adults during both focused and shifting attention. Our data suggest that this increased activation did not reflect new recruitment, but reliance on brain regions typically used by younger adults when task demands are greater. Older adults' activation patterns suggested that even during focused attention conditions they were "shifting" attention to stimuli in the unattended modality. Increased activation during processing of both task-relevant and task-irrelevant information implies age-related loss of processing selectivity. These patterns may reflect both task-specific compensatory neural recruitment and degradation of sensory inhibition.

Selective attention modulates sensory response to enhance selected relative to non-selected information. Electrophysiological studies have shown that the neural response in visual cortex is increased when visual information is attended (Heinze et al. 1994; Hillyard et al. 1998; Mangun et al. 1998). However, attention driven modulation of sensory cortex is not simple signal enhancement (gain), but also reflects neural specificity for the attended information that results from some combination of augmentation of selected and inhibition of non-selected or less relevant stimulation (Murray and Wojciulik 2004).

While selective attention may remain grossly intact with normal aging, some components of attentional processing are affected. Hasher and Zacks (Hasher and Zacks 1988) proposed a model in which age-related deficits in attentional selectivity underlie changes in memory function. They suggested that an ineffective inhibitory system would allow irrelevant information into working memory buffers resulting in the association of large numbers of less specific memory traces. Additionally, an inefficient inhibitory system would affect the ability to suppress irrelevant pathways during memory retrieval and may reflect a central mechanism underlying both distractibility and memory deficits in older adults. A number of studies have suggested that there are age-related decreases in attention modulated neural specificity — most commonly observed as a decreased efficiency in the inhibition of unattended or less relevant information. Single cell recordings in senescent monkeys have shown significant reduction in selectivity of neurons in primary visual cortex that may reflect degradation of cortical inhibitory processes (Schmolesky et al. 2000). In humans, scalp recorded event-related potential (ERP) studies have reported age-related changes in the amplitude, latency and topographic distribution of brain electrical responses, some of which are consistent with a decreased ability to selectively filter incoming information (review: Polich 1996). For example, Dustman and Shearer (Dustman and Shearer 1987) reported significantly increased early somatosensory and visual potentials in the elderly. They suggest this increased activation and altered scalp topography may reflect a general reduction in cortical inhibition and a loss of brain functional specificity (review: Dustman et al. 1996). Similarly, Chao and Knight (Chao and Knight 1997) reported an enhanced primary auditory response in elderly subjects that suggested loss of frontal suppression of auditory information with aging. Alain and Woods (Alain and Woods 1999) found enhanced sensory responses to irrelevant auditory stimuli in healthy older adults during visual attention, adding support for an inhibitory deficit model in aging. Gaeta, Friedman and Ritter demonstrated that while younger subjects showed minimal processing of irrelevant information, in older adults unattended auditory stimuli passed into attentional focus and received unwarranted additional processing (Gaeta et al. 2003). Gazzaley et al have recently provided direct evidence for age-related loss of suppression of task-irrelevant information and the effect of this deficit on working memory function (Gazzaley et al. 2005). In an fMRI design that separated suppression of task-irrelevant information from enhancement of task-relevant information, they demonstrated age-related impaired suppression of irrelevant (unattended) but preserved enhancement of relevant (attended) scenes or faces. Older subjects showing the largest suppression deficits also showed the lowest working memory performance.

A commonly reported finding from fMRI and PET aging studies that may be consistent with loss of specificity in neural circuits is diffuse increased activation in

bilateral prefrontal cortex during tasks that require visual perception and attention (Grady et al. 1994; Madden et al. 1997; DiGirolamo et al. 2001; Milham et al. 2002; Nielson et al. 2002; Cabeza et al. 2004). Several of these studies also report significantly decreased activation in primary visual regions which suggests reduced sensory-perceptual processing (Grady et al. 1994; Nielson et al. 2002; Cabeza et al. 2004). Madden and colleagues (Madden et al. 1996; Madden et al. 1997) found age-related reductions in activity in both primary and ventral processing regions and concluded this represented deficits in visual processing efficiency. Others, however, have reported that older adults showed increased activity in higher level ventral areas and interpreted this as an inhibitory deficit resulting in continued processing of irrelevant information in primary visual cortex (Grady et al. 1994; Milham et al. 2002). Patterns of activation in older adults that include increases in frontal cortex coupled with increases in ventral processing regions and decreases in primary visual sensory areas have generally been interpreted as compensatory processes that may offset the effects of diminished inhibition and deficits in sensory processing (Grady et al. 1994; DiGirolamo et al. 2001; Milham et al. 2002; Nielson et al. 2002; Cabeza et al. 2004).

Conclusions from fMRI and PET studies that suggest processing inefficiencies result from age-related disruption of sensory inhibition are based almost entirely on studies of visual processing. Studies of young adults suggest, however, that the principles of selective processing are similar in other sensory modalities and when shifting attention across sensory modalities (Kawashima et al. 1995; Woodruff et al. 1996). To investigate whether age-related processing inefficiencies observed in visual attention are similar in auditory attention and when shifting attention across modalities, we conducted an fMRI study with healthy younger and older adults. The design required sustained or shifting attention in or between visual and auditory modalities. Efficient processing in this task required both intra- and inter-modality selection of relevant and suppression of irrelevant sensory stimulation. While the older adults in this study performed as well as the younger adults, differences in the patterns of activation suggest age-related reduction of both intra- and inter-modal sensory inhibition.

Methods

Participants

Ten older adults (six females, four males, age range: 65 to 89 years; mean = 70.7 ± 7) and 10 younger adults (six females, four males, age range 18 to 41 years; mean = 27.9 ± 8) were recruited from the community for this study. All participants were right handed, had normal or corrected vision, and had no reported history of major medical illness, neurological or psychiatric disorder, head trauma, or substance abuse. One of the older adults was being treated with an antidepressant medication at the time of testing (bupropion). There was no other use of psychoactive drugs in other study participants. Two of the older subjects (one male, one female) used anti-hypertensive medications (an ACE inhibitor and calcium channel blocker). All study participants are enrolled in an ongoing study of successful aging. There were no significant differences between the two groups in years of education (older: 15.2 ± 1 ; younger: $15.8 \text{ years} \pm 2$) or in general cognitive functioning as measured by the Wechsler Abbreviated Intelligence Scale (WASI) (Wechsler 1999), Verbal IQ: Older = 110.7 ± 8 , Younger =

116.0 ± 8; Performance IQ: Older = 107.9 ± 13, Younger = 114.7 ± 10; Full Scale IQ: Older = 110.5 ± 8, Younger = 117.3 ± 8. Study participants aged 65 and older received a battery of neuropsychological tests to assure normal cognitive function that included the Mini Mental State Exam (MMSE) (Folstein et al. 1975), Dementia Rating Scale (DRS) (Mattis 1988), Wechsler Memory Scale (WMS-III) (Wechsler 1997), and the California Verbal Learning Test (CVLT-II) (Delis et al. 2000). Additionally, all were re-tested 12-18 months following initial testing to assure stable cognitive functioning over time. All older study participants scored in the normal or above normal range on these tests as follows (scaled scores have a mean of 10 and a standard deviation of 3, T-Scores have a mean of 50 and a standard deviation of 10): MMSE mean Total Score = 28.3 ± 2; DRS mean Total Scaled Score = 10.4 ± 1; WMS-III mean Verbal Memory Short and Long Delay (scaled score) = 11.7 ± 2, mean Non-Verbal Short and Long Delay (scaled score) = 11.3 ± 3; CVLT-II mean Short Delay T-Score = 58.1 ± 7.

The Institutional Review Board of the University of California, San Diego, approved the study and informed consent was obtained from each participant prior to participation. Participants received a nominal payment for participation in the study.

Design and Procedure

Auditory-Visual attention task (AV Task): The general design of the AV attention tasks are shown in Figure 1. Visual and auditory stimuli were presented serially in random order. Visual stimuli were light blue and dark blue squares subtending 3° of horizontal and vertical visual angle presented in the center of a grey background over a white cross subtending 1° of horizontal and vertical visual angle. The presentation of the white fixation cross was static throughout the task. Auditory stimuli were 500 and 550 Hz tones presented binaurally through MRI-compatible headphones. The infrequent stimulus in each modality was designated as the 'target' stimulus (20% occurrence within modality) and the frequent stimulus was designated as the 'standard' (80% occurrence within modality). Embedded in the visual and auditory stimulus streams were bimodal stimuli of 'LOOK' and 'HEAR' that served as attention shift cues in the AV shift task. Bimodal stimuli consisted of bright orange capital lettering presented at the central fixation (3° horizontal visual angle) and a simultaneous binaural presentation of the word in the voice of a male, native English-speaker at the same volume as the auditory stimuli.

Experimental conditions: There were three experimental conditions: a focus auditory condition (Focus-Auditory), a focus visual condition (Focus-Visual), and a shift attention condition (Shift). In each condition, participants were instructed to press a button on a custom-made response device using their right hand index finger when they saw or heard the specified target stimulus. In the Focus-Auditory and Focus-Visual conditions, the defined target stimuli were the high tone and light blue box, respectively. During Focus tasks, participants were instructed to ignore stimuli in the alternate modality and to ignore the bimodal shift cue stimuli. In the Shift condition, participants were instructed to attend to the bimodal shift cues and direct their attention to that modality to identify target stimuli. In all three conditions, participants were instructed to respond as quickly and accurately as possible.

AV task during fMRI data collection: The full fMRI experiment consisted of six task runs that included one task run each of the Focus-Auditory and Focus-Visual conditions and four runs of the Shift condition. fMRI data were collected throughout

each run. Each of the six experimental task runs used a blocked design that alternated between active target detection trial blocks ('task blocks') and blocks of resting periods during which only the central fixation cross was presented ('rest blocks'). After an initial 30 sec rest block, four 39 sec task blocks were presented separated by three 21 sec rest blocks. Each task block contained 78 stimulus presentation trials of 500 ms duration each. A stimulus trial included the presentation of a single auditory stimulus, visual stimulus, or bimodal shift attention cue. Thus, only one stimulus was presented within an individual trial. The auditory and visual stimuli were presented during the initial 100 ms of each trial followed by a 400 ms interstimulus interval. Bimodal shift attention cues were presented during the first 200 ms of a trial followed by a 300 ms interstimulus interval. Each of the task blocks within a run of the shift attention conditions contained, on average, seven bimodal shift attention cues. The time between attention shift cues ranged from 2.5 sec to 8.5 sec (i.e., 4 to 16 intervening stimuli), with an average time of approximately 5.5 sec between shifts (i.e., 10 intervening stimuli). On average, targets in both modalities occurred about once in every five to six stimuli, including bimodal cues, for a total of 28 targets per modality across the four task blocks of each experimental run. This resulted in the same number of attended and unattended target stimuli. A 30 sec rest block followed the fourth task block. Thus, a complete experimental task run required 4 min 39 sec. The Focus-Auditory and Focus-Visual conditions were always acquired before the Shift condition runs. The order of the Focus-Auditory and Focus-Visual conditions was counterbalanced across subjects, as were the four runs of the Shift condition.

Prior to fMRI scanning, each participant was tested in our laboratory in all three experimental conditions to ensure familiarity with the task and to collect behavioral data outside the fMRI environment.

fMRI data acquisition: Imaging data were acquired at Thornton Hospital at the University of California, San Diego, using a 1.5 T Siemens Symphony MR scanner (Erlangen, Germany) equipped with the standard clinical head coil. Within the scanner, participants had their heads secured with foam padding and their foreheads taped to the head coil support to reduce motion. A PC-compatible laptop computer using Presentation software controlled stimulus presentation and behavioral response acquisition (Woods 2003). Stimuli were back-projected onto a screen located at the foot of the scanner bed using a video projector located in the scanner control room. Participants viewed the stimuli using a 90° mirror attached to the head coil above their eyes and indicated their responses were recorded using a custom-designed mouse device.

In each test run, 95 whole-brain T2*-weighted axial images were acquired using a single-shot gradient-recalled echo-planar imaging sequence (28 interleaved slices; 4 mm slab; TR = 3000 ms; TE = 34 ms; flip angle = 90°; FOV = 256 mm; matrix = 64 x 64; in-plane resolution = 4 mm²). A high-resolution 3D MP-RAGE scan was acquired for anatomical localization (magnetization prepared-rapid gradient echo; TR = 11.08 ms; TE = 4.3 ms; flip angle = 45°; FOV = 256 mm; matrix 256 x 256; 180 slices; resolution = 1 mm³) after the last functional run.

fMRI data analysis: fMRI analyses were conducted using the Analysis of Functional Neuroimages package (AFNI; <http://afni.nimh.nih.gov/afni>; (Cox and Hyde 1997). Motion correction and three-dimensional registration were performed using the

automated alignment program 3dvolreg, which co-registered each volume in the experimental run to the fourth volume acquired in that time series (Cox and Jesmanowicz 1999). All of the volumes in the second through sixth experimental runs were then registered to the fourth volume of the first run (i.e., interscan registration). The images within each run were then smoothed spatially with a Gaussian filter using a FWHM = 8 mm kernel.

FMRI analyses of individual participants: The EPI BOLD data from individual participants were analyzed using the AFNI 3dDeconvolve multiple regression analysis program. Convolving a gamma variate function to the stimulus time series created the hemodynamic response function models used for testing. Additional reference functions were created to orthogonally remove activity due to motion artifacts, the global mean, and linear drift. The multiple regression analyses were conducted separately for the three task conditions, with all four runs of the Shift condition analyzed with a single regression analysis. In this latter case, the linear drift and global mean terms were modeled separately for each of the four runs. The resulting voxel-wise statistical results were translated to standardized Z scores by converting the obtained *t* statistics of the linear contrast weights, the measure of BOLD signal of the stimulus reference function, to Z scores and then the resulting Z score maps were resampled to Talairach space at a resolution of 3 mm³ using the AFNI hand landmarking procedure.

FMRI group analyses: The individual Z score maps for the Focus-Auditory, Focus-Visual, and Shift conditions were submitted to a 2 x 3 nested mixed-effects analysis of variance (ANOVA) using group (older and younger adults; between-subjects; fixed effect) and condition (Focus-Auditory, Focus-Visual, and Shift; within-subjects; fixed effect) as main factors. Subject was treated as a repeated-measures factor nested within group (random effect). The ANOVA was conducted using the GroupAna program from the AFNI Matlab Library. To establish significant brain activity above baseline levels in all three conditions, a voxel-cluster threshold correction was used to correct the whole-brain statistics for multiple comparisons to yield an overall corrected alpha of $P < .05$ (Forman et al. 1995). This correction, which was based on a Monte Carlo simulation, required a voxelwise threshold of $P \leq 0.001$ ($t_9 \geq 4.78$) within a cluster of at least 17 contiguous significant voxels (459 μl ; FWHM autocorrelation estimate = 7.5 mm). Pairwise comparisons between the older and younger adult groups in the focus and shift attention conditions were limited to an examination of only those regions that had proven sensitive to task effects relative to the baseline condition (i.e., the pairwise contrasts were masked to only include the regions demonstrated as significantly active in the older and/or younger groups as described in Figures 3 & 4). Within these areas, differences between the older and younger adult groups were defined as significant if the voxelwise threshold was $P \leq .001$ within a cluster of at least five significant voxels (135 μl ; FWHM autocorrelation estimated = 7.5 mm).

Results

Behavioral Findings

The group mean percent correct target detection and response time results from the three AV task conditions are shown in Figure 2. There were no statistically significant differences between groups in target detection accuracy, although the older

adult group accuracy was numerically lower than the younger adult group, particularly in the two focus attention conditions. Both the older and younger adult groups were more accurate in visual target detection than auditory target detection across the Focus-Visual, Focus-Auditory, and Shift tasks, $F_{1, 17} = 9.70$, $P < .01$ (mean percent correct: auditory = 88.7%, visual = 95.7%, SEM = 2.5 & 1.6, respectively). No other main effects or interactions approached significance, $P_s > .10$.

There were no significant differences between groups in response times. For both groups, response times were faster for targets in the two focus conditions than in the Shift condition target detection, $F_{1, 17} = 27.01$, $P < .001$ (mean of Focus-Visual & Focus-Auditory = 443.4 ms, Shift = 469.2 ms; SEM = 12.9 & 16.2, respectively). Post-hoc comparisons of a significant attention condition x modality interaction ($F_{1, 17} = 4.74$, $P < .05$) showed that response times to visual targets were faster than response times to auditory targets in the focus attention conditions (mean response times: Focus-Visual = 434.2 ms, Focus-Auditory = 492.0 ms; SEM = 10.2 & 16.2, respectively; $t_{18} = 5.67$, $P < .001$). This was also true in the Shift condition, but the overall difference between visual and auditory targets was smaller (mean response times: Shift visual = 468.1 ms, Shift auditory = 503.4 ms; SEM = 14.6 & 16.8, respectively; $t_{19} = 5.15$, $P < .001$).

In summary, the accuracy and reaction time results across all three conditions suggest that both older and younger adults performed well on both the focused attention and shift attention tasks. In general, for both groups, performance during visual target detection was superior to performance during auditory target detection. The response time results indicate that for both groups, the Shift attention condition was more difficult than either of the focus conditions.

FMRI Findings

Focus Attention Conditions (Focus-Auditory & Focus-Visual): The FMRI results from the auditory and visual focus attention conditions (Focus-Auditory & Focus-Visual) for the older and younger adult groups are shown in Figure 3. Older and younger adults produced nearly the same amount of gross activation in the Focus Auditory task (Focus-Auditory condition: older & younger adults = 39.2 cl & 41.5 cl, respectively). However, older adults produced approximately nine times the gross activation observed in younger adults in the Focus-Visual condition (122.8 cl & 13.6 cl, respectively). As can be appreciated in Figure 3, a substantial proportion of the additional activity produced by older adults in the Focus-Visual condition was co-localized to activity that was observed in the Focus-Auditory task (“yellow” areas in Fig. 3). That is, many brain regions in the older adult group did not distinguish between attention focused within auditory or visual channels, and instead were active in both conditions. This differed from the overall activation pattern observed in the younger adult group. Both groups produced significant activation within the bilateral superior temporal region (Brodmann’s area (BA) 22), centered on the transverse temporal gyrus (primary auditory cortex, BA 41) in both focus attention conditions. However, only the older adult group produced significant activation in both focus attention conditions in the lateral inferior frontal gyrus bilaterally (BA 9; Talairach coordinates (x, y, & z) and mean Z score relative to baseline of most intense voxel, left: 39, 5, 29, visual Z = 3.50, auditory Z = 3.45; right: -35, 5, 29, visual Z = 3.46, auditory Z = 2.70; all $P_s < .001$), left hemisphere insula (37, 12, 16, visual Z = 3.04, auditory Z = 2.69; all $P_s < .001$), and left hemisphere fusiform gyrus (BA

46; -47, -8, visual $Z = 2.64$, auditory $Z = 2.32$; all $P_s < .001$. The meaning of this non-discriminate attention-related activation is likely related to increased cognitive demands for monitoring and/or suppressing activity in the non-target modality. This interpretation is suggested from the evidence that many of the regions activated in the older adult group that were not active in the younger group during the focus attention conditions were employed by the younger adult group in the shift attention condition. This can be seen in Figure 4, and is discussed below in greater detail in regards to Shift condition findings.

The direct pairwise comparison of activity between the old and young adult groups showed that the older subjects produced greater activity in bilateral superior and lateral parietal cortical regions in the focus visual condition. These differences are highlighted in the top panel of Figure 3. Specifically, BOLD activation in the older group was significantly greater than the young adult group in the right hemisphere inferior parietal lobule (IPL) extending anterior to include the postcentral gyrus and precentral gyrus regions (Talairach coordinates ($x, y, & z$) and mean Z score difference of most intense voxel, IPL (BA 40), 25, -35, 55, Z difference = 2.56, $t_{36} = 4.16$, $p < .001$; Precentral gyrus (BA 4), 16, -26, 60, Z difference = 2.60, $t_{36} = 5.58$, $p < .001$). The older adult group also produced significantly greater activation within the right hemisphere precentral gyrus (BA 3) (Talairach coordinates and Z score of most intense voxel of difference, -52, -16, 36, Z difference = 3.21, $t_{36} = 4.29$, $p < .001$). In the right parietal area, the difference between groups was maximal within the superior parietal lobule (BA 7; Talairach coordinates ($x, y, & z$) and Z score of most intense voxel of difference, -22, -50, 56, Z difference = 2.61, $t_{36} = 3.79$, $p < .001$). No significant group differences were observed in the Focus-Auditory condition.

Shift Attention Condition: The results from the Shift attention condition are shown in Figure 4. The results depicted in Figure 4a indicate regions where BOLD activity in the Shift and Focus conditions (Focus-Auditory plus Focus-Visual) was significantly greater than baseline in both adult groups. Regions in red indicate where observed activity in the Shift condition was greater than the baseline condition and greater than Focus attention (whether or not the Focus was greater than baseline). Regions in blue indicate where both Shift and Focus attention conditions produced above baseline activity that was not significantly different. In other words, these regions did not discriminate between the Shift and Focus conditions.

In reviewing the results from the younger adult group, it is clear that in the Shift condition, they produced widely distributed activation that was unique to the Shift condition and significantly greater than activity in the Focus attention conditions (red regions in Fig. 4a, lower panel). These regions are described in Table 1. Of note, many of the regions that were selectively active in the Shift condition for young adults corresponded to areas that were active in the older adults in the Focus attention tasks. The pattern of activation in the older adult group stood in stark contrast to the younger group. As can be seen in Figure 4a, many of the regions active during the Shift condition were jointly active during the Focus conditions, and the level of activity was similar across conditions (blue areas, top panel Figure 4a). This pattern of results suggest that the older adult group were not recruiting new areas to support focus attention performance, but instead were activating brain regions required for multi-

channel attention performance.

The results from the pairwise comparison between the older and younger adult groups in the Shift attention condition are shown in Figure 4b, and described in Table 2. Note that in nearly all cases, the older adults produced significantly greater activation during the Shift condition than the younger adults. Younger adults produced significantly greater activity than older adults in only three regions, all within the superior temporal gyrus. Notably, younger adults produced significantly greater activation bilaterally in the region of the primary auditory cortex (i.e., transverse temporal gyrus, BA 41), suggesting that within the auditory channel, younger adults engaged sensory functions, perhaps such as gating of distracting auditory information, at a much earlier point in the processing stream than the older adults.

Discussion

The most striking age-related differences in BOLD responses from this study were bilateral frontal and parietal regions of significantly increased activation in older adults during both focus and shift tasks. Considered separately, results from the focus attention tasks are consistent with a number of studies reporting that older adults typically produce more widespread activation than younger adults when task performance is similar. Quite often, this is interpreted as evidence that older adults recruit additional brain regions to compensate for reduced capacity in brain regions used by younger adults. Such compensatory processes are proposed to offset the effects of diminished inhibition and deficits in sensory processing (Grady et al. 1994; DiGirolamo et al. 2001; Milham et al. 2002; Nielson et al. 2002; Cabeza et al. 2004).

However, consideration of findings from the focus task in conjunction with those from the shift attention condition, which raised the cognitive demands, suggests a different interpretation. Younger adults showed bilateral frontal and parietal activation during the shift attention task that was not present during focus tasks. In contrast, older adults showed similar activation in these same regions during both focus and shift attention tasks. This suggests that the regions observed in the focus attention conditions by older adults were not new recruitment, but reliance on brain regions typically used by younger adults with increased task demands. That is, when younger adults were required to shift between modalities they utilized additional frontal-parietal regions that were not used when tasks required a simple focus on information in a single modality. These additional regions may reflect the necessity for maintenance of the appropriate target representation and control of the shifting of this information. A critical feature of this control would be the efficient selection of the cued target which would involve both enhancement of information in the cued (attended) modality and some suppression of information in the uncued (unattended) modality.

Regions active in younger subjects only during shifting attention are consistent with those reported by Shomstein and Yantis (Shomstein and Yantis 2004) from healthy subjects in the same age range as our young subject group in a task that required shifting attention between streams of auditory and visual letters and digits. These shift-only activations included superior and inferior frontal regions and both superior (including the precuneus) and inferior parietal regions. In our older adults, these regions were active during both shift and focus attention.

In a study that required shifting between two different visual tasks, DiGirolamo et al (DiGirolamo et al. 2001) reported that younger and older adults showed large areas of activation in dorsolateral and medial frontal regions thought to serve executive function. As in our study, younger adults in the DiGirolamo study activated these frontal regions only during task shifting while older adults recruited these same regions during task shifting and when performing individual tasks in isolation. DiGirolamo and colleagues concluded that older subjects recruited more effortful executive frontal networks even in simpler non-shifting tasks to compensate for reduced efficiency of sensory and cognitive processing. An alternative explanation in our task may be that older adults were unable to inhibit the alternate task even during focused attention conditions. Our results from the focused attention tasks are consistent with this model. For example, many brain regions in the older adult group did not distinguish between attention focused within auditory or visual channels, and instead were active in both conditions (yellow regions in Figure 3). In essence, older adults may have “shifted” attention even during the single focused attention tasks so that activation patterns during focus and shift tasks were nearly identical. A related possibility is that the diffuse bilateral frontal patterns of activation we observed in older subjects across tasks may reflect a nonspecific recruitment that results from failure of inhibitory processes (Logan et al. 2002). Recent studies examining white matter diffusion show age-related decreases in white matter integrity that may be related to reduced functional connectivity (O’Sullivan et al. 2001; Pfefferbaum et al. 2005). Degradation of white matter is particularly prominent in frontal regions. Reduced functional integrity of anterior fiber pathways and the subsequent degradation of information flow could result in nonselective activation of processes that reflect an inevitable breakdown rather than active compensation. In either case, these results are consistent with models that suggest there is generalized degradation of inhibitory processes with aging (Hasher and Zacks 1988; Gazzaley et al. 2005).

In younger adults, regional activations tended to be quite succinct and focal. Overall, older adults showed patterns of activation that were quite similar to those seen in younger adults, but activity was more widespread during all attention conditions, covering significantly greater area in activated regions. In younger adults, activation during auditory attention was primarily focal in and around auditory sensory processing regions. During focused visual attention, younger adults showed very limited activation within the extrastriate cortical regions, specifically to a region in the left hemisphere lingual gyrus (BA 18). In contrast, activations for older subjects during focused visual attention were widespread, covering large swaths of the extrastriate regions bilaterally. This suggests less efficient processing mechanisms, perhaps due to failure of within channel inhibition of irrelevant visual information. This increased activation may also reflect compensatory neural recruitment (i.e., an attempt to increase relevant signal) that serves to offset distraction from irrelevant visual and auditory sensory information (i.e., noise). Weissman and his colleagues reported exactly this sort of recruitment in young adults (Weissman et al. 2004). They found that as activity in sensory cortices processing relevant information increased, behavioral effects of distraction decreased.

Excess activation in older adults was particularly prominent in frontal and parietal regions and in sensory cortices. In both subject groups, robust activations in primary and association auditory cortex were due to auditory attention task but also reflected brain responses to the bimodal cues (“LOOK” and “HEAR”). Word processing in both

visual and auditory modalities would be expected to activate these regions, particularly on the left. Regions where the young adults show activation in all three attention conditions include bilateral superior temporal cortex, bilateral medial pre-central frontal cortex and left extrastriate cortex. In functional imaging studies, these regions have been consistently associated with processing words (Fiez et al. 1996; Binder et al. 2000; Vorobyev et al. 2004). Cross-modal integration of the cue information would also be expected to activate these regions bi-laterally (Laurienti et al. 2003; Sekiyama et al. 2003; Miller and D'Esposito 2005). We believe these patterns of activation across all conditions are a response to the bimodal cue which taps visual, auditory and word processing as well as cross-modal integration of auditory-visual spoken words in all three tasks.

Previous studies have reported age-related increases in activation in frontal cortex and higher level visual processing regions combined with decreased activation in primary visual cortex. These patterns have generally been interpreted as compensation for losses in sensory processing and reduced inhibition of irrelevant information (Grady et al. 1994; DiGirolamo et al. 2001; Milham et al. 2002; Nielson et al. 2002; Cabeza et al. 2004). Our data are consistent with these earlier findings, except that, we did not observe reduced activation in primary visual cortex in our older adults. The visual baseline in our task reduced activation in primary visual cortex in both subject groups, and may have obscured small group differences in this region. An additional possibility is that compromised sensory processing in our tasks would result not in decreased activation in primary visual cortex, but in age-related increases in the degree of processing required to distinguish between relevant and irrelevant visual material. This would result in additional processing of irrelevant information seen as increased activation in higher level visual processing regions—a prominent effect in our data. A related possibility is that compromised sensory processing is likely to result in decreased selectivity but not necessarily decreased activity. This effect has been observed in the primary visual cortex in aging monkeys (Schmolsky et al. 2000). Degraded selectivity (specification of cell response) in these studies was accompanied by increased cell excitability and increased spontaneous activity. The authors considered this to reflect age-related deterioration of inhibitory processes. While it is, of course, impossible to directly relate increased neural activity to changes in BOLD signal, this study does demonstrate that degradation of sensory processing does not necessarily result in decreased neural activity.

There were no significant group differences in either accuracy or reaction time measures for any of the task conditions (Focus or Shift attention). Younger adults performed the visual focus task with near ceiling accuracy. While this ceiling effect complicates interpretation of the between-group comparison of behavioral performance on this condition (i.e., in a more difficult task younger subjects might have performed better than older subjects), it does not affect interpretation of the fMRI activations. Because older adults performed all tasks as well as younger adults, group differences in activation patterns are not the result of performance differences, but rather reflect age-related differences in brain systems that were active during these tasks. The age-related differences we observed in patterns of BOLD activation in the absence of performance differences raises the question of the nature of the association of brain function and behavioral performance in this study. That is, we have suggested that age-

related BOLD differences may reflect diminished inhibition. If, however, there were no performance differences, to what degree might inhibition be required for successful performance of this task? We suggest that in efficient information processing inhibition of irrelevant information at the sensory level occurs to some degree regardless of task demands. Because it was quite simple, the task in our study could be performed without employing inhibition of stimuli from unattended channels. However, younger subjects showed evidence of inhibition of irrelevant (unattended) information even though it was not necessary for task performance. While older subjects performed this task as well as younger subjects, they showed reduced inhibition. This suggests that in more demanding tasks (where inhibition is required), the reduction of inhibition would result in performance decrements.

Summary and Conclusions. Our data show that in healthy, cognitively intact older adults, there are processing inefficiencies associated with visual, auditory and cross-modal attention. Older adults in this study performed as well as the younger adults, but with striking age-related differences in BOLD responses. While younger adults showed succinct and focal regional activations associated with attention and sensory processing, older adults showed significantly larger and more widespread activation in these same regions, particularly in frontal, parietal and visual association cortices. In fact, older adults' activation patterns suggested that even during focused attention conditions they were shifting attention to stimuli in the unattended modality. Generally increased regions of activation and specifically increased activation to task-irrelevant information may reflect both task-specific compensatory neural recruitment and reduced inhibitory processes.

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Table 1. Summary of brain regions active in the Shift condition that were not active in the Focus attention tasks (i.e., regions recruited specifically during the Shift condition).

<i>Location</i>	<i>Hemi</i>	<i>BA</i>	<i>Talairach Coordinates</i>			<i>Z difference</i>
			<i>x</i>	<i>y</i>	<i>z</i>	
<u>Younger adult group</u>						
Precentral gyrus	L	6	43	3	46	-12.0
Middle frontal gyrus	R	6	-34	10	46	4.62
Precuneus	L	7	27	-57	37	10.81
Precuneus *	R	7	-28	-57	37	10.89
Supramarginal gyrus *	R	40	-38	-44	37	6.28
Middle frontal gyrus	R	9	-46	18	32	4.83
Superior temporal gyrus *	R	22	-53	-43	12	8.77
Middle frontal gyrus	R	10	-31	50	9	4.83
Putamen *	L		22	-4	9	5.45
Anterior insula *	R		-42	14	5	8.29
Inferior occipital gyrus *	R	19	-33	-77	-4	5.51
Lingual gyrus *	R	18	-18	-83	-10	4.77
Fusiform gyrus/Middle occipital gyrus *	L	18/19	35	-76	-11	4.24
Fusiform gyrus	R	19	-33	-73	-14	4.11
Inferior frontal gyrus *	L	44	52	-14	4	3.11
<u>Older adult group</u>						
Precuneus	R	7	-6	-63	39	7.05
Middle frontal gyrus	L	9	39	-20	29	9.07
Precuneus	L	7	26	-61	35	10.89

Notes: L = left hemisphere, R = right hemisphere; BA = Brodmann's area; * = region of activity observed in Older group during Focus attention conditions. Pairwise comparison threshold = $P < 0.05$ (corrected) using a cluster-threshold correction. Only voxels where Shift condition activity exceeded baseline and where Shift activity was greater than Focus activity are described ("red" regions in Fig. 4a). Regions similar to those activated in either of the Focus attention tasks (see Fig. 3) are not included. The x, y, and z coordinates of Talairach space are defined with positive indicating the mm to the left, anterior, and superior of the anterior commissure, respectively. All region labels and Brodmann's areas were determined using the AFNI implementation of the Talairach daemon (Lancaster et al, 2000). *Z difference* scores are the Z score difference between the Shift condition and the mean of the Visual and Auditory Focus conditions at the voxel indicated by the Talairach coordinates.

Table 2. Group BOLD activation differences from the Shift attention condition.

Location	Hemi	BA	Talairach Coordinates			Z difference
			x	y	z	
<u>Older > Younger</u>						
Inferior Frontal gyrus	L	9	40	8	30	3.98
Precentral gyrus & Middle Frontal gyrus	L	6	28	-8	56	3.62
Inferior Frontal gyrus	L	47	51	20	-4	2.68
Cingulate gyrus	L	32	14	10	38	2.85
Inferior Frontal gyrus	R	46	-38	32	12	3.04
Middle Frontal gyrus	R	6	-26	-4	56	3.63
Middle Frontal gyrus	R	9	-32	8	36	3.46
Inferior Frontal gyrus	R	9	-44	8	24	3.21
Middle & Inferior Temporal gyrus	R	37	-52	-58	0	4.16
Superior Temporal gyrus	R	22	43	-29	0	4.60
Superior Temporal gyrus	R	22	-59	-38	19	4.59
Inferior Parietal lobule	L	40	44	-40	44	3.81
Precuneus	L	7	20	-56	44	4.06
Inferior Parietal lobule / Supramarginal gyrus	R	40	-43	-41	38	4.52
Superior Parietal lobule / Precuneus	R	7	-27	-50	44	4.54
Fusiform gyrus, Middle Occipital gyrus, Inferior Temporal gyrus	L	37	46	-44	-10	4.23
Middle Occipital gyrus	R	18	-28	-80	8	4.68
Thalamus	L		10	-16	-4	3.62
Putamen & Thalamus	R		-22	-10	8	3.45
Midbrain	R		-8	-20	-6	2.89
<u>Younger > Older</u>						
Transverse Temporal gyrus	L	41	44	-26	12	3.20
Transverse Temporal gyrus	R	41	-44	16	6	3.29
Superior Temporal gyrus & Insula	R	22	-46	-2	0	2.57

Notes: L = left hemisphere, R = right hemisphere; BA = Brodmann's area; Activation differences are depicted in Figure 4b. Pairwise comparison threshold = $P < 0.05$ (corrected) using a cluster-threshold correction. Only voxels where Shift condition activity exceeded baseline levels in either or both the older and young adults groups were considered. The x, y, and z coordinates of Talairach space are defined with positive indicating the mm to the left, anterior, and superior of the anterior commissure, respectively. All region labels and Brodmann's areas were determined using the AFNI implementation of the Talairach daemon (Lancaster et al, 2000). Z difference scores are the mean Z score difference between the old and young groups across the entire cluster of contiguously active voxels.

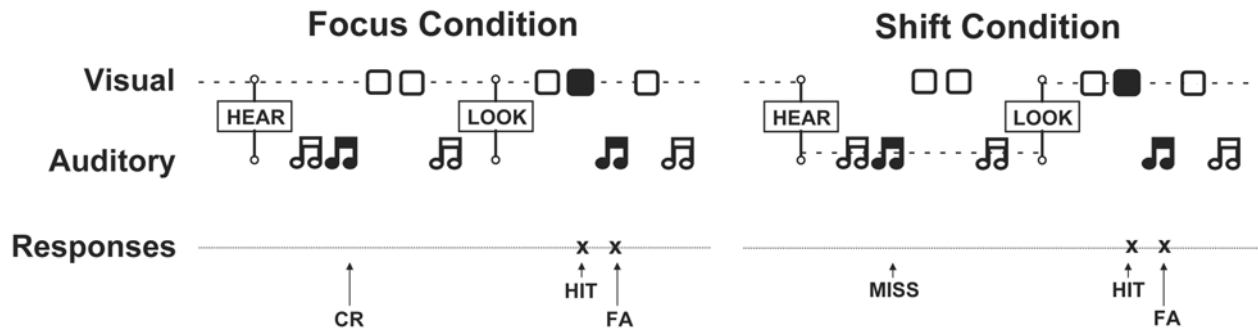


Figure 1. Schematic description of task stimuli and attention conditions. Both visual and auditory stimuli were presented together with bimodal cues to shift attention. Non-target stimuli are represented by outlined boxes for visual stimuli and notes for auditory stimuli, and infrequent target stimuli are shown filled in; a dashed line indicates which modality is to be attended. In the Focus conditions (e.g., in Visual Focus, represented on the left), participants ignored shift cues and responded to stimuli in only one modality for the duration of the run. In the Shift condition (represented on the right), participants used the cues to determine which modality to attend, responding to targets in that modality while ignoring those of the other modality. Sample responses are shown on the bottom line, coded as follows: HIT = correct response to target in attended modality; MISS = failure to respond to target in attended modality; FA = response to target in unattended modality or to non-target in either modality; CR = correct rejection (i.e., no response) of target in unattended modality.

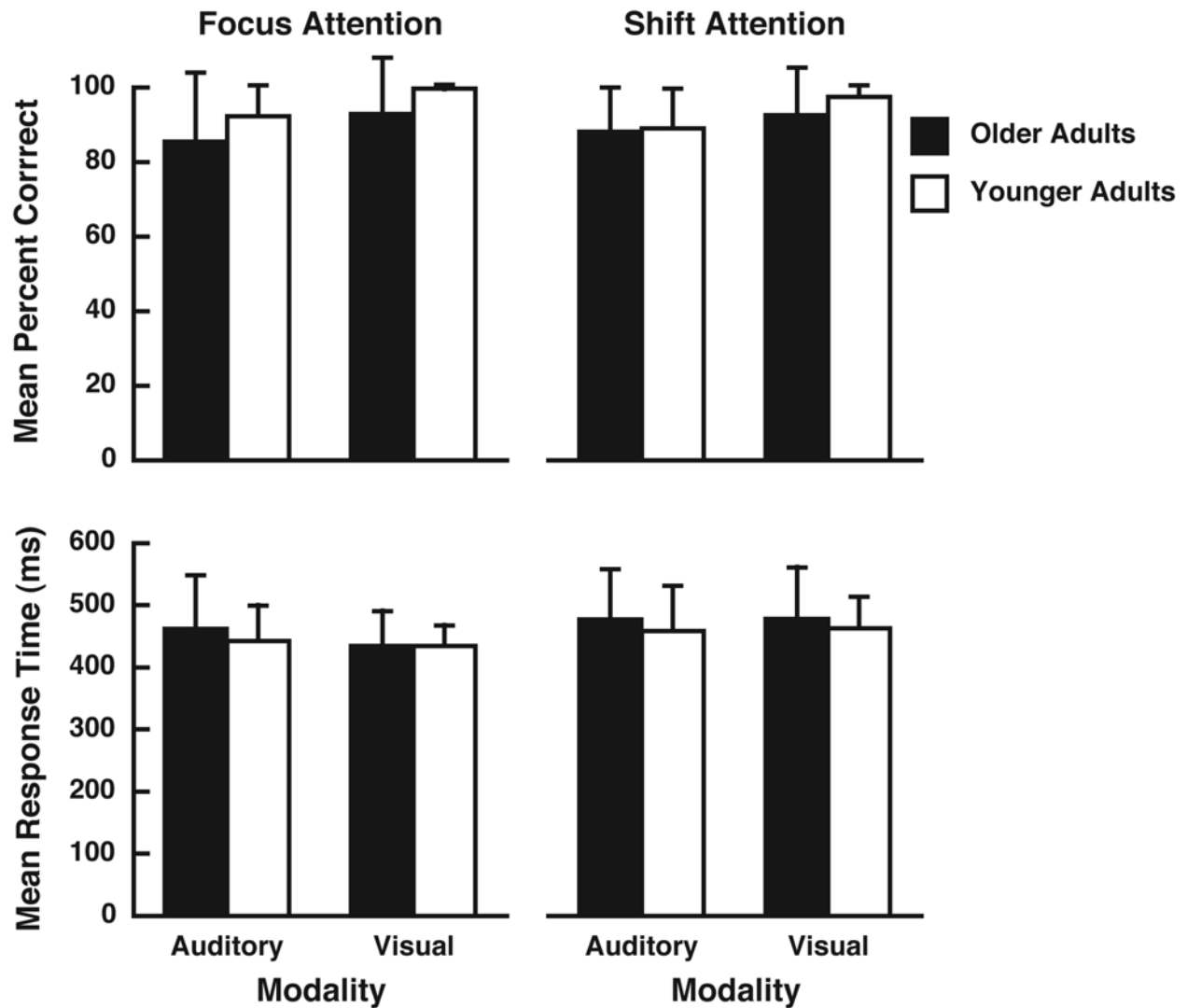


Figure 2. Behavioral results from the three attention conditions for the older adults (black bars) and younger adults (white bars). The top two panels display the target detection accuracy as mean percent correct for the Focus-Visual and Focus-Auditory conditions (left panel) and the Shift condition (right panel). The bottom two panels show the mean response time results for correct target detections. The Shift condition panels display results for visual and auditory target stimuli separately. These were considered together in the analysis of the fMRI results. Error bars indicate standard deviation.

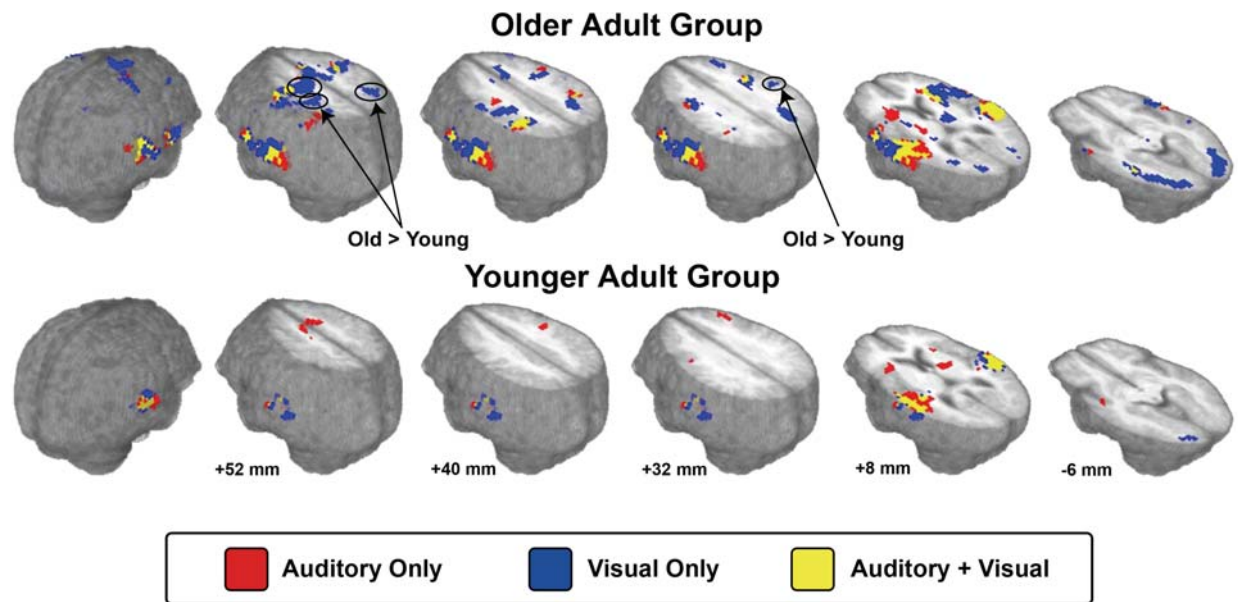


Figure 3. Functional activation conjunction (FAC) maps using color-coding to display regions of significant (greater than baseline) BOLD activation during performance of the Focus Auditory task (red), Focus Visual task (blue), and regions co-active in the Auditory and Visual Focus tasks (yellow). Results from the older adult group (top panel), and the younger adult group (bottom panel) are shown for both Focus attention tasks. Regions where activity was significantly greater in the older adult group are shown circled in the top panel (“Old > Young”; $p < .05$, corrected). There were no regions where activity in the young adult group was significantly greater than in the older adult group. The FAC maps are displayed on the rendered structural anatomy based on the averaged structural images from all 20 participants. The levels of the slices, relative to a plane centered through the anterior and posterior commissures, is shown in the lower figure in each panel.

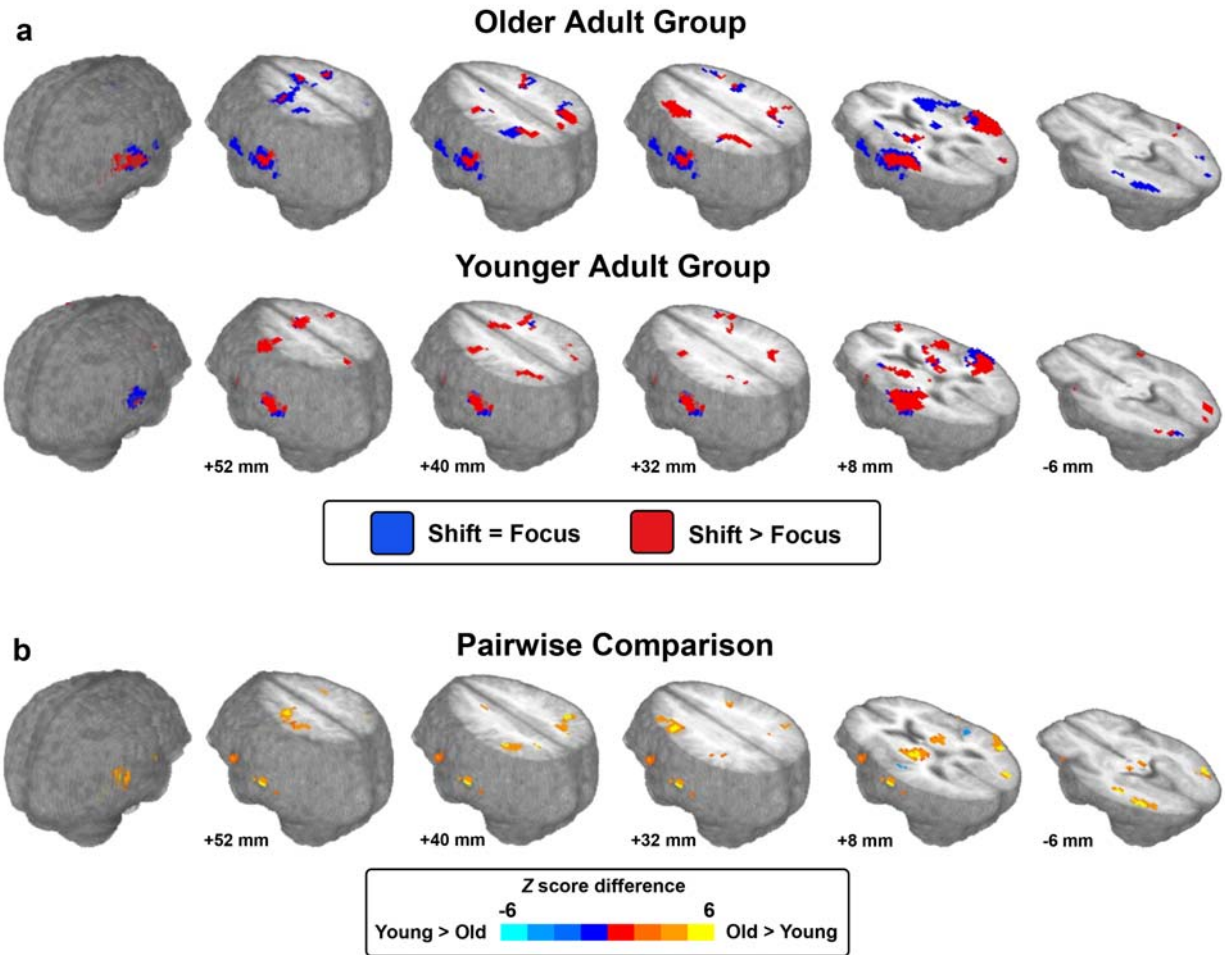


Figure 4. a) Functional activation conjunction (FAC) maps using color-coding to display regions of significant (greater than baseline) BOLD activation observed during the Shift attention task. The maps display regions where Shift activity was greater than activity observed in the combined auditory and visual focus conditions, regardless of whether focus attention was greater than baseline, (red), and regions where Shift and focus activity were both significantly greater than baseline but not different from one another (blue). The results from the older adult group are shown in the top panel, and the results from the younger group in the lower panel. **b)** Results from the pairwise comparison between the older and younger adult groups in activity during the Shift condition. Only regions that were active in either or both the older and younger adult groups in panel (a) were considered in the pairwise contrast (i.e., pairwise results were masked to include only the voxels that were active in the FCA maps in the panel above). Regions in warm colors (e.g., red/yellow) indicate that the Shift condition activity in the older adult group was significantly greater than the younger adult group, and vice versa for the cool colors (e.g., blue). All results are displayed on the rendered structural anatomy based on the averaged structural images from all 20 participants. The levels of the slices, relative to a plane centered through the anterior and posterior commissures, is shown in the lower panel.