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Age-related changes in feature-based object memory retrieval as measured by event-related potentials

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ABSTRACT

To investigate neural mechanisms that support semantic functions in aging, we recorded scalp EEG during an object retrieval task in 22 younger and 22 older adults. The task required determining if a particular object could be retrieved when two visual words representing object features were presented. Both age groups had comparable accuracy although response times were longer in older adults. In both groups a left fronto-temporal negative potential occurred at around 750 ms during object retrieval, consistent with previous findings (Brier, Maguire, Tillman, Hart, & Kraut, 2008). In only older adults, a later positive frontal potential was found peaking between 800 and 1000 ms during no retrieval. These findings suggest younger and older adults employ comparable neural mechanisms when features clearly facilitate retrieval of an object memory, but when features yield no retrieval, older adults use additional neural resources to engage in a more effortful and exhaustive search prior to making a decision.

1. Introduction

Many aspects of semantic memory are separable from the neural systems and mechanisms that underpin episodic and procedural memory (Binder & Desai, 2011; Martin, 2007; Tulving, 1972). Several current models of semantic memory are supported by evidence indicating that an object is represented in multiple neural systems that are closely related to those systems activated originally upon experiencing the features of that object (Allport, 1985; Hart & Gordon, 1992; Martin, 2007; Martin & Chao, 2001). Features associated with objects, either living or non-living things, typically span multiple sensorimotor and cognitive domains and are an essential part of object representation (Goldberg, Perfetti, & Schneider, 2006; Hart et al., 2007; Kellenbach, Brett, & Patterson, 2001; Noppeney & Price, 2002). For example, a lion can be linked to more concrete features such as its roar and mane as well as to more abstract features such as being threatening (Kraut, Kremen, et al., 2002; Kraut, Moo, Segal, & Hart, 2002; Kraut, Pitcock, et al., 2006).

Since features are represented in a distributed fashion in the brain (Binder & Desai, 2011; Hart et al., 2007; Martin & Chao, 2001), one would expect age-related functional and/or structural alterations, including changes in the white matter that mediates synchronized connectivity between different brain regions (Grady, 2012; Hedden & Gabrieli, 2004), to affect long-range communication demanded by memory retrieval from this distributed representation. However, semantic memory, unlike other cognitive functions such as episodic memory, attention, and executive function, does not seem to undergo as much change with age (Levine, Svoboda, Hay, Winocur, & Moscovitch, 2002; Li et al., 2004). How then does the neural mechanism support semantic memory in normal older adults such that only minimal age-related changes are noticeable?

Our goal in this study is to examine how age affects semantic memory retrieval by studying younger and older adults using EEG, a non-invasive tool which provides a high temporal resolution measure of neural activity (Kiefer & Pulvermüller, 2012; Luck, 2005; Luck & Kappenman, 2012). We used the Semantic Object Retrieval Task (SORT), which examines how objects are retrieved via explicit evaluation of object-associated features (Kraut, Cherry, et al., 2006;

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Kraut, Kremen, et al., 2002; Kraut et al., 2007). For example, in the SORT paradigm, presenting the features "humps" and "desert" normally facilitates retrieval of "camel". By eliciting the process of combining these features that are represented across the brain to retrieve an object memory, we could untangle the dynamic neural mechanisms that operate to integrate object features to form a coherent object representation. The SORT task has been applied as an effective measure to detect impairment in lexico-semantic memory retrieval in various clinical populations and thus serves a useful task to examine age-related changes in retrieval (Mild Cognitive Impairment, MCI, and Alzheimer's disease, AD: Kraut, Cherry, et al., 2006; Kraut et al., 2007; schizophrenia: Assaf, Rivkin, et al., 2006; Gulf War Illness: Calley et al., 2010; aging effects of concussion in former professional football athletes: Hart, Kraut, et al., 2013).

Successful performance in the SORT requires successful retrieval of semantic object memory. Data from previous activation, brain stimulation, and lesion studies suggest that the retrieval process of semantic memory involves the left inferior frontal gyrus (IFG) with its sub-regions subserving semantic selection and controlled retrieval (Badre & Wagner, 2002; Thompson-Schill et al., 1998; Whitney, Kirk, O'Sullivan, Lambon Ralph, & Jefferies, 2012). Other areas that may also assist in semantic memory retrieval localize to the left angular gyrus (AG) and left poster middle temporal gryus (MTG) (Noonan et al., 2013; Whitney et al., 2012). In addition to these regions, activation studies on the SORT have shown object memory retrieval elicited increased BOLD signal in the pre-supplementary area (pre-SMA) of the medial frontal cortex, caudate, and thalamus (Assaf, Calhoun, et al., 2006; Kraut, Calhoun, Pitcock, Cusick, & Hart, 2003; Kraut, Kremen, et al., 2002; Kraut, Moo, et al., 2002). Lesion studies using the SORT have shown relatively selective deficits in object memory retrieval compared to other semantic memory tasks (e.g., category, association) in patients with localized thalamic strokes (Pergola et al., 2013; Segal, Williams, Kraut, & Hart, 2003). Based on these findings, Hart, Maguire, et al. (2013) proposed a central role of the pre-Supplementary Motor Area (pre-SMA)-thalamus-caudate circuit in mediating the semantic memory retrieval process, especially in tasks such as the SORT that involves feature integration, as part of the Neural Hybrid Model of semantic memory (Hart et al., 2007; Hart, Maguire, et al., 2013).

An ERP study of young adults using the SORT showed a left fronto-temporal component starting at around 750 ms post-stimulus that was more negative in retrieval than non-retrieval stimulus pairs (Brier, Maguire, Tillman, Hart, & Kraut, 2008). A power analysis of the EEG changes during the SORT showed earlier alpha desynchronization (8–12 Hz)/delta synchronization (~1 Hz) as well as later frontal beta synchronization (20–35 Hz, after one second post-stimulus), which were posited to represent semantic search and object retrieval, respectively (Ferree, Brier, Hart, & Kraut, 2009; Hart, Maguire, et al., 2013). Moreover, Slotnick, Moo, Kraut, Lesser, and Hart (2002) recorded intra-thalamic electrical activity while a patient was performing the SORT task and found beta synchronization at long latency in both thalamic hemispheres time-locked to stimulus. This 750 ms ERP component appears later than typical N400, a negative scalp evoked potential considered to be a marker of semantic processing that peaks at about 400 ms post-stimulus onset in response to semantic/contextual incongruity (Kutas & Federmeier, 2000; Kutas & Hillyard, 1980).

The majority of the previous ERP studies involving the N400 effect have used tasks based on semantic priming, contextual constraints, etc. (Kutas & Federmeier, 2000; Wlotko, Lee, & Federmeier, 2010). Most of these tasks do not mandate retrieval of a specific concept (e.g., objects) but are related to processing of meaning, inquiring about category or semantic relatedness between stimuli (probed as individual words/pictures or in the context of a sentence; Kiefer, 2001; Kutas & Hillyard, 1980). Tasks based on priming do not even require direct (explicit) evaluation of semantic information. For example, subjects are asked to judge if the second stimulus is a real word or not, while the relations between the first (prime) and second stimuli (target) are manipulated to examine priming effects due to semantic association, category, etc. (Holcomb and Anderson, 1993; Kiefer, 2005). The SORT task is characteristically different from these noted above in that participants are required to directly evaluate whether the features result in retrieval of an object memory or not and to indicate so by making an explicit response. In terms of the neural basis of semantically-based ERPs, N400 is most consistently associated with access to semantic memory storage represented in the temporal regions such as the left MTG, inferior temporal gyrus, and anterior medial temporal lobe (Lau, Phillips, & Poeppel, 2008; McCarthy, Nobre, Bentin, & Spencer, 1995; Nobre & McCarthy, 1995). On the other hand, the semantic retrieval process is more strongly associated with longer latency waveform characteristics ("post-N400 positivity", Van Petten & Luka, 2006), especially in the case of semantic selection and effortful retrieval, which may involve frontal areas such as the left IFG (Lau et al., 2008; Van Petten & Luka, 2006). FMRI findings on the SORT (Assaf, Calhoun, et al., 2006; Kraut, Kremen, et al., 2002) also support this contention, finding that only object memory retrieval (during the SORT) elicited increased signal in the bilateral inferior frontal gyri, pre-SMA, caudate, and thalamus, whereas both SORT and object association (i.e., semantic association judgment) elicited increased BOLD in left MTG, angular gyrus, and inferior temporal gyrus. These findings suggest that the ERP marker related to the SORT task involves frontal (pre-SMA, left IFG) and/or temporal (left MTG, inferior temporal) semantic systems that are engaged in semantic selection and integrative retrieval processes.

Other late ERP effects that occur after the N400 time window, such as P600, a positive deflection occurring at around 600 ms post-stimulus onset, have been suggested to be associated with other semantic related processes such as processing sentences with conflicting semantic structure (Bornkessel-Schlesewsky & Schlesewsky, 2008), with conflicting thematic structures (Kuperberg, 2007; Kuperberg, Sitnikova, Caplan, & Holcomb, 2003), and with incongruous syntactic structures (Van Petten & Luka, 2012). These late components have been dissociated from N400 in some experiments, thus suggesting their functional roles different from N400 (Kuperberg, 2007). Also, these late effects are not exclusive to sentence-level processing or verbal content, and have also been observed when stimuli are single words (Hill, Strube, Roesch-Ely, & Weisbrod, 2002; Meyer & Federmeier, 2007; Swaab, Brown, & Hagoort, 1998) or pictures (Ganis & Kutas, 2003; McPherson & Holcomb, 1999; Mudrik, Lamy, & Deouell, 2010; Sitnikova, Holcomb, Kiyonaga, & Kuperberg, 2008).

ERP studies that have examined the effects of age on lexico-semantic tasks have shown varying age-related effects on several components. General findings include delayed N400 latency and/or decreased N400 amplitude as well as difference in lateralization due to age (Federmeier & Kutas, 2005; Giaquinto, Ranghi, & Butler, 2007; Kutas & Iragui, 1998) with some exceptions (Grieder et al., 2012). In terms of later components, prior studies have observed attenuated amplitude (Meyer & Federmeier, 2010) and qualitative changes in scalp distribution (Galdo-Alvarez, Lindín, & Díaz, 2009; Harbin, Marsh, & Harvey, 1984) in older adults. The reason for these variable findings in age-related effects might reflect variations in task designs. It has been posited that older adults may recruit a decreased amount of neural resources when message-level or executive processing is required, but they can still show comparable activity at word-level processing compared to younger adults (Federmeier, van Petten, Schwartz, & Kutas, 2003; Wlotko et al., 2010). Therefore, in view of the word stimuli used in the SORT, we hypothesized that older adults would present differences