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Interactions between visual and semantic processing during object recognition revealed by modulatory effects of age of acquisition

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ABSTRACT

The age of acquisition (AoA) of objects and their names is a powerful determinant of processing speed in adulthood, with early-acquired objects being recognized and named faster than late-acquired objects. Previous research using fMRI (Ellis et al., 2006. Traces of vocabulary acquisition in the brain: evidence from covert object naming. NeuroImage 33, 958–968) found that AoA modulated the strength of BOLD responses in both occipital and left anterior temporal cortex during object naming. We used magnetoencephalography (MEG) to explore in more detail the nature of the influence of AoA on activity in those two regions. Covert object naming recruited a network within the left hemisphere that is familiar from previous research, including visual, left occipito-temporal, anterior temporal and inferior frontal regions. Region of interest (ROI) analyses found that occipital cortex generated a rapid evoked response (~75–200 ms at 0–40 Hz) that peaked at 95 ms but was not modulated by AoA. That response was followed by a complex of later occipital responses that extended from ~300 to 850 ms and were stronger to early- than late-acquired items from ~325 to 675 ms at 10–20 Hz in the induced rather than the evoked component. Left anterior temporal cortex showed an evoked response that occurred significantly later than the first occipital response (~100–400 ms at 0–10 Hz with a peak at 191 ms) and was stronger to early- than late-acquired items from ~100 to 300 ms at 2–12 Hz. A later anterior temporal response from ~550 to 1050 ms at 5–20 Hz was not modulated by AoA. The results indicate that the initial analysis of object forms in visual cortex is not influenced by AoA. A fastforward sweep of activation from occipital and left anterior temporal cortex then results in stronger activation of semantic representations for early- than late-acquired objects. Top-down re-activation of occipital cortex by semantic representations is then greater for early than late acquired objects resulting in delayed modulation of the visual response.

Introduction

Cognitive neuroscience has taught us a great deal about the neural basis of object naming and lexical processing. The broad structure of the underlying neural networks has been identified and accompanied by analyses of the functions of the different nodes in that network and their patterns of interconnectivity (see Cattinelli et al., 2013; DiCarlo et al., 2012; Martin, 2007; Price, 2012, for reviews). At the same time, a substantial body of work in cognitive psychology and psycholinguistics has shown that some objects and words are recognized and named consistently faster and with fewer errors than others, and has explored the contribution of factors such as age of acquisition, frequency, imageability and distinctiveness to generating those reliable differences (see Brysbaert and Cortese, 2011; Cortese and Schock, 2013; Davies et al., 2013; Juhasz, 2005). We know relatively little, however, about how such factors modulate neural processing. fMRI studies have helped to identify the brain regions whose activity levels are influenced by different properties of objects and words (e.g., Carreiras et al., 2006; de Zubicaray et al., 2012; Ellis et al., 2006; Graves et al., 2007; Zhuang et al., 2011), but exactly how and when those factors exert their influence remains poorly understood.

The present study was concerned with identifying how and when object recognition and naming are affected by *age of acquisition* (AoA), one of the most powerful determinants of object and lexical processing speed in adults (Alario et al., 2005; Cuetos et al., 1999; Ellis and Morrison, 1998; Juhasz, 2005; Lagonaro and Perret, 2011; Monaghan and Ellis, 2010). The benefits of early learning in object and word recognition are consistent across both participants and languages, and are

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observed over and above the contributions of other factors such as object familiarity and word frequency (Ghyselinck et al., 2004; Izura et al., 2011; Pérez, 2007). In the only previous neuroimaging study of AoA effects in object recognition, Ellis et al. (2006) presented pictures of early and late acquired objects to participants for covert naming. Functional MRI identified two regions where BOLD responses were stronger to early- than late-acquired objects — the left temporal pole and visual cortex at the occipital pole. The left anterior temporal region has been associated with the representation of concepts abstracted from perceptual and action-based experience (Patterson et al., 2007; Visser et al., 2010). The discovery of an AoA effect at this location is compatible with suggestions that early-acquired semantic representations are richer and more densely interconnected than later acquired semantic representations (Belke et al., 2005; Brysbaert et al., 2000; Steyvers and Tenenbaum, 2005). Neuropsychological studies have found that damage to anterior left temporal regions results in an impairment of object naming that is more severe for early- than late-acquired objects (Lambon Ralph et al., 1998; Woollams, 2012; Woollams et al., 2008), providing further evidence for an influence of AoA at the left temporal pole.

The observation by Ellis et al. (2006) that posterior occipital activity is also modulated by AoA during object naming was unexpected. It has, however, been argued that AoA may have effects at multiple loci within the object and word processing systems, and that one of those loci may be the perceptual analysis of visual object features (Brysbaert and Ghyselinck, 2006; Hernandez and Li, 2007; Holmes and Ellis, 2006; Johnston and Barry, 2005; Navarette et al., 2013). For example, Catling et al. (2008) found that overlaying irrelevant contours on object pictures increased the magnitude of the AoA effect on naming speed and argued that this reflected a perceptual component in the AoA effect on object recognition (see also Catling and Johnston, 2009).

One way that AoA might come to have effects at multiple loci is if its influence lies in the way that patterns of association ("mappings") between representations develop over time. Ellis and Lambon Ralph (2000) trained an artificial (connectionist) network to associate patterns expressed across input units with patterns expressed across output units. Some pairs of associated input and output patterns ("early items") were introduced at the start of training while others ("late items") were only introduced after the network had spent some time learning the early pairs. The frequency with which early and late items were trained was varied, making it possible to demonstrate that the mature network showed an advantage for representing the early items compared with the late items that could not be explained in terms of differences in frequency of exposure but seemed to be related to changes over the course of training in the plasticity of the network. Those effects are greater when the relationships between input and output representations are arbitrary and unpredictable than when they are consistent and reliable (Lambon Ralph and Ehsan, 2006; Monaghan and Ellis, 2010). Some of the mappings between the visual features of objects and other aspects of semantic knowledge are relatively predictable. For example, animals tend to have eyes, ears, legs, rounded outlines and soft, non-shiny surfaces while man-made objects are more likely to have straight edges, sharp corners and hard, shiny surfaces. There are numerous exceptions to those generalizations, however, and some semantic knowledge does not derive predictably from visual features (e.g., Is an animal wild or domesticated? Is a berry edible or poisonous? Is a man-made object normally found inside or outside the house?). Inconsistent or unpredictable aspects of the mappings between visual features in occipital cortex and semantic knowledge in anterior temporal cortex should create the conditions required for AoA effects to arise. We note in this context that Johnston and Barry (2005) found AoA effects on reaction times (RTs) in a behavioral task that required adult participants to decide whether pictured objects were typically found inside or outside the house. The relations between objects and their names are, of course, arbitrary (Monaghan et al., 2011), so large AoA effects would be expected in naming tasks (Alario et al., 2005; Cuetos et al., 2009; Ellis and Morrison, 1998).

Woollams (2012) found that object naming by semantic dementia patients with anterior temporal damage was influenced by both AoA and the typicality or distinctiveness of depicted objects. In a second study, naming latencies to pictured objects were measured in healthy adult participants before and after the application of repetitive transcranial magnetic stimulation (rTMS) to the left anterior temporal region. Naming latencies post-TMS showed an impact of typicality (slower to distinctive than typical objects) that was not apparent before stimulation. In contrast, the impact of AoA on naming latency after TMS was as strong as before TMS. Woollams (2012) proposed that these findings could be explained if typicality exerts its effects within the semantic representations in anterior temporal cortex (e.g., by virtue of the fact that typical concepts share more semantic features with other concepts than distinctive concepts do) while AoA effects arise in the mappings between visual and semantic representations.

Visual processing in occipital cortex and semantic processing in anterior temporal cortex can be seen as lying at opposite ends of a 'ventral stream' that is concerned with individuating and identifying objects and is distinct from a dorsal stream that is more concerned with attention and action (Goodale and Milner, 1992; Ungerleider and Mishkin, 1982; see Cloutman, in press; DiCarlo et al., 2012; Martin, 2007, for reviews). Early visual areas (V1, V2 and V3) project to area V4 which provides input to ventral processing routes that project to posterior, central and anterior temporal regions. Part of that processing involves creating visual representations that preserve object identity across transformations of position, scale, pose, etc. The ventral stream culminates in anterior temporal cortex where, according to one view, visual information is combined with inputs from other sensory modalities, along with action-based and functional knowledge, to create amodal semantic representations of objects and concepts that bring together information that is otherwise distributed around modality-specific regions of the brain (Patterson et al., 2007; Visser et al., 2010).

The present study used magnetoencephalography (MEG) to explore the modulatory effects of AoA at the occipital and anterior temporal ends of the ventral stream during object recognition and naming. As Laaksonen et al. (2012) observed, previous MEG studies of object naming have converged upon the proposal that cortical activity during object recognition and naming begins with a strong but transient occipital response (<200 ms) which is not always reflected in the BOLD signal, possibly because of its brief duration. That short-lived occipital response is followed by more sustained responses in parietal and temporal regions (>200 ms) and in prefrontal cortex (>300 ms) (Hultén et al., 2009; Indefrey and Levelt, 2004; Liljeström et al., 2009; Maratos et al., 2007; Salmelin et al., 1994; Sörös et al., 2003; Vihla et al., 2006). Laaksonen et al. (2012) also noted, however, that previous MEG studies of object recognition and naming have used analysis methods sensitive only to phase-locked (evoked) responses. Laaksonen and colleagues reanalyzed three previous MEG studies of object recognition and naming (Hultén et al., 2009; Liljeström et al., 2009; Sörös et al., 2003; Vihla et al., 2006) using methods sensitive to either phase-locked responses (equivalent current dipole modeling and minimum norm estimation) or event-related modulations of spontaneous rhythmic activity (event-related Dynamic Imaging of Coherent Sources; Laaksonen et al., 2008). The analysis of evoked responses produced a similar pattern to the one noted above, with a transient response in visual cortex (<200 ms) followed by more sustained occipital activation and a salient parietal response with activation of temporal and frontal cortices after ~300 ms. Modulation of rhythmic activity (induced responses) tended to be more long-lasting and was observed in visual and motor cortices; also in parietal and superior temporal regions. Overlap between sources of evoked responses and rhythmic activity was relatively limited, on the basis of which Laaksonen et al. (2012) concluded that evoked responses and cortical rhythms may provide complementary information about neural processing in high-level cognitive tasks.