Neural Basis for Verb Processing in Alzheimer’s Disease: An fMRI Study

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Patients with probable Alzheimer’s disease (AD) have difficulty understanding verbs. To investigate the neural basis for this deficit, the authors used functional magnetic resonance imaging to examine patterns of neural activation during verb processing in 11 AD patients compared with 16 healthy seniors. Subjects judged the pleasantness of verbs, including MOTION verbs and COGNITION verbs. Healthy seniors and AD patients both activated posterolateral temporal and inferior frontal regions during judgments of verbs. These activations were relatively reduced and somewhat changed in their anatomic distribution in AD patients compared with healthy seniors, particularly for the subcategory of MOTION verbs, but AD patients showed minimal activation in association with COGNITION verbs. These findings imply that poor performance with verbs in AD is due in part to altered activation of the large-scale neural network that supports verb processing.

Patients with probable Alzheimer’s disease (AD) are thought to have difficulty understanding single words (Chertkow & Bub, 1990; Cox, Bayles, & Trosset, 1996; Grossman et al., 1996; Hodges, Patterson, Graham, & Dawson, 1996; Martin, 1992). Although this deficit has been the subject of considerable investigation for nouns, the impairment for verbs in AD is less well understood. In this study, we investigated the neural basis for verb comprehension difficulty in AD with blood oxygen level-dependent (BOLD) functional magnetic resonance imaging (fMRI).

Patients with AD appear to have greater difficulty with verbs than with nouns (Buschell & Martin, 2002; Cappa et al., 1998; K. M. Robinson, Grossman, White-Devine, & D’Esposito, 1996; van der Lem et al., 2002; White-Devine et al., 1996). Although exceptional cases have been described (Parris & Weekes, 2001; G. Robinson, Rossor, & Cipolotti, 1999), and a recent study involving many axial verbs (Fung et al., 2001) failed to confirm earlier observations, the verb impairment in AD has been shown with several different techniques, including confrontation naming, word–picture and word–video matching, and word–definition matching. The basis for relative difficulty with verbs in AD is unclear. Some have associated verb deficits with the loss of sensory–motor feature knowledge, and particularly with degraded motor–function features of a verb (Bird, Howard, & Franklin, 2000; Johnson & Hermann, 1995; Parris & Weekes, 2001). However, verb-naming difficulty does not appear to correlate with visual perceptual performance in AD (K. M. Robinson et al., 1996). Moreover, we have observed greater difficulty in AD patients’ comprehension of COGNITION (we use capitals to indicate a concept) verbs that are not dependent on sensory–motor features compared to MOTION verbs (van der Lem et al., 2002). Verbs are relatively rich in their grammatical features, and another possibility is that a grammatical deficit contributes to impaired verb comprehension. However, verb naming difficulty does not appear to correlate with grammatical comprehension in AD (K. M. Robinson et al., 1996). In the acquisition of a new verb, moreover, AD patients were able to learn about some of the grammatical properties of the new word (e.g., that it is subcategorized grammatically as a verb), even though they were quite limited in their ability to acquire the new verb’s meaning or its thematic relations (e.g., who does what to whom; Grossman, Mickanin, Onishi, Robinson, & D’Esposito, 1997). Another hypothesis holds that verbs are more difficult than nouns because verbs generally contain more information (e.g., meaning, grammatical restrictions, thematic relations) that must be coordinated for their proper usage. According to this approach, verb comprehension requires executive resources that are known to be limited in AD (Baddeley, Bressi, Della Sella, Logie, & Spinmler, 1991; LaFleche & Albert, 1995; Patterson, Mack, Geldmacher, & Whitehouse, 1996). However, an unpublished word–picture matching study of AD patients performed during concurrent administration of a secondary task in our lab failed to support this hypothesis.

In the present study, we gained additional information about the status of verb meaning in AD from a different
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Thus may have been due to their semantic deficit, or to relative task performance difficulty in AD patients compared with healthy control subjects. To minimize this confound, a recent study investigated comprehension of noun categories with a “pleasantness” judgment task that was performed equally well by AD patients and healthy seniors (Grossman et al., 2003). This study showed limited left temporal–parietal activation in AD patients, relative to healthy seniors, for both ANIMAL and IMPLEMENT categories of knowledge. This brain region contains heteromodal association cortex, where the connectivity pattern involves reciprocal projections with modality-specific association cortices. Because this change was seen for both categories of knowledge, we hypothesized that this area supports a category-neutral process important for processing the meanings of words. We also observed a change in the anatomic distribution of activation in other regions of the left hemisphere in AD that contain modality-specific association cortex and are associated with a specific category of knowledge. For example, left ventral temporal–occipital activation associated with ANIMALS in healthy seniors was evident about 20 mm anteriorly in AD patients. We also observed up-regulation of right hemisphere regions, particularly for IMPLEMENTS. These findings are consistent with a dual-component model of semantic memory involving both category-specific feature knowledge and category-neutral processes that integrate these features in semantic memory for the purpose of developing meaning representations useful for semantic categorization (Grossman et al., 2003).

In the present study, we investigated the integrity of left hemisphere regions during AD patients’ verb comprehension. On the basis of changes in recruitment patterns for nouns in AD patients relative to healthy seniors, we hypothesized that verb comprehension in AD would be associated with limited activation of heteromodal temporal and frontal regions in the left hemisphere that have been related to verb comprehension in healthy young adults. We also expected to observe changes in the activation of modality-specific brain regions in AD patients that are not activated in healthy seniors. If these novel areas of activation are related in part to compensatory up-regulation that helps AD patients achieve partial comprehension of verbs, we would expect to see less activation of novel regions for COGNITION verbs than for MOTION verbs, reflecting AD patients’ relative accuracy within this domain of verb knowledge.

**Method**

**Subjects**

We studied 16 healthy, right-handed seniors and 11 patients with mild-to-moderate dementia diagnosed as probable AD by a board-certified neurologist, according to National Institute for Neurological and Communicative Disorders and Stroke–Alzheimer’s Disease and Related Disorders Association criteria (McKhan et al., 1984). Other neurologic, psychiatric, and medical conditions that can interfere with cognitive performance were ruled out in the AD patients and healthy seniors. None of the subjects were taking medications with sedating properties that can
imperior cognition or that can change blood flow, but the AD patients were taking a medically acceptable dose of an acetylcholinesterase inhibitor. The control subjects were screened with a semistructured medical history interview to ensure their physical and mental health and to eliminate subjects taking centrally acting medications. Mini-Mental State Examination scores were greater than 27. Structural images were inspected for disease. The demographic features of the AD patients and the age- and education-matched healthy seniors are summarized in Table 1. These subjects and their legal representatives participated in an informed consent procedure approved by the Institutional Review Board at the University of Pennsylvania.

Materials

We presented blocks of printed words to subjects that included citation forms of two categories of verbs: MOTION verbs (e.g., CRAWL, WRITE) and COGNITION verbs (e.g., BELIEVE, ENJOY). This was done to avoid unwarranted generalizations about all verbs that may be relevant only for one subcategory of verbs. The words were either unambiguously verbs, or if not, a word’s frequency of occurrence as a verb was at least 5 times its frequency of occurrence as a noun, according to class-sensitive frequency measures (Francis & Kucera, 1982). The categories of verbs were matched for mean frequency (Francis & Kucera, 1982): cognition = 16.1; motion = 13.8, t(118) = 0.83, ns. A cohort of 42 native English-speaking undergraduates assessed the words for familiarity: The meanings of all the words were known to all students, and all but 11 of the 120 words were judged to be highly familiar by over 90% of these students (1 MOTION verb was judged familiar by only 90% of students, 5 COGNITION verbs and 2 MOTION verbs were judged familiar by only 86% of students, and 3 COGNITION verbs were judged familiar by only 83% of students).

Subjects were asked to judge the “pleasantness” of each stimulus. We chose this single probe for all words to avoid explicit categorization of verb subcategories, in which the content of the word category can influence the nature of the categorization process and thus confound the interpretation of the results. This also allowed us to minimize contaminating the content associated with category-specific activations by avoiding foils (stimuli that are not members of a target category and to which subjects would have responded “no” in something like a category membership judgment task). Pleasantness decisions of this sort have been used for over 30 years to probe deep or semantic knowledge (Warrington & Weiskrantz, 1968). Moreover, pilot testing indicated that this task can be performed easily by AD patients, thus minimizing interpretive confounds associated with impaired task performance (Price & Friston, 1999). Each printed stimulus word was available for 3 s, followed by a 1-s interstimulus interval, and each 10-word block lasted 40 s. Subjects indicated their judgment of each word as pleasant or not by depressing one of two buttons (the “pleasant” button with the right thumb or the “not pleasant” button with the left), and response and latency were recorded by the computer presenting the stimuli. A technical error prevented us from collecting pleasantness judgments and latency data in 1 healthy senior. Words were presented continuously, and blocks were presented in a random fixed order without a break between blocks of different categories. Subjects were not informed that different categories of words were being administered.

Each run included two blocks of each category of verb (four blocks of verbs in total). Each run also included six blocks of filler words (nouns), and three baseline blocks (including two blocks of pronounceable pseudoword stimuli and one block of pseudofont stimuli) interspersed among the blocks of verb stimuli. Subjects also made pleasantness judgments of these stimuli. We chose to use the pseudoword stimuli as a sensory–motor control because the semantically neutral character of these graphemic sequences allowed us to avoid the interpretive confounds associated with verb activations relative to a baseline containing meaningful material. Many studies have shown that nouns are associated with different distributions of activation depending on the specific content of these words (Farah & Aguirre, 1999; Joseph, 2001), and our use of a baseline containing meaningful nouns would have potentially changed the pattern of activation in a manner that is not related to verb meaning. We were particularly sensitive to this issue in the present study because of the possibility of different profiles of noun comprehension difficulty in AD that may vary depending, in part, on the specific semantic content of the words. We chose to use pronounceable pseudowords rather than pseudofont stimuli because we wanted to control in part for the phonemic and graphemic properties of words. Between-group comparisons were made relative to the pseudoword baseline rather than with direct contrasts of verb stimuli because the pseudoword baseline also allowed us to control in part for potential differences in reading processes known to be present in some AD patients compared with healthy seniors (Glosser et al., 2002; Noble, Glosser, & Grossman, 2000). Three runs containing nonrepeated stimuli were presented in total. Before each run, longitudinal magnetization was allowed to attain equilibrium while subjects were acclimated to the MRI environment during a 20-s period of viewing the words Get Ready on the screen. Images corresponding to this period were discarded. Brief rest periods (about 1 min) were included between runs.

Our stimulus presentation system (Epson 5000 LCD projector), compatible with high magnetic fields, back-projected the printed words onto a screen at the magnet bore. The subject viewed the screen through a system of mirrors. A portable computer (Macintosh 1400C or G3) outside the magnet room used PsyScope presentation software (Cohen, MacWhinney, Flatt, & Provost, 1993) to present stimuli and record response accuracy and latency. Subjects were familiarized with the task prior to entering the magnet bore, and the task was practiced by each subject.

Table 1
Mean (± SD) Demographic Characteristics of Alzheimer’s Patients and Healthy Seniors

<table>
<thead>
<tr>
<th>Measure</th>
<th>Healthy seniors</th>
<th>Alzheimer’s patients</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age (years)</td>
<td>73.9 (3.6)</td>
<td>73.0 (4.9)</td>
</tr>
<tr>
<td>Education (years)</td>
<td>13.8 (1.8)</td>
<td>15.3 (2.9)</td>
</tr>
<tr>
<td>MMSE (maximum = 30)</td>
<td>29.7 (0.7)</td>
<td>20.2 (6.1)</td>
</tr>
<tr>
<td>Gender (male/female)</td>
<td>9/7</td>
<td>8/3</td>
</tr>
<tr>
<td>Verb comprehensiona</td>
<td>95.0 (2.8)</td>
<td>77.3 (15.0)</td>
</tr>
<tr>
<td>MOTION verbs</td>
<td>97.3 (2.9)</td>
<td>80.0 (15.1)</td>
</tr>
<tr>
<td>COGNITION verbs</td>
<td>92.8 (4.8)</td>
<td>74.5 (15.1)</td>
</tr>
</tbody>
</table>

Note. MMSE = Mini-Mental State Examination.

a Verb comprehension was assessed with an 80-item multiple-choice paradigm requiring subjects to match one of four verbs with a brief video clip or a verbal description of an action. Half of the stimuli were MOTION verbs, and half were COGNITION verbs. Performance on this protocol was available in 5 of the Alzheimer’s disease patients participating in this study, and this was compared with a group of 10 healthy, age- and education-matched seniors.

Imaging Data Acquisition and Statistical Analysis

The experiment was performed at 1.5 T on an Echospeed scanner (General Electric, Milwaukee, WI) capable of ultrafast
imaging. We used a standard clinical quadrature radiofrequency head coil. Firm foam padding was used to restrict head motion. Each imaging protocol began with a 10–15-min acquisition of 5-mm thick adjacent slices for determining regional anatomy, including sagittal localizer images (TR = 500 ms, TE = 10 ms, 192 × 256 matrix), T2-weighted axial images (FSE, TR = 2,000 ms, TEFf = 85 ms), and T1-weighted axial images of slices used for fMRI anatomic localization (TR = 600 ms, TE = 14 ms, 192 × 256 matrix). Gradient echo echoplanar images were acquired for detection of alterations of blood oxygenation accompanying increased mental activity. All images were acquired with fat saturation, a rectangular FOV of 20 × 15 cm, flip angle of 90°, 5 mm slice thickness, an effective TE of 50 ms, and a 64 × 40 matrix, resulting in a voxel size of 3.75 mm × 3.75 mm × 5 mm. The echoplanar acquisitions consisted of 18 contiguous slices in a transaxial plane covering most of the brain every 2 s. A separate acquisition lasting 1–2 min was needed for phase maps to minimize distortion in echoplanar images (Alsop, 1995). Raw data were stored by the MRI computer on digital audio tape and then processed offline.

Initial data processing was performed with Interactive Data Language (Research Systems) on a Sun Ultra 60 workstation. Raw image data were reconstructed with a two-dimensional fast Fourier transformation with a distortion correction to minimize artifact caused by magnetic field inhomogeneities. Individual subject data were then prepared for a fixed-effects analysis and analyzed statistically by means of statistical parametric mapping (SPM) developed by Wellcome Department of Cognitive Neurology (Frackowiak, Friston, Frith, Dolan, & Mazziotta, 1997). The SPM99 system, operating on a MatLab (MathWorks, 1998; Version 5.2) platform, combines raw difference images from individual subjects into a statistical t map. In brief, the images in each subject’s time series were registered to the initial image in the series. The images were then aligned to a standard coordinate system (Talairach & Tournoux, 1988) through the use of the Montreal Neurologic Institute template (Evans et al., 1993). The data were spatially smoothed with a 12-mm Gaussian kernel to account for small variations in the location of activation and subtle interindividual differences in gyral anatomy across subjects, and low-pass temporal filtering was implemented to control autocorrelation with a first-order autoregressive method. Global means were normalized by proportional scaling. The data were analyzed parametrically with t-test comparisons converted to z scores for each compared voxel. We compared verb–pseudoword contrasts within groups and then between groups with a Group x Task interaction using these conditions. To test our hypotheses about relative activation in healthy seniors and AD patients, we accepted a statistical threshold of p < .001 uncorrected for multiple comparisons. Clusters were larger than 18 adjacent voxels.

Results

Behavioral Observations

As summarized in Table 1, a subset of 5 AD patients had difficulty on a multiple-choice verb comprehension procedure relative to healthy seniors, t(13) = 3.75, p < .002. These AD patients also had relative difficulty with COGNITION verbs compared with their own performance with MOTION verbs, t(4) = 3.77, p < .02.

Pleasantness judgments and response latencies during imaging are summarized in Table 2. As can be seen, healthy seniors and AD patients did not differ in their pleasantness judgments of VERBS. This was true for MOTION verbs, $t(24) = 1.42, \text{ ns}$, and COGNITION verbs, $t(24) = 1.05, \text{ ns}$. However, control subjects, $t(14) = 3.24, p < .01$, found MOTION verbs to be less pleasant on average than COGNITION verbs, whereas AD patients, $t(10) = 3.19, p < .01$, found COGNITION verbs to be less pleasant on average than MOTION verbs. The AD patients were marginally slower than the healthy seniors to respond to VERBS. This was true for MOTION verbs, $t(24) = 2.21, p = .04$, and COGNITION verbs, $t(24) = 1.97, p = .06$. Both control subjects, $t(14) = 1.54, \text{ ns}$, and AD patients, $t(10) = 2.11, p = .06$, were a little slower to respond to MOTION verbs than to COGNITION verbs. Pseudowords were judged less pleasant than real words (controls: 31 ± 35, AD patients: 17 ± 19) to an equal extent in both groups, $t(25) = 1.29, \text{ ns}$, and these judgments did not differ in latency across groups (controls: 1,443 ± 312 ms; AD patients: 1,388 ± 483 ms) to an equal extent in both groups, $t(25) = 0.36, \text{ ns}$.

Imaging Observations

Table 3 summarizes the coordinates of the peak loci and the Brodmann areas associated with activation in healthy subjects and AD patients for verb categories compared with the pseudoword baseline. The activated clusters for healthy seniors are illustrated in Figure 1. Figure 1A shows that judgments of VERBS minus the pseudoword baseline recruited left posterolateral temporal–parietal, right inferior frontal–anterior temporal–insula, and bilateral cingulate–striatal regions in healthy seniors. We also observed right anteromedial prefrontal activation. Figure 1B shows that MOTION verbs activated left posterolateral temporal–parietal cortex. Figure 1C shows that COGNITION verbs recruited left posterolateral temporal–parietal cortex, right inferior frontal–anterior temporal–insula regions, and bilateral anteromedial prefrontal cortex. Direct contrasts of motion verb and cognition verb categories are also provided in Table 3. These are discussed in another report examining healthy seniors relative to younger adults.

In AD patients, as summarized in Table 3 and shown in Figure 2A, judgments of VERBS minus the pseudoword baseline revealed activation of left posterolateral temporal
cortex. Figure 2B shows that MOTION verbs recruited the left striatum. For COGNITION verbs minus the pseudoword baseline, Figure 2C shows that right anteromedial prefrontal cortex was activated in AD patients. Table 3 also shows that the subtraction of MOTION verbs minus COGNITION verbs demonstrated differential activation of striatum and anterior temporal cortex. There were no areas showing significantly greater activation for COGNITION verbs than MOTION verbs in AD patients.

We directly contrasted activation associated with each verb category in AD patients and healthy seniors. Table 4 summarizes the coordinates of the peak loci and the Brodmann areas associated with these activation contrasts in healthy subjects and AD patients for verb categories compared with the pseudoword baseline. The clusters where AD patients have less activation than healthy seniors are illustrated in Figure 3. Figure 3A shows that, during judgments of VERBS minus pseudowords, AD patients had less activation than healthy seniors in the sulcal depths of left posterolateral temporal–parietal cortex, right medial and lateral temporal regions, left inferior frontal cortex, and right striatum. By comparison, Figure 4 shows areas where AD patients have greater activation than healthy seniors. Figure 4A shows that AD patients had greater activation than healthy seniors in left lateral mid-temporal cortex for VERBS, implying a change in the anatomic distribution of temporal activation in AD patients inferiorly, anteriorly, and superficially in comparison to healthy seniors for the same materials.

We also examined direct contrasts of activation patterns in healthy seniors and AD patients for each category of verbs. Figure 3B shows that, during judgments of MOTION verbs minus pseudowords, AD patients had less activation of right temporal cortex than healthy seniors. By comparison, Figure 4B shows that AD patients had greater activation than healthy seniors in the left striatum and left inferior frontal cortex during motion verb judgments. For COGNITION verbs, Figure 3C shows that AD patients had significantly less activation of the right striatum and the left striatum–cingulate region than healthy seniors. However, there were no areas where AD patients had greater activation than healthy seniors for COGNITION verbs.

**Discussion**

Patients with AD appear to have difficulty with verbs on several kinds of behavioral tasks such as naming and word–picture matching (Bushell & Martin, 2002; Cappa et al., 1998; K. M. Robinson et al., 1996; van der Lem et al., 2002; White-Devine et al., 1996), although this is not a universal finding (Fung et al., 2001; Parris & Weekes, 2001; G. Robinson et al., 1999). In the present study, we demonstrated differences in brain activation patterns for verbs in AD patients compared with age-matched healthy seniors. Healthy seniors activated several brain regions for verbs that are also recruited in studies of young healthy subjects (Damasio et al., 2001; Grabowski et al., 1998; Grossman et al., 2002b; Perani et al., 1999). However, AD patients appeared to recruit only a portion of the activations seen in healthy seniors. Direct comparisons showed that some activations in AD patients are less robust statistically than the activations seen in healthy seniors, whereas other activa-
tions in AD patients appear to be in an anatomic distribution that is relatively unactivated in healthy seniors. Moreover, these changes appeared to depend in part on the specific verb subcategory being probed: Increased activation in AD patients relative to healthy seniors was seen for MOTION verbs, but not COGNITION verbs. We discuss the activation profile associated with verb processing and with each verb subcategory below. By way of anticipation, we argue that reduced verb comprehension in AD patients is related in part to their limited neural activation of brain regions critical to understanding verb meaning. We also speculate that areas of increased activation in AD patients relative to healthy seniors represent compensatory changes in the face

Figure 1. Activation of verb categories compared with a pronounceable pseudoword baseline in healthy seniors. A: VERBS minus baseline. B: MOTION verbs minus baseline. C: COGNITION verbs minus baseline.

Figure 2. Activation of verb categories compared with a pronounceable pseudoword baseline in Alzheimer’s disease patients. A: VERBS minus baseline. B: MOTION verbs minus baseline. C: COGNITION verbs minus baseline.
of a neurodegenerative disease that allow these patients to achieve partial comprehension of MOTION verbs.

**Activation Patterns Associated With Verbs in Healthy Seniors**

Healthy seniors activated left posterolateral temporal cortex during presentation of VERBS in comparison with a pronounceable pseudoword baseline. This distribution of activation has been seen in previous functional neuroimaging work with a variety of tasks involving verbs in healthy young subjects. For example, these reports described posterolateral temporal activation in investigations of verb generation (Fiez, Raichle, Balota, Tallal, & Petersen, 1996), probes of action knowledge associated with object words and pictures (Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995), and lexicality decisions about printed verbs (Perani et al., 1999). The precise locus of activation was not identical across these studies; this difference was probably related to multiple sources of differences involving the tasks and the imaging techniques. Nevertheless, left posterolateral temporal cortex has been implicated in lexical–semantic processing based on structural imaging studies of patients with insult to this region (Chertkow, Bub, Deaudon, & Whitehead, 1997; Hart & Gordon, 1990; Hillis et al., 2001), correlations of performance on semantic tasks with functional neuroimaging studies obtained at rest in AD patients who have impaired lexical comprehension (Desgranges et al., 1998; Grossman, White-Devine, et al., 1997), and positron emission tomography and fMRI activation studies in which healthy subjects were challenged to understand the meaning of a noun (Grossman et al., 2002a; Martin, Wiggs, Ungerleider, & Haxby, 1996; Price, Moore, Humphreys, & Wise, 1997; Warburton et al., 1996; Whatmough, Chertkow, Murtha, & Hanratty, 2002). We too observed recruitment of left posterolateral temporal–parietal cortex for VERBS in the present study, extending this basic finding to a population of healthy senior subjects.

One account attributes this distribution of activation to the visual motion thought to be an important component of the knowledge associated with VERBS. Indirect evidence consistent with this explanation comes from other fMRI work that associates this posterolateral temporal distribution of activation with visual motion that is thought to be a critical feature of IMPLEMENT knowledge (Bonda et al., 1996; de Jong et al., 1994; Kourtzi & Kanwisher, 2000; Patzwahl et al., 1996; Puce et al., 1998). However, recent observations have begun to cast doubt on this sensory–motor feature approach to interpreting the activation patterns associated with word meaning (Farah & Aguirre, 1999; Grossman et al., 2002a; Joseph, 2001; Kellenbach et al., 2001; Noppeney & Price, 2002). With respect to VERBS, it is noteworthy that most studies in fact have used motion verb stimuli. Cognition verbs are generally impoverished in their sensory–motor features, yet studies involving this verb subcategory also reported activation of the posterolateral temporal area of the left hemisphere (Grossman et al., 2002b; Perani et al., 1999). Tyler and her coworkers (Tyler, Russell, Fadili, & Moss, 2001) reported posterolateral temporal activation for nouns and verbs, regardless of whether they were high imageability or concrete on the one hand, or low imageability or abstract on the other hand, in both lexical decision and semantic categorization tasks. Left posterolateral temporal cortex thus appears to be associated with the comprehension of VERBS, but this is unlikely to be due entirely to the sensory–motor features associated with this class of words, as COGNITION verbs activating this area are quite impoverished in sensory–motor features such as visual motion. In the present study, we confirmed the left posterolateral temporal–parietal distribution of activation for both MOTION verbs and COGNI-

### Table 4

**Locus and Extent of Peak Activations for Direct Contrasts of Healthy Seniors and Alzheimer’s Patients During Pleasantness Judgments of MOTION Verbs and COGNITION Verbs in Comparison With a Pronounceable Pseudoword Baseline**

<table>
<thead>
<tr>
<th>Contrast</th>
<th>Activation locus (Brodmann area)</th>
<th>Coordinates</th>
<th>Activation extent (no. of voxels)</th>
<th>z</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alzheimer’s patients with less activation than healthy seniors</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>VERBS</td>
<td>Left posterolateral temporal-parietal (22)</td>
<td>–28</td>
<td>–56</td>
<td>16</td>
<td>114</td>
</tr>
<tr>
<td></td>
<td>Left inferior frontal (45)</td>
<td>–32</td>
<td>32</td>
<td>16</td>
<td>97</td>
</tr>
<tr>
<td></td>
<td>Right temporal (21)</td>
<td>40</td>
<td>–40</td>
<td>0</td>
<td>843*</td>
</tr>
<tr>
<td></td>
<td>Right striatum</td>
<td>28</td>
<td>16</td>
<td>4</td>
<td>843*</td>
</tr>
<tr>
<td>MOTION</td>
<td>Right midlateral temporal (22)</td>
<td>36</td>
<td>–36</td>
<td>8</td>
<td>71</td>
</tr>
<tr>
<td>COGNITION</td>
<td>Left cingulate-striatum (24)</td>
<td>–28</td>
<td>–12</td>
<td>24</td>
<td>229</td>
</tr>
<tr>
<td></td>
<td>Right striatum</td>
<td>28</td>
<td>12</td>
<td>0</td>
<td>75</td>
</tr>
<tr>
<td>Alzheimer’s patients with greater activation than healthy seniors</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>VERBS</td>
<td>Left lateral midtemporal (21)</td>
<td>–40</td>
<td>–28</td>
<td>–8</td>
<td>58</td>
</tr>
<tr>
<td>MOTION</td>
<td>Left inferior frontal-striatum (45)</td>
<td>–20</td>
<td>–12</td>
<td>4</td>
<td>74</td>
</tr>
</tbody>
</table>

* The peaks of these regions were part of the same, larger cluster.
TION verbs in healthy seniors. This neuroanatomic recruitment profile for COGNITION verbs parallels activation associated with abstract nouns in healthy subjects (Beauregard et al., 1997; Grossman et al., 2002a; Kiehl et al., 1999; Perani et al., 1999). An alternate possibility is that the left posterolateral temporal region helps integrate the complex network of associative knowledge that underlies the meaning of words, including abstract words that are impoverished in sensory–motor features. Some evidence to support this alternate account comes from recent work examining the anatomic distribution of activation associated with the categorization process that is critical to understanding word meaning. These studies demonstrated left posterolateral temporal activation during the processes involved in semantic categorization of object descriptions and acquiring the meaning of a new semantic category (Grossman, Smith, et al., 2002; Koenig, Smith, DeVita, et al., 2002). Additional work is needed to determine the specific role that left posterolateral temporal cortex plays in lexical semantic comprehension.

Many functional neuroimaging investigations of verb knowledge also have reported activation in a frontal distribution (Fiez et al., 1996; Martin et al., 1995; Perani et al., 1999). We too observed activation in frontal cortex for all VERBS in healthy seniors. One hypothesis associates this with the motor-action knowledge contributing to MOTION verbs being used as stimuli in most studies of verb comprehension (Decety et al., 1994; Gallese et al., 1996; Jeannerod et al., 1995; Rizzolatti, Fadiga, Matelli, Bettinardi, Paulesu, & Perani, 1996; Rizzolatti, Fadiga, Matelli, Bettinardi, Paulesu, Perani, & Fazio, 1996). When we examined the circumstances associated with frontal activation in the present study, we found that the frontal distribution of recruitment was associated more strongly with COGNITION verbs than with MOTION verbs. Given the impoverished motor feature component of COGNITION verbs, it is unlikely that the frontal activation is related to motion feature knowledge. One alternate possibility is that the frontal distribution of this activation contributes to the retrieval process associated with a lexical comprehension task (Demb et al., 1995; Thompson-Schill, D’Esposito, Aguirre, & Farah, 1997). However, activations related to retrieval are often located in the left inferior frontal region, and inferior frontal activation in the present study was localized to the right hemisphere in healthy seniors. Moreover, the identical component of our baseline task is likely to have minimized frontal activation as a result of this process. Previous work using a variety of techniques in healthy subjects, split-brain patients, and aphasic patients with conditions like deep dyslexia have emphasized that lexical representations in the right hemisphere are likely to be more robust for words that are richly endowed with concrete features (Coltheart, 1980; Kounios & Holcomb, 1994; Zaidel, 1978). Although this may seem at first inconsistent with activation for a class of verbs impoverished in their sensory–motor features, other work suggests that words with less precise meaning, such as abstract verbs denoting cognition may be more dependent on right hemisphere-based processes (Beeman et al., 1994), possibly related to the sustained activation needed to process abstract words. Another possibility is that right inferior frontal activation is related to a lexical retrieval process (Nyberg, Cabeza, & Tulving, 1996; Tulving, Kapur, Craik, Moscovitch, & Houle, 1994). This may have been more evident in healthy seniors than in the young adults from our previous work (Grossman et al., 2002b), in which we did

Figure 3. Areas of reduced activation in Alzheimer’s disease patients in direct contrasts with healthy seniors for verb categories compared with a pronounceable pseudoword baseline. A: VERBS minus baseline. B: MOTION verbs minus baseline. C: COGNITION verbs minus baseline.
not see right frontal activation using the same paradigm, because of the relative difficulty associated with lexical retrieval in older subjects (Albert & Knoefel, 1994; Barresi, Nicholas, Connor, Obler, & Albert, 2000; Ramsay, Nicholas, Au, Obler, & Albert, 1999). Several studies investigating age-related changes in the encoding and retrieval of words have reported right frontal activation during retrieval in young subjects, but bilateral frontal activation in healthy seniors (Backman et al., 1997; Cabeza et al., 1997; Madden et al., 1999). Differences between these studies and the results described in the present report may be due to the many differences in the nature of the material being retrieved and the tasks and baselines used to investigate age-related lexical knowledge. Additional work is needed to

Figure 4. Areas of increased activation in Alzheimer’s disease patients in direct contrasts with healthy seniors for verb categories compared with a pronounceable pseudoword baseline. A: VERBS minus baseline. B: MOTION verbs minus baseline. There was no increased activation in Alzheimer’s disease patients compared with healthy seniors for COGNITION verbs.
assess the basis for right inferior frontal activation for verbs in healthy seniors.

We also observed anterior medial frontal activation for VERBS in an anatomic distribution that is not typically associated with motor-action features. One account for this activation focuses on the affective component of the pleasantness task we used to probe meaning in this study (Simpson, Snyder, Gusnard, & Raichle, 2001). For example, medial prefrontal activation has been associated with materials that require the integration of cognitive and emotional attributes (Drevets & Raichle, 1998; Shalman et al., 1997). We may have observed medial prefrontal activation in healthy seniors, but not in our previous studies of young subjects with the same materials, because an age-related limitation in executive resources may have been less effective at suppressing the pleasantness component of the task in healthy seniors while they were considering the verb’s meaning (Hasher & Zacks, 1988). Anterior medial prefrontal activation was particularly prominent for COGNITION verbs, and we cannot rule out the possibility that the more pleasant nature of COGNITION verbs somehow activated this brain region in a category-specific manner. Alternately, the complex network of associations implicated in the meaning of verbs—particularly abstract word categories such as COGNITION verbs (Gentner, 1981)—may have recruited this anterior medial prefrontal region to help support interpretation of the massively interconnected network of associations underlying these words (Braver & Bongiolatti, 2002; Koechlin, Basso, Pietrini, Panzer, & Grafman, 1999; Koechlin, Corrado, Pietrini, & Grafman, 2000). We have also seen recruitment of this area in fMRI studies of semantic categorization (Koenig, Smith, DeVita, et al., 2002).

We observed striatal and cingulate activation for VERBS in healthy seniors as well. Since the striatum is an important component of a frontal–striatal–thalamic loop mediating motor functions (Alexander, Crutcher, & DeLong, 1990), we had hypothesized in our previous work with young adults that this distribution of activation was related to knowledge of motor features associated with MOTION verbs (Grossman et al., 2002b). However, the striatum also contributes to other frontal–striatal–thalamic loops that are unrelated to motor functioning (Alexander et al., 1990). One possibility is that the striatum is part of a frontal–striatal–thalamic loop mediating affective processing. We noted above that limited inhibitory control in healthy seniors may have allowed the pleasantness component of our task to play a greater role in the overall activation pattern seen in the present study, including recruitment of anterior medial prefrontal cortex. Another possibility is that striatal activation is part of a different frontal–striatal loop involving the cingulate that is important in the support of executive resources. Several recent functional neuroimaging studies in young subjects emphasize the role of the striatum in executive resources such as working memory for nonlinguistic problem solving (Poldrack, Prabhakaran, Seger, & Gabrieli, 1999; Rympa, Prabhakaran, Desmond, Glover, & Gabrieli, 1999) and understanding complex linguistic stimuli such as sentences (Cooke et al., 2000). Studies of age-related differences in sentence comprehension also appear to relate striatal activation to the working memory resources needed to understand complex sentences (Grossman, Cooke, et al., 2002). The cingulate itself has been associated with selective attention, monitoring response selection, and regulating the implementation of executive resources (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999; Carter et al., 1998, 2000). In this context, it is possible that cingulate and striatal activation were due in part to the effort associated with comprehension of a complex lexical category like VERBS. Cingulate recruitment may have been seen in the present report, but not our previous study of verbs in young subjects (Grossman et al., 2002b), because of a relative limitation of age-related executive resources. Against this account is the finding that MOTION verbs were marginally more difficult to process than COGNITION verbs because they were judged somewhat less rapidly, even though there was no preferential activation of cingulate and striatal regions for MOTION verbs. Additional work is needed to interpret the basis for cingulate and striatal activation during verb comprehension in healthy seniors.

**Activation Patterns Associated With Verbs in Alzheimer’s Patients**

Consider in this context the activation pattern for VERBS in AD patients. Like healthy seniors, AD patients activated left posterolateral temporal cortex during judgments of VERBS. However, activation of this brain region appeared to be less robust than in healthy seniors, on the basis of a direct comparison of activation patterns across these groups of subjects. It is not simply that AD patients could not activate this brain region that is so critical to processing the meanings of individual words. Instead, the peak of activation in AD patients, when directly compared with healthy seniors (see Table 4 and Figure 4A), was changed in its anatomic distribution such that it was localized inferiorly by more than 20 mm, anteriorly by more than 20 mm, and superficially by more than 10 mm in comparison to the peak of activation for VERBS in healthy seniors relative to AD patients (see Table 3 and Figure 3A). Much work with a variety of techniques has pointed out the critical contribution of left posterolateral temporal cortex to semantic memory (Chertkow et al., 1997; Desgranges et al., 1998; Grossman et al., 1997; Hart & Gordon, 1990; Hillis et al., 2001), and recruitment changes in this area in the present study are consistent with the hypothesis that verb comprehension difficulty in AD is related in part to impairments of left posterolateral temporal cortex functioning. Our observation of activation changes in this region during comprehension of verbs in AD extends our finding of a similar pattern of change in the anatomic distribution of activation in AD patients relative to healthy seniors during probes of noun meaning (Grossman et al., 2003).

Changed activation in left posterolateral temporal cortex associated with poor verb comprehension in AD provides an important beginning in our attempt to understand the basis for comprehension difficulty in these patients. However,
this observation does not provide specific information about the role played by this brain region in semantic memory. One possibility is that partial activation of left posterolateral temporal cortex during verb comprehension in AD may reflect partial degradation of verb knowledge in these patients, such as difficulty with visual-motion features. However, we have not found a correlation between verb naming and visual–perceptual functioning in AD (K. M. Robinson et al., 1996). We discussed above several other problems with attributing changes in temporal–parietal activation to visual-motion feature knowledge. Another possibility relates reduced left posterolateral temporal activation to a deficit in the process of semantic categorization. For example, the interpretation of word meaning requires the integration of feature knowledge that may be represented in a distributed manner in several cortical regions. The anatomical connectivity pattern of this heteromodal brain area with multiple sensory–motor association regions (Mesulam, van Hoesen, Pandya, & Geschwind, 1977; Seltzer & Pandya, 1978) is consistent with this integrative role. Recent fMRI work directly assessing this integrative function for the purpose of semantic categorization has demonstrated posterolateral temporal activation as well (Koenig, Smith, Moore, et al., 2002), and patients with AD are compromised on these semantic categorization measures (Grossman, Smith, Koenig, Glosser, Rhee, & Dennis, in press; Koenig, Smith, Moore, et al., 2002). Regardless of the specific role in impaired verb comprehension played by partial left posterolateral temporal activation, one possible explanation for this observation is related to the histopathologic distribution of disease in AD. Thus, AD patients may have a relatively greater disease burden in the anatomic area most strongly activated in healthy seniors, but less disease in the portion of the left temporal lobe that they did activate. Although this may have allowed AD patients to activate a portion of the left posteriorlateral temporal area contributing to verb comprehension, the relatively reduced area of activation in AD patients compared with healthy seniors may explain in part their limited comprehension of verbs.

Several other brain regions were recruited by healthy seniors, but not AD patients. Limited activation of frontal, striatal, and right temporal regions in AD thus may contribute to their poor comprehension of VERBS as well. This conclusion should be viewed cautiously, however, since these differences may have been due in part to the limited power associated with a study involving only 11 AD patients. Evidence consistent with this latter possibility comes from the observation that AD patients showed activation in some of these regions for subcategories of verbs, such as recruitment of the striatum for MOTION verbs and anterior-medial prefrontal cortex for COGNITION verbs. Additional work is needed to determine the basis for this limited activation in AD patients relative to healthy seniors. Regardless of the specific explanation, the observation of increased activation in a portion of the left temporal lobe in AD patients compared with healthy seniors implies that areas of limited recruitment in AD are not easily explained by something like a global, nonspecific reduction in brain activity in these patients. Healthy seniors and AD patients both recruited the left inferior frontal region as well, although this was evident only in the direct contrasts across groups and not readily apparent in the activation pattern of each group compared with the pseudoword baseline. The loci of peak activation were somewhat different across these two groups of subjects. Left inferior frontal activation in AD patients for VERBS thus was about 30 mm posterior and 10 mm inferior to that seen in healthy seniors for MOTION verbs. Because left inferior frontal cortex is thought to contribute to grammatical processing (Constable et al., 1998; Dapretto & Bookheimer, 1999; Kang, Constable, Gore, & Avrutin, 1999; Ni et al., 2000), one possibility is that changes in left inferior frontal integrity in AD, reflected in a changed anatomic distribution of activation, may reflect AD patients’ limited retrieval of the grammatical properties contributing to verb comprehension. AD patients do have some difficulty on measures of grammatical comprehension (Croft, Hodges, & Patterson, 1999; Kontiola, Laaksonen, Sulkava, & Erkinjuntti, 1990; Swihart, Panisset, Becker, Beyer, & Boller, 1989; Tomoeda, Bayles, Boone, & Kasznia, 1990), although this appears to be closely related to a working memory limitation that also contributes to these measures of grammatical comprehension (Grossman & Rhee, 2001; Grossman & White-Devine, 1998; Kempler, Almor, Tyler, Andersen, & MacDonald, 1998; Waters, Caplan, & Rochon, 1995). Moreover, grammatical comprehension does not appear to be correlated with verb naming in AD (K. M. Robinson et al., 1996). An alternate account focuses on several studies showing age-related increases in left inferior frontal activation during the retrieval phase of verbal anterograde memory tasks (Backman et al., 1997; Cabeza et al., 1999; Madden et al., 1999). Although generalizations from studies of anterograde memory to studies of semantic memory must be conducted only with great caution, one possibility suggested by this work is that differences in left inferior frontal activation in healthy seniors and AD patients may reflect differential retrieval efficiency in anterograde memory compared with semantic memory. This would also be consistent with imaging observations of healthy adults suggesting that left inferior frontal cortex contributes to some aspect of retrieval from semantic memory (Demb et al., 1995; Thompson-Schill et al., 1997; Wagner, Pare-Blagoev, Clark, & Poldrack, 2001). The role played by changes in left inferior frontal activation during verb comprehension in AD requires additional investigation. Regardless of the specific consequences of changed activation in a left inferior frontal distribution, partial activation of this region in AD may be related to the histopathologic distribution of their disease, thus allowing these patients to recruit only a portion of the region involved in verb comprehension and consequently limiting their verb comprehension performance.

Direct contrasts with healthy seniors also showed that AD patients have relatively reduced right temporal activation, particularly for MOTION verbs. Although we did not observe activation for MOTION verbs in the right hemisphere in healthy seniors that exceeded our statistical threshold, the relative reduction of right hemisphere activation during
motion verb judgments in AD may have contributed to AD patients’ limited comprehension of this verb subcategory. For example, some workers have emphasized the spatial-temporal properties associated with motion verb knowledge (Jackendoft, 1983). These features may be represented in the right hemisphere, and AD patients may be less effective than healthy seniors at recruiting these particular features of verbs. This account must be treated cautiously, however, since we did not observe a relationship between verb-naming difficulty and visual–perceptual processing in our previous behavioral work with AD patients (K. M. Robinson et al., 1996). On the basis of activation of ventral frontal temporal cortices in AD patients for MOTION verbs relative to COGNITION verbs, another possibility is that AD patients are attempting to activate features related to object form/shape that are more appropriate for noun meaning—such as the object associated with a motion—than for verb meaning. Other possibilities include a change in the nature of the processes associated with understanding complex categories of words such as MOTION verbs (Beeman et al., 1994). Additional work is needed to understand the role of reduced right temporal activation in AD patients’ limited comprehension of MOTION verbs.

AD patients did activate the left striatum during their comprehension of MOTION verbs relative to the pseudoword baseline, although this region was not recruited to a statistically significant degree for MOTION verbs by healthy seniors. Indeed, a direct contrast of activation for MOTION verbs in these subject groups demonstrated that AD patients had significantly greater striatal recruitment, accompanied by significantly greater activation of a portion of left inferior frontal cortex, than was seen in healthy seniors. The precise role played by the increased inferior frontal–striatal activation for MOTION verbs in AD is not clear. One possibility is that up-regulation of these regions helps support AD patients’ motor-action knowledge. We suggested above several reasons to doubt this feature-based account. An alternate possibility is that lexical retrieval is more difficult for AD patients than it is for healthy seniors. Confrontation naming difficulty is a well-known characteristic of AD (Bayles, Tomoeda, & Trosset, 1990; Dennis, Koenig, Moore, Patel, & Grossman, 2002; Hodges et al., 1996; Huff, Corkin, & Growdon, 1986; Lambon Ralph, Patterson, & Hodges, 1997; Martin, Brouwers, & Lalonde, 1986; Shuttleworth & Huber, 1988), including difficulty naming actions with verbs (Cappa et al., 1998; K. M. Robinson et al., 1996; White-Devine et al., 1996). Thus, increased frontal–striatal activation may support the need to meet relatively greater resource demands associated with lexical retrieval in AD patients compared with healthy seniors.

We also found that AD patients, like healthy seniors, activated anteromedial prefrontal cortex during comprehension of COGNITION verbs. However, this activation was unilateral in AD patients, compared with the bilateral activation in healthy seniors. The reduced activation of this area in AD patients relative to healthy seniors may contribute to AD patients’ relatively poor comprehension of COGNITION verbs. Moreover, direct contrasts of these subject groups showed that AD patients have reduced cingulate–striatal activation for COGNITION verbs in comparison to healthy seniors for COGNITION verbs, and this also may play a role in AD patients’ relatively reduced comprehension of COGNITION verbs. Finally, we did not see any areas of increased activation for COGNITION verbs in AD patients relative to healthy seniors for COGNITION verbs, nor any increased activation for COGNITION verbs in AD patients relative to their own activation for MOTION verbs. This is unlike judgment of VERBS, in which AD patients showed relatively greater left lateral temporal activation than healthy seniors, and unlike judgment of MOTION verbs, in which AD patients showed relatively increased left fronto–striatal activation compared with healthy seniors. The apparent absence of increased activation in AD patients compared with healthy seniors in any brain region for COGNITION verbs may also contribute to the relatively poor comprehension of these words in AD patients compared with healthy seniors, and in comparison to their own performance with MOTION verbs. Thus, at least three factors appear to contribute to AD patients’ relative difficulty with COGNITION verbs: reduced activation in an area activated by both groups, apparent failure to activate an area that is recruited by healthy seniors, and the absence of activation in novel brain regions that are not activated by healthy seniors.

A unique feature of AD patients’ activation profiles was the absence of areas of increased activation relative to healthy seniors only for COGNITION verbs, which are thought to depend on a complex and massively interconnected network that derives knowledge from the associations represented in this network (Gentner, 1981). In a progressive neurodegenerative condition such as AD, in which associative networks may be degraded over time (Gonnerman, Andersen, Devlin, Kessler, & Seidenberg, 1997; Tyler, Moss, Durrant-peatfield, & Levy, 2000), one possibility is that comprehension of COGNITION verbs may not be supportable. Another possibility is that AD patients may not be able to marshal the processing resources needed to support interpretation of the complex network underlying the meanings of COGNITION verbs. For example, healthy seniors may depend in part on anteromedial prefrontal cortex to help organize knowledge represented in the complex associative network underlying COGNITION verbs, and may use cognitive resources supported by cingulate–striatal activation to help them selectively attend to a category of knowledge like COGNITION verbs that is relatively difficult to process. However, this mechanism may be limited in AD patients because they apparently do not fully recruit anteromedial prefrontal cortex or a cingulate–striatal loop during cognition verb processing. Moreover, unlike the activation seen with MOTION verbs, we did not see increased activation for COGNITION verbs in AD patients compared with healthy seniors for COGNITION verbs. Several previous functional neuroimaging assessments of AD in other cognitive domains appeared to show up-regulation during task performance that was thought to compensate in part for the AD patients’ reduced activations (Becker et al., 1996; Grady, Furey, Pietrini,
with AD patients understand some aspects of verbs. This would be consistent with AD patients’ relative success understanding MOTION verbs compared with COGNITION verbs. The potential contribution of compensatory up-regulation in AD may parallel functional neuroanatomic observations of reorganization following stroke, in which areas of increased brain activation have been shown to contribute to recovery of linguistic function in aphasia (Heiss, Kessler, Thiel, Ghaemi, & Karbe, 1999; Rosen et al., 2000). The biological basis for this compensatory activation in AD may be the axonal sprouting and biochemical changes associated with cortical reorganization that are described in these patients (Geddes et al., 1985; Kowall & McKee, 1993; Scheibel & Tomiyasu, 1978).

There are several shortcomings associated with this study that must be kept in mind when considering our results. We do not have behavioral measures of comprehension accuracy in all of the AD patients we studied. Although we used a pseudoword baseline to control for reading differences and other potential sensory–motor differences between subject groups, the pseudoword baseline itself may be associated with activations that limited our ability to identify brain areas important for word meaning in our subtractions. Subtle differences in cerebral anatomy caused by regional atrophy in AD may have contributed to some of the changes seen in these patients relative to healthy seniors. Although the AD patients we examined were mildly demented and thus had minimal atrophy, the normalization algorithm we used nevertheless may not have been able to map AD patients’ brain volumes as accurately as healthy seniors’ brain volumes onto the anatomic template we used to analyze activation. In addition, although our work was intended to assess cerebral activation patterns associated with verbs, the examination of subcategories of MOTION verbs and COGNITION verbs also proved quite informative, but at a cost of reduced statistical power. The statistical analyses thus may have been limited because of several effects that only approached our statistical threshold for significance for a word subcategory. MOTION verbs showed some activations in AD patients that differed from the activations seen in healthy seniors, but a similar pattern of selectively greater activation for COGNITION verbs was not seen. This leaves open the possibility that COGNITION verbs were more difficult than MOTION verbs in some nonspecific sense.

With these limitations in mind, our observations suggest that limited performance on tasks requiring verb knowledge may be due in part to changes in AD patients’ activation of the large-scale neural network implicated in the comprehension of verbs. Left posterolateral temporal and inferior frontal regions are partially activated in AD to support verb comprehension, and the distribution of these activations in AD patients are changed relative to that of healthy seniors. We believe that these areas are implicated in processes important for word meaning such as integrating feature knowledge distributed throughout modality-specific association cortices. Other brain regions that apparently contribute to verb processing in healthy seniors are less activated in AD, although category-specific compensatory up-regulation for MOTION verbs may allow AD patients to achieve partial comprehension of MOTION verbs compared with COGNITION verbs. These category-specific changes may be related to the neural representation of knowledge specific to MOTION verbs.

References


Tulving, E., Kapur, S., Craik, F. I. M., Moscovitch, M., & Houle, S. (1994). Hemispheric encoding/retrieval asymmetry in epi-


