

Traces of vocabulary acquisition in the brain: Evidence from covert object naming

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One of the strongest predictors of the speed with which adults can name a pictured object is the age at which the object and its name are first learned. Age of acquisition also predicts the retention or loss of individual words following brain damage in conditions like aphasia and Alzheimer's disease. Functional Magnetic Resonance Imaging (fMRI) was used to reveal brain areas differentially involved in naming objects with early or late acquired names. A baseline task involved passive viewing of non-objects. The comparison between the silent object naming conditions (early and late) with baseline showed significant activation in frontal, parietal and mediotemporal regions bilaterally and in the lingual and fusiform gyri on the left. Direct comparison of early and late items identified clusters with significantly greater activation for early acquired items at the occipital poles (in the posterior parts of the middle occipital gyri) and at the left temporal pole. In contrast, the left middle occipital and fusiform gyri showed significantly greater activation for late than early acquired items. We propose that greater activation to early than late objects at the occipital poles and at the left temporal pole reflects the more detailed visual and semantic representations of early than late acquired items. We propose that greater activation to late than early objects in the left middle occipital and fusiform gyri occurs because those areas are involved in mapping visual onto semantic representations, which is more difficult, and demands more resource, for late than for early items.

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Introduction

Functional imaging studies of object naming have identified a number of brain areas involved in recognizing objects and producing their names (Murtha et al., 1999; Humphreys et al., 1999; Price, 2000; Tyler et al., 2004). Relatively few connections

have been made, however, between that literature and the extensive body of research on the factors that affect the speed and accuracy with which healthy adults can name pictures of objects, or with research on the factors that make objects easier or harder to name by patients with neurological disorders. The present study is concerned with the possible neural correlates of age of acquisition (AoA), a property of objects and their names that has been shown to be a strong predictor of the speed with which normal speakers can name pictures of objects and the probability that brain-injured patients will retain or lose the ability to name those objects.

Carroll and White (1973) were the first to provide evidence that, all other things being equal, early learned objects are named faster than later learned objects. That claim has since been supported by a large number of studies of object naming speed in English (e.g., Barry et al., 1997; Meschyan and Hernandez, 2002; Snodgrass and Yuditsky, 1996). For example, Ellis and Morrison (1998) used multiple regression to analyze naming response times (RTs) to 220 line drawings of familiar objects taken from Snodgrass and Vanderwart (1980) and Morrison et al. (1997). The measure of AoA for each object was the youngest age at which 75% of children could name that item (Morrison et al., 1997). AoA made a highly significant contribution to predicting naming speed (faster naming of earlier learned items). Word frequency (Celex; Baayen et al., 1993) also made a significant contribution. Effects of AoA on object naming speed have subsequently been reported in Spanish (Cuetos et al., 1999), Italian (Bates et al., 2001), Icelandic (Pind and Tryggvadóttir, 2002), French (Bonin et al., 2002), Greek (Bogka et al., 2003) and Dutch (Ghyselinck et al., 2004). Effects of AoA on object naming accuracy have also been reported in patients with a range of neuropsychological conditions. Better preservation of early than late acquired vocabulary has been observed in aphasia following left hemisphere stroke or other forms of brain damage (Cuetos et al., 2002; Ellis, in press; Nickels and Howard, 1995); also in Alzheimer's disease (Forbes-MacKay et al., 2005; Holmes et al., in press; Silveri et al., 2002), semantic dementia (Lambon Ralph et al., 1998) and following left anterior temporal lobectomy

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in patients with intractable mesial temporal lobe epilepsy (Bell et al., 2000).

A number of theories have been put forward to explain the genesis of AoA effects in object naming and a wide range of other tasks, including object decision, face naming, lexical decision, word naming and semantic categorization (see Juhasz, 2005, for a review). One possible explanation was offered by Ellis and Lambon Ralph (2000) who trained a simple, three-layer neural network to associate patterns expressed across the input units of the network with patterns expressed across the output units. Some ‘early’ patterns were entered into training from the outset while the introduction of other, ‘late’ patterns was delayed until the network had spent time learning the early patterns. Even after extensive training on early and late sets together, the early items had representations in the network that were superior to the representations of the late items. The benefit of being early acquired seems to arise because early changes to connection strengths (weights) in untrained networks are large whereas later changes become progressively smaller. Early items are able to configure the network into a shape that is optimal for representing those items. They do that by directing the large initial changes to connection strengths. Late items can generally only cause small changes to the connections, and if the late items seek to reconfigure the network into a form that is different from that which best suits the early items, those attempts at weight change will be resisted by the early items which continue to be experienced alongside the late ones. Damaging a network trained in this way produces a more deleterious effect on late than early items, providing a possible account of the effects of AoA in brain-injured patients (Ellis and Lambon Ralph, 2000). This account of AoA effects suggests that they will arise wherever neural networks (artificial or real) create associations between inputs and outputs. The effects will be particularly large when the associations (or ‘mappings’) between inputs and outputs are arbitrary and uncorrelated, as is the case for the association between an object and its name (Lambon Ralph and Ehsan, 2006). Hence, AoA effects appear to be larger in tasks that involve the arbitrary mappings of word forms onto meanings (e.g., object naming) than in tasks that involve predictable, correlated mappings (e.g., rapid word naming in alphabetic scripts; Bates et al., 2001; Juhasz, 2005; Monaghan and Ellis, 2001).

The mapping hypothesis implies that AoA could exert an influence whenever a brain area is involved in associating different representational systems, and hence could affect multiple loci in the brain. Other theories have sought to identify a single locus where AoA effects might originate. The fact that AoA effects were first identified in naming objects and reading words aloud led to the proposal that those effects might occur at the process of retrieving spoken word-forms (Brown and Watson, 1987; Gerhand and Barry, 1999). This view is still extant, though it is challenged by the presence of AoA effects in tasks which do not require overt or covert name retrieval (e.g., Moore et al., 2004; Holmes and Ellis, 2006). An alternative single-locus proposal is that the order in which concepts are acquired influences the structure of the developing semantic system with the result that AoA effects are greatest in tasks like object naming that require semantic representations to be accessed (Brysbaert et al., 2000). Steyvers and Tenenbaum (2005) showed how, in a growing semantic network, early acquired concepts may end up being more richly interconnected to other concepts in the network than is the case for later acquired concepts.

Three studies have looked for AoA modulated effects in brain responses, one using event-related potentials (ERPs) (Tainturier et al., 2005) and two using fMRI (Fiebach et al., 2003; Hernandez and Fiebach, 2006). Tainturier et al. (2005) employed an auditory lexical decision task, replicating previous reports of an AoA effect on reaction times (Turner et al., 1998). ERPs showed a classical N1/P2 complex potential for both words and nonwords, but this complex showed no sensitivity to AoA. In contrast, a later positive potential (P300) showed greater amplitude to words than to nonwords, and greater amplitude to early than to late acquired words.

Fiebach et al. (2003) reanalyzed data from a previous event-related fMRI study involving auditory and visual lexical decision that had originally been devised for examining word frequency effects (Fiebach et al., 2002). Behavioral data involving lexical decision RTs were also collected. When AoA values for the words were employed alongside frequency values, regression analyses found that visual lexical decision RTs were influenced by both AoA and frequency, being fastest for early acquired, high frequency words and slowest for late acquired, low frequency words. In the neuroimaging data for visual lexical decision, there was a tendency for low frequency written words to produce stronger activation in the left inferior frontal gyrus and in the left anterior insula when AoA was partialled out. When frequency was partialled out, there was reliable increased activity for early relative to late acquired written words in the precuneus bilaterally (BA 7) and there were indications of increased activity in the left temporal operculum, encompassing the middle portion of Heschl's gyrus (auditory cortex). In contrast, there was reliable increased activity for late relative to early words in the left inferior frontal gyrus (BA 45 and 47/12), extending into the anterior insula, as well as in the caudate nuclei of both hemispheres.

In the auditory lexical decision task, analysis of the behavioral data found that AoA was a significant predictor of RTs to words while the effect of word frequency was not significant, a similar pattern to that reported by Turner et al. (1998). No effects of word frequency were found in the neuroimaging data when AoA was entered as a covariate. When covarying for frequency, late acquired spoken words generated increased activity in the superior temporal gyri bilaterally. No significant differences in activity between early and late spoken words were found when the same level of significance threshold as used in the analysis of the visual lexical decision task was chosen. With a less conservative threshold, there was greater signal change in response to early words in the precuneus close to the site of activation observed in the visual lexical decision task. When the individual contrast images from the visual and auditory tasks were combined in a cross-modal random effects model, greater activation to early than late words was seen in the precuneus while greater activation to late than early words was seen in the left inferior frontal cortex and anterior insula.

In a subsequent study, Hernandez and Fiebach (2006) changed from visual lexical decision to word naming (pronouncing the words silently) and from the German to the English language. fMRI responses and word naming RTs were compared to early and late acquired words matched on frequency. Compared with a resting baseline, both early and late acquired words showed increased activity in the posterior–superior portion of the left inferior frontal gyrus extending into premotor cortex (BA 44/46) as well as in the pars triangularis of the inferior frontal gyrus (BA 45) and part of the middle frontal gyrus (BA 46). There was also bilateral activity in the precuneus and in the left inferior parietal lobule. When responses to early and late acquired words were

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