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The brain bases of reading late learned words: Evidence from functional MRI

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Abstract

Age of Acquisition (AoA) effects for reading have been documented in the literature. Recent studies have suggested that more effortful phonological retrieval is involved in picture naming for late learned words. Here we use functional magnetic resonance imaging to determine the neuroanatomical correlates of AoA effects in reading, and to explore whether AoA effects in the brain modulate activity in areas devoted to phonological processing. Participants were asked to covertly name blocks of early and late learned words while being scanned with functional MRI. Results revealed a relative increase in neural activity for late learned words in a set of brain areas involved in auditory-phonological processing (the planum temporale of the posterior-superior left temporal lobe) and articulatory motor planning (BA 44, putamen, and globus pallidus) . These findings support the view that late learned words involve more effortful phonological retrieval, but in addition point to a second locus of the AoA effect in the articulatory component of the reading system.

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The fact that early learned words are processed differently than late learned words has been established for over thirty years (Carroll & White, 1973; Gilhooly & Watson, 1981). This effect of the age of a word's acquisition was shown in a number of domains including word reading, auditory and visual lexical decision, picture naming and face recognition (e.g., Christopher Barry, Morrison, & Ellis, 1997; Cuetos, Ellis, & Alvarez, 1999; Ellis & Morrison, 1998; Gerhand & Barry, 1998, 1999a, b; Gilhooly & Gilhooly, 1979; Lewis, 1999; Meschyan & Hernandez, 2002; Morrison, Chappell, & Ellis, 1997; Morrison & Ellis, 1995, 2000). Theoretical accounts of these findings, however, are still under debate. Brown and Watson (1987) found that earlier learned words are named faster than late learned words and suggested that these items have more complete phonological representations in the phonological output lexicon. According to this account, pronouncing late learned words involves the generation of phonological information not directly represented in the phonological lexicon. A recent study by Monaghan and Ellis (2002) tested one prediction of this 'phonological completeness hypothesis', i.e., the assumption that late learned words should be faster to segment than early learned words because they have more fragmented phonological representation. However, the results reported by Monaghan and Ellis (2002) do not support the phonological completeness hypothesis. Furthermore, others have pointed out that this approach does not capture the entire range of empirical findings (Lewis, Chadwick, & Ellis, 2002; Moore & Valentine, 1999). For example, the phonological completeness hypothesis cannot account for Age of Acquisition (AoA) effects in tasks which do not require the overt pronunciation of words such as lexical decision or face recognition tasks. Despite the lack of support for this specific model, the assumption has confirmed that the locus of AoA effects in picture naming and word naming might be traced

back to the sublexical phonological level (C. Barry, Hirsh, Johnston, & Williams, 2001). Under this account, the pronounciation of later learned words during picture and word naming tasks would be more effortful because the phonological representations of late learned words are not as easily accessed as those of early learned words (Barry et al., 2001).

More recently, a connectionist network was designed to explicitly model AoA effects (Ellis & Lambon Ralph, 2000). This network was trained on sets of items that were introduced early or late in training in order to simulate differences in the words' acquisition age. At the end of cumulative training, early learned items could be recognized more easily by the network than late learned words. Ellis and Lambon Ralph (Ellis & Lambon Ralph, 2000) suggest that a gradual reduction in plasticity of the network model is a mechanism that can account for AoA effects. Under this assumption, early learned words have a greater influence on the structural organization of the distributed representations of words in the mental system, and have better-optimized representations.

The simulation by Ellis and Lambon Ralph (2000) provides a viable alternative to the phonological completeness hypothesis by offering an account that generalizes beyond lexical tasks. At the same time, it postulates mechanisms underlying the AoA effect that are very similar to those assumed in the phonological completeness hypothesis. Both models argue that early acquired words influence the structure of the representational system more profoundly, and that later representations are built around the former, resulting in a disadvantage for late learned words. However, while the phonological completeness hypothesis specifies the representational level at which these structural differences should be observable (i.e., the phonological output lexicon), the Ellis and Lambon Ralph (2000) model allows for a broader locus of the AoA effect in the cognitive system.

Despite increased work in the behavioral domain in recent years, relatively few studies have investigated the neural basis of AoA effects. Fiebach, Friederici, Müller, von Cramon and Hernandez (2003) asked participants to make visual and auditory lexical decisions to words and pronouceable pseudowords while being scanned with fMRI. Results across both modalities revealed increased activity for late learned words in left inferior prefrontal cortex (IPFC; BA 45) extending to lateral orbito-frontal cortex (BA 47/12) and in the precuneus for early learned words. In addition, increased activity in the region of the left temporal operculum near Heschl's gyrus was observed for early learned words in the visual modality. Because of the involvement of auditory association cortices, Fiebach et al concluded that when making lexical decisions to visually presented early learned words, participants automatically coactivated auditory representations possibly facilitating word recognition. The increase in inferior frontal activity during processing of late learned words is compatible with suggestions found in the neuroimaging literature regarding the role of left IPFC in semantic processing. Left IPFC is assumed to be critical for the effortful or strategic activation of information from the semantic knowledge system (Fiez, 1997; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997). Hence, processing of late learned words, at least when making lexical decisions, is likey to involve more complex semantic retrieval or selection processes instantiated by inferior frontal brain areas.

However, the lexical decision task is not necessarily representative of natural word recognition processes. In the behavioral literature, very often multiple tasks such as lexical decision and reading aloud are employed in order to compensate the influence of specific task demands on the effects of interest (e.g., Carreiras, Perea, & Grainger, 1997). In functional neuroimaging studies, it was observed that the cortical networks modulated by word frequency differ between reading (Fiez, Balota, Raichle, & Petersen, 1999) and lexical or semantic

decisions tasks (Chee, Hon, Caplan, Lee, & Goh, 2002; Fiebach, Friederici, Muller, & von Cramon, 2002). For this reason, it is likely that the brain regions affected by AoA in our earlier study are (at least to some extent) specific to the lexical decision task. AoA effects in reading aloud, as suggested by the phonological completeness hypothesis, might be due to differences between early and late words in the organization of their phonological representations in the speech output system, a system not necessarily involved in making lexical decisions. In the current study, a group of English speakers were asked to perform a reading task to blocks of matched early and late acquired words, once to gather reaction times to overt reading in the laboratory, and once while being scanned with functional MRI . What predictions could be made regarding the difference between early and late learned words? In general, reading words involves a distributed network of cortical brain regions including lateral and medial occipital cortices, basal occipito-temporal regions, inferior and superior portions of the postero-lateral temporal lobe, inferior parietal regions as well as inferior frontal areas (e.g., Price, 2000; Pugh et al., 2001). This network involves brain regions specialized to certain aspects of word processing. The exact functional-anatomical correlations, however, are still under debate. For example, word form processing has been attributed to medial occipital areas (Petersen et al., 1990), to left lateral occipito-temporal areas (Pugh et al., 2001), or to the mid-portion of the left fusiform gyrus (Cohen et al., 2000; Dehaene et al., 2001). Phonological recoding of visually presented words is often associated with the region around the parieto-temporal junction which encompasses the angular gyrus and supramarginal gyrus in the inferior parietal lobe and the posterior aspect of the superior temporal gyrus (Wernicke's Area) (Benson, 1994; Black & Behrmann, 1994 ; Geschwind, 1970; Pugh et al., 2001). Finally, areas in the fronto-opercular region, encompassing the posterior inferior frontal gyrus (BA 44), ventral premotor and motor cortex, as well as the

deep frontal operculum and insular regions are involved in the planning and execution of articulation (Bates et al., 2003; Blank, Scott, Murphy, Warburton, & Wise, 2002; Dronkers, 1996; Wise, Greene, Buchel, & Scott, 1999).

Given the literature reviewed above, it would be logical to predict that one or more of the areas described should be affected by AoA in the reading task. If different areas are affected differentially by early and late learned words, the functional specification of these areas will allow us to draw conclusions regarding the cognitive components involved in the processing of late as compared to early learned words. In contrast, an overall modulation of the reading network, without regional AoA-related differences, would be evidence in favor of a more general account of the locus for AoA effects. In addition, it will be of interest to determine if AoA effects in single-word reading are in line with those previously seen for the lexical decision task. But note that activation differences between the present study and our earlier work employing lexical decision tasks might also be due to differences in the orthographic opacity of the two languages used, i.e., English and German (see, e.g., Paulesu et al., 2000).

Method

Participants

Sixteen subjects (7 female and 9 male) from the Santa Barbara and Los Angeles communities with a mean age of 22.3 (sd= 1.35, range 19 to 24) participated in the current experiment. None had any history of neurological or psychiatric disorders and none were currently using medication. All were right handed as assessed by our internal handedness questionnaire and reported no left handed members in their immediate family. Informed consent

was obtained from all participants according to protocols approved by both the UCLA and UCSB Human Subjects Committees.

Materials

For the fMRI study, we chose an item set of 96 words, i.e., 48 per condition. All words were between 3 and 10 letters in length. The average length in letters was 5.6 letters for early learned words and 5.6 letters for late learned words ($t(94) = 1.1$; $P < 0.3$). The average syllable length was 1.6 syllables for early learned words and 1.7 syllables for late learned words (range 1 to 3 syllables; $t(94) = -.6$; $P = .6$). The two experimental conditions were matched on frequency using CELEX database (Baayen, Piepenbrock, & Gulikers, 1995). Early and late learned words had comparable frequencies (19.0 and 15.8 in one million, respectively; $t(94) = .84$; $P = .4$) and were equated in their logarithmic frequencies (2.3 and 2.4, respectively; $t(94) = -.229$; $P = .8$). All nouns used were imageable. Using the MRC psycholinguistic database (Coltheart, 1981), early and late learned words were matched for subjectively rated imageability as much as possible (i.e., 554.1 and 489.1, respectively, on a scale ranging from 100 to 700; $t(77) = 5.2$; $P < .000$). Early items were chosen such that they were learned before the age of 5 and late learned items were chosen such that they were learned after the age of 6 , $t(94) = -22.519$; $P < .000$). Age of acquisition was determined using age-of-acquisition norms reported by Szekeley et al. [, 2003 #1249]. An analogous set of items was created for the behavioral word reading study which was conducted prior to the fMRI study.

Procedure

Behavioral testing was conducted for each subject prior to the fMRI sessions.

Functional MRI imaging was performed with a General Electric 3.0 Tesla magnetic imager equipped with echo-planar imaging (EPI) from Advanced NMR (Wilmington, MA). For

each subject, a conventional sagittal scout scan was first obtained from which the functional images were prescribed. Using an EPI gradient echo sequence (TR = 3000 ms; TE = 25 ms; a 64 x 64 scan matrix with a 24 cm FOV) 108 images were obtained for each subject over axial 19 slices (4 mm thick / 1 mm gap). According to the atlas of Talairach and Tournoux (1988) the most inferior and superior slices approximately corresponded to z = -24 and z = +65, respectively. A set of coplanar high-resolution EPI structural images (TR=4000 ms; TE = 65 ms; matrix size 128 X 128; FOV = 20 cm) was also collected at the same time and used to spatially normalize each subject's data into a standardized template.

The functional scan session lasted 5 minutes and 12 seconds and consisted of four activation blocks of 48 seconds length each. During each block, 24 words were presented at the rate of one every two seconds. Two blocks consisted of late learned words and two blocks consisted of early learned words, resulting in 48 words per condition. Participants were shown a cue, a plus sign for 200 ms, followed immediately by a target word which was presented for 600 ms which the participants were instructed to read covertly. A 1200 ms delay was introduced prior to the next stimulus presentation. The activation blocks alternated with five baseline periods of 24 sec each, during which the subjects were instructed to rest.

Data Analyses

To correct for head motion, the functional images for each subject were realigned with Automated Image Registration (AIR) (Woods, Mazziotta, & Cherry, 1993) using an eight parameter rigid body transformation model. The realigned data were then spatially transformed into a standard reference system (Woods, Dapretto, Sicotte, Toga, & Mazziotta, 1999) using polynomial non-linear warping to allow for intersubject averaging. As a final preprocessing step,

all images were smoothed using an 8 mm FWHM isotropic Gaussian kernel to increase the signal-to-noise ratio.

All statistical analyses were done using the Statistical Parametric Mapping software(SPM '99; Friston, 1995). The analysis consisted of two steps. The first was a fixed effect analysis in which contrast images are calculated for each subject. These contrast images were then jointly analyzed in a second step using a random effects model which was thresholded at $p < 0.001$ (uncorrected for multiple comparisons). An extent threshold of 10 consecutive voxels was used in order to eliminate spurious activity. Figures were created using the Brain X software (Kris Singh, Aston University) and a template brain from the Montreal Neurological Institute (Collins, Neelin, Peters, & Evans, 1994).

Results

Behavioral Data

Reading time data from the behavioral pretesting were placed into a one-way within-subjects ANOVA. Results revealed a main effect of AoA in terms of reaction time, $F(1,15) = 10.65, p < 0.01$, such that subjects were faster for early words (570 ms) compared to late words (583 ms).

Neuroimaging

Early learned words when compared to a rest baseline revealed increased activity in a set of areas. This included in the frontal lobes the posterior-superior portion of the inferior frontal gyrus extending into premotor cortex (Brodmann areas/BA 44/6) as well as in the left hemisphere the pars triangularis of the inferior frontal gyrus (BA 45) and part of the middle frontal gyrus (BA 46). In addition, we saw activity bilaterally in the precuneus and in the left

inferior parietal lobule. Late learned words compared to rest activated the same network, and in addition showed activity in the medial frontal lobe (BA 9) bilaterally, as well as laterally in the left precentral gyrus, insula and in subcortical structures.

The direct comparison between early and late learned words revealed significantly greater activity for late learned words in temporal, frontal and subcortical brain regions (see Figure 1 and Table 1). In the temporal lobe, there was greater activity for late learned words in the left supratemporal plane posterior to the transvers temporal gyrus of Heschl. More specifically, this effect was seen in the anterior-middle portion of the planum temporale, in Brodmann area (BA) 42. In addition, we saw greater activation for late than for early learned words in a deep portion of the pars opercularis of the right inferior frontal gyrus (BA 44), in the medial portion of the superior frontal gyrus (BA 9) and in the right basal ganglia involving the globus pallidus and putamen[1]. For early learned words, there were no areas of increased activity relative to late learned words.

Discussion

In the introduction, different models to account for AoA effects were presented. The phonological completeness hypothesis (Brown & Watson, 1987) argues that early learned words are represented in a more complete manner than late learned words in the phonological output lexicon. According to this account, pronunciation of late learned words involves of the assembly

[1] Note that it is higly unlikely that the reported activation differences are due to the remaining differences in imageability between early and late learned words, as none of the reported areas has been associated with imageability before (e.g., Wise et al., 2000; Fiebach et al., 2003).

of the word's phonological form from fragmented phonological representations. Related accounts suggest that the ease of the retrieval of lexical phonological representations during word production – which might or might not be related to the structural organization of the representation – differs between early and late learned words (Barry et al., 2001). A further model, based on simulation studies reported by Ellis and Lambon Ralph (2000), offers a more general mechanism for AoA effects. Words learned earlier have a more substantial influence on the internal organization of the distributed knowledge system. According to these authors, AoA effects appear because the word representation system is subject to a gradual loss of plasticity during development. Later learned words are organized in the cognitive system in a less optimal way. Ellis and Lambon Ralph's (2000) model can be viewed as a more general account of AoA effects that assumes representational differences similar to those of the phonological completeness hypothesis but not restricted to phonological representations. Such an assumption is supported by evidence in the literature which finds AoA effects for tasks which do not require phonological output such as, for example, face processing tasks.

In the current study, we used fMRI to look at the brain areas involved in a simple covert reading task. FMRI studies of reading had established involvement of areas in the fronto-opercular region for articulation (e.g. Fiez et al., 1999) (Price, 2000; Wise et al., 1999), the temporo-parietal juncture for a likely involvement in phonological recoding or in the integration of orthographic and phonological information (e.g. Geschwind, 1970; Pugh et al., 2001) and areas in the lateral and basal occipito-temporal area that are postulated in relation to visual word form recognition (e.g. Cohen et al., 2000; Dehaene et al., 2001; Fiebach et al., 2002; Pugh et al., 2001). If AoA effects in reading are the product of a general mechanism as proposed by Ellis and Lambon Ralph (2000) we would expect to see a general modulation of activity in a

distributed network of reading areas in the brain, encompassing all those mentioned. Our results, however, did not support such a general mechanism account of AoA effects in reading, at least at the functional-neuroanatomical level. Specifically, we saw increased activity for late learned words only in a subset of the reading network including the anterior middle portion of the left planum temporale as well as in the right hemisphere the posterior portion of the inferior frontal gyrus and basal ganglia structures.

For reading late learned words, a relative increase of activation was observed in a circumscribed subregion of the temporo-parietal junction area implicated in reading. Reading models suggest that this region is involved in the integration of orthographic, phonological, and semantic information (e.g. Geschwind, 1970; Price, 2000; Pugh et al., 2001). However, the fact that the supratemporal area identified in the present study for late words (i.e., the anterior portion of the planum temporale) is in the immediate vicinity of the gyrus of Heschl and attributed to secondary auditory cortex rather than to multimodal association cortex, suggests that its function in reading is more associated with the acoustic-phonological form of words rather than high-level cross-modal aspects of orthographic-phonological integration. In a recent review of the function of the planum temporale, it was proposed that it is involved in the spectrotemporal analysis of incoming acoustic signals, and the matching of these signals to stored auditory patterns in speech but also in other domains of auditory processing (Griffiths & Warren, 2002). With respect to speech processing, it was suggested that this area is crucial for the construction of sound-based representations of words (for an overview see Hickok & Poeppel, 2000).

The present results suggest that sound-based word representations accessed via the planum temporale are also involved when reading words aloud, as the planum temporale is

activated during reading of both early and late words - but relatively more for late learned words. An involvement of the planum temporale in speech production and reading is supported by recent functional neuroimaging data. For example, Paus and collaborators (Paus, Perry, Zatorre, Worsley, & Evans, 1996) associated the planum temporale with phonological demands during speaking, based on their finding of increasing activity in this area with increasing rate of speech production. Other studies found activation in the same brain region during silent object naming (Hickok et al., 2000) or, slightly more posteriorly in the planum temporale, during overt articulation (Wise et al., 2001). Nakada et al. (2001) reported activation of the planum temporale in both reading of visually presented words and listening to auditorily presented words. Thus, there is converging evidence that the planum temporale is involved in phonemic processing during speech production (Hickok & Poeppel, 2000) or, as suggested by Wise and colleagues (2001), has the role of an interface between speech perception or lexical recall on the one hand and speech production on the other. As the planum temporale was more strongly activated in the present study for late words, it appears to be the case that the assumed activation of stored acoustic-phonological word representations for these items is more demanding or less automatic than for early acquired words. This conclusion is consistent with findings of increased phonological processing when naming pictures of late learned objects. Finally, the fact that this increase is observed for late learned words conflicts (at least on the surfacts) with that observed by Fiebach et al. (2003), a point we will return to later.

In single word reading, the posterior inferior frontal lobe and fronto-opercular region involving also the ventral premotor cortex and underlying insular cortex are generally associated with articulation and articulatory planning (e.g., Wise et al., 1999; Price, 2000; Pugh et al.,

2001), but also with effortful phonological processes associated with articulatory mechanisms. The latter aspect, however, is generally attributed to the left superior portion of the posterior inferior frontal gyrus, extending into premotor cortex, BA 44/6 (Bookheimer, 2002; Friederici, 2002; Poldrack et al., 1999). Therefore, it is not likely that the right BA 44 activity seen in the present study is involved in controlled phonology. It is more plausible to assume that the additional inferior frontal component seen in the present study for late learned words is associated with the increased difficulty of articulating late learned words. As it is not the primary motor component of word reading that is modulated by AoA but a more anteriorly located region, we suggest that the difficulty for late learned words arises during the stage of articulatory planning or preparation. A comparable modulation of BA 44 in reading was seen in other studies for words that were difficult to pronounce due to spelling-to-sound irregularity (Fiez & Petersen, 1998; Herbster, Mintun, Nebes, & Becker, 1997) or due to the words' low frequency of occurrence (Fiez et al., 1999). A particularly great demand on motor planning for late learned words is also supported by the increased activity observed in the globus pallidus and putamen of the basal ganglia. These are known to play a role in motor planning (Menon, Anagnoson, Glover, & Pfefferbaum, 2000; Wildgruber, Ackermann, & Grodd, 2001; Wise et al., 1999). The increased activity in BA 44 and the basal ganglia suggests that verbal motor planning during covert reading of late learned words is more effortful relative to early learned words. This increased effort, however, appears to be reflected in the additional recruitment of right-hemispheric areas.

The joint activity in both the planum temporale and a frontal-subcortical circuit likely to be involved in articulatory mechanisms suggests that both phonological processing and verbal motor planning are harder for late learned words during covert reading. Thus, late learned words

require more effort in order to be retrieved and produced. This conclusion based on functional neuroanatomical considerations is not fully consistent with the assumptions derived from Ellis and Lambon Ralph's (2000) simulation studies regarding a general mechanism for AoA effects applying to multiple levels of representation. On the other hand, this findings is consistent with the view that reading of late learned words involves more complex phonological processing (for evidence from picture naming see C. Barry et al., 2001). The current study is consistent with this view but suggests that it must be extended to include processing disadvantages for late learned words during the articulation component of reading as well.

One final area of increased activity was in the medial frontal lobe, where late learned words also elicited greater activity than early learned words. This area is typically seen domain-independently in studies which ask participants to exert metacognitive control (for a review see Zysset, Huber, Ferstl, & von Cramon, 2002). This interpretation, however, is difficult to apply to the present study as participants were asked to simply read single words in blocks which either contained early-learned or late-learned items, and participants were not aware of the AoA manipulation. It might be more plausible to associate the fronto-medial involvement seen for late learned words with an unspecific increase in processing difficulty (Paus, Koski, Caramanos, & Westbury, 1998).

The current study yielded results which are not completely consistent with previous findings for age of acquisition effects using the lexical decision task (Fiebach et al., 2003). In particular, there were no brain areas identified which might be associated with the facilitation of reading in early learned words. Also, it is crucial to note that although both studies showed a modulation of supratemporal areas in the vicinity of the left auditory cortex, these effects had

opposite directions in the two studies. Whereas the present results show increased activity for late learned words posterior to the gyrus of Heschl, the visual lexical decision study yielded greater activity for early words anterior to the gyrus of Heschl. While it is truly remarkable that both neuroimaging studies exploring AoA effects showed activation modulation in the left supratemporal region for visually presented words, it is not clear why reading and lexical decisions result in opposite activation patterns. This might be due to possible differences in task-specific processes operating on information represented in this region.

The consideration of the specific brain areas identified in the present study (which are known to be involved in reading) compared to the areas seen in the previous study suggests that the differences are likely to be induced by the varying demands of the behavioral tasks employed, i.e., reading vs. lexical decision. However, differences between the two studies might also be caused by differences between the two languages in which the studies were conducted (i.e., English vs. German) which vary in orthographic transparency. Languages possess different scripts which vary from logographic (in which a symbol represents a word; e.g. Chinese) up to alphabetic languages in which symbols represent sounds which compose a word (e.g. most Indo-European languages). In alphabetic languages, the orthographic transparency can vary tremendously from completely transparent in which most letters have one corresponding sound (e.g. Spanish) up to opaque where each letter can have many different sounds (e.g. English). German is more transparent than English which has a large number of exception words. Studies which have investigated reading cross-linguistically, have found that transparency modulates neural activity. For example, Paulesu et al. (2000) reported that activation in the left superior temporal, posterior inferior temporal and left inferior frontal cortex differed between

monolingual Italian and English speakers when reading words and pseudowords in their native language. It remains to be seen whether the differences seen between AoA effects in reading and lexical decision can be attributed to task differences, language differences such as transparency, or other factors not identified yet. Future studies which investigate AoA (and other variables) across a number of tasks are needed in order to yield a more detailed understanding of the organization of reading in the brain.

In summary, the current study found that the age of word acquisition modulates activity in a subset of brain regions for reading known from previous studies. In particular, reading late learned words resulted in increased activity in a set of areas involved in auditory-phonological processing and higher-level motor planning during reading . These findings are consistent with the theoretical models that associate disadvantages in the production of late learned words with increased difficulty of phonological retrieval, but suggest that such models have to be extended to consider also that late learned words induce increased effort at the level of articulatory motor planning in reading. As such the present study demonstrates the role that fMRI can play in constraining and validating cognitive models of AoA.

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Appendix. Experimental items and corresponding characteristics.

Early Acquired Words							**Late Acquired Words**						
Stimulus	IMG	NSYL	LNFR	Fr	AOA	LEN	Stimulus	IMG	NSYL	LNFR	Fr	AOA	LEN
balloon	583	1	1.9	7	3.8	7.0	ax	597	1	2.3	10	6.2	2.0
bear	526	1	2.8	17	4.0	4.0	balcony	-	3	2.6	14	7.1	7.0
bell	543	1	3.3	28	4.4	4.0	barrel	487	2	3.1	22	6.4	6.0
bicycle	-	3	1.8	6	4.4	7.0	bomb	566	1	3.7	42	6.4	4.0
bird	614	1	0.0	1	3.4	4.0	bra	575	1	1.9	7	8.0	3.0
butterfly	481	3	2.4	11	4.0	9.0	bride	-	1	2.6	13	6.3	5.0
button	573	2	3.3	27	4.4	6.0	canon	424	2	1.9	7	6.8	5.0
can	620	1	2.3	10	4.2	3.0	cigarette	573	3	4.3	72	6.4	9.0
carrot	539	2	2.2	9	4.1	6.0	column	491	2	2.8	17	8.1	6.0
cat	582	1	4.2	68	3.0	3.0	drill	473	1	2.2	9	7.1	5.0
cheese	588	1	3.5	32	4.0	6.0	flute	496	1	1.4	4	6.9	5.0
clock	608	1	3.7	40	4.3	5.0	funnel	-	2	1.099	3	7.87	6.0
cloud	553	1	4.0	57	4.2	5.0	harp	430	1	1.4	4	7.3	4.0
clown	511	1	1.6	5	4.1	5.0	heel	524	1	3.4	30	6.1	4.0
comb	-	1	1.8	6	4.2	4.0	helmet	528	2	2.6	14	6.2	6.0
cookie	600	2	1.6	5	3.1	6.0	hinge	-	1	1.6	5	7.9	5.0

crib	-	1	0.7	2	4.1	4.0	hoe	489	1	1.4	4	7.5	3.0
elephant	459	3	3.2	25	4.3	8.0	hoof	401	1	2.2	9	6.4	4.0
frog	507	1	2.3	10	4.0	4.0	knight	608	1	2.6	14	6.1	6.0
ghost	505	1	3.5	32	4.4	5.0	leopard	431	2	2.2	9	6.1	7.0
giraffe	571	1	1.1	3	4.6	7.0	lobster	472	2	1.4	4	6.6	7.0
grape	591	1	0.0	1	4.1	5.0	microscope	493	3	2.2	9	7.8	10.0
hamburger	-	3	1.8	6	4.3	9.0	monkey	531	2	3.9	50	8.5	6.0
jacket	596	2	3.8	43	4.3	6.0	octopus	370	3	1.1	3	6.1	7.0
kite	597	2	1.8	6	4.4	4.0	ostrich	358	2	1.4	4	6.7	7.0
knife	573	1	3.8	45	4.3	5.0	package	497	2	3.0	21	6.1	7.0
leaf	556	1	1.1	3	4.8	4.0	pelican	-	3	1.1	3	6.8	7.0
lion	511	1	3.3	26	4.3	4.0	pipe	535	1	3.5	32	6.4	4.0
mirror	593	2	3.9	50	4.1	6.0	pliers	499	2	0.7	2	7.7	6.0
pea	524	1	0.0	1	4.4	3.0	pyramid	386	3	2.1	8	6.9	7.0
pencil	598	2	3.0	20	4.1	6.0	razor	511	2	2.3	10	7.3	5.0
present	569	2	2.9	18	4.1	7.0	scarf	-	1	2.6	13	6.1	5.0
pumpkin	-	2	1.1	3	4.2	7.0	soldier	517	2	4.4	84	6.3	7.0
rabbit	523	2	3.0	20	4.0	6.0	statue	444	2	3.2	24	6.4	6.0
rainbow	431	2	2.1	8	4.3	7.0	syringe	-	2	2.8	17	9.5	7.0
sandwich	-	2	0.0	1	4.1	8.0	thread	522	1	1.9	7	6.2	6.0
sink	599	1	2.8	16	4.2	4.0	tomb	450	1	3.1	22	8.1	4.0
sled	-	1	0.7	2	4.9	4.0	trumpet	490	2	2.2	9	6.7	7.0

spider	526	2	2.1	8	4.3	6.0	vase	563	1	2.1	8	6.0	4.0
strawberry	539	3	1.9	7	4.0	10.0	vest	472	1	2.1	8	6.4	4.0
tail	533	1	3.6	37	4.2	4.0	volcano	461	3	1.9	7	6.3	7.0
telephone	605	3	4.7	106	4.3	9.0	waiter	-	2	3.1	23	6.8	6.0
towel	570	2	3.1	23	4.2	5.0	walnut	538	2	1.8	6	6.3	6.0
truck	620	1	3.6	37	4.0	5.0	wheat	510	1	3.4	30	7.1	5.0
turkey	-	2	1.8	6	4.3	6.0	whip	476	1	2.7	15	6.5	4.0
turtle	509	2	1.6	5	4.3	6.0	wig	518	1	2.6	14	7.0	3.0
wagon	443	2	2.5	12	4.2	5.0	windmill	368	2	2.3	10	6.6	8.0
wall	596	1	0	1	4.1	4.0	wrench	-	1	1.4	4	7.2	6.0
M	554.1	1.6	2.3	19.0	4.2	5.6	*M*	489.1	1.7	2.4	15.8	6.9	5.6

LEN Length in letters NSYL Number of syllables. LNFR Natural Log of Frequency (Celex) Fr Celex Frequency. AOA Rated Age of acquisition (Szekely et al., 2003) FAM Familiarity (Szekely et al., 2003). (Note that mean imageability values are based on 40 and 39 words for early and late learned words, respectively.)

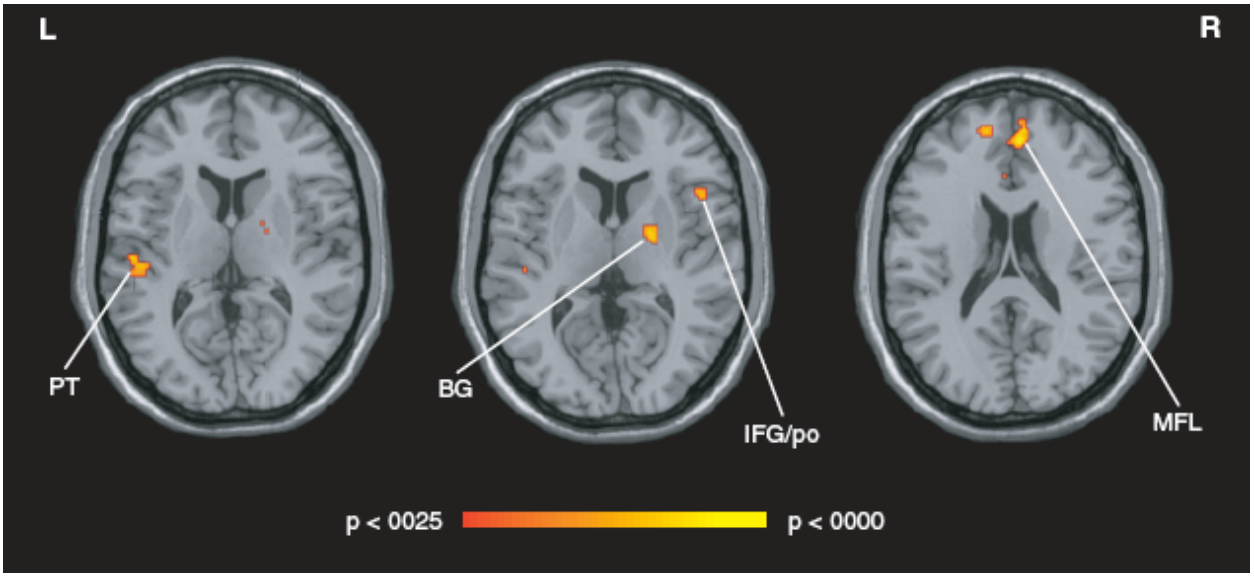
.

Table 1. Areas showing greater activity for late than for early acquired items. Coordinates given are in MNI space.

Region (Brodmann Area)	left					right				
	x	y	z	Z	mm^3	x	y	z	Z	mm^3
Superior Temporal Gyrus, anterior-middle portion of the planum temporale (BA 42)					128	---	---	---	---	---
	-52	-20	10	3.83						
Inferior Frontal Gyrus, pars opercularis (BA 44)	---	---	---	---	---					
						48	16	6	3.52	104
Superior Frontal Gyrus, pars medialis (BA 9)	---	---	---	---	---					
						6	46	20	4.01	168
Putamen	---	---	---	---	---					
						20	-10	6	3.6	168
Globus Pallidus	---	---	---	---	---					
						12	-4	2	3.91	128

Figure Caption

Figure 1. Brain areas showing greater activity for late than for early learned words. Increased activity for late learned words relative to early learned words is displayed on axial sections of a template brain from the Montreal Neurological Institute (Collins et al., 1994). For purposes of visualization, a statistical threshold of $p < .0025$ was applied. PT, planum temporale; BG, basal ganglia; IFG/op, deep portion of the pars opercularis of the left inferior frontal gyrus; MFL, medial frontal lobe.


L
R
PT
BG
IFG/po
MFL
p < 0025
p < 0000