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Aging and Attentional Guidance During Visual Search: Functional Neuroanatomy by Positron Emission Tomography

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Abstract

Positron emission tomography (PET) was used to examine adult age differences in neural activation during visual search. Target detection was less accurate for older adults than for younger adults, but both age groups were successful in using color to guide attention to a subset of display items. Increasing perceptual difficulty led to greater activation of occipitotemporal cortex for younger adults than for older adults, apparently as the result of older adults maintaining higher levels of activation within the easier task conditions. The results suggest that compensation for age-related decline in the efficiency of occipitotemporal cortical functioning was implemented by changes in the relative level of activation within this visual processing pathway, rather than by the recruitment of other cortical regions.

Neuroimaging investigations of visual perception and attention, especially those using positron emission tomography (PET) and functional magnetic resonance imaging (fMRI), have validated a distinction between dorsal and ventral processing pathways for vision (Ungerleider & Mishkin, 1982) that derives from anatomical work on nonhuman primates. These processing pathways both originate in primary visual (striate) cortex. The dorsal pathway is composed of

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occipitoparietal cortical regions and is critical for the analysis of the spatial relationships among objects. The ventral pathway is composed of occipitotemporal cortical regions and mediates the visual feature analyses leading to object identification (Haxby et al., 1991, 1994).

Neural activation in these visual processing pathways is modulated by widely distributed networks that represent different aspects of attentional functioning (Handy, Hopfinger, & Mangun, 2001; Kastner & Ungerleider, 2000; Knight, 1997; Mesulam, 1990; Posner & Petersen, 1990). Activation within the occipito-temporal regions, for example, may be enhanced by top-down attentional processing, such as expectations of the occurrence of the upcoming visual display (Heinz et al., 1994; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999). In visual tasks, parietal and prefrontal regions are the most important cortical components of the attentional network (Gitelman et al., 1999; Nobre et al., 1997). Regions in posterior parietal cortex play an important role in orienting and shifting an attentional focus across spatial locations (Corbetta, Shulman, Miezin, & Petersen, 1995; Hopfinger, Buonocore, & Mangun, 2000). Medial regions of the prefrontal cortex provide access to a motor map that integrates this attentional focus with exploratory behavior (especially eye movements; Petit et al., 1996, 1999). More lateral prefrontal regions appear to be related to working memory and associated executive control processes (Hartley & Speer, 2000; McCarthy et al., 1996). The role of the anterior cingulate is often attributed to processes such as the preparation for task performance and inhibition of irrelevant responses (Murtha, Chertkow, Beauregard, Dixon, & Evans, 1996; Paus, Petrides, Evans, & Meyer, 1993). Activation of these attentional networks is usually bilateral but often is more prominent for cortical regions in the right hemisphere (Gitelman et al., 1999; Grady et al., 1996; Kim et al., 1999). Subcortical regions that include the basal ganglia and thalamus are often activated during visual attention tasks, which may represent an enhancement of information flow in response to frontal-mediated top-down control (LaBerge, 2000).

Bottom-up (stimulus-driven) processes, in addition to top-down attentional control, modulate activation in the occipitotemporal pathway. Kastner, De Weerd, Desimone, and Ungerleider (1998) demonstrated that with attention held at fixation, the extrastriate activation associated with peripherally presented displays was decreased when the display items were presented simultaneously, relative to when the items were presented sequentially. Kastner et al. (1998) proposed that in the absence of directed attention, there is a competitive interaction among multiple visual stimuli that suppresses their cortical representation (Duncan & Humphreys, 1989). Sathian et al. (1999) reported that when the task required participants to count the number of targets (vertical bars) among a larger number of display items (16 horizontal and vertical bars), both performance and neural activation differed when the 16-item display contained four or fewer targets compared with when it contained more than four targets. The smaller number of targets allowed participants to respond on the basis of a "subitizing" process that involved minimal attentional demands: The function that related reaction time to the number of targets was substantially steeper for five to eight targets than for one to four targets. The subitizing condition, relative to a single-target condition, was associated with activation in right extrastriate cortex. Counting five to eight targets, compared with the subitizing condition, led to activation throughout the dorsal and ventral processing pathways and in right inferior prefrontal cortex.

Behavioral measures of adult age differences in visual search and classification performance have indicated that some components of attention undergo age-related decline (Hartley, 1992; McDowd & Shaw, 2000). In particular, the requirement to divide attention among multiple stimulus inputs or tasks appears to be more problematic for older adults than for younger adults. In visual search, age-related increases have been observed both in the time that is required to identify individual display items (Ellis, Goldberg, & Detweiler, 1996) and in the time that is required to shift attention across display locations (Madden, 1992; Madden,

Connelly, & Pierce, 1994). However, if a specific stimulus dimension (e.g., color or spatial location) is available that partitions relevant and irrelevant information, older adults are frequently as efficient as younger adults in attending selectively to this dimension and using it to improve perceptual performance (Humphrey & Kramer, 1997; Madden & Plude, 1993). That is, younger and older adults are often comparable in the ability to use some feature dimension to guide attention (Wolfe, 1994, 1998a) to relevant display items, although the dividing of attention among items undergoes age-related decline. It is likely that age differences in divided attention performance are to some extent the result of a generalized age-related slowing of information processing. Independent of specific task demands, the magnitude of age-related decrements in performance tends to increase as a function of increasing task complexity, and age-related variance is often shared across related measures of cognitive performance, rather than being unique to specific measures (Madden, 2001; Salthouse, 1985, 1996).

Neuroimaging research has begun to identify the changes in the central nervous system that mediate age-related cognitive change (Anderson & Grady, 2001; Cabeza, 2001; Grady, 1998; Langley & Madden, 2000; Raz, 2000). One general theme that is emerging from this research is that although age-related decline is evident in both structural (e.g., cortical volume) and functional (e.g., resting metabolic rate) measures, aging is associated with a substantial degree of functional plasticity. Grady et al. (1992, 1994), using PET measures of regional cerebral blood flow (rCBF), found that the functional dissociation between the dorsal and ventral visual processing pathways was less pronounced for older adults than for younger adults and that activation near the visual sensory (striate) cortex was relatively greater for the younger adults. Older adults, however, exhibited relatively greater activation in prefrontal cortex, especially during the spatial task. Grady et al. (1992, 1994) concluded that older adults' activation of neural regions outside of the task-relevant network may represent a form of functional compensation for age-related decline in the efficiency of sensory processing regions. Consistent with this account, increasing perceptual difficulty (e.g., increasing visual noise in a face-matching task) led to different patterns of covariation between neural activation and task performance for younger and older adults (Grady, McIntosh, Horwitz, & Rapoport, 2000). A related view is that the differences between younger and older adults' activation patterns represent an age-related reduction in the hemispheric specialization of cognitive function (Cabeza, 2002).

Madden et al. (1997) compared younger and older adults' performance in selective and divided visual attention conditions and obtained age differences in rCBF activation consistent with those of Grady et al. (1992, 1994, 2000). Participants searched through series of nine-letter displays for the presence of a target letter that either occurred predictably in the central location or could appear in any of the nine display positions. When participants could attend selectively to the central display position, there were minimal age differences in either visual search performance or in rCBF activation relative to a passive viewing condition. The requirement to divide attention among the display positions, however, led to a greater increase in error rate and reaction time for older adults than for younger adults. The divided attention condition was in addition associated with different patterns of rCBF activation for the two age groups. Activation in the occipitotemporal pathway was greater in magnitude for younger adults than for older adults, whereas activation in prefrontal cortex was relatively greater for older adults. For each age group, the rCBF activations were correlated positively with the changes in reaction time across the task conditions. These findings suggested that for younger adults the additional processing demands of the divided attention condition, relative to the selective attention condition, led primarily to an increased involvement of letter identification processes mediated by the ventral processing pathway, whereas for older adults these additional demands led to the recruitment of higher order control processes that are mediated by the prefrontal cortex.

In this experiment, we examined whether the pattern of age differences in cortical activation observed by Madden et al. (1997), in terms of an age-related decline in the activation of the ventral processing pathway and an age-related increase in the activation of regions outside of this pathway, would also occur in response to a different form of attentional selectivity. One feature of the Madden et al. study was that the display location of the target was constant in the selective attention condition (i.e., the center of the display) and was unpredictable in the divided attention condition. Participants' ability to attend selectively thus depended on their ability to use this spatial dimension to guide attention to the target item (Wolfe, 1994, 1998a). In this experiment, we used a task in which a subset of target-relevant display items was defined by the color of the items, and the distribution of the potential locations of the target in the display was random in each task condition. Color provided a dimension that participants could use as a basis for attentional guidance, but the spatial location of the target was independent of this dimension.

The search task required participants to determine whether a single upright L target was present among rotated L distractors. Unless there is some additional basis on which to differentiate the target from the distractors, this type of task requires a slow and inefficient (i.e., difficult) form of search (Wolfe, 1998b) because the distractors are different conjunctions of the individual features of the target (a short line, a longer line, and a right angle). We examined age differences in rCBF activation in three task conditions that varied the similarity among the display items (see Figure 1). The display location of the target was not predictable in any of the conditions.

In the least difficult condition (feature search), the distractors were always a different color than the target was (e.g., a black target among 17 white distractors). It is well established that search is highly efficient when the target is defined by a unique feature (Treisman & Gelade, 1980). In the most difficult condition (conjunction search), one half of the display items contained the target's color (e.g., a black target among 8 black distractors and 9 white distractors). In the guided search condition, a smaller subset of items shared the target's color (e.g., a black target among 2 black distractors and 15 white distractors). When a subset of the display items can be defined as potentially containing the target, it is often possible to increase search efficiency by guiding attention to the relevant subset even though, as in the present instance, the subset is distributed unpredictably across the display (Friedman-Hill & Wolfe, 1995). Madden, Gottlob, and Allen (1999) reported that younger adults were more accurate than older adults were in detecting an upright L among rotated Ls but that both age groups were successful in guiding attention to a target-relevant subset that was defined by color.

Because the search for an upright L among rotated Ls, especially in the conjunction condition, requires feature identification processes as well as shifting attention across display locations, we expected that rCBF activation for conjunction search, relative to feature search, would be evident prominently in both the occipitotemporal and occipitoparietal pathways. Other aspects of search performance, such as maintaining the target in working memory and deciding when to terminate the search, would likely lead to activation in the cortical components of the attentional network outside of the visual processing pathways (e.g., prefrontal cortex). If older adults' conjunction search performance depends on the recruitment of prefrontal neural systems to compensate for a decline in perceptual processing (Grady et al., 1992, 1994, 2000; Madden et al., 1997), then activation in the dorsal and ventral processing pathways should be greater in magnitude for younger adults than for older adults, whereas the activation outside of these regions, especially in prefrontal cortex, should be relatively greater for older adults.

The pattern of rCBF activation associated with the guided condition, relative to the feature and conjunction conditions, was of particular interest. In our guided condition, there were only three items in the display that shared the target's color. Both younger and older adults are able to guide attention to a relevant subset in this type of task (Madden, Gottlob, et al., 1999), but

the neural systems that mediate this form of attentional guidance may change as a function of age. The findings of Sathian et al. (1999) suggest that, for younger adults, identifying a subset of four or fewer display items from among a larger group is mediated by extrastriate cortex and does not involve the frontal and parietal components of the attentional network. If, for older adults, guiding attention to a relevant subset requires the involvement of compensatory mechanisms (Grady et al., 1992, 1994, 2000; Madden et al., 1997), then the guided condition would be more likely to lead to neural activation outside the visual processing pathway for older adults than for younger adults. Thus, in the present task, the guided search condition may not lead to substantial activation beyond the feature search baseline for younger adults, whereas in this condition, older adults may be more likely to exhibit activation throughout the attentional network in a manner similar to the pattern of activation that is associated with conjunction search.

Method

Participants

The participants were 12 younger adults between 20 and 27 years of age and 12 older adults between 60 and 77 years of age (see Table 1). Each age group contained 5 men and 7 women. The research procedures were approved by the Institutional Review Board of the Duke University Medical Center, and all participants gave written informed consent.

The younger adults were recruited from the Duke University campus. The older adults were recruited from the Duke Aging Center Subject Registry and from advertisement in the local media. Participants were right handed, had completed at least a high school education, and had no current health problems (e.g., diabetes, hypertension, arteriosclerosis) or previous significant medical events (e.g., head injury with loss of consciousness more than 5 min, stroke, transient ischemic attack, heart attack, heart surgery) as determined by a screening questionnaire (Christensen, Moye, Armson, & Kern, 1992). All participants scored at least 27 (out of 30) on the Mini-Mental State Exam (MMSE; Folstein, Folstein, & McHugh, 1975).

Participants completed the Vocabulary subtest of the Wechsler Adult Intelligence Scale-Revised (WAIS-R; Wechsler, 1981) and a computer version of the WAIS-R Digit Symbol Substitution subtest (Salthouse, 1992). The latter test measures both accuracy and median time per item to code digit-symbol pairs. Corrected binocular acuity for near vision was measured with a Keystone Telebinocular vision tester (Mast/Keystone, Davenport, IA), using split-ring slides. Participants had acuity of at least 20/40. The younger and older adults were equivalent in mental status (MMSE), education, digit-symbol coding accuracy, and verbal knowledge (WAIS-R Vocabulary), but an age-related decline was evident in digit-symbol coding time and visual acuity (Table 1).

Prior to PET testing, structural MR images were obtained for all participants. Transaxial MR images were acquired with a 1.5 T scanner (Signa; GE Medical Systems, Milwaukee, WI). The slice thickness was 3 mm with no interslice gap. The repetition time (TR) for the T₁-weighted images was 600 ms, and the echo delay time (TE) was 20 ms, with two excitations (NEX). The T₂-weighted images had a TR of 2.50 s, TE values of 20 ms and 80 ms, and 1 NEX.

All of the MR images were reviewed by the same neuroradiologist (one of the authors: James M. Provenzale) for evidence of significant cerebral atrophy or structural abnormality. For both age groups, participants were excluded from PET testing if, in the neuroradiologist's judgment, the MR image contained any signal abnormality indicating a mass, ventricular enlargement, or atrophy atypical for age; flow signal abnormality within intracranial vessels; extra-axial fluid collection; or any focal signal abnormality within caudate, putamen, globus pallidus, thalamus, brain stem, or cerebellum. For younger adults, any focal area of hyperintensity on

T₂-weighted images was also an exclusion criterion, whereas for older adults, the criterion was the presence of focal supratentorial hyperintense white matter signal abnormalities that were greater than 3 mm. This latter criterion was chosen to take into account the age-related increase in the occurrence of these white matter signal abnormalities, at the same time setting a conservative limit with respect to the probability of disease (Yetkin, Fischer, Papke, & Haughton, 1993). Five participants, all older adults, were excluded from the experiment on the basis of the MR findings. We estimated the total volume of gray matter (covaried for participants' height) from each participant's MR image, using the method described by Madden et al. (1996). The height-adjusted gray matter volume was significantly greater for younger adults than for older adults (Table 1).

Apparatus and Stimuli

Presentation of the visual displays and measurement of participants' responses were controlled by a 486-processor (66-MHz) microcomputer (Gateway 2000, N. Sioux City, SD). Displays were presented on a Gateway Vivitron 15-in. video monitor, with a 285 mm × 213 mm display area. The monitor was positioned above the gantry opening of the PET scanner, facing downward at an approximately 45° angle, at a viewing distance of approximately 81 cm.

On each trial, participants made a *yes-no* decision regarding the presence of an upright L (the target) among rotated Ls (distractors). Examples of the displays are presented in Figure 1. The background for the entire screen was gray, with a luminance of 19 cd/m². Each display was presented in an area in the center of the video monitor subtending 4.70° × 4.70° visual angle. Each display item was either white or black. Luminance was 44 cd/m² for white items and less than 1 cd/m² for black items, as measured by a Spectra Mini-Spot silicon cell photometer (Photo Research, Burbank, CA). Each display contained 18 items, either a target and 17 distractors or 18 distractors, distributed across 25 display positions. The display positions, which were not explicitly marked, were arranged in a 5 × 5 position grid. Display positions were 0.45° wide × 0.56° high. There was 0.48° between adjacent rows and 0.61° between adjacent columns. Item distribution was random, with the constraint that a target occurred equally often at each display position across a block of trials. Participants responded on each trial by means of a two-button response box connected to the game port of the microcomputer. Participants rested the index and middle fingers of the right hand on the two response buttons. One button was assigned the *yes* (target present) response, and the other button was assigned the *no* (target absent) response.

There were three search conditions that varied the difficulty of the search task by varying the similarity of the target and distractor items. In the feature search condition, the distractors were all the same color, and the target was always the single item of a different color (e.g., a black upright L among white rotated Ls). The feature condition was presumably the easiest form of search, because the target differed from all of the distractors on a single feature: color. The detection of any item of the target's color was sufficient for a *yes* response. In the conjunction search condition, the similarity between the target and distractors was higher. Each display in the conjunction condition contained nine black items and nine white items that were distributed randomly. The guided search condition was an intermediate case, in that each display contained three items that were distributed randomly and shared the target's color (e.g., 3 black items and 15 white items). Thus, if a target was present in the display, it would be one of these three items. Relative to the conjunction condition, the feature condition allowed the target to stand out on the basis of color, and the guided condition allowed participants to restrict their search to the three items that shared the target's color.

The assignment of the target as either a white L or a black L was constant for each participant but varied across participants. There were three types of rotated-L distractors: flipped (i.e., reflected) horizontally: J, flipped vertically: 7, and rotated 180°: 1. Each of these three types

could be presented in either black or white, which yielded a complete set of six distractors. All display items were presented in a sans serif type font. The item counterbalancing was similar on the *yes* and *no* trials, except that on the *yes* trials one of the distractors was replaced with a target. On the *no* trials, the 18 items in each display were counterbalanced in the following manner: In the conjunction condition, the six types of distractors each occurred three times. In the feature condition, only the three distractors of the opposite color from the target were used, with each distractor occurring six times. In the guided condition, there were always three items sharing the target's color, either the target and two distractors (*yes* trials) or three distractors (*no* trials). On the guided-search target-absent trials, the three distractors that shared the target's color each occurred once, and the three distractors of the opposite color each occurred five times.

Procedure

All participants performed a practice version of the search task prior to PET testing on a separate day, during which the psychometric and visual acuity tests were administered. There were 900 trials in the practice task, 300 trials in each of the three search conditions. During this practice task, participants were encouraged to maintain central fixation during display presentation, and eye movements were monitored with a video camera. Eye movements occurred on less than 1% of the trials. So that practice would be specific to the task rather than to the stimuli, participants who searched for a black upright L target during the practice task searched for a white target during PET testing and vice versa.

The PET testing involved 12 measurements of rCBF, and participants performed a single task condition (in a block of 100 trials) during each of the 12 PET scans. There were four blocks of trials for each of the three search conditions. Each block contained a random sequence of 50 *yes* trials and 50 *no* trials. For the 50 *yes* trials, the target occurred twice at each of the 25 display positions. In the sequence of 12 blocks, each search condition was represented once in each set of three successive blocks, and the same search condition never occurred in two adjacent blocks. Twelve block orders were constructed such that, across the orders, each of the search conditions occurred four times at each of the 12 serial positions. Each block order was used by one participant in each age group. The assignments of the *yes* response (left vs. right response button) and type of target (black vs. white L) were varied across participants, with the result that three participants in each age group received each combination of *yes*-response and target type. (The left-right assignment of *yes-no* responses was maintained between the practice session and PET testing for each participant, although in the practice session the two responses were assigned to separate hands rather than to the same hand.)

The experimenter explained the differences among the search conditions and emphasized that participants should concentrate their visual fixation in the center of the screen. Each trial began with a fixation point (an asterisk) in the center of the viewing screen for 500 ms. The display occurred immediately following the offset of the fixation point and remained on the screen for 1 s. A blank screen was presented during the intertrial interval. To reduce the predictability of the initiation of a trial, this interval varied randomly in duration from 800 ms to 1,200 ms. The experimenter emphasized that performance would be maximized if the participant could maintain central fixation during display presentation, but eye movements were not monitored. Accuracy was emphasized more than was speed. The computer recorded the participant's response on each trial and the time between the onset of the display and the response.

Positron Emission Tomography

The measurement of rCBF was conducted with a General Electric Advance whole-body PET scanner that contained 18 detector rings. Data were acquired simultaneously from 35 imaging planes (18 direct planes and 17 cross planes) separated by 4.25 mm. The axial field of view

was 15 cm, and the intrinsic in-plane and axial spatial resolutions were approximately 5-mm full width half maximum (FWHM). Data acquisition was performed in the septa-out, three-dimensional mode (DeGrado et al., 1994).

Radiotracer injection was performed through an intravenous catheter placed in the participant's left arm at the beginning of the testing session. The participant was positioned in the tomograph with his or her head aligned in a plane approximately parallel to the glabella-inion line. Alignment was conducted with the assistance of a low-power laser. Prior to the emission scans, a 5-min transmission scan was performed using a pair of 3-10 mCi ^{68}Ge rotating pin sources. Following the transmission scan, participants performed three blocks of 10 practice trials, one block for each of the feature, guided, and conjunction conditions. The practice trial data were not included in the task performance analyses.

During the 12 emission scans, the radiotracer was administered as an intravenous bolus injection of approximately 10 mCi of $\text{H } ^{15}_2\text{O}$. Prior to each radiotracer injection, participants were reminded of the instructions and response button assignment for the upcoming task condition. Presentation of the visual displays was initiated 30-60 s prior to radiotracer injection and continued for approximately 4 min. The PET data acquisition began automatically when the radioactivity count rate exceeded a preset threshold of 75,000 counts/s (random corrected) and continued for 1 min. Radiotracer injections were separated by 10 min. Reconstruction of the PET image data was performed with filtered back-projection using a Hann filter transaxially and a ramp filter axially (Kinahan & Rogers, 1990). Images were 128×128 pixels ($2 \times 2\text{mm}^2$) for each of 35 slices. The data were corrected for random coincidences, attenuation, scattered radiation, and dead time.

Changes in rCBF between task conditions were analyzed with the 1996 version of the Statistical Parametric Mapping software (SPM96; Wellcome Department of Cognitive Neurology, London, England; Friston et al., 1995). As noted previously, there were four scans for each of the three task conditions. Participants performed each task condition twice in the first half of the testing session (Scans 1-6) and twice in the second half (Scans 7-12). Preliminary analyses indicated that there was no significant change in the pattern of rCBF activation as a function of one half of testing session. For each participant, therefore, a mean PET image was derived from the four scans that were associated with each task condition. The 12 scans for each subject were reordered to the same sequence of task conditions and then realigned by using the scan for the first conjunction condition as a reference. The scans were normalized and transformed after realignment into a standard stereotaxic space (Talairach & Tournoux, 1988). This procedure began with a 12-parameter affine transformation, followed by piecewise (contiguous transverse slices) nonlinear matching that was constrained by a set of smooth basis functions (Friston et al., 1996). An additional 15-mm FWHM isotropic Gaussian kernel was used to smooth the spatially normalized images.

The SPM analyses of the task condition contrasts used a fixed effects model of the mean PET images. An analysis of covariance (ANCOVA) was applied to the PET counts on a voxel-by-voxel basis and included global activity as a confounding covariate. The increase in rCBF between task conditions was represented by a linear contrast (i.e., image subtraction), which was reversed to yield the corresponding decrease in rCBF. The resulting set of voxel t values for each subtraction formed the statistical parametric map $\text{SPM}\{t\}$. The t values were transformed to the unit normal distribution $\text{SPM}\{Z\}$ and then characterized in terms of the peak height (u) and spatial extent (k) of the local maxima. Voxels were thresholded for height at $Z = 2.33$ ($p = .01$, uncorrected). The local maxima were defined as voxels with Z values that were greater than all voxels within 8 mm.

Significance of the peak height was estimated by using distributional approximations from the theory of Gaussian fields. The significance level referred to the probability that the observed peak height of the local maximum of activation is greater than would be expected by chance ($p[Z^{\max} > u]$). Corrected p values that were obtained for estimates applied to the entire volume that was analyzed. Up to ten local maxima were obtained for each region. Regions of rCBF change were considered to be significant statistically if there were at least 100 contiguous voxels and the probability level for the peak height of the local maximum (corrected for multiple comparisons) was less than .05.

The SPM contrasts for conjunction minus feature, guided minus feature, and conjunction minus guided were examined. As noted in the Participants section, the two age groups differed in cortical volume. We therefore included height-adjusted cortical volume as a confounding covariate in all of the SPM analyses. We used the method reported by Lane et al. (1998) to adjust SPM contrasts for a covariate that has a single value per participant. For contrasts between two task conditions (i.e., those in which the condition codes were 1 and -1), the same covariate (volume) values were used in each condition, but the sign of the values was reversed for the condition that was coded -1.

To assess the age differences associated with each of these subtractions, the rCBF data for the two age groups were combined, and a masked analysis was conducted that included two simultaneous linear contrasts: one that represented the task condition subtraction of interest (for all subjects combined) and another that represented the difference between the two age groups. The task condition contrast was used as a mask for the age difference contrast. The resulting SPM $\{Z\}$ map for these interaction contrasts contained those voxels that differed as a joint function of age group and task condition. The p values for the interaction contrasts were corrected on the basis of the number of regions identified in the contrast that was used as the mask. Additional analyses were conducted on the PET radioactivity counts of the voxels that were identified as local maxima in the SPM maps. To examine the relationship between rCBF and performance, we also conducted SPM analyses, in which search accuracy was a covariate of interest.

Results

Search Performance

Trials on which participants failed to respond to the current display before the onset of the subsequent trial (approximately 2,200 ms) were excluded from analysis. Trials on which the reaction time to the current display was less than 150 ms were also excluded. The mean proportion of excluded trials was less than .02 for each search condition and did not differ significantly between the age groups.

Recognition accuracy—Search performance was near ceiling for both age groups in the feature and guided conditions but was substantially lower in the conjunction condition. As is typically observed in visual search tasks (Chun & Wolfe, 1996; Madden, Gottlob, et al., 1999; Zenger & Fahle, 1997), failures to detect the target (incorrect *no* responses) were more frequent than false alarms (incorrect *yes* responses) were. The false-alarm rate was less than .05 for each combination of age group and search condition. Corrected recognition accuracy (proportion hits minus proportion false alarms) is presented in Figure 2. We focus primarily on the accuracy data as an index of search performance because reaction time data are difficult to interpret when accuracy is well below ceiling (Santee & Egeth, 1982).

An analysis of variance (ANOVA) was performed on corrected recognition accuracy with age group as a between-subjects variable and search condition (feature, guided, conjunction) as a within-subjects variable.¹ This ANOVA yielded significant main effects for both age group,

$F(1, 22) = 8.73$, $MSE = 0.03588$, $p < .01$, and search condition, $F(2, 44) = 243.70$, $MSE = 0.01332$, $p < .0001$. The level of recognition accuracy averaged across the task conditions was .066 higher for younger adults than for older adults. Averaged across age group, accuracy decreased from .983 in the feature condition to .931 and .641 in the guided and conjunction conditions, respectively. Each of these differences between the search condition means was significant by Bonferroni-corrected t tests, with critical $t(44) = 2.49$, at $p = .05$.

The Age Group $\times$ Search Condition interaction, $F(2, 44) = 18.63$, $MSE = 0.01332$, $p < .0001$, was also significant. In the conjunction condition, the age-related decline in corrected recognition was .182, which was significant, $F(1, 22) = 17.67$, $MSE = 0.04484$, $p < .001$. The age difference did not exceed .025 and was not significant in either of the other conditions. Bonferroni-corrected paired comparisons were conducted on the simple main effect of search condition for each age group, with critical $t(22) = 2.59$ at $p = .05$. For both age groups, accuracy in both the feature condition and the guided condition was significantly higher than it was in the conjunction condition. For both age groups, performance in the guided condition was slightly lower than it was in the feature condition. This difference was not significant for younger adults (.025) but was significant for older adults (.069).

In addition to considering the three search conditions as qualitatively different tasks, we also analyzed performance as a continuum of similarity, based on the incidence probability of target-relevant items. In the feature condition, the target-absent trials did not contain any items that shared the target's color. Thus, across an equal number of target-present and target-absent trials, the incidence probability of items that shared the color of the target in the feature condition was .028 (1 target per 36 display items). In the guided condition, the incidence probability of the target-relevant items was .167 (6/36), and the corresponding value was .50 (18/36) in the conjunction condition. The increase in this probability across the conditions represents a change in stimulus similarity, in the direction of both an increase in similarity between the target and distractor items and a decrease in similarity among distractor items. This type of change in stimulus similarity typically leads to a decrease in the efficiency of search (Duncan & Humphreys, 1989).

The decline in corrected recognition accuracy as a function of the increasing stimulus similarity was linear for each age group (median $r^2 = .96$ for younger adults and .97 for older adults). The magnitude of this decline, as reflected in the slope of the linear function relating recognition accuracy to increasing incidence probability of target-relevant items, was significantly greater for older adults than for younger adults, $F(1, 22) = 22.80$, $MSE = 0.04554$, $p < .0001$. The mean slope value was -0.541 ($SD = 0.188$) for younger adults and -0.957 ($SD = 0.236$) for older adults.

To determine the degree to which the age-related variance in the recognition slopes was shared with other perceptual variables, we conducted a series of hierarchical regression analyses. When age group (coded as 0 or 1) was the only variable in the model predicting the recognition slope values, the proportion of age-related variance was .509, $F(1, 22) = 22.80$, $MSE = 0.04559$, $p < .0001$. Adding visual acuity as a predictor reduced the age-related variance to .338, but age group remained a significant predictor, $F(1, 21) = 14.66$, $MSE = 0.07116$, $p < .001$. When both

¹Analyses conducted on signal-detection measures of sensitivity and bias yielded results that were comparable to those reported for the corrected recognition (hits minus false alarms) measure. It is worth noting that although accuracy was lower in the conjunction condition than in the other conditions, conjunction performance was well above chance. In difficult search tasks, participants typically set a cautious response criterion, requiring a high degree of evidence that a target was present before responding *yes* (Chun & Wolfe, 1996; Madden, Gottlob, et al., 1999; Zenger & Fahle, 1997). As a result, the false-alarm rate is low, and the majority of the errors are misses, as was observed in this experiment. Target detectability can remain well above chance with this pattern of error rates. The d' value in the conjunction condition was 2.77 for younger adults and 2.0 for older adults. That is, participants' decisions were based on a substantial separation of at least two standard deviations between the evidence distributions for the target-present and target-absent displays. Chance performance (complete overlap of the distributions for the two types of displays) would yield a d' of zero.

visual acuity and digit symbol coding time were entered into the model prior to age group, the age-related variance was only .087, and age group was marginally significant as a predictor, $F(1, 20) = 3.58$, $MSE = 0.04946$, $p = .073$. Thus, .829 of the age-related variance in the recognition slopes $(.509 - .087)/.509 = .829$ was shared with the visual acuity and digit symbol measures.

Reaction time—As noted previously, we focus on accuracy as the most valid measure of search performance in this task. The reaction time data (Figure 3), however, were generally consistent with the accuracy data. We performed an ANOVA of the reaction time for correct responses, with age group as a between-subjects variable and response type (i.e., hits vs. correct rejections) and search condition as within-subjects variables. All of the main effects were significant: age group, $F(1, 22) = 8.53$, $MSE = 63,214$, $p < .01$, response type, $F(1, 22) = 155.11$, $MSE = 4,141$, $p < .0001$, and condition, $F(2, 44) = 348.06$, $MSE = 9,342$, $p < .0001$. Correct responses were 122 ms slower for older adults than for younger adults, and correct rejections took 134 ms longer than hits took. Bonferroni paired comparisons indicated that the 299-ms increase in reaction time from the feature condition to the guided condition was significant at $p < .05$, as was the 219-ms increase from the guided condition to the conjunction condition.

The only significant interaction in the reaction time data was the Search Condition $\times$ Response Type effect, $F(2, 44) = 119.72$, $MSE = 1,944$, $p < .0001$. This interaction occurred because correct rejection responses were slower than hit responses were by 264 ms in the conjunction condition, $F(1, 22) = 148.20$, $MSE = 5,667$, $p < .0001$, and by 149 ms in the guided condition, $F(1, 22) = 139.53$, $MSE = 1,905$, $p < .0001$, whereas hit responses were 13 ms slower than correct rejections were in the feature condition, $F(1, 22) = 4.24$, $MSE = 456$, $p = .052$. The simple main effect of search condition was significant for both hits and correct rejections, with $F(1, 22) > 300.0$, $p < .0001$, in each case. For both response types, the difference in reaction time between each pair of task conditions was at least 150 ms, which was significant by Bonferroni t at $p < .05$.

Cerebral Blood Flow

The increases in rCBF associated with the task condition subtractions are presented in Table 2, and the corresponding decreases are presented in Table 3. Tables 2 and 3 also list the coordinates of the local maxima in a standard stereotaxic space (Talairach & Tournoux, 1988), the Brodmann's area (BA) designation, and the gyral location. As noted previously in the Method section, there were no significant practice-related changes in rCBF, and we consequently averaged the rCBF data for the four PET scans that were associated with each task condition.² The rCBF activations for the younger adults are presented in Figure 4, and the older adults' activations are presented in Figure 5.

²Practice-related changes were quite pronounced, however, in the performance measures. Because there were two instances of each of the three task conditions in each half of the testing session (i.e., six blocks of trials per half), we compared the first half with the second half of the testing session. Analyses of the recognition accuracy slopes revealed a significant improvement in this accuracy measure with practice, $F(1, 22) = 15.64$, $MSE = 0.00923$, $p < .001$, which did not vary significantly as a function of age group ($F < 1.0$). We also examined practice effects for the mean reaction time of hits and correct rejections within each task condition. There were substantial practice effects in the conjunction and guided conditions. In the conjunction condition, there was a 69-ms decrease in reaction time for hits between the first and second halves of the testing session, $F(1, 22) = 20.75$, $MSE = 5,492$, $p < .001$, and 85-ms decrease in the reaction time for correct rejections, $F(1, 22) = 16.45$, $MSE = 10,511$, $p < .001$. The guided condition yielded a 58-ms practice effect for hits, $F(1, 22) = 66.48$, $MSE = 1,211$, $p < .0001$, and a 65-ms practice effect for correct rejections, $F(1, 22) = 47.74$, $MSE = 2,142$, $p < .0001$. For the feature condition, only the correct rejection reaction time decreased significantly (by 20 ms) with practice, $F(1, 22) = 7.98$, $MSE = 1,211$, $p < .01$. None of the reaction time practice effects varied significantly as a function of age group.

The practice analyses demonstrate that even though participants had previous experience with this search task (during the screening procedures), performance was not asymptotic at the beginning of PET testing. In addition, both younger and older adults were sufficiently engaged in the task to improve both their accuracy and speed of responding during the PET testing. Practice-related improvements in performance have been found to lead to decreases in neural activation, especially in prefrontal regions (Garavan, Kelley, Rosen, Rao, & Stein, 2000; Madden, Turkington, et al., 1999). The reason for the rCBF measures in the present task remaining constant as a function of practice deserves further investigation.

Conjunction minus feature—Relative to the feature condition, the conjunction condition was associated with extensive activation bilaterally in both the dorsal (occipitoparietal) and ventral (occipitotemporal) visual processing pathways. For both younger and older adults, this activation occurred as a single cluster, with local maxima in extrastriate cortex (BA 18) and parietal cortex (BA 7) bilaterally. Both age groups also exhibited activation in the left cerebellum. Prefrontal activation was significant for the medial and lateral regions of the right hemisphere (BAs 32, 6, and 9 for younger adults; BAs 32, 6, and 10 for older adults). The interaction contrast indicated that activation in striate and extrastriate cortex in the right hemisphere (BAs 17 and 19) was greater for younger adults than for older adults.

This subtraction yielded extensive regions of decreased rCBF, primarily in medial prefrontal (anterior cingulate, insula) and temporal cortex, for both age groups. Older adults exhibited a greater rCBF decrease than young adults exhibited in the middle temporal gyrus (BA 21) of the right hemisphere.

Conjunction minus guided—For the younger adults, this subtraction yielded a pattern of rCBF activation similar to the conjunction minus feature contrast, except that the posterior cortical activations were located primarily in the ventral pathways of the visual processing regions (BAs 18 and 19). The younger adults also exhibited activation in the anterior cingulate (BA 32) and middle frontal gyrus (BA 9) of the right hemisphere and in the left cerebellum. For the older adults, this subtraction yielded only activation in the insular cortex of the right hemisphere. The interaction contrast indicated that local maxima in the striate cortex (BA 17) of the right hemisphere and the ventral extrastriate cortex bilaterally (BA 19) were greater in magnitude for younger adults than for older adults.

The younger adults' decreases in activation associated with this subtraction involved the temporal and medial prefrontal regions of the left hemisphere. These included the middle temporal gyrus (BA 39), insular cortex, and medial and superior frontal gyri (BAs 9 and 10). There were no significant decreases for older adults. Changes similar to those exhibited by the younger adults did occur, although to a smaller degree, and as a result the age difference tested by the interaction contrast was not significant.

Guided minus feature—This contrast was associated with different regions of activation for the two age groups, but the difference was not of sufficient magnitude to yield a significant interaction effect. For the younger adults, the rCBF increase in the middle occipital gyrus (BA 19) of the right hemisphere was significant. The older adults exhibited extensive activation in the left hemisphere, including the cerebellum, striate cortex (BA 17), and precentral gyrus (BA 6).

For the younger adults, there was no significant rCBF decrease. The older adults exhibited a decrease in the middle temporal gyrus of the right hemisphere (BA 21). The interaction contrast indicated that the decrease was greater for older adults than for younger adults in BA 39 of the right middle temporal gyrus and in the anterior cingulate bilaterally (BAs 25 and 32).

PET radioactivity counts—A limitation of the method of measurement of rCBF used in this experiment is that, without arterial blood sampling, it is not possible to compare younger and older adults' rCBF values within a condition, in absolute units (e.g., milliliters per 100-gm tissue per minute). Thus, although we have determined that there are several regions for which the rCBF increase that was associated with the conjunction condition, relative to the feature and guided conditions, was greater in magnitude for younger adults than for older adults, this result could represent different patterns of age-related change. The age difference could have occurred as the result of a relatively higher level of activation for younger adults in the

conjunction condition or a relatively lower level of activation for younger adults in the feature condition or both.

To address this issue, we analyzed variation in the PET counts as a function of age group and task condition. These counts, representing the tissue concentration of H_2^{15}O , are a nearly linear function of rCBF (Herscovitch, Markham, & Raichle, 1983). We obtained the PET counts (see Table 4) for the five regions that were associated with significant age-related change in rCBF increases as determined from SPM (Table 2). We analyzed the PET count data for each voxel that corresponded to these local maxima, normalized to each participant's whole-brain gray matter mean value for the corresponding task condition. These latter values were obtained from all of the voxels that were above 80% of the mean voxel value for the entire brain image (for each participant and task condition), which were averaged to yield gray matter mean values. The voxel count values thus represent the level of activation within each task condition, relative to the whole-brain mean, whereas the SPM contrasts represent differences in the level of activation between task conditions.

We first confirmed that the age differences in these voxel counts were consistent with the SPM results. For each of the five voxels listed in Table 4, the difference in normalized counts between the task conditions, covaried for height-adjusted gray matter volume, was greater for younger adults than for older adults, with $F(1,21) > 4.86$, $p < .05$ in each case. In addition, the task condition effect that was associated with each voxel was significant for younger adults, with $F(1, 11) > 9.35$, $p < .01$, in each case, whereas none of the task condition effects was significant for the older adults. As is evident in Table 4, the normalized count values were generally higher for older adults than for younger adults in both the conjunction condition and the comparison condition (feature or guided). Analyses of the age difference within each task condition indicated that the two groups did not differ significantly in the count values for the right fusiform gyrus in the conjunction condition. All of the other comparisons yielded a significantly higher normalized count value for older adults than for younger adults, with $F(1, 22) > 9.55$, $p < .01$, in each case.

Covariation between search performance and rCBF—To examine the relationship between the accuracy of visual search performance and rCBF activation, we conducted an SPM analysis in which search accuracy was included as a covariate of interest. The same thresholds and levels of significance were used as in the paired comparisons of the task conditions that were reported in the previous section. Cortical volume was included as a confounding covariate. Because the difference in search accuracy between the feature and guided conditions was only .05 (although significant statistically), this analysis was conducted with all three conditions included rather than as paired comparisons. The resulting SPM map represents regions of covariation between accuracy and rCBF activation. To represent the covariation between increasing task difficulty and rCBF as a positive relationship (i.e., activation), the covariate of interest was 1.0 minus the corrected recognition score.

The results of this analysis are presented in Table 5. The data resemble the conjunction minus feature condition subtraction, in that the covariation was evident for voxels throughout the occipitotemporal cortex for both age groups. Outside this ventral processing pathway, covariation was also present for younger adults (middle frontal gyrus and anterior cingulate) and older adults (cerebellum, insula, and thalamus). The interaction contrast indicated that the relationship between activation in the ventral processing pathway and increasing task difficulty was more pronounced for younger adults than for older adults. This age difference was evident for BA 19 of the left hemisphere and for BAs 17, 19, 31, and 37 of the right hemisphere. The relationship between activation in the right middle frontal gyrus (BA 6) and task difficulty was also more pronounced for younger adults than it was for older adults.

The covariation between decreasing rCBF and increasing task difficulty was significant for the younger adults' left medial frontal region (BA 10) and for the older adults' right medial and lateral temporal regions (amygdala and BAs 21 and 36). For one region in the right middle temporal gyrus (BA 21), the relationship between decreasing rCBF and increasing task difficulty was more pronounced for younger adults than for older adults. There were no regions for which the covariation between performance and rCBF (either increases or decreases) was more pronounced for older adults than for younger adults.

Discussion

Visual Search Performance

Analyses of the visual search accuracy data (Figure 2) yielded two main findings. First, when the incidence probability of target-relevant information was highest, in the conjunction condition, the age-related decline in target detectability was most apparent. Second, both younger and older adults were able to improve performance in the guided condition by using the color of the display items to attend selectively to a relevant subset. These findings are consistent with the Madden et al. (1997) PET study of visual selective attention. In that study, younger and older adults' performance was comparable when participants could attend selectively to the center of the display, but an age-related decline was apparent when it was necessary to divide attention among nine display positions. In the Madden et al. experiment, however, the search task conditions differed in their distribution of the target across the display positions, and the opportunity to attend selectively was defined by this change in spatial distribution. The distribution of the target in the present experiment was comparable across task conditions, and task-relevant items were defined on the basis of color rather than on the basis of display location.

We obtained some evidence of relatively greater success in attentional guidance for younger adults. Search accuracy for both age groups was higher in the guided condition than it was in the conjunction condition, but only for the younger adults did accuracy in the guided condition reach the level of accuracy in the feature condition. Older adults' accuracy in the guided condition was slightly (.069) but significantly lower than it was in the feature condition. The important point is that both age groups were successful in attending selectively when the relevant dimension was distributed across the display rather than when it was restricted to a single display position. Madden, Gottlob, et al. (1999) also found that, in this type of search task, target detectability in the conjunction condition was worse for older adults than for younger adults, but that both age groups were able to use the color of the display items as a means of improving search performance.

The fact that the decrease in search accuracy was a relatively linear function of the incidence probability of items that shared the target's color suggests that search performance, for both age groups, was significantly influenced by stimulus similarity. As the incidence probability increased, the similarity of the target to the distractor items increased, and the similarity among the distractors decreased. Both of these types of changes impair the efficiency of target detection (Duncan & Humphreys, 1989; Wolfe, 1998a). The slope of this linear decline was steeper for older adults than for younger adults, which suggests that this effect of stimulus similarity (as well as related sensory-level effects in target luminance, contrast, etc.) differentially affected the older adults' performance. This age-related effect was not attributable entirely to sensory-level changes and appears to reflect a decline in processing efficiency at a more central level. In the hierarchical regression analyses of the recognition accuracy slopes, entering visual acuity before age group in the regression model substantially reduced the age-related variance, but age group remained a significant predictor. Adding both a measure of perceptual motor speed (digit-symbol coding time) and acuity as predictors before

age group, however, indicated that most (.829) of the age-related variance in the accuracy slopes was shared with these other two variables (Madden, 2001; Salthouse, 1985, 1996).

Accuracy measures are typically more informative than reaction time is when performance is below ceiling (Santee & Egeth, 1982), as in the conjunction condition, but the findings for reaction time in the present experiment were in general agreement with the accuracy results (Figures 2 and 3). Averaged across the search conditions, responses were slower and less accurate for older adults than for younger adults. Responses for both age groups were, in addition, slowest and least accurate in the conjunction condition. Unlike the accuracy data, however, the age difference in reaction time was relatively constant across the task conditions and did not increase differentially in the conjunction condition. It is likely that in this particular task, the 1-s display duration prevented participants from inspecting all of the relevant items in the conjunction condition, and thus participants responded before obtaining sufficient information for an accurate decision. Under more resource-limited conditions (e.g., displays available until the response), age differences in reaction time typically increase as a function of increasing task complexity (Madden, 2001; McDowd & Shaw, 2000).

As noted previously, accuracy was somewhat lower in the guided condition than it was in the feature condition for the older adults, but accuracy was near ceiling for both age groups in these conditions. The reaction time data revealed that responses were slower in the guided condition than they were in the feature condition by nearly 300 ms. Friedman-Hill and Wolfe (1995) also reported that subset selection requires time. Thus, the opportunity to use selective attention in the guided condition led to improved performance relative to the conjunction condition but did not make the task as easy as the feature search baseline was.

Cortical Volume

Aging is associated with a variety of structural changes in the brain and central nervous system that may contribute to changes in cognitive performance (Raz, 2000; Scheibel, 1996). Age-related decreases in the thickness of the cortical mantle and changes in gyral and sulcal curvature occur in a manner similar to (though less pronounced than) atrophic changes (Magnotta et al., 1999). The age-related decline that we observed for the volume of cortical gray matter (Table 1) has been reported previously by investigators using MR-based volumetric estimates (Raz, Torres, Spencer, & Acker, 1993; Raz et al., 1997). Raz (2000) noted that the age-related decline in cortical volume is approximately 2% per decade, and this estimate fits the present data quite well. The mean height-adjusted volume of cortical gray matter for our younger adults (all in their 20s) was 707 cm³. Starting from this value, a decline of 2% per decade would lead to a volume of 652 cm³ for individuals in their 60s. The volume for the present sample of older adults was 654 cm³. We consequently used the cortical volume data as a covariate in the analyses of rCBF activation, and the age differences that we observed, in both the SPM data and the PET radioactivity counts, were significant independently of the age-related changes in cortical volume. The cortical volume measure that we report is a crude estimate of structural integrity, however, and it is possible that age differences in rCBF are related to changes in cortical volume or structure at a more fine-grained level of analysis.

Regional Cerebral Blood Flow

In the Madden et al. (1997) experiment, the pattern of rCBF activation resembled the performance data, in that age differences were more clearly apparent in the divided attention condition than they were in the selective attention. Relative to a passive viewing baseline, activation associated with the selective attention (central) condition was minimal for both age groups. In the divided attention condition, in contrast, both age groups exhibited activation in the dorsal and ventral visual processing pathways and in prefrontal cortex. Activation in occipital cortex was greater for younger adults than it was for older adults, whereas activation

in prefrontal cortex was relatively greater for the older adults. This pattern was consistent with the findings of Grady et al. (1992,1994), who suggested that the recruitment of prefrontal regions represents a functional compensation for an age-related decline in the initial stages of visual processing.

The present results resemble those of Madden et al. (1997) in that, relative to the feature search baseline, the conjunction search condition was associated with widespread activation in the dorsal and ventral visual processing pathways and in prefrontal cortex for both age groups (Table 2; Figures 4 and 5). These activations correspond to the components of a widely distributed network that mediates spatial attention (Gitelman et al., 1999; Hopfinger et al., 2000; Kim et al., 1999). The higher degree of perceptual difficulty in the conjunction condition (in terms of a higher level of target-distractor similarity and a lower level of similarity among distractors) would increase the number of display items that needed to be inspected before a target present-absent decision could be made. Although individual cortical regions may contribute to multiple attentional functions, it is likely that activation of this network represents specific aspects of search in the conjunction condition. These include shifting attention across the display (occipitoparietal cortex), identifying individual display items (occipitotemporal cortex), programming eye movements (medial prefrontal cortex), and holding the results of individual inspections in memory in preparation for a decision (lateral prefrontal cortex). Within each age group, the activation of posterior cortical regions was bilateral, although there was a rightward asymmetry to the prefrontal activation that has been noted previously (Gitelman et al., 1999; Grady et al., 1996; Kim et al., 1999).

We predicted that the conjunction search condition would be associated with an age-related decline in rCBF activation in the dorsal and ventral processing pathways and an age-related increase in activation in prefrontal cortex, which would represent functional compensation for an age-related decline in the efficiency of visual processing. The test of age differences in the conjunction minus feature subtraction partially supported this prediction. There was clearly an age-related decline in activation in occipital cortex of the right hemisphere. Two local maxima were associated with this age difference, one in the striate cortex (BA 17) and one located more ventrally in the fusiform gyrus (BA 19). The magnitude of activation in prefrontal and superior parietal regions, however, was comparable for the two age groups.

Both the behavioral results and the rCBF activation data demonstrated an age-related decline in perceptual identification processes, but there was no evidence for a compensatory recruitment of neural regions outside the visual processing pathways as we had initially expected. This type of functional compensation is thus not an inherent feature of older adults' cognitive performance. Similarly, the prefrontal activation was located primarily in the right hemisphere for both age groups, and the present results appear to be an exception to the trend of age-related reduction in hemispheric asymmetry (Cabeza, 2002). The types of tasks that were used in previous experiments, such as face matching and discrimination (Grady et al., 1992, 1994, 2000) and visual search with letter displays (Madden et al., 1997), may be more amenable to complex performance strategies (e.g., generating a verbal description of a face as a basis for the discrimination response) than is the search for an upright L among rotated Ls.

The pattern of age differences associated with the conjunction minus guided subtraction was generally consistent with that obtained when feature search was used as a baseline. The interaction contrast demonstrated that rCBF activation in both the striate cortex of the right hemisphere and ventral extrastriate cortex (BA19) bilaterally was greater for younger adults than for older adults. There was no evidence of an age-related increase in activation outside the ventral processing pathway. The results of the contrasts within each age group, however, were somewhat different from those obtained using feature search as a baseline. The conjunction minus guided subtraction yielded significant activation in occipital cortex (BAs

18 and 19) for younger adults but not for older adults. This result suggests that the age difference for the conjunction minus guided contrast was due not entirely to greater activation for younger adults in the conjunction condition, but also to a relatively higher level of activation for the older adults' guided condition.

This interpretation of the age differences in the guided condition is partially supported by the results of the guided minus feature subtraction. This latter contrast, performed within each age group, demonstrated that for younger adults activation was limited to the middle occipital gyrus (BA 19) of the right hemisphere. This finding is similar to that of Sathian et al. (1999), who found that their subitizing condition (counting four or fewer targets in a multielement display), when compared with a single-target baseline, was primarily associated with activation in right extrastriate cortex. The older adults in the present experiment, however, exhibited a different pattern of activation for the guided minus feature contrast, composed of extensive activation throughout the ventral processing pathway, with local maxima in the left striate cortex (BA 17), and cerebellum. The older adults also exhibited activation in the left precentral gyrus (BA 6). The contrast representing age differences in the guided minus feature subtraction, however, was not significant.

The overall results suggest that, in this task, attentional guidance leads to a decrease in level of activation throughout the attentional network, and that this decrease is more pronounced for younger adults than it is for older adults. That is, in terms of the magnitude and extent of activation, the guided condition was similar to the feature condition for the younger adults but was more similar to the conjunction condition for the older adults. It is possible that in this type of task, which relies heavily on the discrimination of the spatial orientation of features, compensation for the decreased level of perceptual functioning (at the cortical level) is expressed by changes in the relative level of activation within the ventral processing pathway rather than by the recruitment of cortical regions outside this pathway.

The analyses of the PET radioactivity counts (Table 4) were also consistent with the idea that activation was relatively higher for older adults. These counts represent the level of activity at a particular voxel, within the task conditions, relative to the whole-brain mean. The five voxels corresponding to the local maxima of significant age differences between task conditions (from the SPM analyses) were all located in either the striate cortex or ventral extrastriate region (fusiform gyrus). For all of these voxels, the task condition effect was greater in magnitude for younger adults than it was for older adults, which was consistent with the SPM results. The analyses of the count data provided additional information by demonstrating that the age differences in the task condition effects represented a higher level of activation for the older adults within the easier task conditions (feature and guided), rather than a higher level of activation for the younger adults within the more difficult (conjunction) condition. Older adults showed strong activations in the ventral processing pathway within the feature and guided conditions as well as within the conjunction condition, whereas younger adults showed low levels of activation in these cortical regions during feature and guided search and increased activation in the conjunction search condition.³ The older adults' increased activation in visual processing regions may represent a signal enhancement as the result of top-down attentional control, mediated by the frontal and parietal regions (Kastner et al., 1999). Network analyses (Nyberg & McIntosh, 2001) of the present data would be particularly informative regarding this possibility.

³This interpretation, however, is tempered by the fact that in the voxel count analyses, the task condition effects were significant only for the younger adults and not for the older adults. This pattern differs from the SPM analyses, in which task-related activation was evident for both age groups.

The analysis of the covariation between rCBF activation and search performance (Table 5) is useful because both age groups' performance changed as a linear function of the perceptual similarity among the display items, and the pairwise subtractions of these task conditions represent the comparison of somewhat arbitrary points along this perceptual continuum. This analysis is also important because rather than simply measuring changes in rCBF between task conditions, which may occur for a variety of reasons, it identifies regional activation that is correlated specifically with participants' performance. The results of the covariance analysis underscore the central findings from the task condition subtractions. As the accuracy of search performance declined (as a function of increasing perceptual similarity among display items), covariation in the ventral processing pathway and prefrontal cortex increased for both age groups. The local maxima within these general regions differed for the two age groups, however, and the interaction contrast indicated that occipital activation in both the left and right hemispheres covaried with search accuracy more consistently for younger adults than it did for older adults. There was, in addition, relatively greater covariation for the younger adults in the right middle frontal gyrus (BA 6). Thus, increasing perceptual difficulty appears to lead to an increased level of activation in a widely distributed attentional network, and this activation covaries more reliably with task performance for younger adults than it does for older adults. There was no evidence in the present task, however, indicating a compensatory age-related increase in this covariation for either prefrontal or other cortical regions.

The decreases in rCBF were located primarily in temporal cortex for both age groups (Table 3). Neuroimaging investigations of visual tasks have frequently reported reductions in the activity of cortical regions that mediate auditory processing (Haxby et al., 1994; Petit et al., 1999; Shulman et al., 1997). The most straightforward interpretation of these decreases is that they represent the suppression of auditory input during visual processing. It is also possible that these decreases result from the withdrawal of attention to auditory input or to some combination of active suppression and attentional withdrawal. Relatively few regions of decreased rCBF were associated with age differences, and the relationship between rCBF change and performance was less prominent for the decreases in rCBF than it was for the increases (Table 5).

In this experiment we observed an age-related decline in activation of occipitotemporal cortex but did not obtain the expected age-related increase in activation outside of this cortical region. This pattern may be related to age differences in the noise level of the hemodynamic signal. Investigations using event-related fMRI to estimate the time course of the hemodynamic response have reported that the noise level of individual voxels increases as a function of age (D'Esposito, Zarahn, Aguirre, & Rypma, 1999; Huettel, Singerman, & McCarthy, 2001), which can influence the measurement of rCBF activation. Specifically, an age-related increase in voxelwise noise can lead to an age-related decline in activation as measured from task condition subtractions. As a result, the measured change in activation might represent an age-related disruption of the coupling between neural activity and the hemodynamic response rather than a decline in neural activity per se. The analyses of the PET radioactivity counts, however, were not consistent with this latter interpretation. At the local maxima of age group differences within occipitotemporal cortex, the level of neural activity within each task condition (relative to the whole-brain mean) was actually greater for older adults than it was for younger adults. An age-related decoupling between neural activity and the hemodynamic response would have led, in contrast, to a decline in the older adults' level of normalized counts.

Conclusions

The performance data demonstrate that the perceptual detectability of the target declines as a function of increasing similarity among display items and that this decline is more pronounced for older adults than it is for younger adults. Both age groups, however, are able to use a spatially

distributed feature-the color of the display items-to guide attention to a relevant subset. At the highest level of task difficulty (conjunction search), rCBF activation is evident in a widely distributed network that includes the dorsal and ventral visual processing pathways and medial and lateral regions of prefrontal cortex. The cortical regions that are activated by this visual search task are similar for younger and older adults. The efficiency of visual identification processes mediated by the ventral processing pathway is lower for older adults than it is for younger adults, as indicated by the age-related decline both in the magnitude of occipitotemporal activation between task conditions and in the relationship between this regional activation and search performance. This decline appears to reflect increased activation for older adults within the easier task conditions rather than increased activation for younger adults within the more difficult conditions.

Attentional guidance, as indexed by participants' use of a subset of display items to improve search performance, is associated with a decrease in activation throughout the attentional network. This decrease is more clearly evident for younger adults than it is for older adults, which may be related to the older adults maintaining a higher level of neural activation within the easier task conditions, perhaps in compensation for the decline in perceptual efficiency. This form of compensation, however, does not involve the recruitment of cortical regions outside the occipitotemporal pathway.

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Figure 1.

Examples of displays presented in the visual search task. The participants' task was to respond *yes* or *no* regarding whether an upright L (the target) was present in a display of rotated Ls (distractors). The figure shows examples of displays in which the target is a black L.

Assignment of the target as either a black L or a white L was varied across subjects. As presented to the participants, the displays contained solid black and white items against a gray background. Each display contained 18 items, distributed in a 5×5 character position grid. In the conjunction search condition, the display items were divided equally between black and white Ls. In the feature search condition, all of the distractors were of the same color, and the target always differed from the distractors in color (i.e., a difference in color specified the presence of a target). In the guided search condition, there were three display items with the target-relevant color for both *yes* and *no* trials. In this latter condition, color defined the subset of three display items that could potentially contain the target.

Figure 2.
Visual search accuracy (hits minus false alarms) as a function of age group and task condition.

Figure 3.
Visual search reaction time for correct responses as a function of age group and task condition.
Hits = *yes* responses; correct rejections = *no* responses.

Figure 4. (opposite). Areas of increased rCBF between task conditions for younger adults. See the legend to Figure 1 for a description of the task conditions. Regions of rCBF increase were identified from the SPM {Z} map, using a threshold for the peak height of voxel change (u) of $Z = 2.33$, $p = .01$ (uncorrected). Regions of rCBF increase ($p < .05$, corrected) are superimposed (blue color scale) on a composite MR image of the 12 younger participants. Images are axial slices between -20 mm and +52 mm on the superior-inferior dimension (in 8-mm steps) with negative values referring to locations inferior to the AC-PC line. Images are presented in standard neurologic orientation (right = right; anterior = top). Regions with significant local maxima are listed with their three-dimensional coordinates in standardized (Talairach & Tournoux,

1988) space and Brodmann's area designations in Table 2. The red color scale represents those voxel clusters for which the local maxima were significantly greater ($p < .05$, corrected) than in the corresponding task condition subtraction for the older adults' data.

Figure 5. (opposite). Areas of increased rCBF between task conditions for older adults. See the legend to Figure 1 for a description of the task conditions and the legend to Figure 4 for a description of image parameters. Regions of rCBF increase ($p < .05$, corrected) are superimposed (blue color scale) on a composite MR image of the 12 older participants. Regions with significant local maxima are listed with their three-dimensional coordinates in standardized (Talairach & Tournoux, 1988) space and Brodmann's area designations in Table 2. None of the local maxima were significantly greater than those obtained in the corresponding task condition subtraction for the young adults' data.

Table 1
Participant Characteristics

Variable	Younger adults		Older adults	
	M	SD	M	SD
Age (years)	23.00 _a	2.13	66.50 _b	4.96
Education (years)	15.42 _a	1.38	15.67 _a	3.28
Vocabulary	62.83 _a	3.56	63.50 _a	5.21
Digit symbol (accuracy)	96.17 _a	3.01	94.75 _a	5.05
Digit symbol (time)	1,144.75 _a	122.57	1,700.08 _b	221.58
Acuity	15.42 _a	1.44	22.50 _b	9.17
MMSE	29.50 _a	1.17	28.60 _a	1.15
Cortical volume (cm ³)	706.75 _a	36.24	654.09 _b	65.60

Note. Each age group contained 7 women and 5 men. Means in the same row that do not share subscripts differ significantly by *t* test at $p < .05$. Vocabulary = raw score on the Vocabulary subtest of the Wechsler Adult Intelligence Scale—Revised (WAIS-R; Wechsler, 1981); Digit symbol = percentage correct and median time per item (in milliseconds) on a computer version of the WAIS-R Digit Symbol Substitution subtest (Salthouse 1992); Acuity = denominator of the Snellen fraction for corrected near vision (binocular); MMSE = Mini-Mental State Exam score (Folstein et al., 1975); Cortical volume = height-adjusted volume of cortical gray matter.

Table 2
Regions of rCBF Increase as a Function of Age Group and Task Condition Subtraction

Region size (k)	$p(Z^{\max} > u)$	Z	x	y	z	BA	Location	
18,846	.0001	Conjunction minus feature, rCBF increase for younger adults						
		7.17	27	-81	11	18	Middle occipital gyrus	
		7.04	-33	-79	-11	19	Fusiform gyrus	
		6.55	-24	-87	4	18	Middle occipital gyrus	
		6.33	25	-87	-5	18	Fusiform gyrus	
		6.28	11	-83	-13	18	Lingual gyrus	
		6.16	-1	-73	-25		Cerebellum	
		6.12	20	-65	40	7	Superior parietal lobule	
		5.71	-20	-71	37	7	Superior parietal lobule	
		5.74	3	18	36	32	Anterior cingulate	
8,259	.0001	5.50	34	-5	49	6	Middle frontal gyrus	
		5.04	34	30	29	9	Middle frontal gyrus	
		4.74	-33	-9	43	6	Precentral gyrus	
		Conjunction minus feature, rCBF increase for older adults						
16,144	.0001	7.18	-4	-69	-25		Cerebellum	
		5.67	-24	-89	4	18	Middle occipital gyrus	
		5.65	-34	-65	-25		Cerebellum	
		5.55	-34	-67	-14	19	Fusiform gyrus	
		5.25	-43	-58	-37		Cerebellum	
		4.97	-24	-62	39	7	Superior parietal lobule	
		4.71	-6	-89	-3	17	Lingual gyrus	
		4.70	27	-89	6	18	Inferior occipital gyrus	
		4.51	-20	-85	-19		Cerebellum	
		5.90	22	-65	42	7	Superior parietal lobule	
2,334	.0001	4.38	32	-52	41	7	Superior parietal lobule	
		5.34	-31	16	4		Insula	
		5.31	41	10	2		Insula	
		5.05	11	-5	61	6	Superior frontal gyrus	
606	.001	4.79	36	47	14	10	Middle frontal gyrus	
		4.72	1	20	31	32	Anterior cingulate	
		4.61	47	1	31	6	Precentral gyrus	
		4.48	38	47	-1	10	Middle frontal gyrus	
451	.003	5.05	-12	-17	8		Thalamus	
		Conjunction minus feature, rCBF increase with younger > older						
		3.84	36	-73	-8		Fusiform gyrus	
		3.48	18	-79	3	17	Striate cortex	
348	.036	Conjunction minus feature, rCBF increase with older > younger						
No significant voxels								
6,122	.001	Conjunction minus guided, rCBF increase for younger adults						
		5.29	36	32	28	9	Middle frontal gyrus	
		5.25	-33	-79	-15	19	Fusiform gyrus	
		4.68	25	-89	2	18	Middle occipital gyrus	
		4.65	-24	-89	2	18	Middle occipital gyrus	
		4.46	-13	-79	-18		Cerebellum	
		4.73	4	20	34	32	Anterior cingulate	
		Conjunction minus guided, rCBF increase for older adults						
		4.65	43	8	4		Insula	
		3.97	18	-83	1	17	Striate cortex	
938	.003	3.22	31	-75	-9	19	Fusiform gyrus	
		3.43	-31	-81	15	19	Fusiform gyrus	
		Conjunction minus guided, rCBF increase with older > younger						
383	.024	Guided minus feature, rCBF increase for younger adults						
No significant voxels								

Region size (<i>k</i>)	$p(Z^{\max} > u)$	Z	x	y	z	BA	Location
1,241	.003	5.01	27	-75	15	19	Middle occipital gyrus
12,198	.0001	5.46	-6	-71	-22		Cerebellum
		4.58	-17	-85	9	17	Striate cortex
		4.48	-34	-63	-26		Cerebellum
		4.48	-22	-87	18	19	Superior occipital gyrus
		4.46	34	-75	-22		Cerebellum
1,874	.040	4.41	-31	-83	-17	18	Fusiform gyrus
		4.43	-36	-5	38	6	Precentral gyrus
		Guided minus feature, rCBF increase with younger > older					
No significant voxels		Guided minus feature, rCBF increase with older > younger					
No significant voxels							

Note. See the Method section for a description of task conditions. Probability levels of less than .0001 have been rounded to .0001. Region size (*k*) = number of voxels; *Z* = *t* value of local maximum of activation scaled to a unit normal distribution; $p(Z^{\max} > u)$ = probability that the observed peak height of local maximum of activation is greater than would be expected by chance; *x*, *y*, *z* = coordinates (in mm) in the standard stereotaxic space of Talairach and Tournoux (1988); *x* = right-left hemisphere, negative indicates left hemisphere; *y* = anterior-posterior coordinate, negative indicates posterior to the zero point (anterior commissure); *z* = superior-inferior coordinate, negative indicates inferior to the AC-PC line; BA = Brodmann's area.

Table 3
Regions of rCBF Decrease as a Function of Age Group and Task Condition Subtraction

Region size (k)	$p(Z^{\max} > u)$	Z	x	y	z	BA	Location
7,412 3,237	.022	Conjunction minus feature, rCBF decrease for younger adults					
	.036	4.55	-41	-13	-6		Insula
		4.44	-6	45	-3	32	Anterior cingulate
22,055	.0001	Conjunction minus feature, rCBF decrease for older adults					
	.0001	5.68	48	-48	1	22	Middle temporal gyrus
	.001	5.55	22	-7	-20		Amygdala
	.001	5.35	-4	30	-2	32	Anterior cingulate
	.001	5.34	48	-65	10	37	Middle temporal gyrus
	.001	5.17	36	-11	-24	20	Fusiform gyrus
	.020	4.58	-1	10	-3	25	Anterior cingulate
	.043	4.39	-38	6	-19	38	Superior temporal gyrus
	.048	4.36	52	-5	-11	21	Middle temporal gyrus
	.028	4.50	1	-56	32	31	Anterior cingulate
Conjunction minus feature, rCBF decrease with younger > older							
No significant voxels		Conjunction minus feature, rCBF decrease with older > younger					
		3.76	47	-48	-8	21	Middle temporal gyrus
	.008	Conjunction minus guided, rCBF decrease for younger adults					
		4.50	-45	-69	21	39	Middle temporal gyrus
	.027	4.48	-43	-15	-6		Insula
	.030	4.39	-4	47	6	10	Medial frontal gyrus
	.042	4.36	-20	41	35	9	Superior frontal gyrus
Conjunction minus guided, rCBF decrease for older adults							
No significant voxels		Conjunction minus guided, rCBF decrease with younger > older					
		Conjunction minus guided, rCBF decrease with older > younger					
		Guided minus feature, rCBF decrease for younger adults					
No significant voxels		Guided minus feature, rCBF decrease for older adults					
	.006	4.86	55	-44	1	21	Middle temporal gyrus
	.037	4.43	52	-63	14	21	Middle temporal gyrus
No significant voxels		Guided minus feature, rCBF decrease with younger > older					
		Guided minus feature, rCBF decrease with older > younger					
	.030	3.08	-4	30	-4	32	Anterior cingulate
	.036	3.03	3	8	-5	25	Anterior cingulate
	.049	2.93	45	-69	16	39	Middle temporal gyrus

Note. See the Method section for a description of task conditions. Probability levels of less than .0001 have been rounded to .0001. Region size (k) = number of voxels; Z = t value of local maximum of activation scaled to a unit normal distribution; $p(Z^{\max} > u)$ = probability that the observed peak height of local maximum of activation is greater than would be expected by chance; x, y, z = coordinates (in mm) in the standard stereotaxic space of Talairach and Tournoux (1988); x = right-left hemisphere, negative indicates left hemisphere; y = anterior-posterior coordinate, negative indicates posterior to the zero point (anterior commissure); z = superior-inferior coordinate, negative indicates inferior to the AC-PC line; BA = Brodmann's area.

Table 4
Normalized PET Counts of Local Maxima, as a Function of Age Group and Task Condition

	Younger adults		Older adults	
	M	SD	M	SD
Conjunction minus feature				
Right fusiform gyrus ($x = 36, y = -73, z = -8$; BA 19)				
Conjunction	1.093	0.053	1.122	0.047
Feature	1.074	0.052	1.124	0.045
Right striate cortex ($x = 18, y = -79, z = 3$; BA 17)				
Conjunction	0.948	0.055	1.027	0.050
Feature	0.930	0.054	1.024	0.043
Conjunction minus guided				
Right striate cortex ($x = 18, y = -83, z = 1$; BA 17)				
Conjunction	0.968	0.056	1.036	0.049
Guided	0.952	0.053	1.042	0.054
Right fusiform gyrus ($x = 31, y = -75, z = -9$; BA 19)				
Conjunction	1.055	0.055	1.104	0.052
Guided	1.039	0.048	1.108	0.055
Left fusiform gyrus ($x = -31, y = -81, z = -15$; BA 19)				
Conjunction	1.115	0.049	1.187	0.066
Guided	1.084	0.039	1.181	0.071

Note. Values are the PET radioactivity counts (tissue concentration of $H_2^{15}O$) for the local maximum, relative to the mean gray matter count value within each task condition. For each task condition subtraction, the local maxima refer to the voxels exhibiting significant age-related change in the SPM analysis. Voxels are the local maxima of significant age difference in rCBF increase between task conditions (Table 2); x, y, z = coordinates (in mm) in the standard stereotaxic space of Talairach and Tournoux (1988); x = right-left hemisphere, negative indicates left hemisphere; y = anterior-posterior coordinate, negative indicates posterior to the zero point (anterior commissure); z = superior-inferior coordinate, negative indicates inferior to the AC-PC line; BA = Brodmann's area.

Table 5

Regions of Covariation Between rCBF Change and Search Performance (1 minus Corrected Recognition) Across All Task Conditions as a Function of Age Group

Region size (<i>k</i>)	$p(Z^{\max} > u)$	Z	x	y	z	BA	Location
15,335	.0001	5.65	rCBF increase for younger adults				
	.0001	5.43	25	-85	8	18	Middle occipital gyrus
3,022	.001	5.34	-34	-77	-11	19	Fusiform gyrus
	.001	5.34	32	-3	49	6	Middle frontal gyrus
	.019	4.59	4	16	38	32	Anterior cingulate
8,308	.0001	5.49	rCBF increase for older adults				
	.004	4.96	-3	-69	-27		Cerebellum
	.012	4.71	-41	-56	-38		Cerebellum
4,485	.009	4.76	41	10	2	17	Striate cortex
745	.036	4.43	-31	14	0		Insula
378	.038	4.42	-10	-19	8		Insula
			rCBF increase with younger > older				
2,846	.001	4.21	34	-75	-6	19	Fusiform gyrus
	.002	4.08	22	-83	6	17	Striate cortex
	.004	3.92	45	-50	-12	37	Fusiform gyrus
647	.009	3.78	-33	-79	-11	19	Fusiform gyrus
323	.046	3.34	34	-5	49	6	Middle frontal gyrus
179	.047	3.34	22	-60	23	31	Precuneus
No significant voxels							
3,681	.030	4.48	rCBF decrease for younger adults				
			-4	45	-1	10	Medial frontal gyrus
18,467	.005	4.88	rCBF decrease for older adults				
	.017	4.62	18	-7	-16		Amygdala
	.021	4.57	45	-48	3	21	Middle temporal gyrus
			27	-11	-22	36	Parahippocampal gyrus
146	.026	3.43	rCBF decrease with younger > older				
			62	-23	-8	21	Middle temporal gyrus
No significant voxels							

Note. See the Method section for a description of task conditions. Probability levels of less than .0001 have been rounded to .0001. Region size (*k*) = number of voxels; *Z* = *t* value of local maximum of activation scaled to a unit normal distribution; $p(Z^{\max} > u)$ = probability that the observed peak height of local maximum of activation is greater than would be expected by chance; *x*, *y*, *z* = coordinates (in mm) in the standard stereotaxic space of Talairach and Tournoux (1988); *x* = right-left hemisphere, negative indicates left hemisphere; *y* = anterior-posterior coordinate, negative indicates posterior to the zero point (anterior commissure); *z* = superior-inferior coordinate, negative indicates inferior to the AC-PC line; BA = Brodmann's area.