Doctoral Dissertation

INHIBITORY MECHANISMS IN FACE-NAME RETRIEVAL: DEVELOPMENTAL AND NEURAL INDICES

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1. INTRODUCTION

For a great number of years, researchers have shown that aging entails a general decline in cognitive functioning, with memory being one of the most affected functions. As people get older, they seem to have greater difficulty in remembering and finding words that they easily did in their 20s (Craik, 1994) and become more vulnerable to everyday forgetfulness (such as forgetting to attend a doctor's appointment, or forgetting where they have left their glasses). And not only do adults over 60 report more memory problems in everyday life situations (Cutler & Grams, 1988; Montejo, Montenegro, Fernández, & Maestú, 2012; Ryan, 1992), they also perceive themselves as having less control over their own memory than their younger counterparts (Dixon & Hultsch, 1983). Aditionally to these subjective reports, more objective measures have similarly shown that older adults perform worse in free recall and recognition tests (e.g. Craik & Jennings, 1992; Light, 1991) as well as in neuropsychological tests taping into memory (e.g. LaRue, 1992). Crucially for the scope of this work, previous research has also shown that elders' memory for names and faces of people is poorer than that of younger adults' (Bahrick, 1984; Cohen & Faulkner, 1986; Maylor, 1990).

Being of a social nature, an essential part of humans' life is meeting and interacting with other people. In order to do so, we often need to process and recognize other people's faces in our daily lives and to be able to retrieve information about them. This has a clear evolutionary role too, since it is crucial, for instance, to be able to distinguish our friends from our enemies. Even if face recognition seems like an easy task from a phenomenological point of view, it is remarkable how we are able to distinguish from a range of incredibly similar features (such as mouths, noses or eyes) the combinations that we recognize as being a friend's face, from that of a complete stranger. Thus, from a cognitive perspective, this is actually a rather demanding task, (Bruce & Young, 1986) and it seems to be rendered even more demanding as people age. In fact, naming difficulties are one of the complaints most oftenly reported by older adults (Lovelace & Twohig, 1990; Maylor, 1990).

Along with these subjective reports, empirical evidence has also shown age-related difficulties in face naming. Naveh-Benjamin and col. (2004) showed their participants 40 face-name pairs that they had to retrieve later. Participants were divided in three groups: young adults, older adults and young adults performing a concurrent task (besides the naming one). Results showed that when remembering faces and names separately, older participants performed almost as well as their younger counterparts, with the concurrent task having a greater effect on task performance than aging. Results were different, however, when testing for the recall of face-name associations. When asked to retrieve which name went with each face, older participants performed worse than both younger groups.

This inability to recall names of well-known people in their lives has a considerable impact for elders, since it generates a lack of self-confidence (Light, 1991), elicits negative moods and leads older people to underjudge their own linguistic capacities (Burke & Shafto, 2004). Furthermore, Pike et al. (2012) suggest that deficits in retrieving face-name pairs may help distinguishing between mild cognitive impairment (MCI) and healthy aging, which is especially relevant if we take into account the increased risk of people with MCI to develop Alzheimer's disease (Gauthier et al., 2006). Trying to understand the mechanisms that underlie these naming difficulties becomes then an extremely pertinent topic. The question is how can this age-related impairment be explained? What cognitive and brain changes occur as people get older?

One possibility has been put forward by Hasher and Zacks (1998). According to their Inhibitory Deficit Theory (IDT), most of the age-related cognitive losses, in processes such as memory or attention, are caused by an underlying deficit in inhibitory mechanisms. Consequently, older people's naming difficulties could be due to an inability to suppress competing representations (such as someone's name) that makes it harder to access and choose the desired one (Lustig, Hasher, & Zacks, 2007). Could this inhibitory deficit then explain naming difficulties?

One way that inhibition has been studied is by means of the retrieval practice paradigm (Anderson, Bjork, & Bjork, 1994). In this paradigm, different stimuli are associated to the same cue, creating an interference situation when one of the stimuli needs to be retrieved. What is usually found is that competing items' recall is impaired at a final memory test. The authors propose that interference situations, as when several stimuli compete for retrieval, may be solved by means of inhibitory mechanisms that come into play in these situations to suppress competitor items and promote retrieval of the correct response (Anderson, Bjork, & Bjork, 1994). Importantly, studies investigating how the effect found in this paradigm is affected by aging have shown that it can be reduced as people get older (depending on factors such as age itself and available cognitive resources; see section 1.1) which corroborates the IDT.

It seems as though this could then be the mechanism impaired in face-name retrieval. However, literature has often considered personal representations, such as faces or names, to enjoy a special status in cognition. Concretely, it is thought that these representations are not always subject to the same mechanisms as other objects (e.g. Farah, 1996; Haxby, Hoffman, & Gobbini, 2000; McKone, Kanwisher, & Duchaine, 2006) and that our brain is fine tuned to perceive and recognize them differently than other types of stimuli (e.g. Kanwisher, 2000). Moreover, several face recognition models have been put forth to explain this phenomenon (e.g. Brèdart, Valentine, Calder, & Gassi, 1995; Bruce & Young, 1986; Burton, Bruce, & Hancock, 1999; Burton, Bruce, & Johnston, 1990), and consider specifically how we go about recognizing faces, but not other objects. It is then unclear whether inhibitory mechanisms could also be involved in face recognition and naming, as they seem to in naming other stimuli, and explain difficulties reported by older adults. If faces are processed differently, do they also suffer from interference?

Importantly for the scope of this work, models of face recognition do assume that when a person attempts to recognize a face competition may arise between other faces that share either perceptual features or semantic information with the to-be-recognized one (e.g. Bruce & Young, 1986; Burton et al., 1990). However, these models either do not give detailed explanations of how this interference is overcome or propose a rather automatic mechanism to deal with competition. But could interference amongst personal representations be solved by the same inhibitory mechanisms as those proposed by the IDT and thus help explaining naming difficulties expressed by elders?

In order to be able to better answer this question, we first need to understand how memory in general, and inhibitory capacities specifically, change as a function of aging. Then, we can focus on face and name processing and recognition, as one of the most reported complaints in older people are their difficulties retrieving personal representations (Lovelace & Twohig, 1990; Maylor, 1990).

1.1. How does memory change with normal aging?

Across life span, memory functions that are essential to a great range of aspects in our lives change considerably. These changes entail a general deterioration of general aspects in memory as people get older: older people report having significantly more memory problems than young (Cutler & Grams, 1988; Ryan, 1992) and perceive having less control over their own memory (Dixon & Hultsch, 1983). Though these subjective reports corroborate several stereotypes about aging, Rabbit and Abson (1990) claim they may be more closely related to the elderly being more vulnerable to a state of depression, and might not accurately reflect their actual memory capacities. Thus, one should perhaps take into account more objective measures of memory performance, and studies over the past decades have been doing just so. Interestingly, these empirical studies have gone in the same direction as subjective reports, showing that aging makes people more vulnerable to everyday forgetfulness (e.g. Craik, 1994).

What some of these studies put in evidence, however, is that though memory does suffer from aging in general, different memory systems suffer differently from it. Decline in working memory, for instance, has been shown to be rather small, using measures of both digit span (Parkinson, Inman, & Dannenbaum, 1985) and visuo-spatial span (Spinnler, Della Sala, Bandera, & Baddeley, 1988). Similarly, semantic memory seems rather unaffected by aging, and can even increase in older adults, when using vocabulary measures (Giambra, Arenberg, Zonderman, & Kawas, 1995). In the same line, initial studies on prospective memory found no evidence for age related impairments (Einstein & McDaniel, 1990), though these were later questioned by research showing preservation of event-related but not of time-based prospective memory tasks (Einstein, McDaniel, Richardson, Guynn, & Cunfer, 1995), or even a general aging impairment (e.g. Cockburn & Smith, 1991; Maylor, 1996).

One system that does reunite some consensus is episodic memory, which does seem to suffer dramatically from aging.

This impairment occurs not only in experiments within a somewhat artificial laboratory setting, but also in studies using more ecological materials that mimic everyday life memory situations (e.g. Salthouse, 1991; Wilson, Cockburn, Baddeley, & Hiorns, 1989). The extent of this deterioration may be modulated by factors such as the person's own processing capacity or the environmental support given to subjects during retrieval, with age effects being more clear in free recall tasks (where there are no external clues), in comparison to cued retrieval and in these more than in recognition tests (Craik, Byrd, & Swanson, 1987).

In any case, impairments in episodic memory largely affect the lives of elderly individuals and it is important to try to understand what underlies this deterioration. Several theories have tried to explain this cognitive decline. These theories, such as the Processing Speed (Salthouse, 1996) or the Inhibitory Deficit Theory (Hasher & Zacks, 1988), propose a common mechanism that accounts for cognitive losses. The first posits that a decline in processing speed is the cause of the overall worse performance usually found with older adults, whilst the second, claims that a deficit in inhibitory function is the cause for this impairment. We will focus on the inhibitory theory, which has received wide empirical support, over the following paragraphs.

Aging and inhibition

As previously described it is now widely known that cognitive function is altered with aging (e.g. Raz, 2000), not only within the frame of dementia, but also in normal healthy aging. One of the theories that attempts to explain this cognitive decline is the Inhibitory Deficit Theory (IDT; Hasher & Zacks, 1988), which proposes that a deficit in inhibitory mechanisms underlies the general cognitive losses, across different domains, observed in aging. Revisiting their theory, Lustig, Hasher, and Zacks (2007) propose three different functions of inhibition. Inhibition's first function would be set in an early stage of the processing stream, and would serve to control access to the attention's focus, namely preventing irrelevant information from getting access to it. In accordance to this proposal, Gazzaley, Cooney, Rissman, and D'Esposito (2005) compared three conditions where participants had to attend, ignore or passively view stimuli on the screen. They found that whereas young participants showed a great reduction of activation when comparing the "ignore" to the "passive view" conditions, older adults showed about the same degree of activation on both. Importantly, older adults had no problem in increasing activation for relevant information, as shown by the greater activation in the "attend" condition in comparison to the "passive view". Furthermore, it was the extent to which they were able to reduce activation in the ignore condition, and not the degree to which they increased activation in the attend one, that predicted memory performance. Thus, there seems to be an age-related deficit specific to preventing irrelevant information from accessing attention.

A second function of inhibition would be to delete irrelevant information that a) eluded the first access function, or b) is no longer relevant and thus should be erased from working memory (Lustig et al., 2007). In fact, research has shown that older adults seem to produce more no-longer-relevant information (e.g. May, Zacks, Hasher, & Multhaup, 1999; Zacks, Radvansky, & Hasher, 1996) than younger and that age differences in working memory span may not depend on the size of the mental workspace *per se*, but rather on the ability to keep irrelevant information out of it, in order to use it more efficiently (e.g. Friedman & Miyake, 2004), which further supports this function of inhibition.

Finally, the third and last inhibitory function would be to suppress strong but inappropriate responses (Lustig et al., 2007), in order to make room for more adaptive ones. Note that this function of inhibition is well in line with that proposed by Anderson et al.'s (1994), discussed in section 1.2. This function too seems to be compromised in older adults. Namely, classic paradigms that study inhibition, such as the Go/No Go or the

Stop Signal paradigms have consistently found older adults to perform worse in these tasks (e.g. Bedard, Nichols, Barbosa, Schachar, Logan, & Tannock, 2002). Importantly for the scope of this work, this inhibitory deficit has been seen not only in motor tasks such as those mentioned above, but also in presumably parallel memory tasks.

Anderson and Green (2001) developed a paradigm similar to Go/No Go, which they named Think/No Think (TNT) paradigm that taps onto the voluntary or motivated forgetting of memories. In this paradigm, participants are asked to memorize word pairs, and in a second phase, when prompted with the first word of the pair they are asked to either retrieve or suppress the associated word. What has been consistently found with younger adults is that suppress items are recalled significantly worse than control ones (e.g. Anderson et al., 2001, 2004; Benoit & Anderson, 2012; Depue, Curran, & Barrich, 2007; Hanslmayr, Leipold, Pastötter, & Bäuml, 2009), showing that we are able to willingly inhibit information that we no longer wish to recall. This however, seems not to be the case for older adults, who show no suppression effect in a standard version of the TNT paradigm (Anderson, Reinholz, Kuhl, & Mayr, 2011; but see Murray, Anderson, & Kesinger, 2015). Additionally, studies in Directed Forgetting (DF), another paradigm looking into voluntary memory suppression, have also shown impaired performance for the elders (Sahakyan, Delaney, & Goodmon, 2008). Aguirre, Gómez-Ariza, Bajo, Andrés and Mazzoni (2014) showed that the forgetting effect was conserved when using the standard DF, but that when employing a more refined paradigm such as the Selective Directed Forgetting (Delaney, Nghiem, & Waldum, 2009), older adults were not able to selectively forget a set of no longer relevant information.

More research on the effects of aging has been conducted using the retrieval practice paradigm (Anderson et al., 1994). Differently from the aforementioned paradigms, the type of forgetting produced in retrieval practice is involuntary, and mainly incidental. Interestingly, this type of incidental forgetting resembles more closely a number of everyday situations that older adults go through whenever in need of recalling a desired target (e.g. a grandchild's name) between a set of potential competitors (e.g. the names of all the other grandchildren). Results point towards a weakened Retrieval-Induced Forgetting effect (RIF; see section 1.2) in older adults. RIF effect has been said to depend on controlled inhibitory mechanisms, and thus, the Inhibitory Deficit Theory would predict this effect to disappear in elders. Studies have shown that RIF is indeed hindered in older people, but that there are a few factors which modulate this diminished effect. Both Aslan and Bäuml (2012) and Marful, Gómez-Amado, Ferreira, and Bajo (2015) found that RIF can be preserved in younger old adults (under 75 years old), but disappears in a sample of older old adults (over 75 years old). Thus, even though this supports the appearance of an inhibitory deficit with aging, this deficit may not be visible or measurable with the retrieval practice paradigm until a very old age.

Another important factor is the amount of cognitive resources available. A study by Ortega, Gómez-Ariza, Román, and Bajo (2012) revealed that RIF effect was preserved in older adults when using a standard retrieval practice paradigm, but that the effect disappeared in older (but not in young) participants when an additional task was introduced.

Notably, all of these effects have been shown to be impaired in populations with inhibitory deficits (Go/No Go and Stop Signal: Aron, Robins, & Poldrack, 2004; TNT: Catarino, Kupper, Werner-Seidler, Dalgleish, & Anderson M.C., *in press*; Depue, Burgess, Willcutt, Ruzic, & Banich, 2010; RIF: Soriano, Jiménez, Román, & Bajo, 2009a; Román, Soriano, Gómez-Ariza, & Bajo, 2009; DF: Conway & Fthenaki, 2003; Harnishfeger & Pope, 1996; Soriano, Jiménez, Román, & Bajo, 2009b), which supports the assumption that this could be the underlying mechanism impaired in older adults. We argue that this impairment is responsible for difficulties reported by older people not only in memorizing new names, but also in recalling names of well-known people in their lives.

Further support for the IDT comes from the fact that paradigms used to measure inhibition have been shown to depend on prefrontal brain structures, which are known to be significantly altered in older adults. Thus, we now discuss age-related alterations in the brain.

Aging and the brain

As people get older, the brain undergoes a great number of changes. These changes occur at several different levels such as neurochemical (e.g. Baltes, Lindenberger, & Staudinger, 2006; Dixon, Wahlin, Maitland, Hultsch, Hertzog, & Bäckman, 2004), anatomical (e.g. Simons & Spiers, 2003; Raz, 2005) or functional (e.g. Cabeza, 2002; Johnson, 2001) and play a relevant role in cognition, correlating with a decay in executive function.

At a neurochemical level, for instance, there are changes in neurotransmitters availability (Werkle-Bergner, Müller, Li, & Lindenberger, 2006), such as in the dopamine systems (Bäckman, Nyberg, Lindenberger, Li, & Farde, 2006). Dopamine is a neurotransmitter that positively correlates with cognitive performance, and Bäckman et al. have reported age-related dopamine losses at different neural and molecular *loci*:

dopamine reduction in the *substantia nigra;* reduction of the number of synapses across the brain and loss of the number of proteins *per* cell. Interestingly, Bäckman et al. (2000) found a substantial correlation between the levels of dopamine in the brain and performance on episodic memory tasks. This correlation accounted for 38% of variance in performance in a word recognition task, and for 48% of the variance in a face recognition one. Age entails metabolic changes as well. Pardo et al. (2007), showed a decrease of glucose uptake with aging, especially in anterior cingulate cortex (ACC), medial prefrontal cortex, basal forebrain and dorsomedial thalamus. This decrease in glucose uptake correlated with a decline in measures of cognitive performance.

Neuroanatomical changes are perhaps the most studied ones. Anatomically, the aging brain is known to lose overall volume. Moreover, gray and white matter densities decline in many brain regions; ventricular size increases as well as neuronal death and there is a loss of dendritic density (Werkle-Bergner et al., 2006), though these changes do not seem to affect the brain equally. For instance, though prefrontal cortex shows a steady linear decline from the moment a person reaches their mid 20s on, the hippocampus does not seem to suffer any aging effects up until a person's 50s, and the entorhinal cortex suffers minimal changes over the years (Werkle-Bergner et al., 2006).

Most neuroanatomical studies have focused on changes in prefrontal cortex, since atrophy in the frontal lobe has been closely linked to a decrement in cognitive function (e.g. Nielson, Langenecker, & Garavan, 2002; Raz, 2000). Building a bridge between function and anatomy, Cummins and Finnigan (2007), found altered frontal/ACC theta power in older adults, which they interpreted as an indicator of a disrupted network function, since theta oscillations are important for integrating different brain regions into coherent networks. Thus, they propose theta could be a neurophysiological marker of functional changes in cognitive networks.

Another EEG experiment (Werkle-Bergner et al., 2006) has shown an increase in phase coupling for older compared to younger adults. The authors interpreted it as a marker of functional dedifferentiation or of a general loss of inhibitory connections. However, results from fMRI studies (e.g. Cabeza, 2002) put forth yet another interpretation.

In his study, Cabeza (2002) found that prefrontal cortex activity is less lateralized, that is, more bilateral, in older than in young adults (Hemispheric Asymmetry Reduction in the OLD, or HAROLD model). According to Cabeza, older adults recruit both hemispheres in order to counteract neurocognitive deficits and maintain performance levels. Reuter-Lorenz et al.'s (2000) results support this claim, by finding that greater left hemisphere activation in seniors (compared to younger adults), particularly in posterior areas, was associated with better performance. Thus, our brain could respond to age-related changes in anatomy by reorganizing its functions, that is, the brain could undergo a process of functional compensation.

This seems to occur especially in ventro-medial PFC (vmPFC). Cabeza and Dennis (2013) found that i) increased task related activation was observed in those with greater brain decline; ii) compensatory activity was associated with an increase in task demands and iii) this compensatory activity was positively associated with performance. Moreover, there was an increase in connectivity between vmPFC and parietal networks, as well as with dorsolateral prefrontal cortex. Taken together, these findings indicate that vmPFC and its connectivity to frontoparietal networks support successful compensation in older adults (Lightall, Huettel, & Cabeza, 2014). Interestingly, García-Pacios et al. (2013) have argued that this increased recruitment of prefrontal regions might be related with interference resolution as levels of interference increase.

In the present work, we aimed to assess whether inhibitory mechanisms of a controlled nature, used to reduce interference, could help explaining memory difficulties in aging. In order to do so, we sought for a paradigm that would mimic competition situations that elders go through in everyday life and that would require participants to solve this competition by means of a suppression mechanism dependent on the central executive. The retrieval practice paradigm seemed to fulfill both these requirements, and was thus used across four experimental series.

To our knowledge, how cognitive and brain changes associated with aging affect RIF has not yet been studied. Anatomical changes, namely shrinkage, in prefrontal cortex would predict that these areas might be less engaged in inhibitory tasks and thus, any alterations in the behavioral RIF effect in the elderly should be accompanied by less activation (in comparison to young adults) in ACC and prefrontal cortex. However, a different prediction could be drawn from the HAROLD model, that is, if participants were capable of functionally compensating these neuroanatomical changes, then prefrontal regions should be equally activated for both young and old adults, or even more so in the latter, and no impairment in the behavioral RIF effect should be found for older participants.

We offer a deeper explanation of this paradigm and its effect, as well as its known neural correlates in younger populations over the next section.

1.2. Controlled inhibition and the Retrieval-Induced forgetting effect

In the memory field interference has often been posit to arise whenever several items become associated to the same cue. When the cue is encountered, then all items become active and compete for retrieval (e.g. Anderson, Bjork, & Bjork, 1994). But how do we overcome these interference situations, that is, how is competition between stimuli solved?

One proposal made by Anderson et al. (1994), is that controlled (that is, dependent of the central executive) inhibitory mechanisms are responsible for dealing with competition between different representations. Inhibition is thought to reduce the level of activation of a given representation, preventing it from achieving threshold. In doing so, weaker but more appropriate responses can be made, enabling a more adaptive and context-sensitive behavior.

This type of controlled inhibitory mechanisms has consistently been studied by means of the Retrieval Practice paradigm (Anderson et al., 1994). The standard version of this paradigm consists of three different phases. During the first phase, participants are asked to study a list of word pairs semantically associated to a given category cue (e.g. FRUIT-Orange, FRUIT-Banana, ANIMAL-Elephant). Then, in the retrieval practice phase, participants are prompted with a retrieval cue (e.g. FRUIT-Or_____) and asked to retrieve the word that correctly completes the stem. During this phase, named retrieval practice phase, participants retrieve half the exemplars from half of the categories seen in the study phase. After this phase, three different types of items can be distinguished: practiced items from practiced categories (e.g. Orange, Rp+); unpracticed items from practiced categories, such as Banana (Rp-) and non-practiced items from non-practiced categories (e.g. Elephant, Nrp). This last type of item provides a baseline against which the other two can be compared. Finally, after a distracter task, a surprise memory test takes place, where participants are asked to recall all of the previously studied items.

Two effects are usually found with this paradigm. On the one hand, Rp+ items are recalled better than baseline ones. This facilitation effect should not be surprising, given that practice has been shown to enhance memory performance. On the other hand, an inhibition effect is also usually found: Rp- items' recall is significantly impaired, compared to Nrp items.According to Anderson et al. (1994), this should happen since upon presentation of a category cue such as FRUIT-Or____ during the retrieval practice phase, all previously studied exemplars of that category (e.g., Banana, Apple, etc.) come to mind, and in order to reduce competition between these exemplars and promote the retrieval of the desired item (e.g. Orange), competing items need to be suppressed. Thus, inhibitory mechanisms come in hand to solve competition among simultaneously active competitors rendering these items more difficult to recall on a final phase. This effect became known as Retrieval-Induced Forgetting (RIF).

As Anderson and Spellman (1995) note, inhibitory mechanisms seem both plausible and necessary. Plausible since the brain uses both excitatory and inhibitory processes to perform neural computation and necessary since computational models have shown that inhibitory mechanisms are critical to maintain stability in neural networks (Easton & Gordon, 1984). In spite of this, the inhibitory assumption (or at least the assumption that inhibitory mechanisms underlie the RIF effect) has been questioned by some researchers.

Traditionally, an alternative account for RIF would be one based on associative blocking (e.g. McGeoch, 1942; Mensink & Raaijmakers, 1988). What would happen during retrieval practice, according to this theory, is that the association between the category and the practiced item is strengthened, making the connection between the cue and this particular exemplar stronger than the one between cue and unpractised items. Then later, when Rp- items are tested upon presentation of the category cue, the cue might lead to the activation of the stronger Rp+ item, blocking access to the Rp-.

Another possible explanation put forth recently (Jonker, Seli, & MacLeod, 2013), states that the impairment of unpractised items could be due to contextual effects. This context account posits that in order for RIF to occur, two criteria must be met: 1) there has to be a change in context between study and practice phase and 2) the retrieval practice context (but not the study one) must be reinstated during test. The fact that the same context is elicited during retrieval practice and test would improve memory for items found in this phase (an effect of context congruency) but impair memory for competitor items that were only found previously in the study context, which differed from the test one.

Several studies have shown, however, that RIF occurs independently of the testing situations, which is probably the strongest support for the inhibitory account. RIF is still present not only in free and cued recall tests, but also in recognition ones (Bajo, Gómez-Ariza, Fernández, & Marful 2006; Hick & Starns, 2004; Spitzer & Bäuml, 2007; Verde, 2004) and even using implicit memory tests (Veling & Knipperberg, 2004), which strongly contradicts both blocking and context accounts. For example, RIF effect is still present when tested with novel cues, different from those used during retrieval practice. So for instance, if the Rp- item Banana is tested during the final memory test with an independent probe such as MONKEY (instead of FRUIT), both the blocking and the context hypotheses would predict that RIF should disappear, whereas the inhibitory account would predict that the effect should be maintained, since inhibition should act on the representation of the item itself. In fact, several studies have shown that this is what happens (Anderson, 2005; Anderson, Green, & McCulloch, 2000; Anderson & Spellman, 1995; Weller, Anderson, Gómez-Ariza, & Bajo, 2014; but see Perfect, Stark, Tree, Moulin, Ahmed, & Hutter, 2004, for a discussion on this issue).

Associative blocking could not explain these results, given that the cue MONKEY has not been associated with any other item and thus no other item could block access to the to-be-retrieved Rp-. Context accounts would also have trouble explaining this finding, since the context encountered at test is different from that of both study, and retrieval practice phases. Given that the cues are novel, the retrieval practice context cannot be reinstated (nor the study context, for that matter). These results are, however, consistent with the inhibitory account: since if it is the representation itself that is being inhibited, impairment in performance should generalize to any cue used at test.

Another property of RIF that speaks in favour of the inhibitory account is that it is retrieval specific; that is, competition between stimuli at retrieval is a necessary condition for RIF to occur. Blocking accounts would predict that any strategy that led to the strengthening of the practiced item (like rehearsing or re-studying practiced items) should lead to memory impairment of the Rp- items. However, this has been shown not to be the case (Anderson et al., 2000; Bäuml & Hartinger, 2002; Bäuml & Aslan, 2004; Hanslmayr, Staudigl, Aslan, & Bäuml, 2010), which is consistent with the inhibitory account. Again, this account would predict retrieval specificity since other forms of strengthening do not involve competition between items and should not, therefore, trigger inhibitory mechanisms to suppress Rp- items. Related to this, it has been found that RIF is stronger when competitors are high frequency members of a category (Anderson et al., 1994). For instance, Orange will create greater competition than Guava and thus it is more likely to be inhibited, supporting the inhibitory account.

Studies have also found that the effects of facilitation and forgetting are dissociable. RIF appears to be independent of the amount of strengthening Rp+ items receive, that is, strengthening of Rp+ does not predict forgetting of the Rp- (Anderson, 2003). In a study conducted by Shivde & Anderson (2001), it was found that performing retrieval practice one versus five times led to a substantial increase in memory performance for the practiced items, but that the impairment for unpractised ones remained constant. This clearly contrasts with the blocking accounts that predicts that the more an item is strengthened, the stronger its connection with the cue and the more it should block the access to the unpractised exemplars.

The RIF effect has been generalized to several types of different stimuli, such as lexical categories (Bajo et al., 2006), processes involved in second language acquisition (Levy, McVeigh, Marful, & Anderson, 2007), false memories (Starns & Hicks, 2004), eyewitness testimonies (McLeod, 2001; Shaw, Bjork, & Handel, 1995) and, more interestingly for the scope of this work, perceptual stimuli (Ciranni & Shimamura, 1999; Gómez-Ariza, Fernández, & Bajo, 2012; Waldhauser, Johansson, & Hanslmayr, 2012).

Finally, several electrophysiological and neuroimaging studies speak in favour of the inhibitory account of RIF (e.g. Hanslmayr et al., 2010; Staudigl, Hanslmayr, & Bäuml, 2010; Waldhauser et al., 2012; Wimber, Bäuml, Bergström, Markopoulos, Heinze, & Richardson-Klavehn, 2008; Wimber, Rutschmann, Greenlee, & Bäuml, 2009) by showing that the effect depends on structures linked to conflict detection and resolution and that the competitor items are actively suppressed during retrieval practice. These studies are discussed in a more detailed fashion over the next section.

Neural correlates of the RIF effect

Numerous studies have looked into the neural correlates of RIF, to better understand the mechanisms involved during both retrieval practice and testing phases, using diverse techniques such as analysis of event-related potentials (ERPs; Johansson, Aslan, Bäuml, Gäbel, & Mecklinger, 2007; Hellerstedt & Johansson, 2013), analysis of oscillatory dynamics (Hanslmayr et al., 2010; Spitzer & Bäuml, 2007; Staudigl et al., 2010; Waldhauser et al., 2012) or fMRI (Kuhl et al., 2007, 2012; Wimber et al., 2008, 2009, 2011).

One of the first electrophysiological studies was conducted by Johansson and colleagues (2007) who contrasted a retrieval practice condition to a relearning one. Whereas retrieval should, as discussed earlier, lead to competition between stimuli, relearning should not, given that participants do not need to retrieve any information from memory in a relearning condition. Accordingly, Johansson and colleagues found that retrieval practice induced a more positive component in frontal areas than relearning and that this component was sustained across time. Moreover, this event-related potential predicted later forgetting in that it was more pronounced in a group of high forgetters than in a low forgetting group.

In a more recent study, Hellerstedt and Johansson (2013) also tested the competition-dependence assumption behind the inhibitory theory. They did so by manipulating competition levels, varying the associative strength between cue and competitors, such that some category cues were associated to strongly related exemplars whereas others had a weak category–exemplar associative strength. Notice that, according to the competition-dependence assumption, cues that are strongly associated to their targets should re-activate them more promptly than weakly associated ones, and thus create greater competition. Accordingly, these authors found that competitors with strong relation to the cue were more vulnerable to forgetting and that, upon the presentation of the category cue during retrieval practice, there was a competition-sensitive ERP modulation, with high competition cues eliciting more positive ERPs over anterior regions. This modulation predicted individual differences in forgetting and it should be reflecting the reactivation of the semantically associated items. By confirming the competition assumption, this study clearly gives support to the inhibitory account, and pins the neural correlates underlying it.

Other EEG studies have focused on oscillatory dynamics instead of ERPs. Hanslmayr et al. (2010), and Staudigl et al. (2010), contrasted retrieval practice and relearning conditions and found that the first one led to an increase in mid-frontal theta power (~4-8Hz). Aside from their binding function, theta oscillations have consistently been linked to conflict, using different types of tasks such as Flankers (Cavanagh, Cohen, & Allen, 2009) or Stroop (Hanlsmayr, Pastötter, Bäuml, Gruber, Wimber, & Klimesch, 2008), and could then be a marker of interference, arising whenever items compete for retrieval. In both studies, theta power correlated with subsequent forgetting on the memory test. Additionally, on Staudigl et al.'s study (2010) two cycles of retrieval practice were compared and a reduction in theta amplitude from the first to the second was observed, which should reflect a reduction in the activation of competing items. This effect was specific to the retrieval practice condition (but not to the relearning one) and was localized to the anterior cingulate cortex (ACC), which is consistent with theories assuming that this brain structure plays a relevant role in the detection and mediation of interference (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Kuhl et al., 2007).

Mid-frontal theta band activity has been linked to interference, but it is unclear if it tracks its resolution as well. A study that shed some light onto this question (Waldhauser et al., 2012), did so by associating abstract shapes to a couple of colored squares. Some shapes were associated with two squares of the same color, while others were associated to squares with different colors. In this case, when one of the squares was presented as a target during retrieval practice, the other color would work as a competitor to that target. Cleverly, the colored squares were encoded either in participants' right visual field or in their left one. The researchers found that during retrieval practice, upon presentation of the retrieval cue, beta power increased over the hemisphere that encoded the competitor item, whereas there was a beta desynchronization over the one that encoded the target. Importantly, the increase of beta power was specific to competition situations (when the same shape was associated with two different colors) but did not appear on non-competition ones (shapes associated with only one color). Furthermore, the effect depended on whether the competitor had been correctly encoded during the study phase or not. Finally, the increase of alpha/beta power over the competitor hemisphere predicted later forgetting.

These results seem to indicate that alpha/beta band activity could be a more direct marker of inhibition, with the increase of beta over the hemisphere that encoded competitor items as a reflection of inhibition *per se*. This agrees with previous work pointing towards alpha/beta activity reflecting cortical inhibition (Hanslmayr, Gross, Klimesch, & Shapiro, 2011; Jensen & Mazaheri, 2010; Klimesch, Sauseng, & Hanslmayr, 2007). The fact that this study provides direct evidence that visual memories are actively suppressed during retrieval practice, provides further evidence for the inhibitory account of RIF.

Neuroimaging studies using the retrieval practice paradigm have shown that BOLD signal is reduced across retrieval practice repetitions (an effect parallel to that found in Staudigl et al., 2010), over the ACC and the prefrontal cortex (Kuhl et al., 2007). This finding points to a decrease in cognitive control demands with repeated retrieval. Similar results were found by Wimber et al. (2009), who contrasted retrieval practice and relearning conditions and found increased activation in the ACC and dorsolateral prefrontal cortex for the selective retrieval condition. In both studies, activity in ACC and prefrontal cortex correlated with later forgetting.

Only a few studies have focused on the effects of retrieval practice on the final memory test: an EEG study (Spitzer, Hanslmayr, Opitz, Mecklinger, & Bäuml, 2009) and a couple of fMRI ones (Kuhl, Kahn, Dudukovic, & Wagner, 2008; Wimber et al., 2008). Spitzer et al. (2009) looked into the correlates of RIF on recognition memory and found that recognition of unpracticed items led to reduced theta and gamma power (~60-90 Hz). Accordingly, Wimber et al. (2008) found that retrieval of unpracticed competing items led to greater activation of ventrolateral prefrontal cortex (but see Kuhl et al., 2008), an area shown to be implicated in the retrieval of weak memory traces (Badre & Wagner, 2007). Taken together, these studies show that the memory representation of competitor items is impaired at test, which again is consistent with the idea that these items were inhibited during retrieval practice to promote retrieval of the correct response. Again, these results are also in accordance with Botvinick's theory (2001) that the ACC is responsible for detecting interference (that is, the activation of competing exemplars) whereas dorsal and ventral portions of the lateral prefrontal cortex are in charge of solving this interference, giving room to a perhaps weaker, but more appropriate response.

If older adults suffer from an inhibitory deficit, and if RIF effect, which depends on mechanisms of inhibitory control, is impaired in seniors, then this mechanisms could be held responsible for the difficulties evidenced by this population in recalling personal representations. The question then remains, however, of whether face-like stimuli, could actually be subjected to controlled inhibitory mechanisms, and if so, if they would depend on the same neural substrates discussed here.

Personal representations have often been considered in the literature to enjoy a special status on cognition (e.g. Farah, 1996; Haxby, Hoffman, & Gobbini, 2000; McKone, Kanwisher, & Duchaine, 2006), and authors defending this idea claim that faces and other personal representations are not vulnerable to the same mechanisms as other types of representations. We discuss these assumptions over the last part of this introduction.

1.3. Are personal representations vulnerable to controlled inhibitory mechanisms?

Personal representations' special status on cognition

Given the importance of recognizing faces for our daily life, it is not surprising that from the late 80s on there has been a great deal of research on this phenomenon. In early studies, faces were often considered to enjoy a special status in cognition, given their relevance for human behavior. In fact, this view was widely accepted until a revolutionary paper by Diamond and Carey (1986) was published, which proposed that recognizing a face did not imply any special cognitive processes. According to these authors, faces' advantage lied exclusively on the fact that we, as humans, are extremely expert in perceiving them; thus, recognition of any other object from any other category that we have acquired expertise in should involve the exact same cognitive processes as the recognition of a face. This led to a great number of studies on this topic, either advocating for face specificity or against it, but this question has not, to this day, been fully answered.

Supporting the faces' special status, several authors (e.g. Farah, 1996; Haxby et al., 2000; McKone et al., 2006) proposed that faces are processed in a more holistic or configural manner, in comparison to other types of objects (McKone et al., 2006). For instance, Tanaka and Farah (1993) proposed that the mechanisms underlying face perception see faces as a whole and do not decompose them into smaller parts. Kanwisher (2000) explains that holistic processing of faces could be the result of face-selective cells responding to the whole face instead of responding to only parts of it.

This specificity hypothesis is supported by several behavioral and neuroimaging studies. For instance, at a behavioral level, the inversion effect (Yin, 1969) has often been used to support faces' special status. Concretely, this effect shows that face recognition is disrupted to a much greater extent by the inversion of the stimulus (that is, by its presentation in an upside down position) than other objects' recognition. This finding was used to corroborate the implication of a more holistic and more orientation-sensitive mechanism needed for face recognition. The effect is thought to be due to the disruption of a configural processing during encoding, which would be unique to face-like stimuli (Rossion & Gauthier, 2002).

This interpretation has however been questioned given that a similar pattern of results was found with other object categories. Whenever participants had expertise with the stimuli to be recognized; for instance with dogs (Diamond & Carey, 1986) or handwriting experts (Bruyer & Crispeels, 1992), the same dramatic inversion effects were found, questioning the specificity assumption.

But support for face specificity has also come from neuroimaging studies. ERP studies have identified an electrophysiological component said to be specific to facial stimuli. Concretely, faces will give rise to a much larger ERP negative wave, between 130 and 200 ms, in comparison to other objects. This component, which has been labeled N170, has a latency of approximately 170ms, peaking at occipito-temporal electrodes. A similar component (M170) has also been found in magnetoencephalography (MEG) studies. This component is thought to reflect structural encoding (Itier, Latinus, & Taylor, 2006), extracting perceptual representation of the face in occipito-temporal areas.

Looking into the inversion effect, it was shown that the latency of the N170 component is delayed and its peak larger when participants are presented with inverted faces, whereas no such results were found for other types of objects (Itier &Taylor, 2002; Rossion et al., 2000). This led the authors of these studies to conclude that this component is the earliest one to reflect a difference between face and objects' processing and that it could reflect an early specificity in face processing (Rossion & Gauthier, 2002).

Nonetheless, Itier et al. (2006) found a similar delay on the latency of the N170 for six different categories that included non-facial stimuli (although different categories produced different delays), which seems to indicate that this latency delay could reflect a disruption in early stimuli processing, rather than a face specific response. Additionally, Rossion et al. (2002) found the same inversion effect on the N170 using *greebles* (a class of novel animal-like objects), when participants became experts in discriminating these stimuli. Thus, this electrophysiological face-inversion effect can be extended to non-face objects, but only when such mechanisms are recruited by expertise.

Studies showing a larger N170 for faces than non-face have not only been contradicted by other investigations but have also been largely criticized by some authors, regarding their methodology. Of particular interest is an article published by Thierry, Martin, Downing, and Pegna (2007), where they attributed most of the results found in N170 studies to a lack of control in the way stimuli are presented. These authors argue that whereas faces are usually presented in full frontal view, other stimuli categories' are presented in more perceptually variable views, thus leading to an uncontrolled interstimulus perceptual variance (ISPV). Thierry et al. (2007) compared faces and cars (Experiment 1) and faces and butterflies (Experiment 2), controlling for ISPV (low or high) and found that controlling this variable canceled the N170 face selectivity.

In functional magnetic resonance imaging (fMRI) experiments, a cortical area located in the right fusiform gyrus has been proposed to account for specificity in face recognition (Haxby, Hoffman, & Gobbini, 2002), and has been named accordingly as the fusiform face area (FFA). The presence of faces *per se* seems to determine the response of this area, which supports the domain-specific hypothesis. This brain region shows a greater sensitivity to differences between upright faces and inverted ones (McKone et al., 2006), which speaks in favor of the FFA being the locus of face specific processing. Yovel and Kanwisher (2005) proposed that the lower sensitivity shown by FFA to inverted faces is due to a sharper neural tuning for upright than to inverted faces. Furthermore, these authors showed a clear dissociation between the FFA and other cortical regions that seem to be responsible for object but not face perception, such as the lateral occipital complex (LOC).

Parallel to what happened with the N170 component, face specific activation in FFA has also been questioned. Some studies have shown, for instance, small but significant increases on FFA activation in response to objects participants were experts with, compared to control objects (Gauthier et al., 1999; 2000). Furthermore, studies have found activation in FFA for nonface objects, whenever these are processed at a subordinate level, that is, when one processes “BMW” rather than the general concept of “car” (Haxby et al., 2000; Gauthier, Behrmann, & Tarr, 1999).

It seems then that effects traditionally interpreted as supporting face specific mechanisms may, at least in some instances, be due to the mere fact that we are more expert in recognizing faces than other types of objects, though this controversy has not been yet solved and it is still to date a central debate in the literature.

Importantly for the scope of this work, a line of research looking into the rise and resolution of interference during object and face naming, has also yielded contrasting results. Although there seems to be a consensus for general objects that the naming of a given target can be impaired by the presentation of semantically related distracter items (Glaser & Düngelhoff, 1984; Lupker, 1979; Rosinski, Golinkoff, & Kukish, 1975), results for face naming are not as clear cut. For instance, Vitkovitch, Potton, Bakogianni, and Kinch (2006) conducted three different experiments and found no evidence for interference in face naming, when using a paradigm that had previously been shown to elicit interference between different objects (Vitkovitch, Rutter, & Read, 2001). Vitkovitch et al. (2006) primed the target face with categorically related (Exp. 1), associatively related (Exp. 2) distracter faces and with a categorically related distracter written name (Exp. 3). None of these manipulations led to interference effects between stimuli. The authors concluded that there is no interference present during face naming.

Though, these results seem to speak in favor of a dissociation between the cognitive processes involved in face and other objects' processing, the picture becomes less clear when taking into account studies by Brèdart and Valentine (1992), Darling and Valentine (2005) and by our own lab (Marful, Paolieri, & Bajo, 2014; Marful, Ortega, & Bajo, 2010) that found similar results when comparing interference for both face and other objects' naming,

Thus, it seems that faces might enjoy some sort of special status in cognition (though this is still a controversial issue) and that interference effects might differ when faces or objects are used as stimuli. Importantly, recent studies that have shown interference between faces (Darling and Valentine, 2005; Marful et al., 2010, 2014) come in accordance with widely accepted models of face recognition that put forth the idea that whenever different units (facial features or semantic information) within the same set are activated, they compete for retrieval and competition needs to be solved in order to promote retrieval of the correct representation (e.g. Burton et al., 1990). We now explain these models in more depth.

Face processing models

As mentioned earlier, several models have been proposed in order to explain how face recognition occurs (e.g. Brèdart, Valentine, Calder, & Gassi, 1995; Bruce & Young, 1986; Burton Bruce, & Hancock, 1999; Burton, Bruce, & Johnston, 1990). These models postulate that face recognition happens in different stages that take place either following strict sequential stages, that is, in a serial fashion (e.g. Bruce & Young, 1986) or in a parallel manner, with the different components of the system acting simultaneously (e.g. Burton et al., 1999).

In spite of this core difference, they share several features. Namely, all models suggest that there are different processing units organized together within a given set.

According to these models, the first step for face recognition, occurs when we see a face. When we see a face, a unit in the first set of representations becomes activated: a Face Recognition Unit (FRU), which encodes purely structural features of a known face. These representations (FRUs) are independent of how we see a face, that is, independent of the face's position, angle or lightning (at least for very well-known faces).

When a FRU is activated it is compared against several other facial representations stored in memory. When a match is found, it leads to the activation of a unit in the next set: a Person Identity Node (PIN). Each PIN and each FRU are unique, that is, they are attributed to one face and one person only. PINs can be activated not only from activation being passed on from the FRUs set, but also by seeing a person's name or by hearing their voice. According to Burton et al.'s model (1999) this is the set where all the domains for recognition converge, given that it is the locus of familiarity: when a PIN reaches a certain level of activation, familiarity is signalled and the person recognized. In Bruce and Young's model, familiarity was signalled at the FRUs stage, which helped explaining why sometimes we render a given face as familiar but are not able to retrieve any information about it.

In Burton et al.'s model (1990), when a PIN surpasses a given threshold, it gives access to the next set of units: the Semantic Information Units (SIUs). These units code all the semantic information we know about the person we are recognizing, such as their nationality, profession or name. Names are located in a separate lexical unit in Brèdart et al.'s model, 1995, and following this and Valentine et al.'s (1996) proposals, Burton et al. (1999) posited two additional sets of units: Word Recognition Units (WRUs) and Name Recognition Units (NRUs).

Importantly, models of face recognition conceive that interference may arise during the attempt to recognize a particular face, that is, different units may compete with each other for activation. For instance, serial models assume that the activation of a given unit will elicit activation of other related ones. This should lead to an interference situation where information competes for retrieval. These models do not detail, however, how competition is solved.

A proposal is put forward by later parallel models. Parallel models assume that units of different sets are connected between them by bi-directional excitatory links, whereas units from the same set are linked by inhibitory connections. What these authors propose is a self-regulatory mechanism that maintains the stability of the system. According to this mechanism, when many units receive activation at the same time, the unit that is activated the most will rapidly inhibit the others, making them stabilize, that is, getting back to their initial level of strength. One prediction could then be derived that the more a unit is activated, the more it will inhibit the other competing ones.

This is, however, a rather automatic mechanism, which contrasts with that proposed by the IDT. This theory is based on a conception of inhibitory mechanisms that are dependent on the central executive and are controlled in nature. The type of inhibition proposed by Burton et al. (1990) resembles somewhat more a type of lateral inhibition, acting quickly and automatically. Inhibition proposed by the IDT, however, is more akin to that thought to underlie the RIF effect.

Thus, if naming difficulties that come about with aging were to be explained by an inhibitory deficit, we first need to know whether personal information, such as faces and names, could be vulnerable to inhibitory mechanisms of a controlled nature similar to those acting in the retrieval practice paradigm.

This reasoning led us to posit three questions that we explore in the present work: i) are personal representations (such as faces and names) vulnerable to controlled inhibitory mechanisms, as those proposed by the IDT? If so, ii) what are the neural correlates of this effect? And iii) how does this effect and its neural correlates change with normal aging?

These questions are developed further over the next sections and the experimental series conducted try to answer each one of them, in the hope to ultimately be able to know whether inhibitory mechanisms of a controlled nature could underlie the problems in naming well-known people, reported by elders (Lovelace & Twohig, 1990; Maylor, 1990).

1.4. Outline of the present work

This dissertation is composed by four experimental series, each aiming to answer the aforementioned questions, in order to assess whether inhibitory mechanisms dependent on the central executive could be responsible for face-name retrieval difficulties reported by seniors.

In Experimental Series I we conduct four behavioral experiments that tackle the question of whether faces might be vulnerable to mechanisms of controlled inhibition, to the same extent as other objects are. In order to investigate this issue, we used a version of the retrieval practice paradigm with facial stimuli, to assess if faces too are vulnerable to the RIF effect. In experiments 1a and 2a, we explored this effect at different stages of the face recognition process and in experiments 1b and 2b we sought for further evidence that the obtained results were in fact due to inhibitory mechanisms. This series of experiments has been published in *Acta Psychologica* (Ferreira, Marful, & Bajo, 2014) and is presented here in its published form.

In Experimental Series II and III we move on to explore if the neural correlates of RIF are maintained with a young sample, when using facial stimuli and how they change with healthy aging. Using a paradigm similar to that of Experiment 2b, we conducted two EEG experiments and looked at how brain's oscillatory activity can specifically track the rise and fall of interference in young (Experiment 3) and older (Experiment 4) adults. Experiment 3 has been published in the *Journal of Cognitive Neuroscience* (Ferreira, Marful, Staudigl, Bajo, & Hanslmayr, 2014) and is presented here in its published form.

Finally, in Experimental Series IV we further explored the neural substrates underlying RIF and how these change as people age (Experiment 5). To better achieve this goal in this experimental series we opted to use a technique of greater spatial resolution, namely fMRI. Moreover, to circumvent a potential confound from Experiment 4, in this experimental series we used semantic stimuli instead of faces, and thus followed a procedure closer to that of Wimber et al. (2009).

Over the last chapter of the dissertation, we discuss the results obtained throughout the Experimental Series, and draw from them relevant conclusions and implications to different psychological theories. We finalize this work by pointing to potential future investigations that could be pursued within this line of research.

1. INTRODUCCIÓN

Han sido muchas las investigaciones que muestran cómo el envejecimiento normal se relaciona con un declive en el funcionamiento cognitivo general, siendo la memoria una de las funciones más afectadas. De hecho, según nos vamos haciendo mayores, comenzamos a notar dificultades en tareas que antes no suponían ningún problema, como, por ejemplo, encontrar la palabra adecuada (Craik, 1994) o recordar actividades cotidianas (e.g. recordar acudir a una cita con el médico o dónde se dejaron las gafas por última vez). Las personas mayores de 60 años no sólo manifiestan que presentan más problemas de memoria en situaciones cotidianas (Cutler y Grams, 1988; Montejo, Montenegro, Fernández y Maestú, 2012; Ryan, 1992), sino que, además, suelen mostrar un menor control percibido sobre su propia memoria cuando se les compara con personas más jóvenes (Dixon y Hultsch, 1983). Además de esta evidencia obtenida mediante autoinforme, se han llevado también a cabo pruebas objetivas que indican que, en la misma línea, los mayores muestran un peor rendimiento en pruebas de recuerdo libre y de reconocimiento (e.g. Craik y Jennings, 1992; Light, 1991), así como en medidas de memoria evaluadas mediante test neuropsicológicos (e.g. LaRue, 1992). Más aún, investigaciones previas parecen indicar que el envejecimiento normal se ha relacionado con una mayor dificultad a la hora de recordar nombres y caras de personas conocidas (Bahrick, 1984; Cohen y Faulkner, 1986; Maylor, 1990). Así, este problema de memoria puede resultar determinante para la interacción social de los mayores.

De hecho, para poder interactuar de forma adecuada con otras personas, necesitamos reconocer y recuperar información biográfica muy detallada sobre nuestro interlocutor. Más aún, desde un punto de vista evolutivo, esta habilidad es crucial, ya que nos permite, por ejemplo, distinguir a nuestros amigos de nuestros enemigos. Pese a que el reconocimiento de caras podría considerarse una tarea sencilla a nivel fenomenológico, resulta una actividad realmente complicada desde un punto de vista cognitivo, ya que en un breve intervalo temporal debemos discriminar entre configuraciones facialesmuy similares entre sí (Bruce y Young, 1986). Además, esta tarea ya de por sí demandante parece ofrecer una mayor dificultad conforme las personas envejecen. De hecho, las dificultades de nombrado son una de las quejas más habituales entre los adultos mayores (Lovelace y Twohig, 1990; Maylor, 1990).

Junto a estas quejas subjetivas, la evidencia empírica también apunta a la existencia de dificultades asociadas a la edad en el nombrado de caras. Naveh-Benjamin y cols. (2004) presentaron a sus participantes 40 pares cara-nombre que estos deberían recuperar más tarde. Estos participantes fueron divididos en tres grupos: adultos jóvenes, adultos mayores y adultos jóvenes que realizaban una tarea concurrente a la tarea de nombrado. Los resultados mostraron que cuando los participantes tenían que recuperar caras y nombres por separado, la ejecución de los mayores era similar a la de los jóvenes. Más aún, los jóvenes que llevaron a cabo la tarea concurrente realizaron peor la tarea que las personas mayores, lo que indicaba que la tarea concurrente tenía un efecto más perjudicial en el recuerdo que la edad. Sin embargo, cuando se evaluaba el recuerdo de las asociaciones cara-nombre, los resultados fueron diferentes, de forma que los participantes mayores realizaron peor la tarea que los dos grupos de jóvenes (con y sin tarea concurrente).

Esta dificultad que muestran los mayores a la hora de recuperar nombres de personas conocidas, tiene un impacto considerable en este grupo de edad, ya que les genera una falta de confianza en sí mismos (Light, 1991), les produce estados de ánimo negativos y falta de confianza en sus propias capacidades lingüísticas (Burke y Shafto, 2004). Además, Pike y cols. (2012) sugieren que los déficits en la recuperación de los pares cara-nombre podrían ayudar a distinguir entre deterioro cognitivo leve (MCI, por sus siglas en inglés) y envejecimiento sano, aspecto especialmente relevante si tenemos en cuenta que las personas con MCI presentan un elevado riesgo de desarrollar la enfermedad de Alzheimer (Gauthier y cols., 2006). Por ello, tratar de entender los mecanismos que subyacen a estas dificultades de memoria resulta especialmente relevante. En consecuencia, las preguntas a responder con este trabajo serían, ¿cómo podemos explicar este deterioro relacionado con la edad? ¿qué cambios cognitivos y cerebrales ocurren conforme las personas envejecen?

Una posible explicación ha sido propuesta por Hasher y Zacks (1998). Según su Hipótesis del Déficit Inhibitorio (IDT, por sus siglas en inglés), la mayoría de pérdidas cognitivas relacionadas con la edad, en procesos como memoria o atención, se deben a un déficit subyacente en mecanismos inhibitorios. En consecuencia, los problemas en el nombrado que padecen las personas mayores se podrían deber a su mayor dificultad para suprimir representaciones competidoras (e.g. los nombres de personas relacionadas), que dificultan a su vez el acceso y selección del nombre deseado (Lustig, Hasher y Zacks, 2007). ¿Podría por tanto este déficit inhibitorio explicar las dificultades en el nombrado?

Uno de los paradigmas empleados para estudiar la inhibición sería el denominado paradigma de Práctica en la Recuperación (Anderson, Bjork y Bjork, 1994). En este paradigma, tradicionalmente se presentan diferentes estímulos que están relacionados con una misma clave (e.g. ejemplares de categorías FRUTAS-Manzana, FRUTAS-Naranja, FRUTAS-Plátano). De este modo, cuando se debe recuperar uno de estos estímulos (por ejemplo, el ítem manzana) es muy posible que se cree una situación de interferencia debido a la activación de otros ítems relacionados con esta misma clave (naranja, plátano). Así, para recuperar correctamente el estímulo deseado (manzana) resulta necesario suprimir los ítems competidores (naranja, plátano). De hecho, los resultados obtenidos empleando este paradigma generalmente muestran una disminución en el recuerdo de estos ítems competidores (respecto a una línea de base) cuando se deben recuperar en una prueba final de memoria. Tradicionalmente, este decremento en el recuerdo de los ítems competidores (denominado Olvido Inducido por la Recuperación, en inglés RIF) se ha explicado debido a su previa inhibición para resolver la situación de interferencia (Anderson y cols., 1994). Más aún, en relación directa con los objetivos de este trabajo, las investigaciones que han estudiado el efecto de la edad sobre el efecto RIF parecen mostrar cómo este efecto se reduce conforme avanza el envejecimiento (dependiendo de factores como la edad en sí misma y los recursos cognitivos disponibles; ver sección 1.1).

Por tanto, este déficit inhibitorio observado en el paradigma de práctica en la recuperación durante el envejecimiento normal podría extenderse también a información cara-nombre. Sin embargo, la literatura ha otorgado habitualmente a estas representaciones personales un estatus especial en la cognición humana. Concretamente, se piensa que estas representaciones no están siempre sujetas a los mismos mecanismos que los objetos (e.g. Farah, 1996; Haxby, Hoffman y Gobbini, 2000; Kanwhiser y Duchaine, 2006) de forma que nuestro cerebro está preparado para procesarlas de forma diferente a otros tipos de estímulos (e.g. Kanwhiser, 2000). Además, se han planteado diferentes modelos de procesamientode caras que han intentado dar cuenta de este estatus especial de las caras en la cognición (e.g. Brèdart, Valentine, Calder y Gassi, 1995; Bruce y Young, 1986; Burton Bruce y Hancock, 1999; Burton, Bruce y Johnston, 1990). Por tanto, no existe una respuesta clara sobre si los mecanismos inhibitorios que afectan a los objetos en general estarían también implicados en el reconocimiento y nombrado de caras, y por tanto, si estos mecanismos podrían también explicar las dificultades que las personas mayores manifiestan a la hora de recuperar este tipo de representaciones. Para tratar de responder a estas cuestiones, en primer lugar debemos plantearnos si las representaciones personales (caras y nombres) son también vulnerables a los procesos de de interferencia.

Así, los modelos de procesamiento de caras asumen que cuando intentamos reconocer a una persona conocida, puede producirse una situación de competición entre esta cara a reconocer y las caras de otras personas que comparten configuraciones faciales o información semántica (e.g. Bruce y Young, 1986; Burton y cols., 1990). Sin embargo, estos modelos, o no dan una explicación detallada sobre cómo la interferencia se supera, o proponen un mecanismos automático (y no controlado) para resolver esta competición. Pero, ¿podría la interferencia entre representaciones de personas ser resuelta por el mismo mecanismo inhibitorio que aquellos propuestos por la IDT y, por tanto, el deterioro de estos mecanismos podría explicar las dificultades en el nombrado que padecen los mayores?

Para poder contestar adecuadamente a esta pregunta, necesitamos entender primero cómo la memoria en general, y las capacidades inhibitorias en particular, cambian con el envejecimiento. Podremos, entonces, centrarnos en el procesamiento y reconocimiento de caras y nombres, ya que las dificultades a la hora de recordar caras y nombres sería una de las quejas más habituales manifestadas por los mayores. (Lovelace y Twohig, 1990; Maylor, 1990).

1.1. ¿Cómo cambia la memoria durante el envejecimiento normal?

A lo largo de la vida, las funciones de memoria que son esenciales en diversos aspectos de nuestra vida cambian considerablemente. Estos cambios suponen un deterioro de aspectos generales de la memoria conforme envejecemos: los mayores manifiestan tener más problemas de memoria que los jóvenes (Cutler y Grams, 1988; Ryan, 1992) y consideran además que tienen un menor control sobre su propia memoria (Dixon y Hultsch, 1983). Aunque estas quejas subjetivas son consistentes con los estereotipos existentes sobre el envejecimiento, algunos autores como Rabbit y Abson (1990) sugieren que podrían deberse más bien a una mayor vulnerabilidad a los estados de depresión en los mayores, y por tanto, podrían no reflejar de manera precisa su estado real de memoria. Por tanto, sería conveniente tener en cuenta medidas más objetivas de memoria. De hecho, las investigaciones realizadas en la última década se han centrado principalmente en este tipo de tareas y han mostrado empíricamente que las quejas subjetivas de los mayores, se corresponden efectivamente con fallos en tareas objetivas de memoria (e.g. Craik, 1994).

Sin embargo, algunos de estos estudios ponen en evidencia, que aunque la memoria se ve afectada durante el envejecimiento en general, su impacto sobre los diferentes sistemas de memoria es diferente. El declive en memoria de trabajo, por ejemplo, no resulta demasiado acusado, usando tanto medidas de span de dígitos (Parkinson, Inman y Dannenbaum, 1985) como de span visuo-espacial (Spinnler, Della Sala, Bandera y Baddeley, 1988). De manera similar, la memoria semántica parece no estar afectada por la edad, e incluso puede verse mejorada en adultos mayores cuando se utilizan medidas de vocabulario (Giambra, Arenberg, Zonderman y Kawas, 1995). En la misma línea, estudios iniciales en memoria prospectiva encontraron que esta memoria no sufría cambios con la edad (Einstein y McDaniel, 1990), aunque estos resultados han sido cuestionados posteriormente por investigaciones que muestran cómo sólo la memoria prospectiva de eventos y no la memoria prospectiva basada en el tiempo, está preservada durante el envejecimiento (Einstein, McDaniel, Richardson, Guynn y Cunfer, 1995), o por algunos estudios que muestran deterioro en ambos tipos de memoria prospectiva asociado a la edad (e.g. Cockburn y Smith, 1991; Maylor, 1996).

Por otro lado, en cuanto a la memoria episódica, puede considerarse que existe un amplio consenso respecto a su afectación durante el envejecimiento. Este deterioro no se produce únicamente en contextos relativamente artificiales como los de laboratorio, sino que también se observa cuando se emplean materiales más ecológicos que reproducen situaciones cotidianas de memoria (e.g. Salthouse, 1991; Wilson, Cockburn, Baddeley y Hiorns, 1989). El alcance de este deterioro puede estar modulado tanto por factores relacionados con las capacidades de procesamiento de la persona, como con las ayudas contextuales proporcionadas durante la recuperación. En este sentido, los efectos de la edad se manifiestan más claramente en tareas de recuerdo libre (donde no existen ayudas de recuperación externas), seguidos de las tareas de recuerdo con clave, y en último término en los tests de reconocimiento (Craick, Byrd y Swanson, 1987).

En cualquier caso, el deterioro de la memoria episódica puede afectar de forma significativa a la vida cotidiana de las personas mayores y es, por tanto importante, entender cuáles son sus mecanismos subyacentes. Diversas teorías han intentado explicar este declive cognitivo. Estas teorías, como la de Velocidad de Procesamiento (Salthouse, 1996) o la IDT (Hasher y Zacks, 1988), proponen un mecanismo común que daría cuenta del deterioro cognitivo observado en los mayores. La primera teoría (Velocidad de Procesamiento) plantea que la principal causa de este déficit sería un enlentecimiento generalizado de procesamiento de los adultos mayores, mientras que la segunda teoría (IDT) defiende que un déficit en la función inhibitoria sería la causa de esta afectación. Nos centraremos ahora en la IDT, debido a la gran cantidad de apoyo empírico que ha recibido.

Envejecimiento e inhibición

Tal y como se ha descrito anteriormente, actualmente se asume que las funciones cognitivas se ven alteradas durante el envejecimiento (e.g. Raz, 2000), no sólo en el marco de las demencias, sino también en el envejecimiento normal. Una de las teorías que intenta explicar este declive es la IDT (Hasher y Zacks, 1988). Esta teoría propone que las pérdidas cognitivas asociadas al envejecimiento se pueden explicar por un déficit generalizado en los mecanismos de inhibición. En su trabajo Lustig, Hasher y Zacks (2007) proponen tres funciones diferentes de la inhibición. La primera se situaría en una primera etapa del procesamiento de la información, y serviría para controlar el acceso al foco de atención de la información que no es relevante. De acuerdo con esta propuesta, Gazzaley, Cooney, Rissman y D'Esposito (2005) compararon tres condiciones en las que los participantes tenían que atender, ignorar o ver de forma pasiva los estímulos presentados. Estos autores encontraron que, mientras los participantes jóvenes mostraban una gran reducción de activación cuando se comparaba la condición "ignorar" respecto a la condición "ver de forma pasiva", los adultos mayores presentaban prácticamente el mismo nivel de activación en ambas condiciones. Sin embargo, los adultos mayores presentaban un incremento en la activación cuando se presentaba información relevante, esto es, mostraban más activación en la condición "atender" que en la condición "ver de forma pasiva". Además, el grado en el que los participantes eran capaces de reducir la activación en la condición "ignorar" (y no el grado en que aumentaban la activación en la de "atender") fue lo que predecía la ejecución en la tarea de memoria . Por tanto, estos datos parecen indicar que existe un déficit relacionado con la edad que está específicamente relacionado con el control de la entrada de información irrelevante en el foco atencional.

La segunda función de la inhibición sería el borrado de información irrelevante que a) eludió el primer control de acceso al foco atencional, o b) ha dejado de ser relevante y por tanto debería ser borrada de la memoria de trabajo (Lustig y cols., 2007). De hecho, diferentes estudios han mostrado que los adultos mayores, parecen producir más información que ya ha dejado de ser relevante que los participantes más jóvenes (e.g. May, Zacks, Hasher y Multhaup, 1999; Zacks, Radvansky y Hasher, 1996). Además,es posible que el decremento en el span de memoria de trabajo observado durante el envejecimiento quizá no dependa del tamaño del espacio de trabajo mental en sí mismo, sino más bien de la habilidad para mantener información irrelevante fuera de este espacio, (e.g. Friedman y Miyake, 2004), lo que apoyaría esta función inhibitoria de borrado de la información irrelevante.

Finalmente, la tercera y última función de la inhibición sería la supresión de respuestas dominantes pero contextualmente inapropiadas (Lustig y cols., 2007), en favor de respuestas más adaptativas. Se debería tener en cuenta que esta función de inhibición es coherente con la propuesta de Anderson y cols. (1994), discutida en la sección 1.2. Esta función también parece verse comprometida en los adultos mayores. Específicamente, los paradigmas clásicos que estudian inhibición, como el de *Go/No Go* o el de *Stop Signal*, han mostrado cómo la ejecución de los mayores es peor que la de los participantes más jóvenes (e.g. Bedard, Nichols, Barbosa, Schachar, Logan y Tannock, 2002). Más relevante para el alcance de este trabajo, este déficit inhibitorio se ha observado no sólo en tareas motoras como las anteriores, sino también en tareas similares de memoria.

Anderson y Green (2001) desarrollaron un paradigma similar al de *Go/No Go*, que fue denominado *Think/No Think* (TNT). Este paradigma pretende estudiar el olvido voluntario o motivado de recuerdos. En el TNT, los participantes, en primer lugar deben memorizar pares de palabras. Posteriormente en una segunda fase, se les presenta la primera palabra de uno de los pares, y deben o bien recuperar (instrucciones "pensar") o bien suprimir (instrucciones "no pensar") la palabra asociada. Cuando a continuación se efectúa un test de memoria sobre todas las palabras presentadas, los resultados muestran un decremento en el recuerdo de los ítems con instrucciones de "no pensar" respecto a una línea de base (e.g. Anderson y cols., 2001, 2004; Benoit y Anderson, 2012; Depue, Curran y Barrich, 2007; Hanslmayr, Leipold, Pastötter y Bäuml, 2009). Según los autores, estos resultados muestran que somos capaces de inhibir voluntariamente información que no queremos recuperar. Sin embargo cuando son personas mayores quienes efectúan esta tarea, los resultados no muestran este efecto de olvido de los ítems con instrucciones de "no pensar" (Anderson, Reinholz, Kuhl y Mayr, 2011; Murray, Anderson y Kesinger, 2015). Adicionalmente, estudios de Olvido Dirigido (DF, por sus siglas en inglés), un paradigma que también estudia la supresión voluntaria de recuerdos, han mostrado también cómo los mayores presentan dificultades a la hora de olvidar la información de modo intencional (Sahakyan, Delaney y Goodmon, 2008). Aguirre, Gómez-Ariza, Bajo, Andrés y Mazzoni (2014), por otro lado, mostraron que este efecto de olvido intencional se producía en una versión estándar del paradigma de DF, pero que cuando se utilizaba un paradigma más refinado, como el de Olvido Dirigido Selectivo (Delaney, Nghiem y Waldum, 2009), los adultos mayores no eran capaces de olvidar selectivamente un conjunto de información relevante pero sí los adultos jóvenes.

Otras investigaciones sobre los efectos de la edad se han realizado utilizando el paradigma de práctica en la recuperación (Anderson y cols., 1994). A diferencia de los paradigmas mencionados anteriormente, este tipo de olvido incidental sería más similar a diversas situaciones cotidianas que exigen a la persona mayor recuperar una información especifica (como por ejemplo, el nombre de un nieto) entre un conjunto de competidores potenciales (los nombres de todos sus nietos). Los resultados apuntan hacia un debilitamiento del efecto de olvido inducido por la recuperación (RIF; ver sección 1.2) en estos mayores. El efecto RIF se considera dependiente de mecanismos inhibitorios y, por tanto, la IDT predeciría la desaparición de este efecto en los mayores. Diferentes estudios han mostrado que, efectivamente, el RIF resulta afectado en personas mayores, pero que hay algunos factores modulando esta disminución del efecto. Tanto Aslan y Bäuml (2012) como Marful, Gómez-Amado, Ferreira y Bajo (2015) encontraron que el RIF puede preservarse en adultos mayores relativamente jóvenes (menores de 75 años), pero que desaparece en una muestra de adultos mayores de más edad (mayores de 75 años). Por tanto, pese a que estos resultados apoyan la existencia de un déficit inhibitorio durante el envejecimiento, este déficit puede mostrarse invisible cuando se emplea el paradigma de práctica en la recuperación hasta una edad muy tardía.

Otro factor importante es la cantidad de recursos cognitivos disponibles. Ortega, Gómez-Ariza, Román y Bajo (2012) encontraron que el efecto RIF se encontraba preservado en mayores cuando se utilizaba un paradigma estándar de práctica en la recuperación, pero que este efecto desaparecía (sólo en mayores, no en jóvenes) cuando era introducida una tarea adicional.

En esta línea, todos estos efectos previamente descritos se muestran también alterados en otras poblaciones con déficits inhibitorios (*Go/No Go* and *Stop Signal*: Aron, Robins y Poldrack, 2004; TNT: Catarino, Kupper, Werner-Seidler, Dalgleish y Anderson, *en prensa*; Depue, Burgess, Willcutt, Ruzic y Banich, 2010; RIF: Soriano, Jiménez, Román y Bajo, 2009a; Román, Soriano, Gómez-Ariza y Bajo, 2009; DF: Conway y Fthenaki, 2003; Harnishfeger y Pope, 1996; Soriano, Jiménez, Román y Bajo, 2009b), lo que apoyaría la idea de que este mecanismo estaría afectado en personas mayores. Este trabajo propone que este deterioro inhibitorio el responsable de las dificultades manifestadas por las personas mayores no sólo a la hora de memorizar nuevos nombres, sino también a la hora de recordar nombres de personas conocidas.

Además, existe aún más apoyo a la IDT, proveniente de estudios de neuroimagen. Estos estudios han mostrado que las zonas de las que depende la inhibición, específicamente, zonas prefrontales del cerebro, se ven significativamente alteradas en adultos mayores. Por tanto, en el siguiente apartado discutiremos cuáles son los diferentes cambios cerebrales que se relacionan con el envejecimiento.

Envejecimiento y cerebro

A medida que envejecemos, el cerebro se enfrenta a un gran número de cambios. Estos cambios ocurren a diferentes niveles: neuroquímico (e.g. Baltes, Lindenberger y Staudinger, 2006; Dixon, Wahlin, Maitland, Hultsch, Hertzog y Bäckman, 2004); anatómico (e.g. Simons y Spiers, 2003; Raz, 2005) o funcional (e.g. Cabeza, 2002; Johnson, 2001). A su vez, estos cambios juegan un papel importante en nuestra cognición, correlacionando con un declive en la función ejecutiva.

A nivel neuroquímico, por ejemplo, se producen cambios en la disponibilidad de neurotransmisores (Werkle-Bergner, Müller, Li y Lindenberger, 2006), como es el caso de los sistemas dopaminérgicos (Bäckman, Nyberg, Lindenberger, Li y Farde, 2006). Teniendo en cuenta que la dopamina es un neurotransmisor que correlaciona positivamente con la actuación cognitiva, estos autores han encontrado diferentes focos de pérdidas de dopamina relacionados con la edad en niveles neurales y moleculares: reducción de dopamina en la sustancia negra; reducción del número de sinapsis a lo largo del cerebro y pérdida de número de proteínas por célula. En esta línea, Bäckman y cols. (2000) encontraron una fuerte correlación entre los niveles de dopamina y el desempeño en tareas de memoria episódica. Esta correlación explicaba el 38% de la varianza en una tarea de reconocimiento de palabras y el 48% de varianza en una de reconocimiento de caras. El envejecimiento implica también cambios metabólicos. Pardo y cols. (2007) observaron un decremento en el consumo de glucosa durante esta etapa de la vida, especialmente en el córtex cingulado anterior (ACC, por sus siglas en inglés), córtex prefrontal medial, prosencéfalo basal y tálamo dorsomedial. Este decremento en el consumo de glucosa correlaciona, además, con un decremento en medidas cognitivas.

En cuanto a los cambios neuroanatómicos, estos suponen quizá el grupo de cambios más estudiados. Anatómicamente, el cerebro que envejece pierde volumen en general. Además, la densidad tanto de la materia gris como la blanca se reduce en muchas regiones cerebrales; el tamaño ventricular aumenta, así como la muerte neuronal y la pérdida de densidad dendrítica (Werkle-Bergner y cols., 2006), aunque estos cambios no afectan a todo el cerebro de la misma manera. Por ejemplo, mientras que el córtex prefrontal muestra un decaimiento linear sostenido desde que la persona alcanza la mitad de su veintena, el hipocampo parece no sufrir cambios hasta los 50 y el córtex entorrinal no sufre apenas por el envejecimiento a lo largo de la vida (Werkle-Bergner y cols., 2006).

La mayoría de los estudios anatómicos se han centrado, por tanto, en cambios prefrontales, dado que la atrofia en el lóbulo frontal se ha ligado estrechamente al decremento de funciones cognitivas (e.g. Nielson, Langenecker y Garavan, 2002; Raz, 2000). En un intento de conectar función y anatomía, Cummins y Finnigan (2007) encontraron alteraciones en la potencia de theta en regiones frontales y del ACC en adultos mayores. Esta modulación de theta se interpreta como un indicador de que la función de una red está interrumpida, dado que las oscilaciones theta son importantes a la hora de integrar información de diferentes regiones cerebrales en una red coherente. Por tanto, estos autores proponen que el ritmo theta podría ser un marcador neurofisiológico de cambios funcionales en redes cognitivas.

Otro experimento de electroencefalografía (EEG; Werkle-Bergner y cols., 2006) mostró un incremento en el acoplamiento de fase en personas mayores en comparación con adultos más jóvenes. Los autores interpretan estos resultados como un marcador de desdiferenciación o de una pérdida general de conexiones inhibitorias. Sin embargo, algunos resultados con resonancia magnética funcional (fMRI; e.g. Cabeza, 2002) sugieren otra interpretación. En su estudio, Cabeza (2002) encontró cómo la actividad del córtex prefrontal está menos lateralizada, es decir, es más bilateral en adultos mayores que en jóvenes (Reducción de la Asimetría Hemisférica en personas mayores, o modelo HAROLD, por sus siglas en inglés). Según Cabeza, los adultos mayores reclutan ambos hemisferios para contrarrestar déficits neurocognitivos y mantener niveles de ejecución similares. Los resultados de Reuter-Lorenz y cols. (2000) apoyan esta idea, al encontrar que una mayor activación del hemisferio izquierdo en personas mayores (en comparación con adultos jóvenes), particularmente en áreas posteriores, estaba asociada con una mejor ejecución. Por tanto, el cerebro podría responder a los cambios anatómicos provocados por la edad mediante la reorganización de sus funciones, esto es, el cerebro podría experimentar un proceso de compensación funcional.

Esto parece ocurrir especialmente en el córtex prefrontal ventro-medial (vmPFC, por sus siglas en ingles). Cabeza y Dennis (2013) encontraron que i) la actividad relacionada a la tarea era mayor en aquellos que presentaban un mayor declive cerebral; ii) la actividad compensatoria estaba asociada con un incremento de las demandas de tarea; y iii) la actividad compensatoria estaba relacionada positivamente con el rendimiento. Además, observaron un incremento en conectividad entre el vmPFC y la corteza dorsolateral prefrontal. Estos resultadosparecen indicar que el vmPFC y su conectividad con redes frontoparietales serían los responsables del proceso de compensación en adultos mayores (Lightall, Huettel y Cabeza, 2014). Interesante también en el marco de este trabajo, García-Pacios y cols. (2013) proponen que el mayor reclutamiento de areas prefrontales en adultos mayores, podría relacionarse con la resolución de interferencia.

En este trabajo, nuestro objetivo era evaluar si los mecanismos inhibitorios de naturaleza controlada, que se utilizan para reducir la interferencia, pueden ayudar a explicar los problemas de memoria en el envejecimiento. Para ello, buscamos un paradigma que reprodujese las situaciones de competición a las que los mayores tienen que enfrentarse en su vida diaria y que además, requiriese mecanismos de supresión dependientes del ejecutivo central para su solución. El paradigma de práctica en la recuperación parece satisfacer estas dos exigencias, y por tanto, fue utilizado a lo largo de cuatro series experimentales.

En este sentido, éste es el primer estudio que trata de determinar cómo el efecto RIF puede verse modulado por los cambios cerebrales asociados al envejecimiento. Los cambios anatómicos, específicamente la reducción en la corteza prefrontal, permite predecir que estas áreas podrían estar menos implicadas en tareas inhibitorias y, por tanto, cualquier alteración encontrada en el efecto RIF en personas mayores debería ir acompañada de menos activación (en comparación con adultos jóvenes) en el ACC y el cortex prefrontal. Sin embargo, desde el modelo HAROLD se efectuaría una predicción diferente: así, si los participantes fueran capaces de compensar funcionalmente sus cambios neuroanatómicos, entonces las regiones prefrontales deberían estar, al menos, igualmente activadas en jóvenes y mayores, o incluso se podría predecir una mayor activación en estos últimos. Asimismo, desde esta perspectiva, el efecto RIF comportamental no debería verse afectado en personas mayores.

A continuación ofrecemos una explicación más profunda de este paradigma y su efecto, así como de los correlatos neurales conocidos en poblaciones más jóvenes.

1.2. Control inhibitorio y el efecto de Olvido Inducido por la Recuperación (RIF)

En el campo de la memoria, la interferencia se ha considerado normalmente como un producto de la asociación de varios ítems con la misma clave. Cuando la clave se presenta, todos los ítems se activan y compiten por la recuperación (e.g.

Anderson y cols. 1994). Pero, ¿cómo superamos estas situaciones de interferencia? Esto es, ¿cómo se resuelve la competición entre estímulos?

Una propuesta, hecha por Anderson y cols. (1994), es que mecanismos de control inhibitorio (es decir, dependientes del ejecutivo central) son los responsables de resolver la competición entre diferentes representaciones. Estos mecanismos reducirían la activación de una representación dada, impidiendo que esta activación alcanzase un determinado umbral. Al hacer esto, se permite la selección de respuestas que quizá sean más débiles pero que resultan más apropiadas desde un punto de vista contextual. Así, este mecanismo permite un comportamiento más adaptativo y sensible al contexto.

Este tipo de mecanismos de control inhibitorio han sido sistemáticamente estudiados mediante el paradigma de Práctica en la Recuperación (Anderson y cols., 1994). La versión estándar de este paradigma consiste en tres fases distintas. Durante la primera fase, los participantes deben estudiar una lista de pares de palabras asociadas semánticamente a una categoría determinada (e.g. FRUTA-Naranja, FRUTA-Plátano, ANIMAL-Elefante). Después, en la fase de práctica en la recuperación, se presenta a los participantes un clave de recuperación para que recuperen de forma repetida la mitad de los ejemplares de la mitad de las categorías (e.g. FRUTA-na_____) Así, en función de esta fase, se pueden distinguir tres tipos de estímulos: ítems practicados de categorías practicadas (e.g. Naranja, Rp+); ítems no practicados de categorías practicadas (e.g. Banana, Rp-) e ítems no practicados de categorías que no fueron practicadas (e.g. Elefante, Nrp) que funcionarán como línea de base

Finalmente, tras una tarea distractora, se lleva a cabo un test sorpresa de memoria en el que los participantes tienen que recuperar todos los ítems estudiados.

Los resultados de este test de memoria tradicionalmente muestran dos efectos diferentes: Por un lado, los ítems Rp+ se recuerdan mejor que los de línea base. Este efecto de facilitación se explica por la recuperación repetida de los ítems Rp+ durante la fase de práctica. Por otro lado, y más interesante, los resultados suelen mostrar también un efecto de inhibición. Así, se observa un menor recuerdo de los ítems Rp- en comparación con ítems Nrp. Según Anderson y cols. (1994), este efecto de olvido del ítem Rp- se explicaría por su previa inhibición durante la fase de práctica en la recuperación. Así, durante esta fase, la presentación de la clave de recuperación FRUTA na____, provocaría la activación de todos los ejemplares previamente estudiados, dando lugar a una situación de interferencia. Para reducir la competición y recuperar adecuadamente el ítem Naranja, deben suprimirse todos los competidores. Por tanto, los mecanismos inhibitorios actúan para resolver la competición entre diferentes competidores activados de manera simultánea, provocando que estos mismos competidores (Rp-) sean posteriormente más difíciles de recordar en el test final de memoria. Este efecto de olvido de los competidores es conocido como efecto de Olvido Inducido por la Recuperación (siglas en inglés, RIF).

Como Anderson y Spellman (1995) puntualizan, los mecanismos inhibitorios parecen no sólo plausibles, sino necesarios. Plausibles en tanto que el cerebro utiliza tanto procesos excitatorios como inhibitorios para realizar computaciones neurales. Necesarios en tanto que los modelos computacionales han demostrado que los mecanismos inhibitorios son críticos para mantener la estabilidad en redes neurales (Easton y Gordon, 1984). Sin embargo, el supuesto inhibitorio (o al menos, el supuesto de que los mecanismos inhibitorios subyacen al efecto RIF) ha sido cuestionado por algunos investigadores.

Tradicionalmente, una postura alternativa al RIF sería una basada en bloqueo asociativo (e.g., McGeoch, 1942; Mensink y Raaijmakers, 1988). De acuerdo con esta teoría, durante la fase de práctica la asociación entre la categoría y el ítem practicado se fortalece, haciendo que la conexión entre la clave y el ejemplar concreto sea mayor que la existente entre la clave y ejemplares no practicados. Más tarde, esta fuerte asociación clave de recuperación–ítem Rp+ provocaría el bloqueo del ítem Rp- durante el test final de memoria.

Otra explicación posible presentada recientemente (Jonker, Seli y MacLeod, 2014), plantea que el olvido de los ítems competidores podría deberse a efectos contextuales. Esta postura basada en el contexto sugiere que, para que se produzca RIF, deben cumplirse dos criterios: 1) tiene que haber un cambio entre el contexto de estudio y el de práctica; y 2) el contexto de práctica (pero no el de estudio) debe reactivarse de nuevo durante la fase final. El hecho de que el mismo contexto se reactive durante la práctica y la prueba final mejoraría el recuerdo de ítems presentes en la fase de práctica (efecto de congruencia de contexto) pero afectaría al recuerdo de competidores que sólo se presentaron en el contexto de estudio, que era diferente del contexto de test.

Diferentes estudios han mostrado, sin embargo, que el efecto RIF ocurre con independencia de la situación de prueba, lo que supone un fuerte apoyo a la postura inhibitoria. El efecto RIF aparece no sólo en tests de recuerdo libre y recuerdo con claves, también se muestra en tests de reconocimiento (Bajo, Gómez-Ariza, Fernández y Marful, 2006; Hick y Starns, 2004; Spitzer y Bäuml, 2007; Verde, 2004), e incluso usando pruebas de memoria implícita (Veling y Knipperberg, 2004). Estos resultados contradicen tanto la explicación del bloqueo asociativo como la basada en el contexto. Más aún, el efecto RIF también aparece cuando se utilizan claves nuevas en el test, diferentes a las utilizadas durante la fase de práctica. Por ejemplo, si para recuperar el ítem Rp- "plátano" se presenta durante el test final de memoria la clave de recuperación "MONO" (en vez de FRUTA), las dos hipótesis alternativas predecirían que el efecto RIF desaparecería, mientras que la postura inhibitoria apostaría por el mantenimiento del efecto, ya que la inhibición actuaría en la representación del ítem en sí mismo. Efectivamente, los resultados muestran que, a pesar de que la clave de recuperación proporcionada durante el test final de memoria es independiente de la clave empleada durante el estudio, el efecto de olvido inducido por la recuperación se mantiene (Anderson, 2005; Anderson, Green y McCulloch, 2000; Anderson y Spellman, 1995; Weller, Anderson, Gómez-Ariza y Bajo, 2014; pero véase Perfect, Stark, Tree, Moulin, Ahmed y Hutter, 2004 para una discusión sobre el asunto) Así, el bloqueo asociativo no podría explicar estos resultados, dado que la clave MONO no ha sido previamente asociada con ningún otro ítem y por tanto no existen ítems que bloqueen el acceso al Rp- que ha de ser recuperado. Por su parte, la hipótesis contextual tampoco podría explicar este descubrimiento, ya que el contexto en la fase de prueba es diferente tanto al de la fase de estudio como al de la práctica. Dado que las claves son novedosas, el contexto de práctica en la recuperación no puede restituirse (así como tampoco el de estudio). Estos resultados, sin embargo, son consistentes con la postura inhibitoria: ya que sería la representación en sí misma la que está siendo inhibida, de este modo, el olvido del ítem Rp- se observa independietemente de la clave de recuperación empleada.

Otra propiedad del RIF que apoya la visión inhibitoria, sería la especificidad en la recuperación, es decir, es necesario que exista competición entre estímulos durante la recuperación para que se produzca el efecto RIF. Así, la postura de bloqueo asociativo predeciría que cualquier estrategia que llevara al fortalecimiento del ítem practicado (como ensayar o volver a estudiar la lista de ítems practicados) debería empeorar el recuerdo de los ítems Rp-. Sin embargo, desde la postura inhibitoria, se predeciría el efecto RIF únicamente cuando existe una fase de práctica en la recuperación en la que se produzca competición entre ítems relacionados que favorezca la inhibición de los competidores. Así, los resultados empíricos parecen apoyar esta última propuesta, de forma que el efecto RIF únicamente aparece cuando se produce esta situación de competicíon y no cuando se fortalece la conexión clave-ítem practicado mediante el estudio o la re-exposición (Anderson y cols., 2000; Bäuml y Hartinger, 2002; Bäuml y Aslan, 2004;

Hanslmayr, Staudigl, Aslan y Bäuml, 2010). En relación con estos resultados, también se ha encontrado cómo el efecto RIF es mayor cuando los competidores son miembros de alta frecuencia en la categoría (Anderson y cols., 1994). Por ejemplo, Naranja creará una competición mayor que Guayaba y, por tanto, su inhibición será más probable, apoyando de nuevo la postura inhibitoria.

Otros estudios también han encontrado que los efectos de facilitación y olvido son disociables. El efecto RIF parece ser independiente de la cantidad de fortalecimiento que reciben los ítems Rp+, esto es, el fortalecimiento de Rp+ no predice el olvido de Rp- (Anderson, 2003). En un estudio llevado a cabo por Shivde y Anderson (2001), se encontró que realizar la fase de práctica una o cinco veces elevaba sustancialmente el recuerdo de los ítems practicados, pero que el recuerdo de los itmes no practicados (y el efecto RIF) se mantenía constante. Esto contrasta claramente con la postura de bloqueo asociativo, que predice que a mayor fortalecimiento de la conexión del ítem practicado con la clave, mayor será el bloqueo de los ejemplares no practicados.

Por otro lado, existe amplia evidenia de la genealización del fenómeno RIF con diversos tipos de estímulos, como categorías léxicas (Bajo y cols., 2006), procesos relacionados con la adquisición de una segunda lengua (Levy, McVeigh, Marful y Anderson, 2007), falsas memorias (Starns y Hicks, 2004), testimonios de testigos (McLeod, 2001; Shaw, Bjork y Handel, 1995) entre otros. Más relacionado con nuestro trabajo, también se ha observado el efecto utilizando estímulos perceptivos (Ciranni y Shimamura, 1999; Gómez-Ariza, Fernández y Bajo, 2012; Waldhauser, Johansson y Hanslmayr, 2012).

Finalmente, varios estudios de electrofisiología y neuroimagen apoyan la explicación inhibitoria del efecto RIF (e.g. Hanslmayr y cols., 2010; Staudigl, Hanslmayr y Bäuml, 2010; Waldhauser y cols., 2012; Wimber, Bäuml, Bergström, Markopoulos, Heinze y Richardson-Klavehn, 2008; Wimber, Rutschmann, Greenlee y Bäuml, 2009) mostrando que el efecto depende de estructuras ligadas a la detección y resolución, y que los ítems competidores se suprimen de manera activa durante la fase de recuperación. Estos estudios se discuten en detalle en la siguiente sección.

Correlatos neurales del efecto RIF

Numerosos trabajados han estudiado cuáles son los correlatos neurales del olvido inducido por la recuperación, con el objetivo de entender mejor qué mecanismos están implicados tanto en fase de práctica como en la de test. Estos estudios han utilizado diferentes técnicas, como por ejemplo el análisis de potenciales evocados (Johansson, Aslan, Bäuml, Gäbel y Mecklinger, 2007; Hellerstedt y Johansson, 2013), análisis de dinámicas oscilatorias (Hanslmayr y cols., 2010; Spitzer y Bäuml, 2007; Staudigl y cols., 2010; Waldhauser y cols., 2012) o fMRI (Kuhl y cols., 2007, 2012; Wimber y cols., 2008, 2009, 2011).

Uno de los primeros estudios electrofisiológicos fue llevado a cabo por Johansson y cols. (2007). Estos autores compararon una condición estándar de práctica en la recuperación con una de re-aprendizaje en la que los ítems se presentaban repetidamente para su estudio. Mientras que la recuperación debería, como se ha comentado anteriormente, desencadenar una competición entre estímulos, éste no sería el caso del re-aprendizaje, ya que en este último los participantes no necesitan recuperar ninguna información de la memoria. En este sentido, Johansson y cols. encontraron que la práctica produjo un componente más positivo en zonas frontales que el re-aprendizaje, y que este componente se mantenía a lo largo del tiempo. Además, este potencial evocado predecía el olvido posterior en el test final de memoria ya que era más pronunciado en los participantes que tenían un mayor efecto RIF que en aquellos cuyo efecto era menor. En un estudio más reciente, Hellerstedt y Johansson (2013) estudiaron cómo el grado de competición modulaba la inhibición de los competidores. Para ello, variaron la fuerza asociativa entre la clave y los competidores, de manera que en algunas categorías, las claves estaban asociadas fuertemente a los ejemplares, mientras que en otras, existía una débil fuerza asociativa entre clave y ejemplar. Habría que tener en cuenta que, de acuerdo con el principio de la dependencia de la competición, las claves que estén fuertemente asociadas con los ejemplares, deben re-activarlos y por tanto generar más competición que aquellas claves poco asociadas con los ejemplares de su categoría. Así, los autores encontraron que los competidores con una fuerte relación con la clave eran más vulnerables al olvido y que la presentación de la clave durante la fase de práctica generaba una modulación en los potenciales evocados asociada a la competición. En este sentido, claves que generaban mayor competición producían potenciales más positivos en zonas anteriores. Esta modulación predijo las diferencias individuales en olvido y debería estar reflejando la reactivación de ítems asociados semánticamente. Al confirmar el supuesto sobre la competición, este estudio otorga clara evidencia en favor de la teoría inhibitoria y señala los correlatos neurales que la subyacen.

Otros estudios de EEG se han centrado en las dinámicas oscilatorias en lugar de los potenciales evocados. Hanslmayr y cols. (2010) y Staudigl y cols. (2010), compararon condiciones de práctica y re-aprendizaje y encontraron que, en condiciones de práctica, se producía un incremento de poder en la banda de tetha (~4-8Hz) en zonas mediales frontales. Aparte de su función integradora, las oscilaciones theta se han asociado de manera consistente al conflicto, usando diferentes tareas, como tareas de flancos (Cavanagh, Cohen y Allen, 2009) o *Stroop* (Hanlsmayr, Pastötter, Bäuml, Gruber, Wimber y Klimesch, 2008), y podrían ser por tanto un marcador de interferencia, originándose ante situaciones de competición cuando los items compiten por la recuperación. En ambos estudios, la potencia theta correlacionó con el olvido posterior durante el test de memoria. Adicionalmente, en el estudio de Staudigl y cols. (2010), dos ciclos de práctica en la recuperación fueron comparados y se observó una reducción de la amplitud theta en el segundo de ellos en comparación con el primero, lo cual debería reflejar una reducción en la activación de ítems competidores. Este efecto era específico de la condición de práctica (no ocurría en la de re-aprendizaje) y fue localizado en el ACC, lo cual es consistente con teorías que proponen que esta estructura del cerebro juega un papel relevante en la detección y mediación de la interferencia (Botvinick, Braver, Barch, Carter y Cohen, 2001; Kuhl y cols., 2007).

La actividad en la banda theta en zonas frontales mediales, por tanto, se ha asociado previamente a interferencia, aunque queda por determinar si esta banda registra también procesos resolutivos. Un estudio que arroja luz acerca de esta cuestión (Waldhauser y cols., 2012) presentaba figuras abstractas asociadas a pares de cuadrados coloreados. Algunas figuras se asociaban a cuadrados del mismo color (situación de competición), mientras que otras se asociaban a cuadrados de diferente color (situación de no competición). En este caso, cuando uno de los cuadrados se presentaba como objetivo durante la fase de práctica, el otro color debería funcionar como competidor. Un aspecto interesante de este estudio fue que los cuadrados de colores eran codificados por los participantes en campos visuales distintos. Los investigadores encontraron que durante la fase de práctica, la potencia de theta aumentaba en la fase de práctica pero sólo en el hemisferio que codificó el competidor. En el hemisferio que codificó la palabra objetivo, sin embargo, se produjo una desincronización de beta. De este modo, el aumento de poder theta era específico de situaciones de competición (cuando la misma figura estaba asociada a dos colores diferentes) pero no tenía lugar en situaciones de no competición (figuras asociadas con un único color). Además, el efecto dependía de si el competidor había sido correctamente codificado durante la fase de estudio o no. Finalmente, el incremento de potencia alfa/beta sobre el hemisferio competidor también permitió predecir el olvido posterior.

Estos resultados parecen indicar que la actividad en bandas alfa/beta podría funcionar como un marcador más directo de inhibición, siendo el aumento de beta en el hemisferio que codifica ítems competidores un reflejo de inhibición *per se*. Esto es coherente con trabajos previos que muestran la relación entre inhibición cortical y actividad alfa/beta (Hanslmayr, Gross, Klimesch y Shapiro, 2011; Jensen y Mazaheri, 2010; Klimesch, Sauseng y Hanslmayr, 2007). El hecho de que este estudio aporte evidencia directa acerca de cómo las memorias visuales se suprimen de manera activa durante la práctica, supone más apoyo a la explicación inhibitoria del efecto RIF.

Otros estudios de neuroimagen con este paradigma han mostrado cómo la señal BOLD se reduce a lo largo de repeticiones de práctica en la recuperación (un efecto paralelo al encontrado en Staudigl y cols., 2010), tanto en el ACC como en la corteza pre-frontal (Kuhl y cols., 2007). Este descubrimiento sugiere que la recuperación repetida va acompañada de un decremento en control cognitivo. Wimber y cols. (2009) encontraron resultados similares al contrastar las condiciones de práctica y re-aprendizaje. En esta situación, tanto el ACC como la corteza dorsolateral prefrontal aumentaron su activación en situaciones de recuperación. En ambos estudios, la actividad del ACC y de la corteza pre-frontal correlacionó con olvido posterior.

Sólo unos pocos estudios se han centrado en los efectos de la práctica en la recuperación sobre el test final de memoria: un estudio de EEG (Spitzer, Hanslmayr, Opitz, Mecklinger y Bäuml, 2009) y dos estudios de fMRI (Kuhl y cols., 2008; Wimber y cols., 2008). Spitzer y cols. (2009) estudiaron los correlatos del RIF en situaciones de reconocimiento y encontraron que el reconocimiento de ítems no practicados implicaba una reducción en la potencia theta y gamma (~60-90 Hz). Este resultado es consistente con la idea de que el efecto RIF se debe a una supresión de representaciones competidoras. De acuerdo con lo anterior, Wimber y cols. (2008) encontraron que la recuperación de ítems competidores no practicados generaba una mayor activación en la corteza ventrolateral prefrontal (pero ver Kuhl y cols., 2008), un área implicada en la recuperación de trazos débiles de memoria (Badre y Wagner, 2007). En conjunto, estos estudios demuestran que la representación en memoria de ítems competidores está afectada durante la fase final de prueba, lo cual es de nuevo coherente con la idea de que estos ítems fueron inhibidos durante la fase de práctica para permitir la recuperación de la respuesta deseada. Asimismo, estos resultados también son consistentes con la teoría de Botvinick (2001) que afirma que el ACC es el responsable de detectar interferencia (esto es, activación de ejemplares competidores) mientras que las porciones dorsales y ventrales de la corteza prefrontal se encontrarían a cargo de resolver esta interferencia, permitiendo una respuesta quizá más débil, pero más apropiada.

Si los adultos mayores sufren un déficit de inhibición, y si el efecto RIF, que depende de mecanismos de control inhibitorio, también está afectado en personas mayores, entonces, estos mecanismos podrían ser considerados responsables de las dificultades en recordar representaciones personales evidenciadas en esta población. La pregunta que queda abierta, sin embargo, es si las representaciones personales podrían estar también sujetas a mecanismos de control inhibitorio y, en caso afirmativo, si también dependerían de los mismos correlatos neurales discutidos previamente.

Las representaciones personales han disfrutado clásicamente de un estatus especial en la cognición (e.g. Farah, 1996; Haxby, Hoffman y Gobbini, 2000; McKone, Kanwisher y Duchaine, 2006). Los autores que defienden este estatus especial consideran que las caras y otras representaciones personales no son igualmente vulnerables a los mecanismos que regulan otro tipo de representaciones como los objetos. En la siguiente sección, discutimos estos planteamientos.

1.3. ¿Son las representaciones personales vulnerables a mecanismos de control inhibitorio?

El estatus especial de las representaciones personales en la cognición

Dada la importancia de reconocer caras en nuestro día a día, no es sorprendente el hecho que desde los años 80 se haya llevado a cabo un gran número de estudios acerca de este fenómeno. En las primeras investigaciones, las caras se consideraban como poseedoras de un estatus especial, dada su relevancia en el comportamiento humano. De hecho, esta visión era ampliamente mayoritaria hasta la publicación del artículo de Diamond y Carey (1986), en el que se proponía que el procesamiento de caras no implicaba ningún proceso cognitivo especial. De acuerdo con los autores, la especificidad de las caras se explicaba únicamente porque se tratan de representaciones muy complejas sobre las que somos expertos. Por tanto, el reconocimiento de cualquier otro objeto que dominemos con maestría debería implicar los mismos procesos cognitivos. Este planteamiento dio lugar a un gran número de investigaciones que obtuvieron resultados tanto a favor como en contra de este carácter especial de las caras en la cognición. De este modo, puede decirse que en la actualidad, esta pregunta continúa abierta.

Varios autores a favor del estatus especial de las caras (e.g. Farah, 1996; Haxby y cols., 2000; McKone y cols., 2006), han propuesto que las caras se procesan de una manera más holística que otros tipos de objetos (McKone y cols., 2006). Por ejemplo, Tanaka y Farah (1993) propusieron que percibimos las caras como un todo y no las descomponemos en pequeñas partes. Kanwisher (2000) explica que este procesamiento holístico de caras podría ser el resultado de células selectivas a caras que responden a la totalidad de las mismas en vez de responder a pequeñas partes.

Esta hipótesis ha sido apoyada por varios trabajos comportamentales y de neuroimagen. Por ejemplo, a nivel comportamental, el efecto de inversión (Yin, 1969) muestra que el reconocimiento de caras se altera de mayor manera al invertirlas (presentándolas boca abajo) que cuando se invierten otro tipo de objetos. Este resultado parece ser consistente con la implicación de mecanismos más holísticos y sensibles a la orientación en el reconocimiento de caras. Así, este efecto se considera un producto de la alteración de un procesamiento de la configuración durante la codificación, algo que sería único de los estímulos faciales (Rossion y Gauthier, 2002).

Esta interpretación, sin embargo, ha sido cuestionada, dado que un patrón similar de resultados se puede encontrar con otras categorías. Así, si los participantes se enfrentan a categorías con las que tienen mucha experiencia, por ejemplo, expertos en perros (Diamond y Carey, 1986) o en escritura a mano (Bruyer y Crispeels, 1992), los efectos dramáticos de la inversión se siguen encontrando para este tipo de estímulos.

Sin embargo, el apoyo a la especificidad de las caras también procede de estudios de neuroimagen. Estudios de potenciales evocados han identificado un componente electrofisiológico considerado específico para estímulos faciales. Concretamente, las caras provocan una onda negativa alrededor de los 130/200ms mucho mayor que otros objetos. Este componente, el cual ha sido etiquetado como N170, tiene una latencia de aproximadamente 170 milisegundos, con picos en electrodos occipito-temporales. Un componente similar (M170) se encuentra también en estudios con magnetoencefalografía (MEG). Este componente se considera un reflejo de codificación estructural (Itier, Latinus y Taylor, 2006), el cual extraería representaciones perceptuales de la cara en áreas occipito-temporales.

En cuanto al efecto de inversión, se ha demostrado que la latencia del N170 se retrasa y su pico es mayor cuando los participantes ven caras invertidas, mientras que esos efectos no se encuentran con otros objetos (Itier y Taylor, 2002; Rossion y cols., 2000). Esto ha llevado a los autores de estos estudios a concluir que este componente es el reflejo más temprano de una diferencia entre el procesamiento de caras y objetos y que podría reflejar una especificidad en el procesamiento (Rossion y Gauthier, 2002).

Sin embargo, Itier y cols. (2006) encontraron un retraso similar en la latencia del N170 para seis categorías diferentes que incluían estímulos no faciales (aunque las diferentes categorías mostraban retrasos diferentes). Estos resultados parecen indicar que este retraso en la latencia podría reflejar una disrupción en el procesamiento temprano de estímulos, más que una respuesta específica a las caras. Adicionalmente, Rossion y cols. (2002) encontraron el mismo efecto de inversión en el N170 utilizando *greebles* (un tipo de objetos complejos novedosos), cuando los participantes se convertían en expertos en discriminar estos estímulos. Por tanto, este efecto electrofisiológico de inversión de caras se puede extender a objetos no faciales, pero sólo cuando estos mecanismos son reclutados por la experiencia.

Los estudios que muestran un mayor N170 para caras que para objetos no faciales no sólo han sido refutados por otras investigaciones, sino que su metodología también ha sido duramente criticada por algunos autores. De particular interés es un artículo publicado por Thierry, Martin, Downing y Pegna (2007), en el que estos autores atribuían la mayoría de resultados encontrados en el N170 a una falta de control en la manera en que se presentaban los estímulos. Estos autores arguyen que mientras que las caras se presentan normalmente desde una perspectiva frontal, otros estímulos se presentan en vistas variables, dando lugar a una varianza perceptual entre-estímulos incontrolable (ISPV, por sus siglas en inglés). Thierry y cols. (2007) compararon caras y coches (Experimento 1) y caras y mariposas (Experimento 2), controlando el efecto de la ISPV (alta o baja) y encontraron que el control de esta variable cancelaba el N170 para las caras.

Utilizando fMRI, algunos estudios han propuesto el giro fusiforme derecho como un área con especificidad a caras (Haxby, Hoffman y Gobbini, 2002) y ha sido etiquetada en este sentido como el área fusiforme de las caras (FFA, por su siglas en inglés). La presencia de caras *per se* parece determinar la respuesta de este área, lo cual apoya la hipótesis de especificidad. Esta región cerebral muestra una mayor sensibilidad a diferencias entra caras normales e invertidas (McKone y cols., 2006), lo cual es coherente con la idea de que la FFA es un centro de procesamiento específico de caras. Yovel y Kanwisher (2005) propusieron que la menor sensibilidad de la FFA a caras invertidas se debe a una mejor configuración del sistema para caras normales que para las invertidas. Además, estos autores mostraron una clara disociación entre la FFA y otras regiones corticales que parecen ser responsables de la percepción de objetos pero no de caras, como el complejo occipital lateral (LOC, por sus siglas en inglés).

De forma paralela a lo que ocurrió con el componente N170, la actividad específica a caras en la FFA también ha sido cuestionada. Algunos estudios han mostrado, por ejemplo, aumentos pequeños pero significativos en la FFA en respuesta a objetos con los cuales los participantes tenían experiencia, en comparación con objetos controles (Gauthier y cols., 1999; 2000). Además, estos estudios han encontrado actividad en FFA para objetos no faciales, siempre y cuando esos objetos se procesen a nivel subordinado, es decir, siempre que uno procese "BMW" en vez del concepto general de "COCHE" (Haxby y cols., 2000; Gauthier, Behrmann y Tarr, 1999).

Parece que los efectos tradicionalmente interpretados como evidencia a favor de mecanismos específicos de caras pueden deberse, al menos en algunas ocasiones, al mero hecho de que somos más expertos en reconocer caras que otro tipo de objetos, aunque esta controversia no ha sido resuelta todavía y es todavía un debate central en la literatura.

De manera importante para este trabajo, una línea de investigación acerca del cómo surge y se resuelve la interferencia durante el nombrado de objetos y caras ha encontrado también resultados opuestos. Aunque parece haber un consenso en cuanto a los objetos, acerca de cómo el nombrado de un *target* puede verse afectado por la presentación de ítems distractores relacionados semánticamente (Glaser y Düngelhoff, 1984; Lupker, 1979; Rosinski, Golinkoff y Kukish, 1975), los resultados para el nombrado de caras no son tan claros. Por ejemplo, Vitkovitch, Potton, Bakogianni y Kinch (2006) llevaron a cabo tres experimentos diferentes y no encontraron evidencia de interferencia en el nombrado de caras, pese a utilizar un paradigma con el que se había comprobado la elicitación de interferencia para objetos. Vitkovitch y cols. (2006) presentaron una cara objetivo que podía estar precedida de otra relacionada categorialmente (Exp. 1), asociativamente (Exp. 2), o podía estar precedida por un nombre categorialmente relacionado (Exp. 3). Ninguna de estas manipulaciones produjo interferencia entre los estímulos, más aún, mostraron el efecto contrario de facilitación. Los autores concluyeron que, por tanto, no existe interferencia durante el nombrado de caras.

Pese a que estos resultados parecen apoyar la disociación entre los procesos cognitivos involucrados en el procesamiento de caras y de otros objetos, el panorama es menos claro cuando se tienen en cuenta los estudios de Brèdart y Valentine (1992), Darling y Valentine (2005) y los de nuestro propio laboratorio (Marful, Paolieri y Bajo, 2014; Marful, Ortega y Bajo, 2010), que encuentran resultados similares cuando se compara la interferencia para el nombrado de caras y objetos.

Por tanto, parece que existe cierta evidencia que apoya que las caras tendrían un estatus especial en la cognición (aunque esto es aún un tema controvertido) y que, en ocasiones, la interferencia puede diferir entre estímulos faciales y otros objetos. En esta línea, estudios recientes que han demostrado interferencia entre caras (Darling y Valentine, 2005; Marful y cols. 2010, 2014) son coherentes con modelos ampliamente aceptados de reconocimiento de caras que apoyan la idea de que en cualquier situación en la que se activan diferentes unidades (características faciales o información semantica) dentro del mismo conjunto, éstas compiten por la recuperación y que la competición necesita ser resuelta para promover la recuperación de la respuesta correcta o del comportamiento adecuado (e.g. Burton y cols., 1990). En la siguiente sección explicamos algunos de estos modelos.

Modelos de procesamiento de caras

Como ha sido mencionado anteriormente, diferentes modelos han sido propuestos a la hora de explicar cómo se produce el reconocimiento de caras (e.g. Brèdart, Valentine, Calder y Gassi, 1995; Bruce y Young, 1986; Burton, Bruce y Hancock, 1999; Burton, Bruce y Johnston, 1990). Estos modelos postulan que el reconocimiento de caras se produce en diferentes niveles que tienen lugar, o bien en términos estrictamente secuenciales, es decir, serialmente (e.g. Bruce y Young, 1986) o en paralelo (e.g. Burton y cols., 1999).

A pesar de esta diferencia central, los modelos comparten diferentes aspectos. Específicamente, todos los modelos sugieren que existen diferentes unidades de procesamiento organizadas dentro de un mismo conjunto. El primer paso de reconocimiento de una cara, de acuerdo con estos modelos, se produce cuando vemos una cara. En este momento se activa una unidad en el primer conjunto denominado Unidad de Reconocimiento de Caras (FRU, por sus siglas en ingles). En este momento únicamente se codifican características puramente estructurales de una cara conocida. Estas FRUs, al menos en caras muy familiares, son independientes de la posición de la cara, su ángulo o su iluminación.

Cuando se activa una FRU se compara con otras representaciones faciales almacenadas en memoria. Si se encuentra una correspondencia, ésta provoca la activación del siguiente conjunto: un Nodo de Identidad de la Persona (PIN, por su siglas en inglés). Cada PIN y cada FRU son únicos, esto es, están asociados a una única cara y a una única persona. Los PINs pueden activarse no sólo mediante la activación que proviene de una FRU si no también al ver el nombre de una persona o al oír su voz. De acuerdo con el modelo de Burton y cols. (1999) este es el conjunto de unidades donde todos los dominios de reconocimiento convergen, dado que es el *locus* de la familiaridad: cuando un PIN alcanza un nivel determinado de activación, la persona es reconocida como familiar. En el modelo de Bruce y Young (1986), la familiaridad se ubica en la etapa del FRU, lo cual ayudaba a explicar por qué en algunas ocasiones consideramos una cara como familiar pero somos incapaces de recuperar información sobre ella.

En el modelo de Burton y cols. (1990), cuando un PIN alcanza un umbral determinado, da acceso al siguiente grupo de unidades: las Unidades de Información Semántica (SIUs). Estas unidades codifican toda la información semántica que disponemos acerca de la persona que estamos reconociendo, como por ejemplo su nacionalidad, su profesión o su nombre. Los nombres se encuentran en una unidad léxica separada en el modelo de Brédart y cols. (1995), y continuando este modelo y las propuestas de Valentine y cols. (1996), Burton y cols. (1999) propusieron dos unidades adicionales: las Unidades de Reconocimiento de Palabras (WRUs) y las Unidades de Reconocimiento de Nombres (NRUs).

Crucialmente, los modelos de reconocimiento de caras conciben que la interferencia puede surgir del intento de reconocer una cara particular, esto es, en situaciones en las que diferentes unidades compiten entre ellas por activación. Por ejemplo, los modelos seriales asumen que la activación de una unidad dada, elicita la activación de otras relacionadas. Esto debería llevar a una situación de interferencia donde la información compite por la recuperación. Estos modelos no detallan, sin embargo, cómo se resuelve la competición.

En este sentido, los modelos en paralelo lanzan una nueva propuesta. Estos modelos asumen que las unidades de diferentes conjuntos están conectadas entre ellas mediante conexiones excitatorias bidireccionales, mientras que las unidades de un mismo conjunto están conectadas de manera inhibitoria. Estos autores proponen la existencia de un mecanismo auto regulatorio que mantiene la estabilidad del sistema. De acuerdo con este mecanismo, cuando muchas unidades reciben activación al mismo tiempo, la unidad que más se active será la que más rápidamente inhiba a las demás. Así, esta unidad más activada inhibirá al resto haciéndolas volver a su nivel inicial de activación. Una predicción podría ser, por tanto, que cuanto más se activa una unidad, más inhibirá al resto de unidades competidoras.

Este mecanismo de inhibición automática, sin embargo, difiere del control inhibitorio planteado desde la IDT. Desde esta teoría se plantea que los mecanismos inhibitorios dependen del ejecutivo central y por tanto son controlados por naturaleza. El tipo de inhibición propuesta por Burton y cols. (1990) se asemeja a un tipo de inhibición lateral, que actua de forma rápida y automática. La inhibición propuesta por la IDT, sin embargo, se parece más al proceso que subyace al efecto RIF.

Por tanto, si las dificultades de nombrado que se asocian al envejecimiento pudieran explicarse por un déficit inhibitorio, primero necesitamos saber si la información personal, como las caras y los nombres, pueden ser vulnerables a mecanismos inhibitorios de una naturaleza controlada, similares a aquellos que actúan en el paradigma de Práctica en la Recuperación.

Desde este planteamiento se derivan tres preguntas a explorar en el presente trabajo: i) ¿son las representaciones personales (como caras y nombres) vulnerables a mecanismos de control inhibitorio, como el propuesto por la IDT? En caso afirmativo, ii) ¿cuáles son los correlatos neurales de este efecto? Y iii) ¿cómo cambia este efecto y sus correlatos neurales con el envejecimiento normal?

Estas preguntas se desarrollan en mayor profundidad en la siguiente sección. Las series experimentales llevadas a cabo intentan responder a cada una de ellas, con el objetivo de determinar, en última instancia, si los mecanismos inhibitorios de naturaleza controlada podrían explicar los problemas en el nombrado de personas conocidas que manifiestan las personas mayores (Lovelace y Twohig, 1990; Maylor, 1990).

1.4. Esquema del presente trabajo

Este trabajo se compone de cuatro series experimentales, cada una de las cuales busca responder a las preguntas mencionadas con anterioridad, para poder evaluar finalmente si los mecanismos inhibitorios dependientes del ejecutivo central podrían ser responsables de las dificultades en la recuperación cara-nombre manifestadas por las personas mayores.

En la Serie Experimental I, realizamos cuatro experimentos comportamentales que tratan de responder a la pregunta de si las caras podrían ser vulnerables a mecanismos de inhibición controlada, al igual que lo son otros objetos. Para investigar este problema, utilizamos una versión del paradigma de práctica en la recuperación con estímulos faciales, y evaluamos si las caras también eran vulnerables al efecto RIF. En los Experimentos 1a y 2a, exploramos este efecto en diferentes niveles del proceso de reconocimiento de caras y en los experimentos 1b y 2b buscamos evidencia de que los resultados obtenidos se deben de hecho a mecanismos inhibitorios. Esta serie experimental ha sido publicada en *Acta Psychologica* (Ferreira, Marful y Bajo, 2014) y se presenta en la forma del artículo publicado.

En las Series Experimentales II y III, pasamos a explorar, respectivamente, si los correlatos neurales del RIF se mantienen en una muestra de jóvenes cuando utilizamos estímulos faciales y cómo estos correlatos cambian en mayores sanos. Usando un paradigma similar al del Experimento 2b, realizamos dos experimentos de EEG y estudiamos si la actividad cerebral oscilatoria puede identificar específicamente la aparición y desvanecimiento de la interferencia en jóvenes (Experimento 3) y mayores (Experimento 4). El Experimento 3 ha sido publicado en *Journal of Cognitive Neuroscience* (Ferreira, Marful, Staudigl, Bajo y Hanslmayr, 2014) y se presenta en la forma del artículo publicado.

Finalmente, en la Serie Experimental IV, exploramos los correlatos neurales del RIF y cómo estos cambian con el envejecimiento (Experimento 5). Para alcanzar este objetivo, en esta serie optamos por utilizar una técnica con mayor resolución espacial, como la fMRI. Además, para evitar explicaciones alternativas del efecto observado en el Experimento 4, en esta serie utilizamos estímulos semánticos en vez de caras, y por tanto seguimos un procedimiento similar al de Wimber y cols. (2009).

En el último capítulo, discutimos los resultados obtenidos a lo largo de las series experimentales, y proponemos las conclusiones relevantes y las implicaciones para diferentes teorías psicológicas. Finalizamos este trabajo describiendo posibles futuros trabajos en esta línea de investigación.

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2. EXPERIMENTAL SERIES I

2.1. Experiment 1a

Introduction

Retrieval of specific information is not a trivial task. Imagine that in a conversation someone mentions the name of Kofi Annan. You will probably be able to retrieve some information about him, such as “he is the former UN's Secretary-General” or “he is from Ghana”. However, it is also possible that you will associate these information to Morgan Freeman's face, given their similar facial features, and retrieve Morgan Freeman's face instead of Kofi Annan's. Likewise, confusion can arise from other features besides physical ones. For instance, semantic information may interfere with the retrieval of personal representation, so that if someone asks the name of the former UN's Secretary General you might access Ban Ki-moon instead of Kofi Annan.

This illustrates that remembering and recognizing a face or other personal representations such as names, is sometimes difficult (Bruce & Young, 1986). For example, in order to correctly recognize a face, one needs to be able to accurately discriminate and select from a multitude of very similar facial patterns the ones that are relevant to the person we are trying to recognize or retrieve (in the example, Kofi Annan's facial features) and reject the irrelevant ones (e.g. Morgan Freeman's). The same holds true for competition between representations that share semantic information (Kofi Annan and Ban-Ki moon, for instance). Thus, how our memory system deals with competition between these similar representations in order to retrieve the desired one is an important topic.

To explain the processes involved in the correct retrieval of personal representations, several models have been proposed (e.g. Brèdart, Valentine, Calder, & Gassi, 1995; Bruce & Young, 1986; Burton, Bruce, & Hancock, 1999; Burton, Bruce, & Johnston, 1990). These models suggest different processing units, organized within different pools. The idea is that when one sees a face, a unit will become activated: a Face Recognition Unit (FRU). This unit contains representations of the structural features of familiar faces. This representation is independent of the way we see the face, that is, of its position, angle or lighting at the moment we see it.

The activation of a certain FRU leads to the activation of a unit in the next pool: the Person Identity Node (PIN). This unit can become active not only by the sight of a person's face, but also by its voice or its name. So, at this level, all the domains for recognition converge (Burton et al., 1999). Each FRU and each PIN are assigned to only one face or one person. In Burton et al.

(1999) the PIN node is the locus of familiarity, which means that when a PIN reaches a threshold of activation, familiarity is signalled. The activation of a given PIN will allow access to the next pool, labelled Semantic Information Units (SIUs), which codes semantic information about known individuals, such as their profession, their hometown, or their name (names are located in a lexical unit in Brèdart et al., 1995).

Importantly for the scope of this work, these models assume that during retrieval, competition from different active nodes may arise and in order to correctly retrieve the desired representation, competition needs to be solved. From this perspective, retrieval of personal information would be subjected to the same type of interference processes than objects and other episodic information. However, several lines of research question this assumption.

First, faces have been said to enjoy a special status in cognition and accordingly are not always vulnerable to the same variables and mechanisms as other objects (e.g. Farah, 1996; Haxby, Hoffman, & Gobbini, 2000; McKone, Kanwisher, & Duchaine, 2007). For example, inversion of stimuli (i.e., its presentation in an upside down position) worsens facial recognition to a much larger extent than object recognition (Farah, 1996). Also, electrophysiological (Itier & Taylor, 2002; Rossion et al., 2000) and neuroimaging studies (Haxby, Hoffman, & Gobbini, 2002) seem to indicate that there are components and brain regions more sensitive to face processing and recognition. Taken together these studies suggest that perceiving and recognizing a face implies specific mechanisms, different from those involved in the perception of other types of stimuli. This could mean that facial and personal representations respond differently than objects to interference processes.

In fact, research comparing interference during object and face naming has yielded contrasting results. Whereas for objects there seems to be a consensus that naming a target can be impaired by the presentation of a semantically related distracter (Glaser & Düngelhoff, 1984; Lupker, 1979; Rosinski, Golinkoff, & Kukish, 1975), results for face naming are not as clear. Though some studies have found similar results when comparing face and object naming (e.g. Brèdart & Valentine, 1992; Darling & Valentine, 2005), others have failed to replicate these results. For instance, in three experiments, Vitkovitch, Potton, Bakogianni, and Kinch (2006) did not obtain any evidence of interference in face naming when employing a paradigm that had previously been shown to elicit interference for objects (Vitkovitch, Rutter, & Read, 2001). In the first experiment, Vitkovitch et al. (2006) primed the target face with categorically related distracter faces; in the second study, the prime was associatively related, and in the last experiment they primed the target face with a categorically related distracter written name. None of these manipulations led to interference effects. Thus, the studies by Vitkovitch et al. (2006) using this paradigm convey the idea that interference might not be present during face naming.

Second, although some models (e.g. Burton et al., 1990, 1999) assume that related personal information interferes and competes for retrieval, the type of inhibitory mechanisms proposed by these models to deal with competition differs from that proposed for other type of information. Whereas face recognition models suggest that inhibitory links are built within the system to resolve competition, retrieval inhibition in episodic and semantic memory is assumed to be the result of a controlled mechanism external to the system (see, Anderson, 2005; Anderson, Bjork, & Bjork, 1994; Anderson & Spellman, 1995). Note that the term "controlled mechanism" does not necessarily involve intentionality. Instead, the term implies that executive control processes underlie the effects found in this paradigm and in fact, many recent studies speak in favor of this assumption (e.g. Román, Soriano, Gómez-Ariza, & Bajo, 2010; Ortega, Gómez-Ariza, Román, & Bajo, 2012).

Face recognition models propose that different pools of units are connected by excitatory links, whereas links within units of a same pool are inhibitory[1] in nature. Links between pools are bi-directional and have, initially, equal strength. Activation passes along these links from one unit to the other and the activation of these units changes over time and tends to stabilize. The total input that leads to the activation of a particular unit is the sum of the input it receives from other related units, plus any external input provided (Burton et al., 1990). This self-regulation mechanism posits that if many units in the same pool receive simultaneous activation, the unit that is activated the most will inhibit the others, forcing them to stabilize, that is, to go back to their initial level of strength (Burton et al., 1999). To make it clearer, imagine that two people sharing very similar facial features (as Kofi Annan and Morgan Freeman), become active and give rise to competition. This should be quickly solved given that one FRU will rapidly inhibit the other. The same would happen at all levels of representation, for instance, the activation of Kofi Annan and Ban Ki-moon (given their shared semantic features) would also imply that the person activated the most would automatically suppress its competitors. Hence, competition would be solved by means of automatic inhibitory links. Evidence for this inhibitory mechanism comes from semantic priming studies (Burton et al., 1990) showing that semantic priming disappears when subjects are asked to recognize a new face and that it does not last for more than 5s (Burton et al., 1990, 1999).

However, outside the face recognition field, many studies have shown that competition during retrieval is solved by means of controlled inhibitory mechanisms that have long lasting consequences (e.g. Anderson & Spellman, 1995; Anderson et al., 1994). For example, Anderson (2005) has suggested that for a given retrieval cue, many memory representations may come to mind and compete for selection. In order to select the desired item, controlled inhibition is triggered to reduce the level of activation of the competing non-target memories (Anderson et al., 1994). Inhibition is thought to reduce the activation level for a given representation, preventing it from achieving threshold and reducing the level of competition.

Controlled inhibition in memory selection has been studied by means of the retrieval practice paradigm (Anderson et al., 1994). In the first phase of this paradigm participants study pairs of semantically associated words (e.g. FRUIT-Orange; FRUIT-Banana; ANIMAL–Elephant). Next, in the retrieval practice phase, participants practice half of the exemplars from half of the studied categories, given a retrieval cue (e.g. FRUIT-Or____). Finally, after a distracter task, participants are asked to retrieve all the exemplars from all studied categories. Therefore, after retrieval practice, we can distinguish three types of items: the practiced items of practiced categories, as Orange (Rp+);

non-practiced items from practiced categories, for instance Banana (Rp-) and non-practiced items from non-practiced categories (Elephant; Nrp). These last provide a baseline against which the Rp+ and Rp- can be compared.

What is usually found is that Rp+ items are recalled above baseline (Nrp), which should reflect the effects of practice. More interestingly however, is that recall of the Rp- items is usually impaired in comparison to Nrp. This effect is known as Retrieval Induced Forgetting (RIF). The authors argue that the retrieval of some members of a given category (Rp+) impairs later recall of unpracticed items from the same category. During retrieval practice phase, Rp- items have to be inhibited in order to reduce their competing effects and facilitate the recall of the Rp+ items.

Although non-inhibitory explanations have also been proposed (such as associative blocking; e.g. Raaijmakers & Jakab, 2012) or change of context (e.g. Jonker, Seli, & MacLeod, 2013), the amount of studies strongly supporting the inhibitory account of RIF is overwhelming (e.g. Anderson & Spellman, 1995; Anderson et al., 1994; Bajo, Gómez-Ariza, Fernández, & Marful, 2006; Hicks & Starns, 2004; Johansson, Aslan, Bäuml, Gäbel, & Mecklinger, 2007; Kuhl, Dudukovic, Kahn, & Wagner, 2007; Román et al., 2009; Staudigl, Hanslmayr, & Bäuml, 2010; Storm, Bjork, Bjork, & Nestojko, 2006; Veling & van Knippenberg, 2004; Wimber, Rutschmann, Greenlee, & Bäuml, 2009; see Storm & Levy, 2012 for a review). Moreover, the controlled nature of RIF is supported by behavioral studies that show that the effect disappears in populations with deficits of executive control (e.g. Soriano, Jiménez, Román, & Bajo, 2009), as well as by several electrophysiological (e.g. Ferreira, Marful, Staudigl, Bajo, & Hanslmayr, 2014; Hellerstedt & Johansson, 2013; Johansson et al., 2007; Staudigl et al., 2010; Waldhauser, Johansson, & Hanslmayr, 2012) and neuroimaging studies (e.g. Kuhl et al., 2007; Wimber et al., 2008; Wimber et al., 2009) showing that the RIF effect is dependent of prefrontal structures, typically associated with conflict detection and resolution, namely the Anterior Cingulate Cortex and the Dorsolateral Prefrontal Cortex.

Given that RIF effects are assumed to be the result of competition (Anderson, Bjork, & Bjork, 2000; Anderson et al., 1994; Bäuml, 2002) and consequent inhibition, the retrieval practice procedure can be a valuable tool to compare interference and inhibition processes in personal representations, namely to assess if, similar to other objects, competition can occur between facial features and names, and if it can also be resolved by controlled inhibitory processes. Hence, in the present study, we aimed to investigate if mechanisms of inhibitory control can also be responsible for memory selection during retrieval of personal representations. In Experiment 1, we explored interference and inhibition at the FRU level, whereas in Experiment 2, we explored these processes during name retrieval. Importantly, this represents an adaptation of the retrieval practice paradigm to a novel and more natural context, such as face feature recognition.

In order to study inhibition of facial features, in Experiment 1 we adapted the procedure used by Ciranni and Shimamura (1999, Experiment 1) to show RIF for perceptual information. In their experiment, Ciranni and Shimamura used different geometric figures, grouped by a distinct dimension (such as location, form or color) and observed that retrieval practice on one dimension of the stimuli (working as a category) impaired later recall of the non-practiced items belonging to the practiced perceptual category. In Experiment 1, we created facial categories by presenting faces that shared the same type of hair (short blond, long blond or red hair). All of the faces differed, however, in the color of their eyes. During the study phase, our aim was to create competition among faces sharing a particular feature (the type of hair). In the retrieval practice phase, participants practiced half of the faces from two categories. They were presented with an image of the hair followed by a black and white face and were asked to choose from a color pallet the color of the eyes corresponding to the presented face. This pre-cuing procedure (see Bajo et al., 2006) is used to enhance competition between stimuli. The assumption is that upon presentation of a category cue (the hair) all the items belonging to that category will become activated and compete for retrieval. This competition has to be solved later, when the retrieval cue (a specific face) is presented.

The eyes were selected as the to-be-recognized feature, since previous studies have shown that this is one of the most salient features when recognizing a non-familiar face (e.g. Bonner, Burton, & Bruce, 2003; Hancock, Bruce, & Burton, 2000; Rakover & Cahlon, 2001). Finally, participants were presented with all of the black and white faces and had to choose the appropriate eye color from the color palette.

In Experiment 1 we addressed the question of whether faces, like objects, are vulnerable to the retrieval inhibition effect. According to the literature discussed above, which defends different mechanisms underlying face and other objects' perception, we should not expect RIF effect to occur when using faces as stimuli. This should be so since, according to the face recognition models (e.g. Burton et al., 1990), an activated unit will rapidly inhibit competing ones, and thus, a controlled inhibitory mechanism (such as the one underlying RIF) would not be necessary. In addition, according to these models, inhibited units (in our manipulation, Rp-) should go back to their initial strength, that is, their recall should resemble that of baseline items (Nrp), but not go below it.

If, however, competition between facial features is resolved by means of inhibitory executive control, we expect that practicing the color of the eyes of some faces during the retrieval practice phase would impair the later recall of the unpractised items from the practiced categories (Rp-) relative to the baseline item (Nrp). Getting back to our example, in Experiment 1 we aimed to investigate if, in order to correctly remember Kofi Annan's facial characteristics, one has to inhibit Morgan Freeman's.

To rule out alternative explanations for the results of Experiment 1a (such as blocking) and ensure they rely on processes engaged to overcome interference created by the retrieval practice, a second experiment was conducted (1b) where instead of having to retrieve the stimuli, participants were simply re-exposed to them without making any retrieval effort. Since in both procedures (retrieval practice and relearning) a given set of items is being strengthened, if the effect on Experiment 1a was being driven merely by interference or response bias at test, then relearning should also lead to a forgetting effect for the unpractised related items.

In Experiments 2a and 2b, we followed the same rationale for name retrieval.

Method

Participants

Thirty undergraduate students from the University of Granada participated in this study. From the total of participants 4 were male (Mean age=22.3, SD=1.9) and the other 26 female (Mean age=21.2, SD=1.2). Participants got credits for their courses for taking part of the experiment. All participants reported normal or corrected to normal vision and were not color blind.

Materials

Sixteen faces from the Karolinska Directed Emotional Faces database - KDEF (Lundqvist, Flykt, & Ohman, 1998) were selected. These faces were then modified, using Adobe Photoshop CS 8.0.1 software so that they could be grouped according to one specific feature. Five types of hair were chosen from de KDEF database faces, isolated and applied to other faces. We created three critical categories of hair that differed both in color and general form (short blond hair, long blond hair and red hair). Four faces were randomly assigned to each one of these types of hair. In addition, two filler categories were created (with two exemplars each) using long gray hair and short gray hair. All images had 9.98cm x 13.55 cm dimension and were put on a white background (see Fig. 1).

The colors of the eyes were transformed in a similar way, in order for each experimental face to have a specific eye's color (a light, a medium and a dark blue hue, light, medium and dark green, light, medium and dark brown, light and dark gray and black). Two more colors were included for the filler items (14 colors in total). Eye colors were assigned so that each category comprised four different colors, that is, a blue, a green, a brown and a gray/black hue. Thus, within the same category there could not be different hues of the same color (for example, dark blue and light blue). The most unnatural colors were assigned to the filler items and we tried to maintain the critical ones' as natural as possible. In sum, materials for study were composed of 12 experimental faces grouped into three categories (according to the type of hair) and four filler faces belonging to two filler categories.

These faces were then converted to black and white images to be used in the retrieval practice and test phases. Isolated images of each type of hair were also created to be used as category cues in the retrieval practice phase and the eyes of each of the 16 colored faces were isolated too, to use in the familiarization phase of the experiment. Each eye for this familiarization phase had a 10 x 5.20cm dimension and was presented on a white background. These images were then reduced to a 2.30 x 2.30cm dimension square to create a color palette from which participants had to select the right eye color during the retrieval practice and final test phases.

In total, 16 colored faces were used in the study phase, 8 black and white faces in retrieval practice and 16 black and white faces in the final memory test. In order to control for possible biases, all faces had a neutral expression.

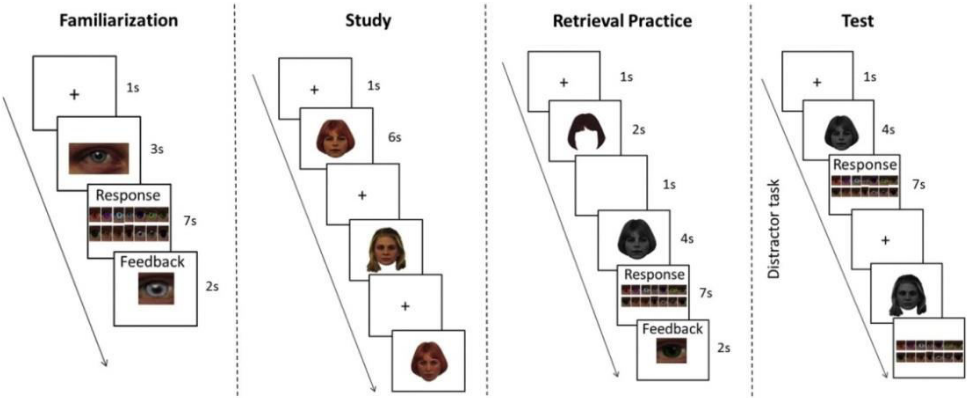

Figure 1. Experimental procedure as employed in Experiment 1a. First, participants performed a familiarization task, in order to get acquainted with the colors used in the experiment. Then the experiment followed the standard 3 phases of retrieval practice paradigm: a study phase, where participants studied 16 colored faces; a retrieval practice phase, where participants were presented with a category cue (the hair), and a retrieval cue (the face) in order to retrieve the eye color of the previously seen face; and a test where all of the faces were presented.

Procedure

As shown in Fig. 1, the first part of the experiment consisted in a familiarization phase so that participants could get acquainted with the colors to be used in the experiment and could learn how to distinguish the different hues. Thus, in the beginning of the experiment, the image of an eye was shown for 3s followed by fourteen colored squares (one for each possible eye color). Participants were asked to click on the square corresponding to the eye they had just seen and feedback was provided right after. Each eye was presented once.

The rest of the experiment followed the retrieval practice procedure. First, in the study phase, participants saw the 16 colored faces, and were given instructions to memorize them, since they would be asked about them later. The presentation was randomized, with some restrictions: the first and the last four faces were always fillers, in order to control for primacy and recency effects, and two faces from the same category could not appear sequentially. Each face was presented five times, for 6s each.

Next, in the retrieval practice phase, participants practiced half of the faces from two of the categories. A category cue (the type of hair) appeared on the screen for 2s, followed by a black and white face (4s), which served as a retrieval cue. Note that all the hair styles were sufficiently different as to be distinguishable from one another, even when presented in black and white. The subject's task consisted on choosing from the 14 eye color pallet presented after the face, the one corresponding to the previously seen face. Participants had 7s to answer and feedback was provided by presenting a square with the correct color for 2s. Feedback was provided so that the task would be as similar as possible to the procedure of Ciranni and Shimamura's (1999) Experiment 1. Each face was presented for practice three times.

Finally, after a 5 min distracter task, an unexpected memory test was conducted. Note that participants knew they would have to retrieve information after our initial instructions, which they did during the retrieval practice phase; thus we argue the final memory test was indeed unexpected. Participants were presented with each of the black and white faces (4s) in pseudo-random order and had to choose the appropriate eye color from the color palette (7s). To avoid output interference explanations, we presented first the unpractised items and half of the baseline items, followed by the Rp+ and the other half of Nrp. Apart from this constraint, order of presentations was random. Three counterbalance versions were created so that each item appeared equally in each condition (Rp+, Rp - or Nrp).

Results and discussion

For this experiment, the mean probability of recall in the retrieval practice phase was .59 (SD=.21). We excluded three participants because their baseline score was 0. The remaining 27 subjects were equally distributed across the counterbalancing conditions (9 *per* condition).

In order to check for facilitation and forgetting effects, in this and the following experiments, we performed two repeated measures ANOVAs on the percentage of recall in the final test. The first analysis involved comparing memory for Rp+ and Nrp items (facilitation), while the second analysis involved contrasting memory for Rp- and Nrp items (forgetting). Results can be seen in Fig. 2A.

The facilitation effect of practice was significant [$F(1,26)=7.63$, $p=.01$, η2=.23] so that Rp+ items were recalled better than Nrp (Fig. 2A). This facilitating effect of practice is usually found in the retrieval practice procedure. In addition, there was a reliable RIF effect, that is, recall of the Rp- items was significantly lower than recall of the Nrp [$F(1,26)=4.97$, $p=.03$, η2=.16].

Hence, our results indicate that inhibition can act during retrieval of facial features. During the retrieval practice phase, the presentation of a particular hair type activated the faces sharing that particular feature; then, when the black and white faces were presented and the corresponding eyes' color had to be selected, inhibition was triggered to suppress the competing irrelevant features so that when they were tested later they became less accessible.

It could be argued here that participants were adopting a guessing strategy, such that when seeing an Rp- item they could eliminate the colors they knew corresponded to Rp+, reducing the number of colors to choose from. This would not happen with Nrp items, since the category was never practiced and no colors were learnt better than others. However, if participants were indeed using such strategy, we would expect to find enhanced recall of the Rp- items, which is the opposite pattern to what we find in this experiment.

In sum, similar to the RIF effect found by Ciranni and Shimamura (1999) with visuo-spatial stimuli, we showed RIF during face feature recognition, namely in an early stage of the face recognition process (FRUs in Burton et al., 1999).

It could, however be argued, that these effects depend on interference, or reflect associative blocking instead of inhibition. To rule out these possible explanations, we conducted Experiment 1b, in which participants were merely re-exposed to the stimuli during the intermediate phase, instead of actively retrieving them. If the effects of Experiment 1a were being driven by interference or response bias at test, then relearning should also lead to a forgetting effect for the unpractised related items.

2.2. Experiment 1b

Method

Participants

Thirty-three undergraduate students from the University of Granada participated in this study. From the total of participants 11 were male (Mean age=20.3, SD=2.8) and the other 22 female (Mean age=19.2, SD=1.2). Participants got credits for their courses for taking part of the experiment. All participants reported normal or corrected to normal vision and were not color blind.

Materials

The materials used were the same as in Experiment 1a.

Procedure

The procedure followed Experiment 1a, except for the retrieval practice phase. In this experiment, instead of having to actively retrieve the eye color of the previously seen faces, participants were given the correct responses.

Thus, during this phase, participants saw half of the faces from two of the categories. A category cue (the type of hair) appeared on the screen for 2s, followed by a face in black and white (4s), which served as a retrieval cue. Then the 14 eye color pallet appeared on screen and a black square surrounded the correct eye color (7s). Each face was presented three times.

Results and discussion

In this experiment, six participants were excluded because their baseline score was 0.

As in the Experiment 1a, two repeated measures ANOVAs were conducted on the percentage of recall in the final test, comparing memory for Rp+ and Nrp items (facilitation), and contrasting memory for Rp- and Nrp items (forgetting). Results can be seen in Fig. 2A.

The facilitation effect of practice was significant [$F(1,26)=28.77$, $p<.001$, $\eta^2=.524$] so that Rp+ items were recalled better than Nrp (Fig. 2A). Facilitation is usually found with relearning of the material, and reflects an effect of practice. However, in this experiment, there was no significant forgetting effect, that is, recall of the Rp-items did not differ from Nrp recall ($F<1$).

According to these results, simply being exposed to the stimuli without the need of an active effort to retrieve information does not yield forgetting of unpractised but related items. This comes in line with previous research showing the same pattern of results (Anderson et al., 2000; Ferreira, Marful, Staudigl, Bajo, & Hanslmayr, 2014; Hanslmayr, Staudigl, Aslan, & Bäuml, 2010).

Thus, Experiment 1b supports an inhibitory explanation of the results found in Experiment 1a. Again, it seems that controlled inhibition comes into play when there is a need to suppress competing irrelevant features. When participants are simply re-exposed to the material no such need arises and recall of unpractised items is not impaired.

2.3. Experiment 2a

Experiment 1 seems to indicate that inhibitory mechanisms might play an important role at early stages of face recognition. Experiment 2 aimed to investigate if these controlled inhibitory mechanisms can also arise at other stages of the face recognition process by focusing on semantic and name information (SIUs). For example, imagine you see the face of an actor (e.g. Eduardo Noriega) and try to remember his name. You will probably access information such as “he is Spanish” or “he is an actor”. This information can lead to the activation of other names associated to similar semantic information, such as Antonio Banderas'. Thus, we hypothesize that in order to correctly retrieve Noriega's name, one would have to inhibit Banderas'.

Therefore, we used the retrieval practice procedure to create competition between names of people that share semantic information (their occupation). If interference does not arise at a semantic level, as posited by Vitkovitch et al. (2006), we should not find RIF effect on Experiment 2. If, however, competition between personal information also arises during name retrieval, and controlled inhibition is triggered to deal with this competition, then we should expect to find standard RIF effects, that is, we should find that the recall of suppressed representations (Rp-) is impaired in comparison to baseline items (Nrp). These results would indicate that interference situations may affect different stages of face recognition and that interference in these cases might be overcome by mechanisms of inhibitory control.

Moreover, the type of recognition demanded from the subjects in Experiment 1 can be considered quite artificial, since in everyday life we are not asked to recognize such narrow features of a face. Experiment 2 tries to address this issue as well, since participants are asked to identify faces in a more holistic fashion.

Method

Participants

Thirty nine undergraduate students (30 females) from the University of Granada (Mean age=20.3, SD=2.5) participated in this experiment in exchange for course credit. Again, all participants reported normal or corrected to normal vision. Importantly for this experiment, all participants were Spanish or had been living in Spain for at least 15 years.

Material

Thirty-six photographs depicting faces of famous people in Spain with neutral to mildly-positive expression were used in this experiment. These photos were divided in four occupational categories, with six photos per category: female singers, female royalty members, male politicians and male actors, plus two filler categories (male presenters and sportswomen), with three exemplars each. Normative data were collected previous to the experiment to assess familiarity. None of the names shared the first two letters.

Since we wanted to make sure that competition would be at work during retrieval practice, the more familiar faces were selected for each category as Rp- items. Two counterbalanced versions of the materials were created, so that every high familiarity face appeared in both unpractised conditions (Rp- and

Nrp-high familiarity) and lower familiarity names appeared in the Rp+ and Nrp-low familiarity conditions. To check for RIF, Rp- items should be compared to the equivalent high-frequency Nrp items (Nrp-high), whereas Rp+ items should be compared to their equivalent low-frequency Nrp items (Nrp-low) to check for potential facilitation (see Bajo et al., 2006, for a similar procedure). Note this manipulation could not have been done in Experiments 1a and 1b, given that the stimuli used were unfamiliar faces, which did not allow us to know a priori which would be the strongest or weakest competitors.

The 36 photographs were presented in color, in 5.19 x 6.99cm dimensions, on a white background. An oval template was applied around each picture in order to standardize silhouettes and background (see Young, Ellis, Flude, McWeeny, & Hay, 1986).

Procedure

First, a refresh phase[2] took place where participants were shown the 36 photographs. Each photograph was presented for 3s, centered on the screen, with the category name (e.g. ACTOR) and the person's name (e.g. Banderas) written underneath. As in the previous experiment, presentation was pseudo-randomized so that two items from the same category would not appear consecutively. Four filler items were presented at the beginning and at the end of this phase to control for primacy and recency effects. (See Fig. 3.)

Then, in the retrieval practice phase, after a fixation point, subjects were instructed to recall the names of Rp+ items three times. Using a pre-cuing procedure (Bajo et al., 2006) the category name (e.g. ACTOR) was presented (2s), followed by a blank screen (1s) and the first two letters of the Rp+ famous name appeared as retrieval cue for 6s (e.g. Ba_____). Subjects were instructed to retrieve half the names from half the categories.

Finally, following a 10 min distracter task, a memory test occurred. Participants saw a fixation point followed by one of the faces (for 4s or until response). All the faces from the refresh phase were presented in random order in the center of the screen, on a white background. Participants were instructed to recall the names one by one, upon presentation of the face, as quickly as possible, preferentially with the previously studied name (i.e., if they saw the name Banderas during the refresh phase, they should say Banderas at test, and avoid saying his first name Antonio instead. Regardless, we did accept both responses as correct).

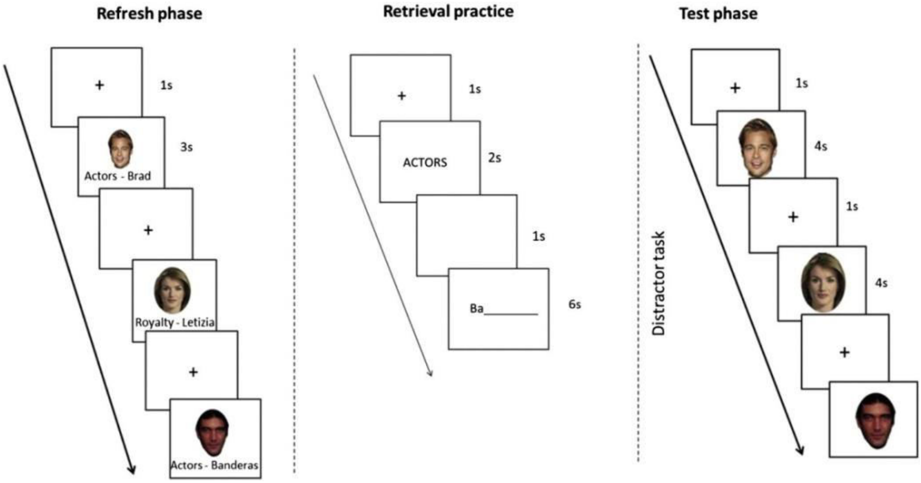

Figure 2. Experimental procedure as employed in Experiment 2a. The experiment followed the standard 3 phases of retrieval practice paradigm: a refresh phase, where participants studies familiar faces along with their profession and names; a retrieval practice phase, where participants were presented with a category cue (profession), and had to retrieve half of the names from half of the categories upon presentation of a retrieval cue (first two letters of the name); and a test where all of the faces were presented again for naming.

Results and discussion

For the data analysis, nine subjects were excluded for having ceiling effects (100% accuracy for both Nrp and Rp-items). For the remaining thirty (15 for each of the two counterbalancing conditions), the average retrieval practice success was .69 (SD=.24).

We obtained a trend for facilitation [$F(1,29)=3.1$, $p=.08$] where Rp+ naming was higher than their Nrp-low baseline (see Fig. 2B, note that because Rp+ and Nrp-low were of lower familiarity relative to the Rp- and Nrp-high items, the level of recall for these items was relatively lower). More importantly, there was a significant RIF effect [$F(1,29)=5.05$, $p<.05$, $\eta^2=.15$]. The probability of retrieving the Rp- names was lower than the probability of retrieving their corresponding Nrp-high baseline names.

Hence, repeatedly retrieving a person's name (e.g. Banderas) during the retrieval practice phase led to the suppression of competitor names (e.g. Noriega), overcoming interference but impairing later access to these competitors in the final naming test.

2.4. Experiment 2b

Following the same logic of Experiment 1, this last experiment aimed to rule out alternate explanations for the results found in Experiment 2a. Thus, the same materials and procedure were used, apart from the retrieval practice phase. In this experiment, participants did not need to actively retrieve the famous person's name, since it was immediately provided to them along with the person's face.

Our assumption is that, similarly to Experiment 1b, no RIF effect will be found, given that no inhibition is needed during this relearning phase.

Method

Participants

Thirty undergraduate students (10 males) from the University of Granada (Mean age=21.7, SD=3.2) participated in this experiment in exchange for course credit. Again, all participants reported normal or corrected to normal vision. As in Experiment 2a, for this experiment, all participants were Spanish or had been living in Spain for at least 15 years.

Material

The material used was the same as in Experiment 2a.

Procedure

The procedure followed that of Experiment 2a, with the exception of retrieval practice phase, which was changed to a relearning phase.

In this phase, after a fixation point, subjects were instructed to attend to some of the faces and names once more. The category name (e.g. ACTOR) was presented (2s), followed by a blank screen (1s) and the name of half the faces from half of the categories for 6s.

Results and discussion

For the data analysis, 8 subjects were excluded for having ceiling effects (100% accuracy for both Nrp and Rp- items).

We obtained a facilitation effect [$F(1,21)=8.54$, $p<.01$, $\eta^2=.23$] where Rp+ naming was higher than their Nrp-low baseline (see Fig. 2B). There was, however, no forgetting effect ($F<1$), with unpractised items and baseline ones being recalled similarly.

Once more, these results speak in favor of an inhibitory explanation regarding Experiment 2a results'. Repeatedly viewing a person's name (e.g. Banderas), with no need for recall, does not seem to lead to forgetting of unpracticed related items. This should be so since no inhibition is needed when participants are passively reading the name of a given person.

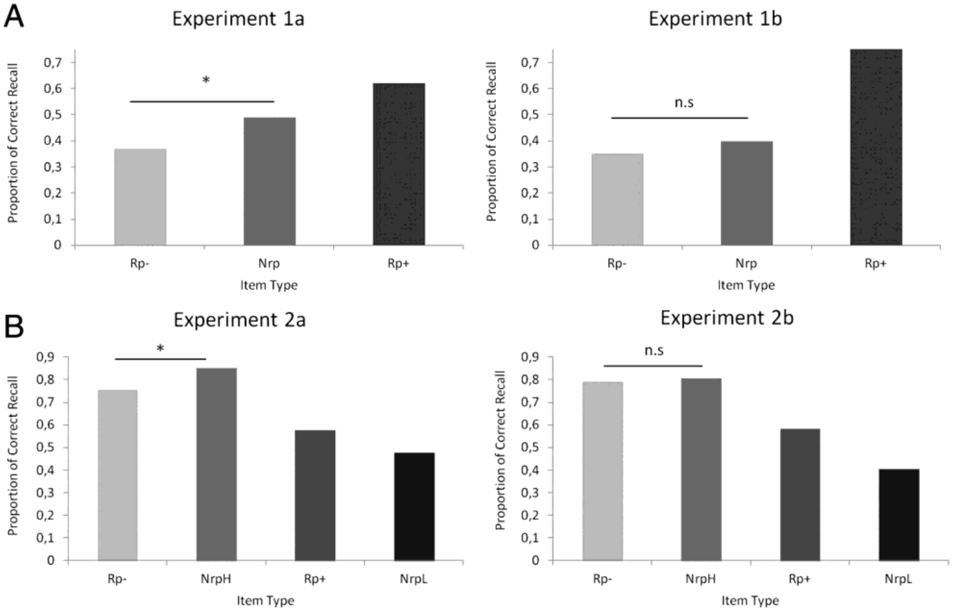

Figure 3. **A)** Results from Experiments 1a (retrieval) and 1b (relearning). **B)** Results from Experiments 2a (retrieval) and 2b (relearning). *p<.05.

General discussion

In two experiments we found evidence of Retrieval Induced Forgetting of facial features (Experiment 1a) and names (Experiment 2a). That is, Rp- items were recalled significantly worse than Nrp baseline in both experiments. During the retrieval practice phase, competition rose between faces that shared some information (the type of hair in Experiment 1 and the occupational category in Experiment 2) and we argue that this competition was solved by means of inhibitory mechanisms that suppressed the competitor (Rp-) items in order to promote the retrieval of the Rp+, thus impairing the recall of these Rp- on the final test. These results have several theoretical implications.

First, results of the two experiments suggest that personal representations, similar to other types of representations, are prone to interference processes. In fact, Retrieval Induced Forgetting has been shown to depend on inhibitory processes triggered to solve competition.

To test this interpretation and ensure the results found in Experiments 1a and 2a were in fact due to inhibitory processes, we conducted two similar experiments (Experiments 1b and 2b) where no competition was created. In these experiments, participants were simply re-exposed to the material without actively retrieving any information. This should create no competition between stimuli and thus, no inhibitory mechanisms would be needed. Accordingly, no RIF effect was found in these experiments.

This comes well in line with previous studies in the literature. For example, Anderson et al., (2000) observed RIF when there was competition during the retrieval practice (e.g. recall orange upon presentation of FRUIT-Or____) but not when competition was not involved (presentation of FR___-Orange, in order to recall Fruit). Employing a similar procedure, some electrophysiological studies found that competitive retrieval conditions elicit higher oscillatory prefrontal theta activity (~4-9 Hz), which has been consistently related to interference (Ferreira et al., 2014; Hanslmayr et al., 2010; Waldhauser et al., 2012).

Given the fact that RIF depends on competition, our results are in line with data showing semantic competition (Brèdart & Valentine, 1992; Darling & Valentine, 2005; Marful, Paolieri, & Bajo, 2014) by showing not only interference in face naming, but also that this interference is solved by means of inhibitory mechanisms. Furthermore, these data support models of facial recognition proposing that competition can arise at several levels of representation (Brèdart et al., 1995; Bruce & Young, 1986; Burton et al., 1990, 1999).

The fact that our results differ from the studies by Vitkovitch et al. (2006), that did not show interference in face naming, could be explained by procedural differences, probably related to a reduced number of naming trials that might not have been enough to elicit interference. Marful, Ortega, and Bajo (2010) used a procedure similar to that of Vitkovitch et al., but incremented the number of naming trials. They replicated the facilitation effect (that is, naming of a prime face facilitated posterior naming of a related target face) when looking at the first naming block. However, this facilitation effect decreased as the naming trials increased, which would then be consistent with our results.

Second, our results suggest that controlled inhibitory mechanisms seem to have an important role on retrieving information related to personal representations. In our two Experiments, competition seems to have been solved by controlled inhibition, since recall of Rp- items was impaired relative to recall of Nrp items. Our data indicate that the inhibitory mechanism by which competition is solved in our experiments differs from the more automatic mechanisms proposed by face recognition models (Burton et al., 1990, 1999).

There are two key predictions from these models that are contradicted by us and other RIF studies. One is that according to the face recognition models (e.g. Burton et al., 1990) inhibited items get back to an initial level of activation but not below it, which could not explain the fact that Rp- items are recalled below baseline (Nrp) ones. The other speaks to the difference between what we here call automatic vs. controlled inhibition. Inhibitory mechanisms proposed by traditional face recognition models greatly resemble a sort of lateral inhibition (e.g. Burton et al., 1990). Thus, these models would predict that the more activated a unit is, the more the competing items would be inhibited. For the retrieval practice paradigm, this assumption would imply that the more activated Rp+ items are, the more inhibition should be observed for Rp-. However, a number of studies have demonstrated that there is no relation between the strengthening of Rp+ and the inhibition of Rp- (e.g. Anderson & Spellman, 1995; Storm et al., 2006). Consequently, the type of inhibition found in the present study could not be explained by the more automatic type of inhibitory mechanisms proposed by face recognition models, but would make sense from a controlled inhibition perspective.

This does not necessarily mean that automatic inhibition does not play a relevant part, but we argue that controlled mechanisms should also be taken into account by models of face recognition given that the type of automatic inhibition proposed by these models cannot fully explain our results.

Recently, another explanation for the RIF effect has been proposed (Jonker et al., 2013) according to which impairment of unpracticed items could be due to contextual effects and not to inhibitory mechanisms. This context-account postulates that two conditions need to be met in order for RIF effect to be found: 1) there should be a context change between study and practice phase, and 2) during the final test, the retrieval practice context (but not the study one) must be reinstated. Even though it could be argued that the first tenet is met in our Experiments, the second one is not, especially in Experiment 2, where participants study the faces and names of famous people and are then prompted to practice the names upon seeing the category cue and the first two letters of the name. Then, during the test phase, participants are prompted with the face again, in order to retrieve the names. Importantly category cues are not shown during this phase. Given these two characteristics of our test, participants should actually re-instate the study phase (when they saw the faces for the last time) rather than the practice one. Thus, the context-account seems to not be able to explain our results.

The idea that this type of controlled mechanism is important to face recognition had already been proposed by authors like Ciranni and Shimamura (1999) and Anderson (2003). In particular, these authors proposed that phenomena such as the Verbal Overshadowing effect (Dodson, Johnson, & Schooler, 1997; Kinlen, Adams-Price, & Henley, 2007; Schooler & Engster-Schooler, 1990) depend grandly on inhibitory mechanisms. This term - Verbal Overshadowing - was first introduced by Schooler and Engster-Schooler (1990) to describe their counterintuitive findings that describing a face in detail can make it more difficult to recognize that same face later. It has been argued that this impairment is due to inhibitory mechanisms (Anderson, 2003; Ciranni & Shimamura, 1999). When making a verbal description of a face it is not possible to describe all its features. So naturally, some of the features will be retrieved while making the description, whereas others will not. Mechanisms involved in this partial retrieval during verbal description can be similar to the mechanisms involved in retrieval practice paradigm.

Accordingly, it is possible that non-practiced but related features will be inhibited, since they compete for retrieval when one makes the description, thus impairing the later recognition of the faces that were practiced.

Note however that, whereas in the Verbal Overshadowing phenomenon competition seems to arise from features within the same face, we believe that in the retrieval practice paradigm we are tapping into interference created between faces, namely, faces that share some particular feature. As mentioned earlier, we believe that upon presentation of the category cue, several faces that share particular information (be it the same type of hair or belonging to the same occupational category) become active and compete for retrieval and it is this competition between different faces that leads to the action of inhibitory mechanisms. In spite of this difference, once more, inhibition seems to influence, in a substantial way, memory and recognition of personal representations.

Third, our results show that inhibition may come in hand at different levels of face and name recognition. Our first experiment seems to indicate that controlled mechanisms of inhibition can occur at the FRU level, where the structural codes are stored, whereas our second experiment demonstrates that inhibition can help overcome interference at a more lexical-semantic level (at the SIU level).

One relevant question regarding Experiment 1 is whether inhibition is taking place at FRU level or whether it could be located at another level of face recognition, namely the PINs. If inhibition was acting at the PIN level, access to the identity of previously presented people should be impaired. If this was the case, RIF effect should still occur when participants are asked to recognize the studied faces (instead of a particular feature). To test this hypothesis, we ran an experiment (N=29; Mean age=19.79, SD=2.54) that followed the same procedure as Experiment 1a, the only exception being that the final memory test consisted on a recognition test, where participants had to make an old/new decision ("was this face presented before?"). In this experiment, RIF effect disappeared ($F<1$), which seems to indicate that the person's identity was not inhibited. Importantly, since Experiment 1a had enough power to detect this effect, we do not believe that the absence of RIF in this experiment could be due to it being underpowered. Taken together, these results indicate that inhibition observed in Experiment 1a could be mainly acting at the FRU rather than at the PIN level.

Accordingly, this sort of mechanisms would have an influence throughout the entire face recognition process. Results from Experiment 1a demonstrate that, at least in some situations (namely in interference resolution), faces are vulnerable to similar mechanisms that act upon other perceptual representations. The same holds true for representations at a lexical-semantic level, as the results from Experiment 2a indicate. Taking this into account, we can assume that, just as other types of information, personal representations are vulnerable to competition from related information during retrieval of faces and names. The relevance of these data lies on the fact that it shows personal representations can be vulnerable to controlled mechanisms of inhibition which could help explaining difficulties and failures in everyday life. For in- stance, it could help explain difficulties reported by older adults when trying to retrieve a particular name or facial feature. Hasher and Zacks (1988) proposed that most cognitive deficits in elder people are related to inhibitory failures, and so, according to our results, naming difficulties could too be explained by inhibitory deficits when dealing with naming interference. In fact, it has been proposed in the Executive Deficit Hypothesis (Levy & Anderson, 2008), that since their executive processes are impaired, older adults fail in using mechanisms of inhibitory control. Recent studies using the retrieval practice paradigm have shown, however, that this impairment may be somewhat gradual, and depending on a number of different variables. For instance, it seems that the effect is maintained in early aging, but disappears during late aging (Aslan & Bäuml, 2012; Marful, Gómez-Amado, Ferreira, & Bajo, 2015). Moreover, early aging participants' ability to inhibit competing items seems to disappear when their memory capacities are overloaded, by introducing, for instance, a dual task (Ortega et al., 2012).

In sum, in two experiments we investigated if faces and names can be subjected to controlled inhibitory mechanism. Our results demonstrate that inhibition, conceived as a general mechanism that allows us to override competition situations, may play an important role at different stages of face feature recognition and help explain some everyday difficulties in face recognition and naming. We argue, therefore, that models of face recognition should take into account this type of mechanisms.

Footnotes

1. Altough the seminal model of face processing developed by Bruce and Young (1986) did not consider inhibitory mechanisms to solve interference, most of the more recent models do assume inhibitory links within same units (e.g. Brèdart et al., 1995; Burton et al., 1900, 1999).

2. Since participants already knew all of the faces, given that they were given that they were very familiar, we named this phase refresh phase instead of study phase. We consider participants were not learning faces or names but just refreshing their memory.

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3. EXPERIMENTAL SERIES II

3.1. Experiment 3

Introduction

Retrieval of a target memory is often challenged by other competing memories, which are irrelevant for the particular information one is trying to retrieve (Anderson & Neely, 1996; Anderson, Bjork, & Bjork, 1994). Consider, for instance, that you are trying to recall a memory from your last summer holidays. Several memories of previous holidays are prone to become activated and compete with the specific memory of the last ones, thereby eliciting retrieval interference. According to the inhibitory theory, mechanisms are needed to detect this interference and engage higher-order control mechanisms that reduce interference by suppressing the competing memories. In this study, we provide evidence that theta oscillations in the medial pFC track the time course of interference during selective memory retrieval. Employing a new experimental paradigm, we here show that theta oscillations in the medial pFC specifically reflect interference (the activation of competing information) and not its resolution, which goes beyond previous studies.

Interference and inhibition during memory retrieval are typically studied by means of the retrieval practice paradigm (Anderson et al., 1994). In this paradigm, after studying pairs of semantically related words (e.g. FRUIT-Orange; FRUIT-Banana, or ANIMAL-Horse), participants engage in a retrieval practice phase, selectively retrieving half of the exemplars from half of the categories, given a retrieval cue (e.g. FRUIT-Or____). In a final test, participants are asked to retrieve all of the exemplars from all of the previously studied categories. Results consistently show that whereas the recall of practiced items (Orange) is improved, recall of unpracticed items that belong to practiced categories (Banana) is impaired relative to control items (items from unpracticed categories; e.g. Horse). This phenomenon is termed retrieval-induced forgetting (RIF). RIF is typically explained by a reactivation of competing items during the retrieval practice phase, which are inhibited to facilitate retrieval of the target item. The results of several behavioral (e.g. Román, Soriano, Gómez-Ariza, & Bajo, 2009; Soriano, Jiménez, Román, & Bajo, 2009; Anderson, 2003; Bäuml & Hartinger, 2002; Anderson & Spellman, 1995), electrophysiological (e.g. Hellerstedt & Johansson, 2013; Waldhauser, Johansson, & Hanslmayr, 2012; Hanslmayr, Staudigl, Aslan, & Bäuml, 2010; Staudigl, Hanslmayr, & Bäuml, 2010; Johansson, Aslan, Bäuml, Gäbel, & Mecklinger, 2007), and neuroimaging studies (Wimber, Rutschmann, Greenlee, & Bäuml, 2009; Wimber et al., 2008; Kuhl, Dudukovic, Kahn, & Wagner, 2007) strongly support this inhibitory account of RIF.

On a neurocognitive level, interference has been consistently associated with oscillatory prefrontal theta band activity (~4–9 Hz) in studies using response conflict tasks, such as Flanker or Stroop tasks (e.g. Cavanagh, Cohen, & Allen, 2009; Hanslmayr et al., 2008). Theta oscillations also seem to index the amount of activated information in memory (e.g. Khader & Rösler, 2011; Mecklinger, Kramer, & Strayer, 1992). Regarding studies using the retrieval practice paradigm, Hanslmayr et al. (2010) found that a competitive retrieval condition elicited higher theta power, when compared with a noncompetitive retrieval condition. This effect was most pronounced over frontal and left parietal sites and correlated with later forgetting. Similar results have been found by Waldhauser et al. (2012) and Staudigl et al. (2010).

Staudigl et al. (2010) compared two cycles of retrieval practice and observed a reduction in theta amplitude from the first to the second retrieval cycle (reflecting reduced activation of competing information), which predicted the amount of RIF. No such effect was found in a reexposure control condition. Importantly, the reduction in theta amplitude across retrieval practice cycles was localized to the

ACC, confirming the results of an fMRI study showing a reduction of BOLD signal in ACC (and in the dorsolateral pFC) with an increase of retrieval attempts (Kuhl et al., 2007). These results are consistent with theories assuming that ACC plays an important role in the detection of interference and its mediation (Botvinick, Braver, Barch, Carter, & Cohen, 2001).

A problem with the prior studies, however, is that by presenting the category cue together with the item-specific retrieval cue, they cannot disentangle the effects of interference, triggered by the cue (which activates previously associated items), from the effects of inhibition, needed to reduce interference. From a theoretical perspective this is a relevant question given that competition is said to precede inhibition. In fact, without competition, there is no need for inhibition to act. So far, however, these temporal dynamics of competition and inhibition have not been addressed. To address this question, we used an adaptation of the retrieval practice paradigm previously introduced by Bajo, Gómez-Ariza, Fernández, and Marful (2006), where the category cue was temporally separated from the item-specific cue.

Underlying this precuing procedure is the idea that the presentation of the category cue will lead to the activation of previously associated items competing for retrieval. This has been demontrated in previous studies showing that presenting a retrieval cue activates associated items and renders retrieval more difficult as the number of associated items increases. This effect held constant both when associations were explicitly learned during study (Anderson & Reder, 1999; Watkins, 1979) and when a given category was naturally connected to more associatively related words (Nelson, Schreiber, & Xu, 1999; Nelson, McEvoy, & Bajo, 1984).

In this study, competition (interference) is elicited by presenting the category cue. Afterwards, upon presentation of the item-specific cue, inhibitory mechanisms should come into play to reduce interference, thereby facilitating retrieval of the target item. Unlike previous experiments, this procedure allows to trace the specific temporal dynamics of competition (as prompted by the category cue), disentangling it from the inhibition-related activity, that should only be present upon presentation of the item-specific cue.

Following prior work (Hanslmayr et al., 2010; Anderson, Bjork, & Bjork, 2000), a competitive and a noncompetitive retrieval condition were contrasted. In the competitive condition, participants were presented with an occupational category that served as a category cue (e.g. Actors), followed by the face of a famous person (the item-specific cue), whose name they should retrieve (e.g. Brad Pitt). In the noncompetitive condition, participants saw the first two letters of the category cue (e.g. Ac____), also followed by the face of a famous person, but were instructed to retrieve the category name. Note that, although both conditions demand participants to actively retrieve information (the category label or the specific name), the competitive condition requires participants to recall a specific item in the presence of competition, whereas in the noncompetitive condition participants are simply asked to retrieve that category label with no need to retrieve the specific names/faces associated to them. Therefore, the category label in the noncompetitive condition does not act as a retrieval cue for the associated items, and thus, no requirement for interference resolution mechanisms is needed.

The assumption is that, in the competitive condition, the presentation of the category cue (e.g. Actor) leads to the activation of items previously associated to it that will compete for retrieval, creating interference, which should subsequently trigger inhibitory mechanisms to reduce competition. These dynamics should be specifically reflected by medial prefrontal theta power. Accordingly, it was hypothesized (i) that presentation of the cue in the competitive retrieval condition elicits higher theta power than presentation of the cue in the noncompetitive condition, (ii) that theta power decreases upon presentation of the target face, reflecting competition reduction, and (iii) that this decrease in theta power from cue to face correlates with later forgetting.

Finally, the use of facial stimuli might help shed light on some controversial topics in the face processing and recognition literature, especially regarding the similarity of the mechanisms underlying faces and other objects' recognition (e.g. McKone, Kanwisher, & Duchaine, 2007; Haxby, Hoffman, & Gobbini, 2000; Farah, 1996) and the issue of whether face naming is subject to interference (Vitkovitch, Potton, Bakogianni, & Kinch, 2006; Darling & Valentine, 2005; Brèdart & Valentine, 1992). If personal representations are inhibited (i.e., if the RIF effect is found for this type of stimuli), this would mean they are vulnerable to interference and that, at least at some instances, mechanisms underlying faces and objects' recognition are of a similar nature.

In summary, in this study, a precuing procedure was used to disentangle competition and inhibition signals during the retrieval practice paradigm. To isolate the inference signal, a competitive retrieval condition was contrasted with a noncompetitive condition. Because we were interested in the temporal dynamics of competition, we collected EEG data. Given the great temporal resolution of EEG, using this technique allowed us to trace the fine-grained temporal dynamics of competition, which would not have been possible using behavioral data only.

Methods

Participants

Twenty (10 women) students from the University of Granada participated in this study (Mean age=24 years, SD=3.1 years). All participants were Spanish or had been living in Spain for at least 15 years. All of them reported normal or corrected-to-normal vision. Participants gave written informed consent before the study and received either course credits or a monetary reward for their participation.

Material

Forty-eight pictures of famous people in Spain from eight occupational categories (male actors, politicians, football players, writers, and TV hosts, and female singers, royalty members, and tabloid stars) were chosen from a set of pictures collected before the experiment to assess the familiarity of each item. The most familiar pictures were selected from this set with the constraint that none of the names of the famous people shared the first two letters. Two additional categories (radio personalities and bull fighters) with three exemplars each were used as fillers to prevent for primacy and recency effects and were not taken into consideration in any of the analyses described. The pictures (5.19 cm x 6.99 cm) were presented in color against a white background. The faces displayed a neutral to mildly positive expression. An oval template was applied around each picture to standardize silhouettes and background (see Young, Ellis, Flude, McWeeny, & Hay, 1986).

Design

The experiment consisted of two blocks (within-participant design). Each block comprised a study phase, a retrieval practice phase, and a final test. The two blocks differed in the list of items provided as well as in the type of selective retrieval performed: competitive or noncompetitive (Figure 4A). From the total of pictures, half (24) were shown in the competitive condition (C), and the other half were presented in the noncompetitive condition (NC). A similar procedure has been used in different RIF studies, such as Gómez-Ariza, Fernández, and Bajo (2012), Hanslmayr et al. (2010), or Anderson et al. (2000).

In the C condition, participants were shown the category cue, which consisted of the occupational category of the target face (e.g. Actor), followed by the item-specific cue (a previously studied face belonging to that same category;

e.g. Brad Pitt). Participants were instructed to retrieve the name of each famous person. In the NC condition, participants saw the first two letters of the to-be-retrieved category (e.g. Ac) and subsequently a face with the corresponding name written below. In this condition, the participants' task consisted in retrieving the category name ("Actor," for instance).

In both conditions, retrieval was performed for half of the items from three of the four studied categories. This created three different types of items: practiced items, unpracticed items (from practiced categories), and control items from nonpracticed categories, which served as baseline items.

Across participants, all items served equally often as practiced, unpracticed, and control items, in both C and NC conditions. Assignment of list to block and presentation order of the blocks was counterbalanced across participants.

Procedure

Study Phase

Each block started with a study list, during which the 24 items were presented successively on a 15-in. computer screen. After a fixation cross (1sec), participants were presented a face together with its respective name and category displayed below (see Figure 4A) for 5sec. Presentation order of the items was randomized with the restriction that the first and the last four faces were filler items, and two faces from the same category did not appear sequentially. Participants were instructed to memorize all faces as well as their name and category, as they would be asked to recall them later.

Retrieval Practice Phase

After studying the 24 items, participants engaged in nine retrieval practice trials, where half of the exemplars from three of the studied categories were presented. In the C condition, a trial started with a fixation cross, with a variable duration (1-1.5sec) followed by a category cue for 2sec (e.g. Actor) and a blank screen (1sec). Thereafter, the item-specific cue (i.e., the face) appeared on the screen for 2.5sec, followed by a blank screen (4sec), during which participants were asked to overtly retrieve the corresponding name (e.g. Brad Pitt). In the NC condition, a trial started with a jittered fixation cross (1-1.5 sec) followed by the first letters of the category cue (e.g. Ac___). Then, a blank screen was presented (1sec) and subsequently a face belonging to that category, along with the corresponding name displayed below (2.5sec). During the following 4 sec, participants were asked to overtly retrieve the corresponding category name (e.g. Actors). To prevent possible speech artifacts in the EEG, participants were instructed to only respond during the 4-sec blank interval.

Test Phase

After a 5-min distracter task (the vocabulary test from the Wechsler Adult Intelligence Scale), each block ended with a memory test, during which each of the studied faces were presented individually, and participants were asked to produce the corresponding name. After a fixation cross (1sec), each face appeared on the screen for 4 sec, and participants were instructed to name the person as quickly as possible. The order for testing was pseudo-randomized, such that unpracticed items and half of the control items were shown first, followed by practiced and the other half of the controls. This was done to prevent blocking effects, that is, to prevent retrieval of the practiced items to block access to the unpracticed ones, which would confound the effects of memory inhibition (Anderson et al., 1994). After a short break, the second block of the experiment was conducted.

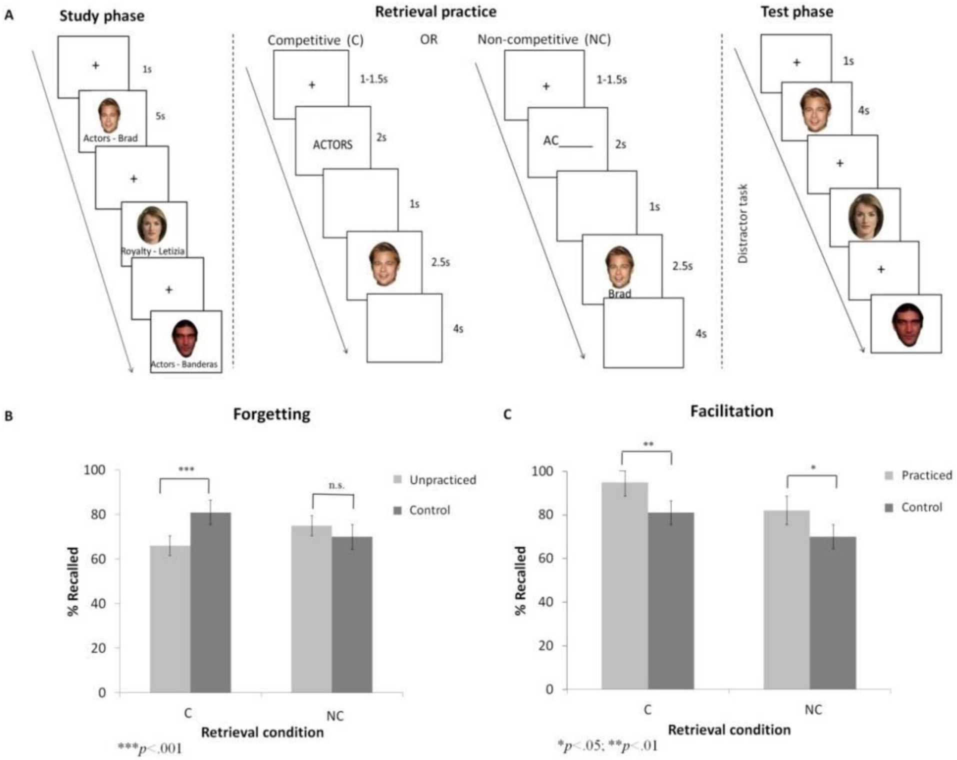

Figure 4. **(A)** Experimental procedure in this study. The experiment consisted of three phases: During study phase, participants studied pictures of famous people, alongside with their name and occupational category. During retrieval practice, participants were instructed to retrieve either the person's name or the name of the category cue, depending on the condition they were performing. Note that during retrieval practice phase, presentation of category cue was temporally separated from the presentation of the item-specific cue. During the final test phase, all of the studied faces were tested using a cued recall test. **(B)** Forgetting, as indicated by the difference in recall rates between nonpracticed and control

items. Significantly less unpracticed items than control items were recalled in the C, but not in the NC, condition. **(C)** Facilitation, as indicated by the difference in recall rates between practiced and control items. Significantly more practiced items than control items were recalled in both conditions. Error bars indicate standard error.

EEG Recording

The EEG was recorded from 64 scalp electrodes mounted on an elastic cap according to the standard 10–20 system. The continuous electrical activity was recorded with Neuroscan Synamps2 amplifiers (El Paso, TX). The EEG was initially recorded against an electrode placed in the midline of the cap (between Cz and CPz) and re-referenced off-line against a common average reference. Each EEG channel was amplified with a band pass of 0.01–100 Hz and digitized at a sampling rate of 500 Hz. Impedances were kept below 5 kΩ. To control for vertical and horizontal eye movements, two additional electrodes were located above and below the left eye and another two at the outer side of each eye. Before data analysis, a high-pass filter (at 1 Hz) was applied, and data were corrected for artifacts such as blinks, horizontal eye movement, and EKG, by performing an independent component analysis that allows an identification of components corresponding to eye blinks, horizontal movements, or EKG artifacts. Remaining artifacts, because of muscle activity or poor artifact correction, were excluded by careful visual inspection.

EEG Analysis

EEG analysis was performed using FieldTrip Matlab toolbox software (Oostenveld, Fries, Maris, & Schoffelen, 2011) and in-house Matlab (The MathWorks, Munich, Germany) codes. The EEG data were segmented into time windows ranging from −2000 msec before and 4000 msec after the onset of the retrieval cue (cues in the C and NC conditions) and from −3000 msec to 4000 msec around face presentation (both C and NC). These broad time windows were chosen to prevent filter artifacts at the edges of the epochs. Analyses were restricted to a 2500-msec time window, ranging from −500 to 2000 msec.

Analysis of the Oscillatory Power

Time–frequency analyses were conducted applying Morlet wavelet transformation (7 cycles) to derive the time–frequency representation. Data were filtered in a frequency range of 1–30 Hz and exported in bins of 50 msec and 1 Hz. To analyze event-related changes, power changes were calculated in relation to a pre-stimulus baseline (set to 500–0 msec before stimulus onset). Analyses were restricted to theta band (6–8 Hz), as explained in the Results section.

Source Localization

To estimate the sources of activity that contributed to the effects at the sensor level, the dynamic imaging of coherent sources (DICS) Beamformer approach was used (Gross et al., 2001). The reliability of Beamforming methods in localizing the source of EEG activity was demonstrated by several combined EEG-fMRI, MEG-fMRI, and MEG-intracranial EEG studies (see, e.g. Singh, 2012; Hanslmayr et al., 2011; Dalal et al., 2009).

For source reconstruction, a standardized boundary element model was used to calculate the leadfield. The standard boundary element model was derived from an averaged T1-weighted MRI data set (MNI, www.mni.mcgill.ca). A previous study demonstrated that similar results are obtained from such a standard head model and individual head models (Fuchs, Kastner, Wagner, Hawes, & Ebersole, 2002).

The DICS algorithm allows performing source reconstruction in a frequency domain, given a time latency and frequency range defined by the user. The Beamformer computes the changes in power from a prestimulus baseline to a poststimulus interval, transforming data into standard MNI space (Montreal Neurological Institute, Montreal, Quebec, Canada). The prestimulus baseline was set from 500 to 0 msec before stimulus onset. The time window for the poststimulus interval and the frequency band were chosen according to the effects on the sensor level.

ERP Analysis

In an attempt to replicate previous findings, ERPs were also analyzed (Hanslmayr et al., 2010). The ERPs were computed for each participant and condition, in a time window from −500 to 2000 msec. The waveforms were low-pass filtered at 15 Hz and high-pass filtered at 1 Hz. For the interaction between the C and NC conditions (cue–face), a time window ranging from 400 to 500 msec was chosen for further analysis, upon visual inspection of the grand-averaged waveform. Analyzing the grand-averaged waveforms, when comparing C and NC conditions upon presentation of the category cue, two time windows were chosen for subsequent analysis: 350–400 and 410–450 msec, according to Hanslmayr et al. (2010). For the comparison between the conditions upon presentation of the item-specific cue (the face), one time window was chosen, ranging from 150 to 180 msec, comprising the well-known N170 component.

Statistical Analyses

Behavioral Data

Two 2x2 repeated-measures ANOVAs were conducted to analyze the behavioral data. To assess the forgetting effect, we calculated an ANOVA with the factors Item Type (unpracticed vs. control) and Retrieval Condition (C vs. NC). Likewise, a second ANOVA was conducted for the facilitation effect, taking as factors Item Type (practiced vs. control) and the Retrieval Condition. The significant effects from these analyses were then followed up by performing planned comparisons with two-tailed paired-samples *t*-tests.

Oscillatory Power

In a first step, an interaction analysis (cue minus face x condition) of the power differences averaged across all electrode sites was conducted to define time–frequency windows for subsequent analyses. To this end, the difference in oscillatory theta power between the face and the cue was computed for each participant for the C and NC conditions, respectively. This difference was then subjected to a dependent samples *t*-test. To account for multiple testing, a Monte Carlo randomization procedure was employed, following Maris and Oostenveld (2007).

This method randomizes the observations and recalculates the statistic for the randomized data after each run. The frequency bands and time windows exhibiting significant interaction effects are then subjected to planned comparisons using cluster-based, dependent sample *t*-tests with Monte Carlo randomization (Maris & Oostenveld, 2007).

With cluster statistics, dependent-sample *t*-tests are first calculated for every sample (channel–frequency– time). Then, samples with *t* values higher than the specified threshold (α=.05) are selected and clustered. Cluster statistics are calculated by taking the maximum sum of *t* values within every cluster. This result is the test statistic by means of which the effect of the experimental conditions is evaluated. Observations in the data are then randomized, and statistics are recalculated for this randomized data (again, taking the maximum sum of the cluster *t* values). This procedure is repeated several times, and the proportion of observations that resulted in a larger test statistic than the observed one is calculated. This proportion is the Monte Carlo significance probability (*p* value). Importantly, for two-tailed tests, such as in this study, alpha value is corrected (that is, considered divided by 2), so that each tail is actually tested with α=.025. From this procedure, clusters of electrodes that significantly differed for each condition (p_{corr}<.05) are obtained.

Following our hypotheses, planned comparisons were made between power changes from cue to face presentation (both in C and NC conditions) and upon presentation of the cue (C vs. NC).

Source Level

Source level statistics were conducted for both retrieval conditions (similarly to oscillatory power: cue to face (in C and NC conditions) and cue (C vs. NC). For the statistical analysis at the source level, we used a parametric test that results in analytic probabilities for the null hypothesis and performed dependent-sample *t*-tests on these probabilities. Only clusters bigger than 100 voxels were taken into account. As reported in the results section, the only comparison that met this criterion was between presentation of the category cue in the C and NC conditions (i.e., all other comparisons resulted in clusters<100 voxels).

ERPs

The mean amplitudes in the time windows previously chosen by analyzing the grand-averaged waveforms (400–500 msec for the interaction, 350–400 and 410–450 msec for cue C vs. NC, and 150–180 msec for face C vs. NC) were subjected to a dependent-samples *t*-test, using the Monte Carlo randomization procedure mentioned above.

Results

Behavioral Results

Forgetting

Mean recall performance in the C condition was 66% (SD=19%) for unpracticed items and 81% (SD=19%) for control ones. In the NC condition, mean recall performance was 73% (SD=21%) for unpracticed items and 67% (SD=32%) for control items, as depicted in Figure 4B.

A two-way ANOVA (Type of Item x Condition), revealed a significant Item Type x Condition interaction, $F(1,19)=7.37$, $p<.01$. No main effects of Item Type or Retrieval Condition were found ($p>.05$). Post hoc *t*-tests showed impaired memory performance for unpracticed items compared with control items, $t(19)=3.80$, $p<.001$, in the C condition, whereas no difference was found for the NC condition, $t(19)=.79$, $p>.05$. These results reveal the typical pattern of RIF in the competitive condition, which was not evident in the noncompetitive condition.

Facilitation

Mean recall performance for practiced items was 95% (SD=12%) for the C condition and 81% (SD=19%) for the NC one, as shown in Figure 4C.

Regarding the facilitation effect, the two-way ANOVA did not yield a significant interaction between Item Type and Retrieval Condition ($F<1$). There was a main effect of Item Type, $F(1, 19)=12.39$, $p<.01$, as well as a main effect of Competition, $F(1,19)=10.26$, $p<.01$. Post hoc analyses showed that practiced items were recalled significantly better than control items [$t(19)=3.16$, $p<.01$ for the C condition and $t(19)=2.19$, $p<.05$ for the NC]. Also, mean recall performance was higher in the C (M=.88, SD=.18) than in the NC condition (M=.74, SD=.27), $t(19)=3.22$, $p<.01$.

Oscillatory Power Results

Interaction Analysis

For the interaction analysis, the difference in oscillatory theta power between the face and the cue was computed for each participant for the C and NC conditions, respectively. The interaction (cue minus face x condition) yielded a significant effect in the theta frequency range (6–8 Hz, 500–1000 msec), as depicted in Figure 5A. For this time window and frequency range, the difference in theta power between cue and face was significantly bigger in C than in NC condition, with the C condition showing a larger decrease in theta power, from cue to face, than the NC condition. As the topography illustrates, the difference was most pronounced over frontal and parietal electrode sites (p_{corr}<.01; Figure 5B). All of the following analyses were based on this time window and frequency range. Theta power results (6–8 Hz, 500–1000 msec) for both retrieval conditions (C and NC), averaged over significant clusters of electrodes, upon presentation of the cue and of the face are depicted in Figure 5C. Planned comparisons on these results are described below.

Cue to Face

Theta power in the C condition decreased upon presentation of the face, over central and left parietal sites (Figure 6A). Nonetheless, this difference was only marginally significant (p_{corr}=.07). Regarding the NC condition, significant differences were also found when comparing theta activity upon presentation of cue and face, with face presentation inducing a significantly larger increase of theta power than the presentation of the cue (p_{corr}<.005), over left parietal and frontal regions (Figure 6B).

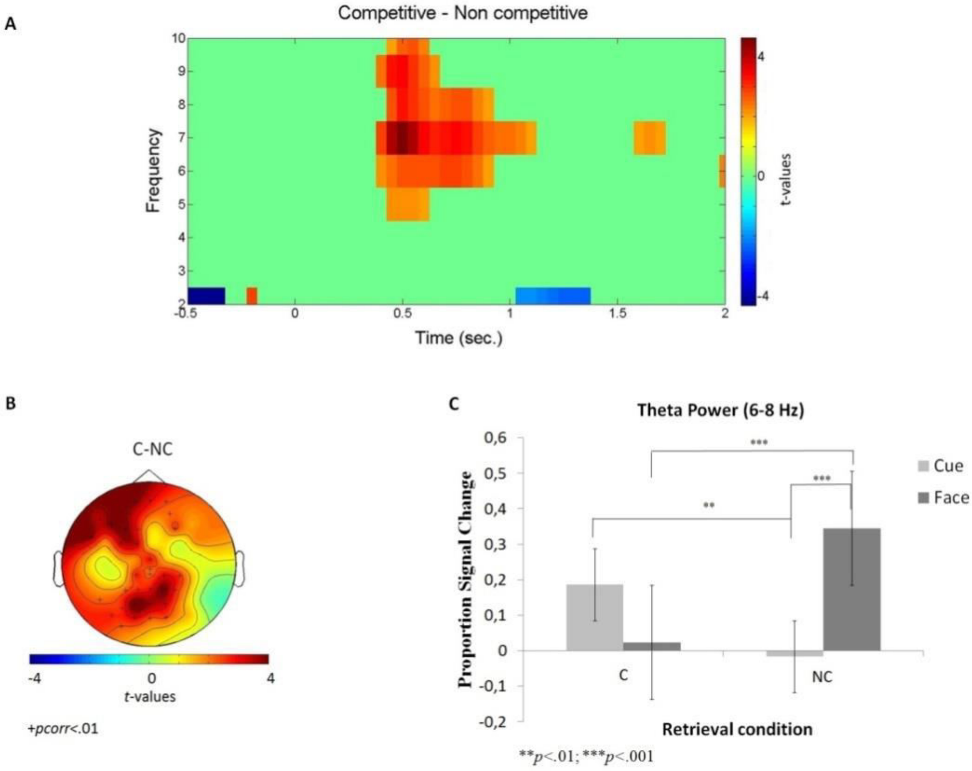

Figure 5. (A) Time–frequency plot showing the significant interaction effects between C (cue vs. face) and NC (cue vs. face) averaged across all electrodes. Note the significant interaction in the theta band (6–8 Hz) from 500 to 1000 msec. **(B)** The topography depicts the differences in theta power between C and NC conditions (cue–face), from 500 to 1000 msec. Significant electrodes yielded by the cluster-based permutation test (p_{corr}<.01) are marked with "+." **(C)** Theta power (6–8 Hz, 500–1000 msec) averaged over the significant clusters of electrodes for both retrieval conditions (C and NC), upon presentation of the cue (light gray) and the face (dark gray).

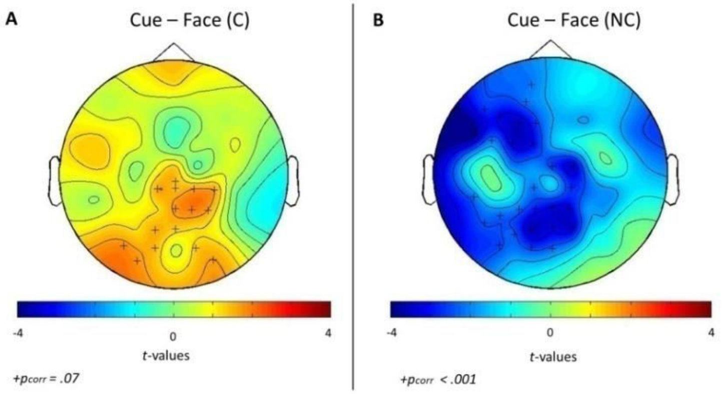

Figure 6. **(A)** Topography representing the marginally significant cluster between theta power from cue to face (C condition; p_{corr}=.07), from 500 to 1000 msec. **(B)** Topography representing the significant differences in theta power between cue and face in the NC condition, from 500 to 1000 msec.

Cue-C versus Cue-NC

Cluster-based permutation tests revealed that theta power (6–8 Hz) significantly increased after presentation of the cue in the C as compared with NC condition (p_{corr}<.01), from 500 to 1000 msec (Figure 7A). This increase was evident over fronto-central and left parietal sites, although only the fronto-central electrodes exceeded the statistical threshold (Figure 7B). Source localization analysis (DICS Beamformer; Gross et al., 2001) of this theta power effect indicated that the biggest cluster of significant voxels (366 voxels) was located in the dorsal part of the right ACC (MNI coordinates: x=4, y=23, z=40; ~BA 32), as depicted in Figure 7C.

Theta Power and Behavioral RIF effect

To test the hypothesis that high theta power is related to stronger RIF effects, we median-split participants according to the difference in theta power from cue to face presentation and compared the between group differences (larger vs. smaller theta power difference) in the forgetting score (recall of control items minus recall of unpracticed items). An independent-samples *t*-test showed significant differences between the two groups, $t(18)=-2.1$, $p<.05$. The large theta difference group had higher forgetting scores (M=.22, SD=.18) than the small theta difference group (M=.07, SD=.14). No such pattern emerged either for the facilitation scores, $t(18)=.35$, $p>.05$, or for the NC condition [for the forgetting score: $t(18)=-.19$, $p>.05$; for the facilitation score: $t(18) =.00$, $p>.05$].

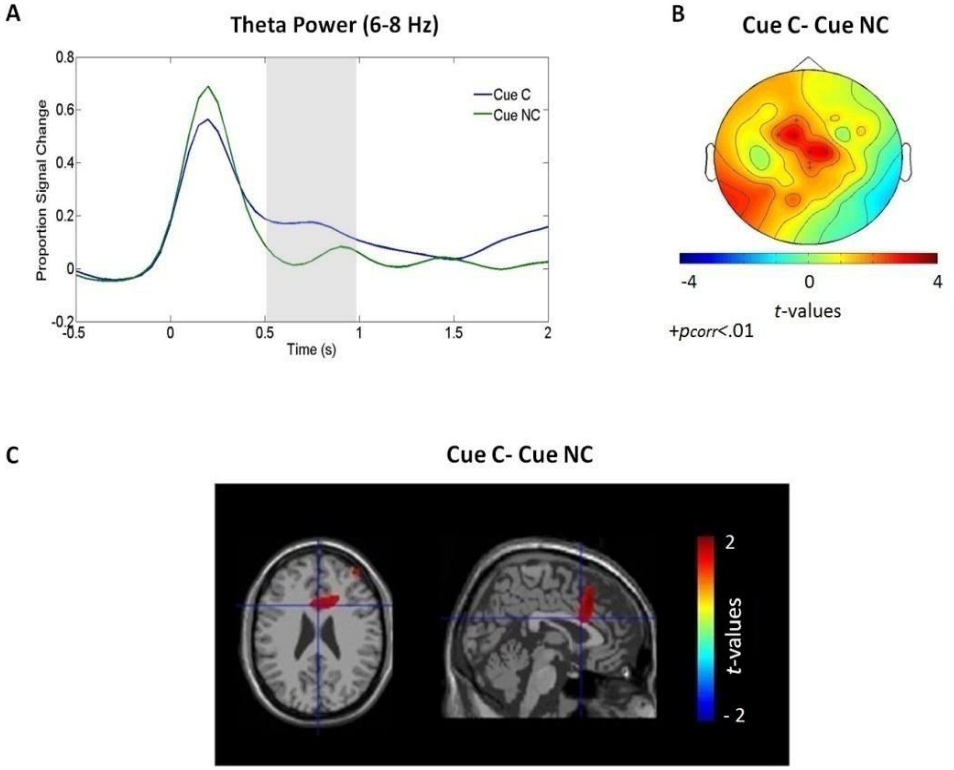

Figure 7. **(A)** Time course of the theta activity (cue C–cue NC) averaged over the significant clusters of electrodes. Highlighted in gray is the time window chosen for analysis. **(B)** Topography representing the significant differences in theta power between the retrieval cues in both conditions (C–NC), from 500 to 1000 msec. Significant electrodes yielded by the cluster-based permutation test (p_{corr}<.01) are marked with "+." **(C)** Source localization (DICS Beamformer) of the difference in theta power between cue in the C and NC conditions (500–1000 msec) in the cingulate gyrus (BA ~32).

ERP Results

Interaction Analysis

The competitive retrieval condition (cue–face) elicited a more positive ERP in comparison with the noncompetitive one, with a midfrontal topography in a time window raging from 400 to 500 msec (p_{corr}<.05) and led to a more negative ERP than the NC condition over midparietal sites (p_{corr}<.05) in the same time window (Figure 8).

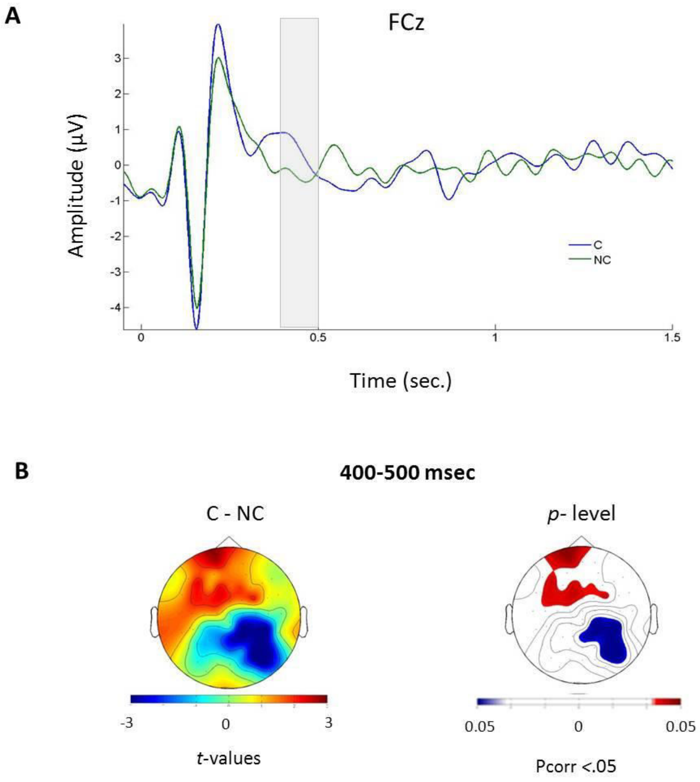

Figure 8. Plot of the results of the ERP analysis comparing competitive (C) and noncompetitive (NC) conditions (cue–face). **(A)** Grand-averaged ERPs for the C and NC category cue plotted for a frontocentral electrode (FCz). The gray bar indicates the time windows where significant differences emerged (p_{corr}<.05). **(B)** Topography of the effects. The left plot indicates the distribution of the amplitude, whereas the right plot indicates the topography of the *p* level.

Cue-C versus Cue-NC

A similar pattern was found for the category cue, where the competitive retrieval cue elicited a more positive ERP in comparison with the cue in the NC condition, both in a time window from 350 to 400 msec and from 410 to 450 msec (p_{corr}<.05) over frontal–central sites. The opposite pattern emerged over midparietal sites, with the C cue showing an ERP wave more negative than the NC (p_{corr}<.05) in the first time window (Figure 9).

Face C–NC

Face in the C condition elicited a more negative N170 (150–180 msec) component when compared with face presentation in the NC condition (p_{corr}<.05) over parietal sites (Figure 10).

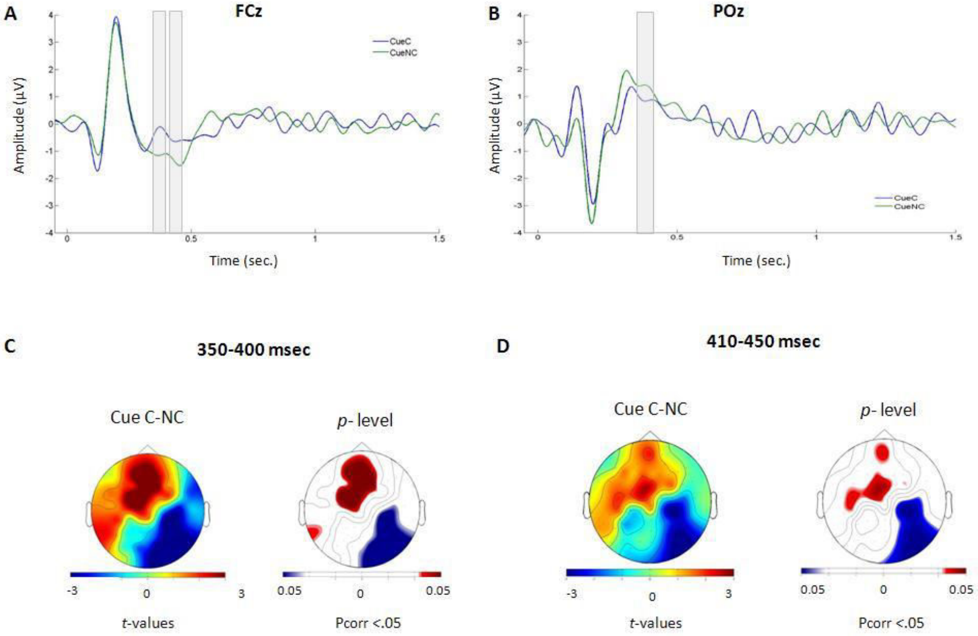

Figure 9. Plot of the results of the ERP analysis comparing competitive (C) and noncompetitive (NC) conditions upon presentation of the category cue. **(A)** Grand-averaged ERPs for the C and NC category cue plotted for a frontocentral electrode (FCz). **(B)** Grand-averaged ERPs for the C and NC category cue plotted for a midparietal electrode (POz). The gray bars indicate the time windows where significant differences emerged ($p_{corr}<.05$). **(C,D)** Topography of the effects. The left plots indicate the distribution of the amplitude whereas the right plots indicate the topography of the *p* level.

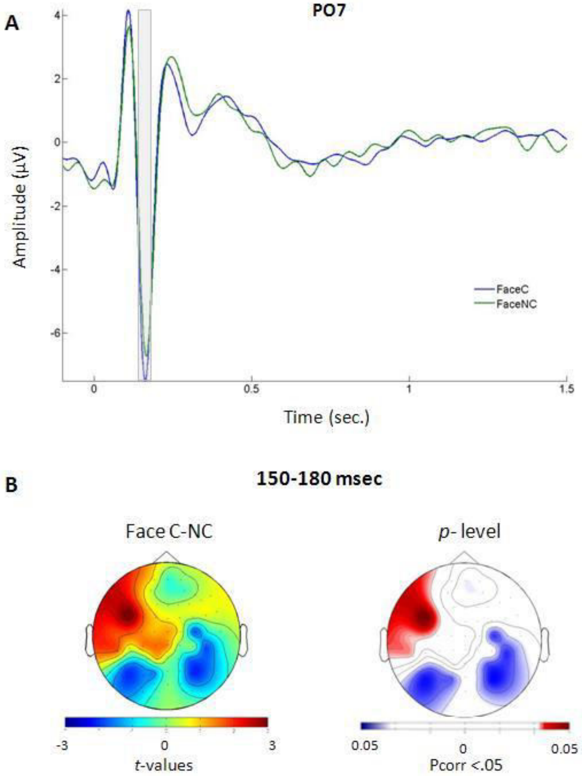

Figure 10. Plot of the results of the ERP analysis comparing competitive (C) and noncompetitive (NC) conditions upon presentation of the face. **(A)** Grand-averaged ERPs for C and NC upon presentation of the face plotted for a parietal electrode (PO7). The gray bar indicates the time windows where significant differences emerged (p_{corr}<.05). **(B)** Topography of the effects. The left plots indicate the distribution of the amplitude whereas the right plots indicate the topography of the p level.

Discussion

The behavioral results replicate those from previous studies, showing that selectively retrieving a subset of relevant items impairs the later recall of related but irrelevant items (Anderson et al., 2000). Importantly, and in contrast to the competitive retrieval condition, the noncompetitive retrieval practice did not induce significant forgetting. Whereas retrieving a subset of items impaired later recall of competing associates, mere exposure to this subset of items did not. These results speak in favor of an inhibitory account of RIF, assuming that related but competing items interfered during the retrieval of target items and were suppressed to reduce this interference in the competitive condition (Anderson, 2003). No such effect was found in the noncompetitive condition, where no interference occurred, and thus, no inhibition was needed. Moreover, our results confirm that the noncompetitive condition can be used as a neural baseline for the competitive condition to isolate effects of interference and interference resolution (Hanslmayr et al., 2010).

Although the inhibitory view of the RIF effect has been questioned by alternative cognitive theories (Anderson, 1983; Raaijmakers & Shiffrin, 1981; see Verde, 2012; Anderson, Bjork, & Bjork, 1994, for a review) there is strong evidence from neurophysiological investigations of RIF, showing that

RIF relies on the reactivation of competing items and their active suppression (e.g. Waldhauser et al., 2012; Kuhl et al., 2011). Waldhauser and colleagues (2012), for instance, showed that, during selective retrieval of the target items, alpha/beta power increased exactly at those brain regions storing the competitor's memory trace. As increased alpha/ beta power has been closely linked to neural inhibition (Jensen & Mazaheri, 2010; Klimesch, Sauseng, & Hanslmayr, 2007) and because this increase in alpha/beta power predicted later forgetting, these results clearly speak against non-inhibitory accounts of RIF.

We expected that the competitive condition elicited higher levels of theta power than the noncompetitive condition, reflecting generally higher levels of interference during competitive memory retrieval (Hanslmayr et al., 2010; Staudigl et al., 2010). Going beyond the prior studies, the design of the current study allowed us to disentangle the effects of competition from the effects of inhibition, as the presentation of the category cue was temporally separated from the presentation of the item-specific cue (face). If theta oscillations track the reactivation of memories and thus memory competition, theta power should already increase upon category cue presentation, in the absence of the item-specific memory cue. Our assumption was that the presentation of the category cue during retrieval practice activated competitor memories. This assumption comes from different lines of research. For example, classic studies on blocking effects showed impairment in recalling semantic information after having retrieved associated items (Brown, Cattoi, & Bradley, 1985; Blaxton & Neely, 1983; Brown, 1981). Evidence for this also comes from a recent study by Hellerstedt and Johansson (2013) who, by varying the associative strength of cue and competitors, found a competition-sensitive ERP modulation after presentation of a category cue, reflecting the retrieval of the semantically associated competitors. Finally, many studies have shown that retrieval is more difficult as the number of associated items increases (Anderson & Reder, 1999; Nelson et al., 1984, 1999).

Additionally, we assume that the competitive and non-competitive conditions differ in the mental operations performed by the participants. When engaging in the competitive condition, participants are aware they will need to retrieve only one item in each trial and this specific retrieval mode should orient their act of retrieval accordingly (Tulving, 1983). Given that participants know that each presentation of a category cue is followed by the retrieval of one specific item, all previously studied items are likely to get preactivated by the category cue and kept in working memory until the target retrieval. The fact that associated items are activated and held in memory until the item-specific cue is presented is what we termed interference in the context of this study.

In contrast, in the noncompetitive condition, where participants only need to retrieve the category name, interference should not be present to the same extent. Thus, even if some items do come into mind upon presentation of the category cue, there is no need for participants to hold them in memory, and therefore, no competition should occur.

Indeed, the present results demonstrate higher levels of category cue-related theta power in the competitive condition than in the noncompetitive condition. The presentation of the category cue in the competitive condition elicited higher theta power than in the noncompetitive one in the time window ranging from 500 to 1000 msec. Hence, shortly after the category cue is presented, items associated to that cue are reactivated in memory leading to interference as reflected by theta oscillations (Staudigl et al., 2010). In line with prior studies (Staudigl et al., 2010; Hanslmayr et al., 2008), the source of this theta interference signal was source localized to the dorsal part of the ACC, suggesting that medial prefrontal theta oscillations track interference, but not its resolution, given that no retrieval (and thus no interference resolution) is actually needed until the presentation of the item-specific cue. When the item-specific cue is presented, interference should be solved, which should be reflected by a decrease in theta power in the competitive condition from the presentation of the category cue to the presentation of the item-specific cue (i.e., the face). Furthermore, this decrease should correlate with later forgetting, if we assume that interference is resolved by inhibition of the competing items. The obtained results corroborate these hypotheses by showing that the theta power decrease from the category cue to the item-specific cue was related to later forgetting. Using the precuing procedure, that is, temporally separating the presentation of the category cue and the item-specific cue, it can be assumed that the results obtained in theta track the time course of the rise and fall of interference during competitive memory retrieval.

As mentioned, the difference in theta power between the category cue in the competitive and the noncompetitive condition was localized to ACC (see Staudigl et al., 2010, for similar localization), which has been consistently associated to the detection of interference (Wimber et al., 2009; Kuhl et al., 2007; Botvinick et al., 2001). Importantly, ACC seems to be involved not only in response conflict (e.g. Aron & Poldrack, 2006; Aron, Robins, & Poldrack, 2004; Menon, Adleman, White, Glover, & Reiss, 2001), but in cognitive conflict in general, as seen in studies using Flankers or Stroop tasks (Cavanagh et al., 2009; Hanslmayr et al., 2008). We argue that, in the current study, there is a conflict between different mnemonic representations that compete for retrieval. According to Botvinick et al. (2001), the cingulate cortex is the responsible for mediating and detecting interference, and theta oscillations seem to underlie such activity (Staudigl et al., 2010).

An alternate explanation would be that theta oscillations reflect task effort or difficulty rather than interference. Namely, the competitive condition seems to be harder than the noncompetitive one, and thus, theta oscillations could be reflecting increased task effort instead of competition. However, previous studies have shown that this is unlikely to be the case because theta oscillations at retrieval actually decrease for items that are difficult to retrieve (e.g. Spitzer et al., 2009; Klimesch et al., 2006; see Hanslmayr et al., 2010, for a similar explanation), which indicates that theta oscillations do not relate positively to retrieval effort.

Regarding interference resolution, it has been shown to depend on other brain regions (namely the dorsolateral pFC; Kuhl et al., 2007; Botvinick et al., 2001). According to the cognitive theory, interference during retrieval practice should be resolved by means of inhibition (e.g. Hellerstedt &

Johansson, 2013; Waldhauser et al., 2012; Hanslmayr et al., 2010; Staudigl et al., 2010; Román et al., 2009; Soriano et al., 2009; Wimber et al., 2008, 2009; Kuhl et al., 2007; Anderson, 2003; Bäuml & Hartinger, 2002; Anderson & Spellman, 1995).

As mentioned earlier, Waldhauser et al. (2012) were able to disentangle the neural representation of the competitor and the target memory via lateralized presentation and found increased alpha/beta power to reflect inhibition of competing visual memories. In the current study, we were not able to investigate such material specific inhibitory markers as the material was presented foveally and therefore encoded in highly overlapping neural assemblies. Presenting stimuli in a lateralized fashion requires that stimuli are shown on the screen for a very short period of time, which would not be optimal when the stimuli being presented are such complex ones as faces.

Although this direct marker of inhibition could not be obtained within this study, its effect, namely interference resolution, could be revealed as indicated by a reduction in theta power from cue to face presentation in the competitive condition. Once participants see an item-specific cue (i.e., a particular face), theta power decreases, presumably indicating interference resolution in the competitive condition (but not in the noncompetitive one). Furthermore, this difference selectively relates to later forgetting, but not with facilitation. Thus, participants with a greater difference in theta power from cue to face presentation (or, in other words, those able to reduce interference), had higher scores of later forgetting. This supports the assumption that interference was solved by the suppression of competing items.

Concerning the ERP effects, the present results showed that the competitive condition elicited midfrontal positivity and right parieto-occipital negativity, when compared with the noncompetitive condition. Inspecting the waveform, this pattern seems to be reversed after 500 msec, which is exactly what one would expect if these components were originated by a theta oscillation. These results should however be interpreted with caution, given that the comparison includes stimuli of different natures, namely words (for the category cue) and faces (for the item-specific cue), which are known to elicit very different ERP components.

ERP results upon presentation of the category cue are considerably more important, and again, the present results showed that the competitive category cue elicited both fronto-central positivity and right parieto-occipital negativity in contrast to the noncompetitive retrieval cue (Hanslmayr et al., 2010). Importantly, these results go beyond prior studies as they demonstrate that these ERP components reflect solely interference and not inhibition in episodic memory retrieval.

For the ERPs obtained upon face presentation, as expected, both conditions elicited a strong N170 component, typically shown to be modulated by faces (e.g. Rossion & Jacques, 2008). However, the competitive face evoked a more negative N170 than the noncompetitive one. This is possibly because of the fact that in the first condition participants were presented with the face alone, whereas in the later, the face was presented along with the corresponding written name below it, which might explain the less negativity found on the N170 for this noncompetitive condition.

An additional goal of this study was to explore the role of memory inhibition of personal representations. According to previous studies, face processing does not engage the same mechanisms as other objects (e.g. McKone et al., 2007; Haxby et al., 2000; Farah, 1996). This raises the question if RIF, which has been shown for a variety of materials, can also be found using faces or other personal representations. Studies investigating object and face naming, point to material specific effects of interference. For objects, naming a target can be impaired by the presentation of a semantically related distracter (Glaser & Düngelhoff, 1984; Lupker, 1979; Rosinski, Golinkoff, & Kukish, 1975); however, using facial stimuli, Vitkovitch et al. (2006) did not find any effects of interference in naming (see Darling & Valentine, 2005; Brèdart & Valentine, 1992, for inconsistent findings). Thus, these studies imply that faces may not be vulnerable to interference, and as a consequence, no inhibitory mechanism would be needed to resolve it.

Models of face processing, on the other hand, do assume that interference may arise between competing personal representations, at different levels of face recognition (e.g. Burton, Bruce, & Hancock, 1999; Brèdart,Valentine, Calder, & Gassi, 1995; Burton, Bruce, & Johnston, 1990; Burton et al., 1990; Bruce & Young, 1986). These models, however, either fail to give a solution for how we deal with interference (e.g. Bruce & Young) or propose very quick, automatic mechanisms that inhibit activated competing representations whenever we try to retrieve a particular face or name. In any of these models, inhibitory processes of a more controlled nature (such as the one found in RIF studies) are taken into account.

The results found in this study, both at a behavioral and neural level, could indicate that personal representations are prone to suffer from interference and that resolution of interference between these type of stimuli could depend on inhibitory processes of a controlled nature. Our design does not allow us to examine where this interference is actually taking place (if at a perceptual or at a semantic level), but both levels should be vulnerable to interference. Thus, it seems that, at least in some instances, mechanisms underlying interference for personal representations and other objects could be similar. These conclusions, however, cannot be fully drawn from the current set of data; thus, more research is clearly needed on this topic.

Finally, our results seem to indicate that the memory interference traced by ACC theta effects generalizes to materials other than words, which could suggest a domain general marker of interference.

Conclusions

Taken together, this study shows that (i) theta oscillations track the temporal dynamics of interference during competitive memory retrieval, disentangling interference from inhibition; (ii) the sources of medial prefrontal theta oscillations are located in the ACC; and (iii) the RIF effect generalizes to personal representations.

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4. EXPERIMENTAL SERIES III

4.1. Experiment 4

Introduction

Human beings need to be able to recognize other people's faces and to retrieve information about them on a daily basis. Though we seem to be able to do so without too much effort, this seemingly effortless task is actually quite demanding from a cognitive point of view (Bruce & Young, 1986) and seems to grow harder as people get older. We all have witnessed, for instance, grandparents struggling to remember the name of one of their grandchildren and in fact, naming difficulties, even when naming well-known people, are one of the most commonly reported complaints made by elders (Lovelace & Twohig, 1990; Maylor, 1990).

Aging encompasses a great number of changes that influence cognitive performance, especially in the brain, and happening at different levels. For instance, at a neurochemical level, Bäckman, Nyberg, Lindenberger, Li, & Farde (2006) have reported that dopamine losses across the brain are related with decay in cognitive function in older adults. Additionally, anatomical changes, such as the decline of both gray and white matter densities, as well as general volume loss (e.g. Raz, 2000;

Werckle-Bergner, Müller, Li, & Lindenberger, 2006) could also help explaining this decay. Of especial relevance are anatomical changes reported in the prefrontal cortex (PFC). PFC, which is thought to be responsible for triggering inhibitory mechanisms (e.g. Aron, Robins, & Poldrack, 2004), suffers from severe tissue loss or shrinkage with aging (Pardo et al., 2007; Raz, 2000) and these losses could be responsible for age-related inhibitory deficits.

As a matter of fact, one of the most accepted theories of aging is the Inhibitory Deficit Theory (IDT; Hasher & Zacks, 1988; Lustig, Hasher, & Zacks, 2007; Treitz, Heyder, & Daum, 2007), which posits that cognitive failures related to normal aging are due to a deficit in inhibitory mechanisms. Concretely, these authors argue that cognitive deficits in attention, language or memory, could be due to an underlying common mechanism: a decline in inhibitory function with increased age. According to this theory, older adults do not have the ability to suppress or inhibit unwanted behavior or information from entering working memory.

Corroborating this idea, studies using inhibitory paradigms, have found age-related impairments in these tasks (e.g. Stop Signal and Go/No go: Bedard, Nichols, Barbosa, Schachar, Logan, & Tannock, 2002; Think/No Think: Anderson, Reinholz, Kuhl, & Mayr, 2011; Murray, Anderson, & Kesinger, 2015). A study by Gazzaley, Cooney, Rissman, and D'Esposito (2005), for instance, compared young and older adults in a task where they had to remember, ignore or passively view the stimuli presented. Whereas young adults showed significantly less activation during the ignore condition in comparison to the passive view one, no such difference was found for older adults, that is, there was equivalent activation under both conditions. Importantly, there were no age differences when it came to increasing activation during the remember condition. Thus, older adults seem to have a specific deficit in preventing irrelevant information from interfering. Furthermore, the degree of reduced activation selectively predicted memory performance, whereas the activation increase (under the attending instructions) did not.

Another commonly used paradigm to investigate inhibitory function has been the retrieval practice paradigm. In this paradigm, participants first study pairs of words belonging to a given category (e.g. FRUIT-Apple; FRUIT-Orange; ANIMAL-Elephant) and are then asked to retrieve half of the words from half of the categories, upon presentation of a cue (e.g. FRUIT – Ap___). When presented with the category cue (e.g. FRUIT) all of the related items previously studied become active in memory (Apple, Orange, Banana…). In such a situation, according to an inhibitory account (e.g. Anderson, Bjork, & Bjork, 1994), our memory needs to suppress the competing words (Apple) in order to promote the retrieval of the correct one. Inhibition is then thought to suppress strong competing responses in order to allow the expression of a weaker but more adequate one (Levy & Anderson, 2002; Anderson, 2003). Concretely, when interference is detected, high-order control mechanisms come into play to reduce interference by inhibiting competing memories. Accordingly, on the final memory test it is usually found that practiced items (e.g. Apple) show a benefit and are recalled significantly better than control items (items that were not studied nor belonged to studied categories) whereas the recall of unpracticed items from practiced categories (e.g. Orange) is significantly impaired in comparison to controls. This later effect has been named Retrieval Induced Forgetting (RIF) effect (Anderson et al., 1994).

Supporting the inhibitory nature of RIF, several electrophysiological and neuroimaging studies have demonstrated that it strongly depends on prefrontal structures involved in interference detection, such as the anterior cingulate cortex (ACC; Ferreira, Marful, Staudigl, Bajo, & Hanslmayr, 2014; Kuhl, Dudukovic, Kahn, & Wagner, 2007; Staudigl, Hanslmayr, & Bäuml, 2010), and its resolution, as the ventro-lateral prefrontal cortex (VLPFC; Kuhl et al., 2007; Wimber et al., 2008; Wimber, Rutschmann, Greenlee, & Bäuml, 2009). Importantly, these studies have shown that, not only does the effect depend on structures related to executive function but that inhibition actively suppresses the competing items rather than, for instance, their association to the cue (Waldhauser, Johnsson, & Hanslmayr, 2012).

Focusing on electrophysiological studies investigating RIF, it has been shown the effect can be traced by mid-frontal theta (~4-8 Hz) and alpha/beta oscillations (~8-12 Hz). These studies (e.g. Hanslmayr, Staudigl, Aslan, & Bäuml, 2010; Staudigl et al., 2010) typically compare a competitive condition (standard retrieval practice) with a non-competitive one (relearning condition). In the latter, participants are simply re-exposed to the material, without having to retrieve any information. Whereas the standard retrieval practice should lead to interference between stimuli and consequent inhibition of competitors, the second should not lead to any competition, since participants do not need to retrieve any particular items. Accordingly, not only does the behavioral RIF effect disappear in the relearning condition (e.g. Anderson, Bjork, & Bjork, 2000), but there is also an increment in theta power when comparing retrieval to relearning (Hanslmayr et al., 2010; Staudigl et al., 2010). This increment is localized to the ACC and predicts later forgetting (Staudigl et al., 2010). A potential problem with these studies, however, is that by presenting the category and retrieval cues alongside they could not entirely disentangle between interference and inhibition mechanisms. With such a design, interference and its resolution are being measured at the same time and the correlates found could be attributable to either.

In order to separate neural activity for these two different mechanisms, Ferreira et al. (2014) presented a category cue (e.g. Actor) and the retrieval specific cue (the face of a specific actor) separated in time. The underlying reasoning was that whenever participants saw the category cue, all of the previously studied items belonging to that category would become activated and generate interference, which should be solved by inhibitory mechanisms upon presentation of the retrieval specific cue (given that, at that point, participants needed to arguably suppress competing names to be able to retrieve a specific one). Therefore, this design allowed tracking the time course of interference specifically, by looking at category cue presentation. Results showed that the category cue in the competitive condition led to a greater increase in theta power than in a non-competitive condition, which was interpreted as a marker of interference itself. An indirect marker of interference resolution was also found in this study: concretely, theta power decreased in the competitive condition from the presentation of the category cue to the presentation of the retrieval cue, reflecting a decrease in interference and hence its resolution. Importantly, this theta power decrease predicted forgetting scores in the final memory test.

Though this effect is quite well studied with young populations, how aging affects RIF and its neural correlates is still fairly unknown. At a behavioral level, the IDT would predict that RIF sould be hindered in elder people. In fact, research has shown that this effect is gradually impaired in older adults, but that it is modulated by factors such as age itself (Aslan & Bäuml, 2012; Marful, Gómez-Amado, Ferreira, & Bajo, 2015) or available cognitive resources (Ortega, Gómez-Ariza, Román, & Bajo, 2012). Regarding neural correlates, there are not, to our knowledge, any electrophysiological or neuroimaging studies evaluating how brain activations related to RIF change with normal aging. In fact, not that much is known about how brain oscillations in general are altered in aging, even despite the fact that research using this technique has become increasingly popular over the past few years.

Thus, in order to shed some light on this question, the present study aims to investigate the oscillatory correlates of interference in older adults. Using a procedure similar to that of Ferreira and col. (2014), we expect to replicate the results found with young adults and to test the effects of aging in this paradigm, looking at brain oscillations.

In the present study we opted to eliminate the non-competitive condition, and compare the neural correlates throughout subsequent cycles of retrieval practice, a more straight forward comparison. Previous studies have shown a reduction in BOLD signal (Kuhl et al., 2007; Wimber et al., 2008) and a decrease in theta power (Staudigl et al., 2010) from one retrieval practice cycle to the next, which is thought to reflect interference resolution across cycles. Thus, comparing younger and older adults' activation upon presentation of the category cue in the first cycle would give us an index of initial levels of interference, whereas comparing the difference between category cue in the first versus third cycle would put in evidence the resolution of that interference across cycles.

Accordingly, we hypothesised that older adults would show greater interference upon presentation of the first category cue than younger adults (reflected in greater theta power in older versus young adults) and that the young sample would show a decrease in theta power from the first to the last retrieval practice cycle. Older people, however, should not be capable of reducing interference arising upon category cue presentation, if inhibitory mechanisms are actually impaired. This should be reflected by theta oscillations; concretely, theta power should not show a decrease (as expected in the younger sample) but should rather be kept constant in the older adults, given their arguable inability to solve interference.

Furthermore, by using a pre-cuing procedure (Bajo, Gómez-Ariza, Fernández, & Marful, 2006; Ferreira et al., 2014) and assessing brain oscillations upon presentation of the cue, we are able to disentangle interference (first presentation of the cue) and inhibition (difference between first and third presentation of the cue) mechanisms. This is of special relevance for the older adults' literature, given that up to date there is still no unanimity about whether impairment in older people's memory is due to them suffering from more interference, being less able to solve it or both. We believe the procedure of the current study could help clarify some of these questions.

Method

Participants

24 students from the University of Granada (17 female; M_{age}=24.7 SD=5.4) and 24 older adults (10 female; M_{age}=68.4; SD=5.1; range 60-79) participated in this study. Older participants were recruited from an association for retired people and were highly educated ($M_{\text{scholarity(years)}}$=13.31; SD=3.25) and living very active lives, engaging in several activities in the association such as chess competitions or language and

informatics courses. Participants were asked to complete the Mini Mental State Exam (MMSE; Lobo, Ezguerra, Gomez, Sala, & Seva, 1979) to rule out possible dementia or severe cognitive impairments. Mean score in the MMSE was of 28.7/30 (SD=1.3) which indicates our participants were going through a process of normal healthy aging. Moreover, we found no significant differences between both groups in working memory, as measured by the digits span test from the Wechsler Adult Intelligence Scale (WAIS III; M_{young}= 15.3, SD_{young}=2.7; M_{old}=13.6, SD_{old}=2.9; $p>.05$).

All participants (young and older) were Spanish or had been living in Spain for at least 15 years and they all reported normal or corrected-to-normal vision. Participants were given all the information about the study and signed an informed consent prior to the study. All subjects received course-credits or a monetary reward for their participation in the study.

For the oscillatory power and ERP analyses, four of the older participants were excluded, due to excessive movement during the task, which severly compromised the quality of the EEG data.

Material

A total of sixty-four pictures were used in this experiment, all of famous Spanish people. Faces were divided into eight occupational categories (male actors, politicians, football players, writers, and TV hosts, and female singers, royalty members, and tabloid stars). These materials had been used in previous experiments (Ferreira, Marful, Staudigl et al., 2014 or Ferreira, Marful, & Bajo, 2014) and were originally chosen from a pilot study that served the purpose of evaluating each item's familiarity. Pictures chosen were the most familiar ones, provided they did not share the first two letters of the corresponding name. Six additional exemplars were chosen as filler items: 3 radio personalities and 3 bull fighters. These were used to control for primacy and recency effects and were not taken into account in any of the reported analyses.

Pictures were presented in color (5.19cm x 6.99 cm) against a white background and in order to standardize them, an oval template was applied around each picture (see Young, Ellis, Flude, McWeeny, & Hay, 1986). All faces displayed a neutral to mildly positive expression. Eight counterbalance versions were created so that all faces were seen in all conditions across participants.

Procedure

The experiment consisted of a version of the Retrieval Practice paradigm, thus comprising a study phase, a retrieval practice phase and a final test, explained next.

Study phase

The experiment started with a study phase, where participants were shown the 64 critical faces sequentially. Presentation was randomized except that the first and last three faces were always filler items, to account for primacy and recency effects. After a 1000ms fixation cross, a face would appear on the screen for 4000 ms with its respective name and profession written below (e.g. Actors – Banderas). Participants' task consisted on pressing a number from 1 to 5 on the keyboard according to how familiar the presented person was for them (1- not known at all; 5- very well known).

This way, not only could we control for possible differences in item familiarity between older and younger participants, but we also made sure participants were attending and processing the stimuli. They were also instructed they should pay close attention not only to the faces but also to their names and professions since they would be asked about them later.

Retrieval practice phase

During this phase, which occurred right after study, participants were asked to retrieve half the exemplars from six of the categories. Participants first saw a fixation point (jittered from 1 to 1.5s) followed by the category cue (e.g. Actors) for 2s, a blank screen (500ms) and a specific face (2.5s). Then a red question mark appeared on the screen and in that moment participants should give their response (naming the person they had seen on screen). Participants were instructed to refrain from responding up until the moment they saw the question mark, to avoid speech artefacts. Faces were presented in a pseudo-random order, so that a whole set would be presented before repeating itself. As in the study phase, the first and last few faces were filler items used to control for primacy and recency effects.

Crucially, there were 3 cycles of retrieval practice, that is, each of the 26 faces used during this part of the experiment was repeated three times, in order to allow comparisons between first and third cycles, similarly to what has been done in previous research (e.g. Kuhl et al., 2007; Staudigl et al., 2010; Wimber et al., 2009).

After retrieval practice, three types of items can be distinguished: practiced items, unpractised items (from practiced categories), and control items (non practiced items from non-practised categories), which serve as baseline items.

Test phase

A 5 minute distracter task followed retrieval practice (digits span test from the WAIS III). Thereafter, a final memory test occurred, where each studied face was presented again for naming. After a fixation cross (1s), a face appeared on the screen for 3s and participants were asked to retrieve the corresponding name as soon as possible. The order of presentation was randomize, such that all unpractised items and half of the baseline items were presented first, followed by practiced items and the other half of the baseline ones. This was done to prevent possible confounds with the forgetting effect. Namely, retrieval of practiced items first, could block access to the unpractised ones, something known in the literature as blocking effect (McGeoch, 1942; Mensink & Raaijmakers, 1988). This was controlled for by ensuring that unpractised items were always presented for naming before practiced ones.

EEG Recording

The EEG was recorded from 64 scalp electrodes, on a standard 10-20 system, mounted on an elastic cap. Four additional electrodes were used to control for eye movements: two set above and below the left eye (controlling for vertical movement) and another two set at the outer side of each eye, to control for horizontal movement.

Continuous activity was recorded using Neuroscan Synamps2 amplifiers (El Paso, TX) and was first recorded against a midline electrode (between Cz and CPz electrodes), but re-referenced offline against a common average reference. Each channel was amplified with a band pass of 0.01-100Hz and digitized at a 500Hz sampling rates. Impedances were kept below 5kΩ.

Prior to analysing the data, a high-pass filter (at 1Hz) was applied and artefacts (such as eye movements and EKG) were removed using independent component analysis.

EEG analysis

For EEG analyses we used the Fieldtrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011) on Matlab (The MathWorks, Munich, Germany). Using self-written code, EEG data was cut into segments ranging from -2000 ms before stimulus presentation to 4000 ms after, around cue and face (first, second, and third cycle in both cases). These large segments were chosen to avoid filter artefacts, but for the analyses, a smaller time window was used (from -500ms to 2000ms), both on the first and third cycle trials.

Analysis of Oscillatory Power

For time-frequency analysis, a Morlet wavelet transformation (7 cycles) was applied to the data. Data were filtered in a frequency range from 1-30 Hz and exported in bins of 50 ms and 1Hz. As in previous experiments (Ferreira et al., 2014b), power changes were calculated in relation to a prestimulus baseline (from -500 to 0ms before category cue onset). Given that prior to this study we had very specific hypothesis, analyses were restricted to activity in theta band (4-8Hz).

Analyses of oscillatory power focused on theta dynamics upon cue presentation. These analyses computed power differences in a region of interest (ROI) defined a-priori, based on previous experiments (Ferreira et al., 2014). The ROI comprised 9 fronto-central electrodes (Fcz, F1, Fz, F2, Fc1, Fc2, C1, Cz, C2) and results from power differences over this ROI were used to define time-frequency windows for subsequent analyses.

Since the main focus of this study was to assess differences between the young and older adult groups, the first step was to look at group differences upon presentation of the first cue, as an index of initial levels of interference, and then perform an interaction analysis (cue cycle 1 minus cue cycle 3 x age group). Differences in power upon presentation of the cue on the first cycle minus presentation of the cue on the third one were calculated for each participant, over the mentioned ROI. These differences were then subjected to an independent samples *t*-test, comparing the two age groups.

Analyses of oscillatory power upon face presentation were also performed in a similar fashion to the analyses of category cue, with the only difference that power differences were computed not for a particular ROI, but rather for all electrodes.

In order to control for multiple comparisons, Monte Carlo randomization was used (see more details on this method in Maris & Oostenveld, 2007 and Ferreira et al., 2014). From this procedure, clusters of electrodes that significantly differed from one cycle to the other were obtained ($p_{corr} < .05$).

Planned comparisons were then made for each group (young and older) separately, comparing first cue and face presentations minus third ones, over the time and frequency windows significant in the interaction analysis.

Analysis of Source Localization

Dynamic imaging of coherent sources (DICS) Beamformer was used in order to determine the source of the differences in activity found at the sensor level, a method that has been proved to be quite reliable (see, for example, Dalal et al., 2009; Hanslmayr, Volberg, Wimber, Raabe, Greenlee, & Bäuml, 2011; Singh, 2012).

For source reconstruction, a standardized boundary element model (BEM) was used to calculate leadfield. The BEM was derived from an averaged T1-weighted MRI data set (MNI, www.mni.mcgill.ca).

In order to compute changes in power, the prestimulus baseline was set to -500 to 0ms before stimulus presentation, whereas the time and frequency windows poststimulus were chosen according to the effects found at the sensor level.

Statistics at the source level were conducted for the two interest conditions (cue first cycle vs. cue third cycle) for both young and older adults. For the statistical analysis at the source level, we used a parametric test that results in analytic probabilities for the null hypothesis and performed *t*-tests on these probabilities.

We first looked into the effects found in the interaction analysis at the sensor level, and then for each age group separately. As in previous experiments, only clusters over 100 voxels were considered.

ERP analysis

For the ERP analyses, the mean amplitudes in the time windows previously chosen by analyzing the grand-averaged waveforms (150-200 and 350-400msec for the interaction, 180-200 and 350-400msec for young adults and 200-250msec for older adults) were subjected to *t*-tests, using the Monte Carlo randomization procedure mentioned above.

Also, to assess whether there were any differences on how younger and older adults were processing the faces upon their presentation, we looked at the N170 face component, in a time window raging from 160-180msec.

Results

Behavioral Results

Mean recall during the retrieval practice phase did not differ between the two age groups (M_{young}=.76; SD_{young}=.16; M_{old}=.67; SD_{old}=.18; $p>.05$)

Two 2x2 repeated measures ANOVA were further conducted to assess forgetting and facilitation effects separately on the final memory test. For both ANOVAs type of item (unpracticed vs. control and practiced vs. control) was used as a within subject variable, and age group (young vs. older) as a between subjects factor. Post-hoc analyses were conducted for each group, using 1-tailed paired-sample *t*-test.

Forgetting

The results of the ANOVA type of item (unpracticed vs. control) x group (younger vs. older) showed a significant effect of group [$F(1,46)=10.03$, $p<.01$, $\eta_p^2=.18$], where younger participants had a higher overall proportion of recall (M=62%; SD=23%) than older participants (M=44%; SD=19%). A marginally significant effect of item type [$F(1,46)=3.64$, $p=.06$, $\eta_p^2=.07$] was also found, with mean recall of unpracticed items (M=50%; SD=20%) lower than mean recall of controls (M=55%; SD=25%). The interaction between age group and item group did not, however, reach significance ($F<1$).

Post-hoc analyses revealed that whereas the difference between unpracticed (M=58%; SD=21%) and control items (M=65%; SD= 24%) was significant for the younger adults [$t(23)=-1.97$,$p<.05$], it was not for the older participants ($M_{unpracticed}$=43%, SD=15%; $M_{control}$= 46%; SD= 22%; $p>.05$; see Fig. 11).

Facilitation

Regarding the facilitation effect, no significant age group x item type interaction was found [$F(1,46)=2.66$, *n.s.*], but there was a significant main effect of age group [$F(1,46)=7.92$, $p<.01$, $\eta_p^2=.78$], according to which younger adults recalled more items overall (M=70%; SD=22%) than older adults did (M=55%; SD=22%). Moreover, item type also reached statistical significance [$F(1,46)=30.26$,$p<.001$, $\eta_p^2=.39$]. Recall of practiced items was significantly better than that of control items ($M_{practiced}$=70%; SD=17%).

Both young [$t(23)=3.1$,$p<.01$] and older [$t(23)=4.6$, $p<.001$] participants recalled practiced items significantly better than controls. For younger adults, mean recall of practiced items was of 75% (SD=17%), whereas older adults' mean recall of these items was of 64% (SD=17%; see Fig. 11).

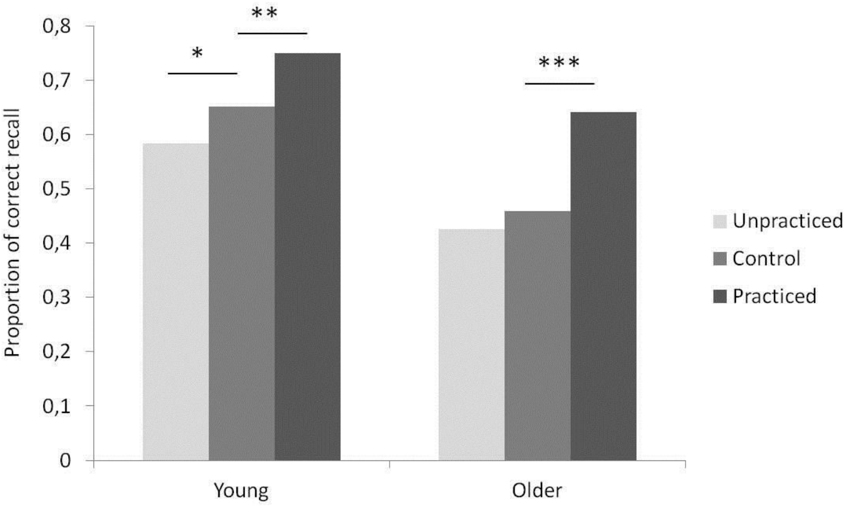

Figure 11. Behavioural results. Forgetting is indicated by the difference in proportion of recall between unpracticed and control items, whereas facilitation is reflected by the difference in recall rates between practiced and control items. Notice that whereas these effects are both significant for the young participants (with unpracticed items being recalled significantly worse than controls, and practiced items significantly better), older adults only show evidence of facilitation.

Oscillatory Power Results

Cue

Differences in theta power upon presentation of the cue on the first and third cycles were computed for each participant in the young and older group.We first report the analysis for the first cycle (Cue 1; interference index) and then the difference between the first and third cycles (Cue 1 vs. 3; inhibition).

Cue 1: Younger *vs.* Older

For the first cue presentation a significant difference in theta power was found between younger and older adults (p_{corr}<.01), such that younger adults showed greater theta power (6-8 Hz) over frontal and parietal areas, in a time window ranging from 0 to 500 msec (Figure 12A).

Cue 1 *vs.* 3: Younger *vs.* Older

The interaction analysis (first cue minus third cue x age group) yielded a significant effect in two different time-frequency window, and in both theta power was bigger for young than for older adults (see Figure 12C). The first time-frequency window ranged from 7-8 Hz in the first 500ms upon stimulus onset (p_{corr}<.001) with a fronto-central and left parietal distribution (Fig. 12B). Source analysis (DICS Beamformer; Gross et al., 2001) on this effect revealed three different clusters that surpassed our criteria, with peak activation in a cluster in right inferior frontal gyrus [46, 22, 17; ~BA 45].

The second significant window ranged from 5-6 Hz at 500 to 1000 ms (p_{corr}<.01) with a predominantly mid-frontal distribution (Figure 12B). Source analysis revealed four different clusters in this time window, with peak activation localized to the left inferior frontal gyrus [-64 9 30; ~BA 9]. Planned comparisons on these effects are described next.

Cue1 *vs.* 3: Young adults

For young adults, we found a significant theta power decrease upon cue presentation from the first to the third retrieval practice at the sensor level, both from 7-8Hz during the first 500 ms (p_{corr}<.01) and from 500 to 1000 ms, at a frequency range from 5-6Hz (p_{corr}<.01). These effects were mostly distributed across frontal and parietal sites, as depicted in Figure 13A.

Finally, in order to get a clearer picture of how theta power progresses from one cycle to the other, we extracted theta power values upon presentation of the category cue, in the significant time window and over the 9 electrode ROI, for the three cycles. As seen in Figure 13C, theta power seems to gradually decrease from one cycle to the other, though only differences between first and third cue were significant [$t(23)= 2.91, p<.01$].

Cue 1 *vs.* 3: Older adults

Regarding the older adult sample, there was a significant difference in the first time window, from 0 to 500ms and from 7-8Hz ($p_{corr}<.05$) with a frontal cluster showing an increase of theta power from the first to the third category cue (Figure 13B). For the other time window (500-1000ms; 5-6Hz) no significant differences were found (all $p_{corr}>.05$).

For older adults, we also extracted theta values upon presentation of the cue for each retrieval practice cycle. As expected from the results found in the interaction analysis, older people seem to have, overall, lower levels of theta power than young. Theta power increases numerically from the first to the second and third retrieval cycles, with differences between first and third cue reaching significance.

Face

The interaction relative to activation upon face presentation (face cycle 1 minus face cycle 3 x age group) was also computed, but did not yield any significant results ($p >.05$).

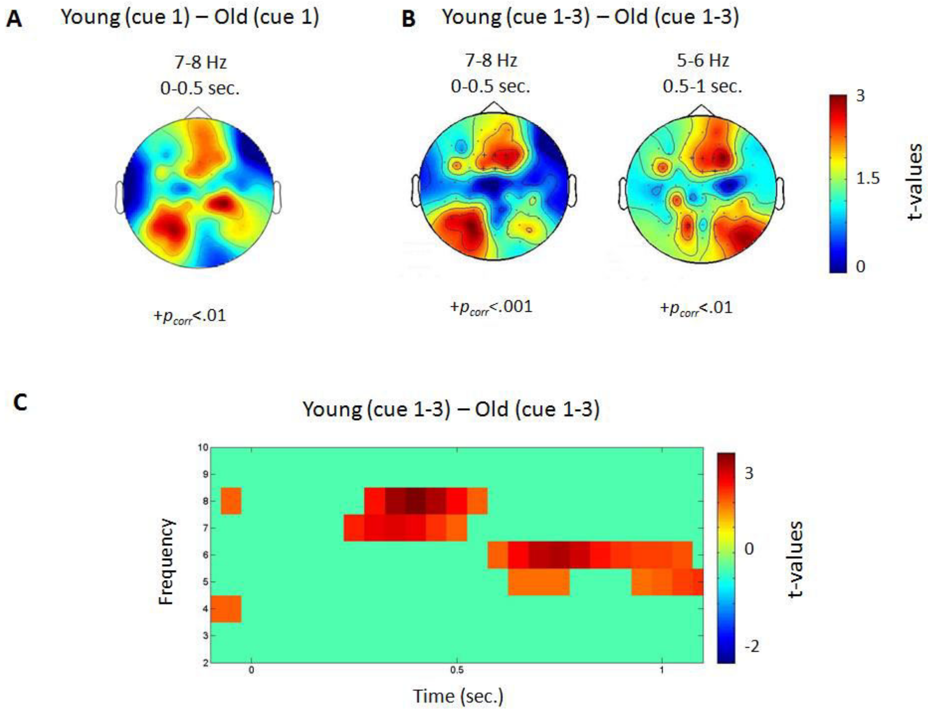

Figure 12. (A) Topography depicting differences between young and older adults, upon presentation of the category cue in the first retrieval cycle. **(B)** Topographies depicting differences in theta power between younger and older adults in the two frequency bands and time windows evidenced in the time-frequency plot. Significant electrodes yielded by the cluster-based permutation test (p_{corr}<.001 and p_{corr}<.01) are marked with "+." **(C)** Time–frequency plot showing the significant interaction effects between Young (cue1-cue3) and Older (cue1-cue3) adults, averaged across a 9 electrode ROI. Note the significant interactions in the theta band (7–8 Hz) from 0 to 500 msec. and from 500 to 1000 msec (5-6 Hz).

Correlation with behavior

To establish correlations with behavior, an inhibitory index was computed, consisting of the difference in recall between control and unpractised items. Correlation analysis showed that theta power at 7-8 Hz, from 0 to 500 msec upon presentation of the first cue, significantly correlated with the inhibitory index (r=0.25, *p*=.05) and at 4-6Hz, from 500 to 1000msec, marginally correlated with inhibition (r=0.21, *p*=.08), so that the more theta power upon presentation of the cue on the first cycle, the more forgetting on the final memory test.

No other significant correlations were found.

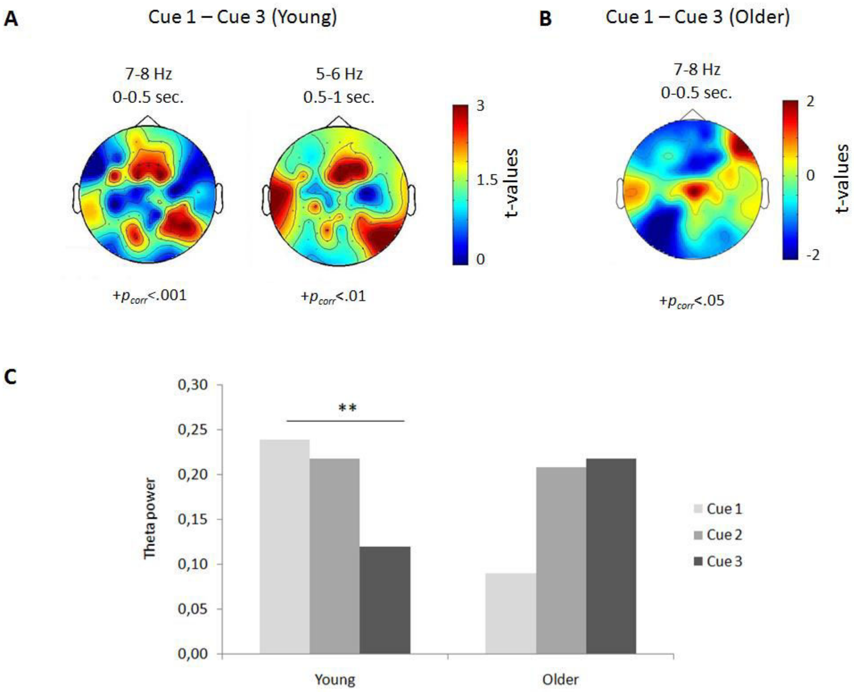

Figure 13. (A) Topographies representing the significant differences in theta power between cue presentation on the first retrieval cycle vs. the third, from 0 to 500 msec. (7-8 Hz) and from 500 to 1000 msec (5-6 Hz) for younger adults. Significant electrodes yielded by the cluster-based permutation test (p_{corr}<.001 and p_{corr}<.01, respectively) are marked with "+." **(B)** Topography depicting the significant differences in theta power between cue presentation on the first retrieval cycle vs. the third, from 0 to 500 msec. (7-8 Hz), for older adults. Significant electrodes yielded by the cluster-based permutation test (p_{corr}<.05) **(C)** Theta power (7–8 Hz, 0-500 msec) averaged over the significant clusters of electrodes for the category cue in retrieval cycles 1, 2 and 3. Notice how theta power gradually decreases from cycle 1 to 3 in the young sample, whereas the opposite pattern is found for the older sample.

ERP Results

Cue

Younger *vs*. Older

For the interaction analysis, we computed differences between ERPs upon first and third cycle of retrieval practice for both age groups, in order to contrast them. Results show that younger participants compared to older ones elicited a more positive ERP over frontal sites (p_{corr}<.05), and a more negative one over paritetal sites (p_{corr}<.01), in a time window raging from 150-200msec. An identical pattern occurred at a later time window, going from 350 to 400msec (see Fig. 14).

Young adults

Results found in the young adults mimic those from the interaction analysis. Concretly, we found greater amplitude upon the first presentation of the cue in comparison to the third over frontal sites, in two time windows raging from 180-200msec and from 350-400msec. This was accompanied by greater negativity over parietal sites for the first time window considered.

Older adults

For older adults, differences between first and third cue were smaller, as indicated by the interaction analysis. In any case presentation of the first cue led to a more positive component than the third from 200-250msec at frontal sites, which again was accompanied by greater parietal negativity in the first versus the third cue.

Face

Comparing ERPs upon face presentation in young vs. older adults, results showed that older adults elicited a more negative component over parietal sites, in a time window raging from 160-180msec, depicted in Figure 15.

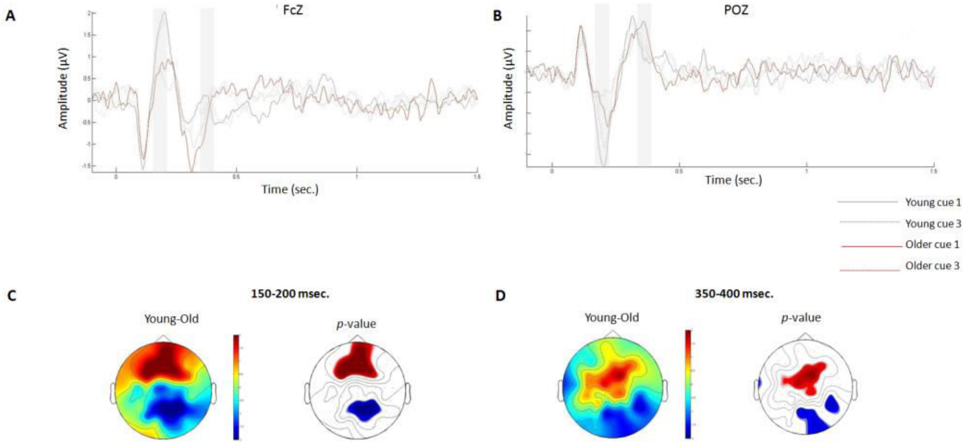

Figure 14. Plot of the results of the ERP analysis comparing first and third category cue for young and older adults. **(A)** Grand-averaged ERPs for the first(solid lines) and third (dashed lines) category cues, for young (gray) and older (red) adults, plotted for a frontocentral electrode (FCz). **(B)** Grand-averaged ERPs for the first and third category cue, for young and older adults, plotted for a midparietal electrode (POz). The gray bars indicate the time windows where significant differences emerged (p_{corr}<.05). **(C, D)** Topography of the effects. The left plots indicate the distribution of the amplitude whereas he right plots indicate the topography of the *p* level.

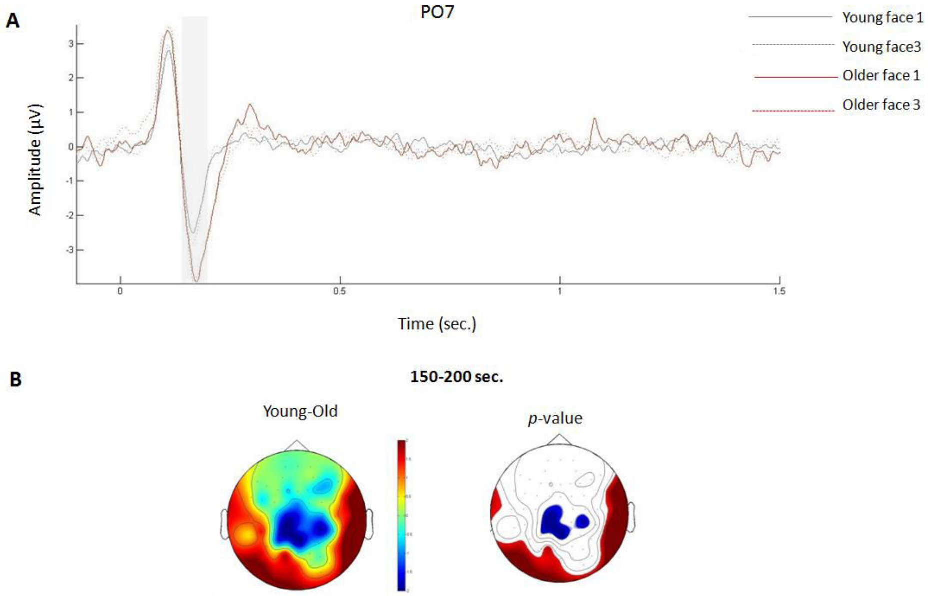

Figure 15. Plot of the results of the ERP analysis comparing first and third category cue for young and older adults. (A) Grand-averaged ERPs for the first (solid lines) and third (dashed lines) category cues, for young (gray) and older (red) adults, plotted for a parietal electrode (PO7). The gray bar indicates the time windows where significant differences emerged (p_{corr}<.05). (B) Topography of the effects. The left plot indicates the distribution of the amplitude whereas the right plot indicates the topography of the *p* level.

Discussion

The goals of this study were, on the one hand, to replicate previous results found in young adults using the retrieval practice paradigm, and on the other hand, to assess how RIF effect and its neural correlates change with normal aging.

In this study, we found the behavioural RIF effect to disappear in a sample of older adults. Concretely, while we did find a facilitation effect for both young and old adults, with practiced items being recalled significantly better than baseline (due to an effects of practice), only younger adults evidenced a forgetting effect, where the recall of unpracticed items belonging to practiced categories is significantly impaired compared to baseline items. According to the inhibitory account this should be due to the fact that, when presented with the category cue (e.g. “Actors”), young participants activate several of the previously studied actors, which leads to a competition between stimuli. This conflict is then solved by means of inhibitory mechanisms that suppress the competing items and promote the correct recall of the target item. Older adults, however, do not seem to be capable of performing this task in a similar manner.

This result then, agrees not only with the Inhibitory Deficit Theory, but also with studies showing an age-related impairment in other types of inhibitory tasks, such as Directed

Forgetting (e.g. Collette, Germain, Hogge, & Van der Linden, 2009; Zacks, Radvansky, & Hasher, 1996) or Think/no Think (Anderson et al., 2011) that find differences in performance in the same direction as that of the present study. More importantly, our results corroborate other RIF studies showing that the effect is often hindered in older subjects (Aslan et al., 2012; Marful et al., 2015, Ortega et al., 2012).

These studies put in evidence that this impairment in inhibitory tasks is modulated by factores such as age (Aslan et al., 2012; Marful et al., 2015) or the amount of cognitive resources available (Aguirre, Gómez-Ariza, Bajo, Andrés, & Mazzoni, 2014, Ortega et al., 2012), or by the specificity of the instructions provided to older participants (Sahakyan, Delaney, & Goodmon, 2008; Murray et al., 2015).

Regarding the age-related modulation, a couple of studies have shown that younger-old adults have a RIF effect similar to that of young adults, but that this effect disappears in older-old adults (Aslan et al., 2012; Marful et al., 2015). Moreover, Ortega et al. (2012) showed that RIF is maintained in older people but easily disrupted when another concurrent task is added. Similarly, Aguirre et al. (2014) showed that older adults have similar DF effect to young ones, but that a more demanding version of this paradigm (Selective Directed Forgetting: Delaney, Nghiem & Waldum, 2009) hinders the effect in the older. These studies seem to indicate that older adults are capable of performing inhibitory tasks when enough cognitive resources are available, but that as cognitive demand increases, the effects usually found become impaired. Finally, studies on DF and TNT paradigms (Sahakyan et al., 2008; Murray et al., 2015) show that inhibitory deficits may be overcome when participants are provided with a precise guided strategy on how to perform the task.

In the case of the present study, we argue that older adults' effect might have been hindered due to our task demands. Concretely, the type of stimuli used in this experiment are rather complex and especially so for older adults, who have been shown to generally perform worse in tasks requiring face-name associations (e.g. Naveh-Benjamin, Guez, Kilb, & Reedy, 2004).

At a neural level, we seem to replicate, with a young adults sample, results from our previous experiment (Ferreira et al., 2014). Using the pre-cuing procedure (Bajo et al., 2006) we were able to disentangle the temporal dynamics of interference and inhibition. Concretely, similarly to our previous experiment, we found that theta power, a marker of interference, decreases from one retrieval cycle to the others. This effect had a mid-frontal and parietal distribution. Still with young adults, we also replicate ERP findings (Hanslmayr et al., 2010; Ferreira et al., 2014), showing a more positive component over frontal areas and a more negative one in parietal sites, when comparing presentation of the first to the third category cue. The pattern of results differed, however, for older adults, with the differences found between theta power in the first and third retrieval practice cycles, upon presentation of the cue going in the opposite direction of the younger adults.

When directly comparing young and older adults, we had hypothesised that older participants might suffer from greater interference than young adults and that they would not be able to solve this interference. Surprisingly, this was not what we found. Comparing activation in young and older adults upon presentation of the first category cue (an index of initial interference levels), we found the first group to actually elicit greater theta power than the second. In fact, extracting the values of activation for the category cues across cycle revealed, on one hand, that young adults had overall higher theta levels than older and on the other hand, that whereas for young adults theta decreased gradually from one cycle to the next, older adults showed the opposite pattern, with theta increasing over retrieval practice cycles. Accordingly, ERP components elicited by younger adults were both more positive at frontal sites and more negative at parietal ones, than the components elicited by older adults.

This should mean that, contrary to what we predicted, younger adults actually seemed to be more prone to interference, suffering from higher interference levels, at least at initial phases of the experiment. Younger adults were then capable of solving this interference, as evidenced by the decrease in theta power from first to third cue. This adds to the idea that our results tap into conflict between stimuli that triggers inhibitory mechanisms. Importantly, we found a positive correlation between theta power upon presentation of the cue in the first cycle and the forgetting effect on the later memory test. Literature has shown that one of RIF's properties is its dependence on interference (e.g. Anderson et al., 2000), so that if there is no competition between stimuli, there is no need for an inhibitory mechanism to act. Accordingly, the more interference participants suffered (the greater theta power) upon cue presentation in the first cycle of the experiment, the more need there was to recruit inhibition, and thus greater forgetting scores on the final memory test.

Older participants then, seem to suffer less from competition between stimuli, since they showed less overall theta power than the younger participants, though theta power seems to increase from the first retrieval practice to the next. This means that, contrarily to our hypothesis, older adults seem to actually suffer less from interference than young ones.

Importantly, research has shown that one of the core characteristics of inhibitory mechanisms is that they are dependent of interference (Anderson et al., 2000), that is, they are put into play in order to face interference situations, and thus no inhibition is needed if stimuli do not compete. Our results could suggest that the reason older people usually perform worst in inhibitory tasks is due to the fact that they do not experience interference in the first place, and therefore do not need to engage inhibitory mechanisms. Though this is a plausible explanation, it does contradict a large number of studies supporting the Inhibitory Deficit Theory (Hasher & Zacks, 1988; Lustig et al., 2007; Treitz et al., 2007).

Another plausible explanation is that older adults are just not processing the category cue that is supposed to elicit interference to the same extend than young adults. If this is the case, by not processing or paying attention to "Actors", names of studied actors should not become active in memory and no interference should arise. This idea is supported by studies showing that older adults have impaired context processing (Braver et al., 2001; Rajah, Languay, & Valiquette, 2010; Rush, Barch, & Braver, 2006). As Rush et al. put it (2006), context processing is what allows individuals to create representations of cues in the environment, which are used to exert control over thoughts and actions.

Braver et al. (2001), for instance, found that this ability is reduced in older people. These authors developed a computational model from which they derived a series of predictions about what would happen when context representations are intact or impaired. They then tested this model with samples of young and older participants who were asked to perform the AX-CPT task, and found their results to be compatible with an age-related deficit in context processing. Moreover, they argued that deficits across other cognitive domains such as attention, inhibition or working memory, could be due to this impairment in context processing, as a common mechanism underlying these processes and that the neurobiological substrate of this deficit is a dysfunction of the dopaminergic system in dorsolateral prefrontal cortex.

Interestingly, Braver et al.'s (2001) theory is consistent with an inhibitory account of age-related deficits. Specifically, the authors argue that "a major function of context is to provide a mechanism by which task relevant information can effectively compete with and suppress task irrelevant information and responses" (Braver et al., 2001). Hence, in the specific case of our study, if participants were not attending to the context (in this case given by the category cue) such mechanism should not be set into action.

We argue that this might be what our older participants are doing. Given that the category cue is not actually essential to be able to perform the task (participants can still recall the name “Banderas” upon face presentation, regardless of whether or not they have read the cue “Actors” beforehand) and that older people seem to exhibit context impairment, they could not be engaging the mechanisms needed to allow relevant information to compete and be suppressed. This is of course, a speculative hypothesis, which we think could be tested by running an experiment identical to the current one, using pairs of words as stimuli instead of faces. By using semantic material, participants would be forced to actually focus on the category cue. This would be so since in order to retrieve Apple upon seeing the retrieval cue Ap___, one needs more information than the word’s stem to promote successful retrieval. This necessary information is given precisely by the category cue, and thus participants would need to process this cue in order to respond correctly.

A related possibility is that older adults are simply using a strategy different than that used by younger ones. Using another inhibitory paradigm (Direct Forgetting), Sahakyan and colleagues (2008) found that younger and elder intentionaly use different strategies to perform the task required. These authors showed that the effect of cost in Directed Forgetting (impaired recall of the “forget list”) disappears for senior participants when performing the standard paradigm, but that providing them with a clear strategy to follow maintains this cost effect. The authors argue that contextual cues (such as the category in our experiment) might not be efficient for older participants at retrieval, due to a difficulty in binding together different components of information (e.g. Naveh-Benjamin, 2000), such as the semantic meaning of an item or its relationship to other items. Thus in the case of the present study, it could be that younger adults were adopting a strategy of focusing on the category cue to be able to answer quickly upon presentation of the item specific cue, whereas older adults were not initiating searching processes until later, when the item specific cue appeared on screen. In accordance to this, our ERP results upon face presentation show that older adults elicit a more negative N170 component than their younger counterparts. This could be due to the fact that younger have all of the faces already “pre-activated” in memory, whilst older participants do not and thus show greater N170 amplitude as a response to face presentation.

Interestingly, according to Sahakyan’s results, this difficulty can be overcome when participants are given the right strategy to do it. To add to this, similar results were obtained in a recent study by Murray et al. (2015) who showed that older adults have a deficit in suppression induced forgetting (measured by the TNT paradigm) when given an open strategy to perform the task, but that offering participants guidance and a focused strategy, along with more precise instruction leads to successful and undiminished suppression induced forgetting. Therefore, providing older adults with specific strategies can attenuate age-related cognitive deficits. We hypothesized that instructing participants to focus on the category cue, or forcing them to do so by changing the study's materials would lead to similar levels of interference between young and older adults. The question then is whether older adults would be able to solve this interference just as well as younger ones.

In sum, we replicate previous findings that mid-frontal theta oscillations track the dynamics of interference in young adults and that it decreases as interference is solved. Older people however, show a different pattern of results and seem to not activate exemplars of a given category to the same extent that younger people do. This difference between older and young was localized to the right inferior frontal gyrus, an area consistently shown to be involved in control processes, namely in mediation of conflict (e.g. Aron et al., 2004).

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5. EXPERIMENTAL SERIES IV

5.1. Experiment 5

Introduction

Memory is often vulnerable to situations of interference, whenever several stimuli compete for retrieval at a given time (e.g. Anderson, 2003). When this happens, our memory system needs a mechanism to face interference and promote the recall of the correct answer, even if it is not the strongest one (Levy & Anderson, 2002). According to the inhibitory theory, this mechanism has an inhibitory nature and is responsible for suppressing memory representations that, though potentially strong, are not appropriate for a given context (e.g. Anderson, Bjork, & Bjork, 1994; Levy & Anderson, 2002). Thus, by suppressing these competing representations, inhibition promotes the recall of appropriate answers.

This phenomenon has typically been studied using the retrieval practice paradigm (Anderson et al., 1994). In this paradigm, participants start by studying a list of category exemplars (e.g. FRUIT-Orange, FRUIT-Banana, ANIMAL-Elephant) and are then asked to recall half of the exemplars from half of the categories, upon presentation of a retrieval cue. This cue usually consists on the category name and the first two letters of the exemplar (e.g. FRUIT-Or____). Afterwards, a distracter task takes place, followed by an unexpected final memory test, where participants are asked to recall all the items from the study list.

What is usually found in this paradigm is that, unsurprisingly, practiced items (e.g. Orange) are recalled significantly better than control items (that is, items that were not practiced during the intermediate phase, nor belong to practiced categories (e.g. Elephant), due to a practice effect. More interestingly, however, is the fact that recall of unpracticed items that belong to practiced categories (e.g. Banana), is significantly impaired, in comparison to controls. Anderson et al. (1994) argued that this should happen since during the intermediate phase, when prompt to recall Orange, all of the previously studied fruits can become activated in memory and consequently compete for retrieval. In order to overcome this competition and promote the correct recall of “Orange”, interfering items need to be suppressed by means of an inhibitory mechanism and are thus recalled more poorly at the final memory test.

This effect has been known as Retrieval-Induced forgetting (RIF), and it has been widely replicated with semantic categories (e.g. Anderson, Bjork, & Bjork, 2000; Anderson, Green, & McCulloch, 2000; Bäuml & Hartinger, 2002), lexical categories (e.g. Bajo, Gómez-Ariza, Fernández, & Marful, 2006), visuospatial stimuli (e.g. Ciranni & Shimamura, 1999; Ferreira, Marful, Staudigl, Bajo, & Hanslmayr, 2014, Ferreira, Marful, & Bajo, 2014; Gómez-Ariza, Fernández, & Bajo, 2012; Waldhauser, Johansson, & Hanslmayr, 2012), etc. Even though a few alternate explanations, such as blocking effects (e.g. McGeoch, 1942; Mensink & Raaijmakers, 1988) or context changes (Jonker, Seli, & McLeod, 2013), have been put forth to account for this effect, evidence supporting the inhibitory account is overwhelming (e.g. Anderson & Spellman, 1995; Anderson et al., 1994; Bajo et al., 2006; Hicks & Starns, 2004; Johansson, Aslan, Bäuml, Gäbel, & Mecklinger, 2007; Román, Soriano, Gómez-Ariza, & Bajo, 2009; Staudigl, Hanslmayr, & Bäuml, 2010; Storm, Bjork, Bjork, & Nestojko, 2006; Veling & van Knippenberg, 2004; Wimber, Rutschmann, Greenlee, & Bäuml, 2009; see Storm & Levy, 2012 for a review)

Part of this evidence comes from neuroimaging studies, demonstrating that this effect is dependent of brain structures typically involved in controlled behaviour, which speaks in favor of a controlled inhibitory mechanism. In one of the first MRI experiments conducted with this paradigm, Kuhl, Dudukovic, Kahn, and Wagner (2007) found that throughout repeated retrieval practice cycles, the engagement of cognitive control related areas, known to detect and resolve competition (anterior cingulate cortex and dorso and ventrolateral prefrontal cortices), was reduced. Disengagement of these areas was interpreted as a reduction in interference throughout retrieval practice cycles, which is exactly what one would expect if inhibition had come into play to solve interference as it arose during the first retrieval practice. Moreover, this disengagement correlated with later forgetting so that the more forgetting participants showed on the final test, the greater the decline of activation in prefrontal cortex from one retrieval practice cycle to the next.

Similar results were found by Wimber et al. (2009), when contrasting a competitive retrieval condition with a non-competitive one. In the competitive condition, participants followed a standard retrieval practice paradigm, thus being asked to retrieve a previously studied item. In contrast, in the non-competitive condition, during the intermediate phase, participants were simply re-exposed to part of the studied material and instructed to study it again. Note that in this second condition, participants did not need to retrieve any information, and thus no competition should arise. This manipulation usually leads to impairment in the recall of unpracticed items compared to control in the competitive condition, but not in the non-competitive one (e.g. Anderson et al., 2000; Ferreira et al., 2014a; Hanslmayr et al., 2010). At a neural level, Wimber and col. found that the competitive retrieval condition led to greater activation of anterior cingulate cortex (ACC) and left ventrolateral prefrontal cortex (VLPFC) and that this activation pattern predicted later forgetting. These results were replicated in a few other studies (e.g. Wimber et al., 2008, 2011).

In sum, both behavioral and neuroimaging studies employing the Retrieval Practice paradigm seem to offer solid evidence in favor of an inhibitory explanation of RIF. From this perspective, it could be hypothesized that individual differences that have been related to changes in inhibitory control would also modulate RIF effect. For example, aging has been shown to lead to a series of changes in the brain, at different levels, such as neurochemical (Baltes, Lindenberger, & Staudinger, 2006; Dixon, Wahlin, Maitland, Hultsch, Hertzog, & Bäckman, 2004); functional (Cabeza, 2002; Johnson, 2001) or anatomical (Giedd et al., 1999; Raz, 2005) that could impair inhibitory control mechanisms in this population. In this line, anatomically, prefrontal structures seem to suffer more from aging than any other brain structures. The hippocampus, for instance does not seem to show age-related changes until people reach their 50s; prefrontal cortex, however, especially in lateral sites, shows a steady linear decline as early as in people's mid 20s (Werkle-Bergner, Müller, Li, & Lindenberger, 2006). As Raz, Rodrigue, and Haacke (2007) point out, there is a generalized reduction of brain volume with aging, but polymodal regions, and especially the prefrontal cortex, are affected to a greater extent than the rest of the neo-cortex. Crucially, age-related atrophy in frontal lobes has been linked to a decrement in executive functions (e.g. Raz, 2000) that largely depend on frontal brain structures.

These neuroimaging studies come in accordance with the Inhibitory Deficit Theory (IDT; Hasher & Zacks, 1988; Lustig, Hasher, & Zacks, 2007), which states that cognitive failures related to normal aging are due to a deficit in inhibitory mechanisms, which would be a result of anatomical and neurochemical changes in prefrontal cortex. According to this theory, older adults do not have the ability to suppress or inhibit unwanted behavior or information from entering working memory.

If this is true, then one could expect RIF effect to be hindered in older adults. Though early studies did not find inhibitory deficits in this population (Aslan, Bäuml, & Pastötter, 2007; Gómez-Ariza, Pelegrina, Lechuga, Suárez, & Bajo, 2009; Hogge, Adam, & Collette, 2008; Lechuga, Gómez-Ariza, Iglesias-Parro, & Pelegrina, 2012), more recent ones have found that RIF is gradually impaired, but modulated by a few of different factors. For example, Aslan and Bäuml (2012) and Marful, Gómez-Amado, Ferreira, and Bajo (2015) found that though the effect is preserved in younger old adults, it disappears in older old people. Another important factor is the amount of available cognitive resources. Ortega, Gómez-Ariza, Román, and Bajo (2012) showed that RIF is maintained in an older sample, when tested with the standard paradigm, but that the effect disappears in this sample (but not in the young adults) when they are required to perform an additional task.

Even though the effects of aging on the behavioural RIF effect have been fairly well studied, to our knowledge, there are no fMRI studies looking into the neural correlates of RIF in healthy aging. Therefore, in this study we aimed to replicate neural results using the retrieval practice paradigm with a sample of young adults and, most importantly, to assess whether these patterns of activity are maintained or change as a function of age.

In a previous EEG experiment looking into the neural correlates of aging in RIF, we found that older adults did not seem to suffer from interference between stimuli, during the retrieval practice phase. Though this came to us as a surprising result, it does come in accordance with research on context processing impairment in seniors (Braver et al., 2001; Rajah, Languay, & Valiquette, 2010; Rush, Barch, & Braver, 2006). This led us to believe that the lack of interference evidenced by elders was due to the nature of the stimuli being used in this experiment, which did not require participants to take the context (given by the category cue) into account.

Concretely, in the previous experiment, participants were first presented with a category cue (e.g. “Actors”) and subsequently with a retrieval-specific cue (e.g. Banderas). Therefore, the category cue was not actually necessary to be able to respond to the retrieval-specific cue, that is, people can still recall Bandera’s name upon seeing his face, even if they have previously ignored the cue “Actors”. We hypothesized that our subjects used different strategies during retrieval practice, with younger adults using the category cue as a way to be able to more rapidly respond to the specific item, whereas older adults might have ignored this cue and focused uniquely on the retrieval-specific cue. By not focusing on the category cue, the elderly did not activate studied exemplars and consequently showed no interference effects.

For this reason, in the present experiment we decided to use semantic material instead of faces and names. By using semantic stimuli, we believe older participants will be forced to attend to the context, since completing a word stem (Ap____) is rendered much more difficult without the context information provided by the category cue FRUIT. Thus, we ran an experiment similar to Wimber et al.’s (2009), introducing just minor changes to their design (see Procedure section).

If we do find the standard behavioural RIF effect in our older adults’ sample, we should expect to find similar brain activations to those of younger adults, or maybe some more extended activation in the older sample, reflecting compensatory mechanisms (e.g. Cabeza, 2002). If, on the other hand, we do not find the inhibitory behavioural effect, then it seems reasonable to assume that the frontal areas linked to detection and resolution of interference that we expect to find more activated in young adults, would be activated to a lesser extent in older adults, when comparing both groups, which would further support the idea that aging renders inhibitory mechanisms impaired.

Methods

Participants

20 young and 18 elder adults living in Granada (Spain) volunteered to participate in this study. One of the younger participants was excluded from the analyses due to both excessive movement in the scanner and poor behavioural performance (Mean recall 3 standard deviations below its group's Mean). Two of the older participants were excluded due to marked brain atrophy.

All the remaining 19 young adults (13 females; Mean age=25.3 years old (SD=4.5) and 16 older participants (7 females; Mean age=64.9; SD=4.5) were native Spanish speakers or had been living in Spain for at least 15 years and they all reported normal or corrected-to-normal vision. No significant differences were found between the two groups in terms of mean years of education (Mean_{young}=16.2, SD=1.4; Mean_{older} = 15.4, SD=2.3; p>.05).

Participants were given all the information about the study beforehand and signed an informed consent prior to it. Young participants from the University of Granada received course-credits for their participation in the study; other young volunteers and older ones received a monetary reward.

Materials

A total of 144 words were used in this experiment, divided into 12 categories (tools, insects, trees, fruits, animals, furniture, vehicles, clothes, drinks, birds, reptiles and toys) with 12 exemplars each.

Within the same category, no items shared the first two letters. Moreover, within each category, 6 exemplars were highly representative of that category (to be used as competitor items) and another 6 (used as practiced items) were poor representatives. Indices of frequency and rank were considered for each item, respective to its category were taken from Marful, Díez, and Fernández (*in press*), using the database NIPE (Norms and Indices for Experimental Psychology; Díez, Fernandez, & Alonso, 2014). Mean frequency was of 8.9 for practice items and 168.7 for competitors. Rank scores were around 8.2 and 4.8 for practice and competitor items respectively.

Procedure and design

In this experiment, we replicated the procedure used by Wimber and col. (2009). Thus, similarly to their study, ours consisted in 12 separate runs, each comprising a study phase, a retrieval practice or relearning phase, a distracter task and a test phase (see Figure 16A).

The runs differed between them in the list of items presented to the subject, and critically, in the procedure followed during the intermediate phase (retrieval practice or relearning). Thus, in six of the runs (retrieval practice runs) participants were presented with a word stem and asked to covertly retrieve the word that completed that stem, out of the previously studied ones. In the remaining six runs (relearning runs), participants were presented again with some of the words from the previously studied list, and instructed to attend to them since they would be asked about them later.

The runs were divided in blocks of three, so that participants performed three runs of one condition, followed by three of the other and so on. Four counterbalance conditions were created so that order of run presentation and assignment of list to run were balanced across subjects. Item presentation within each list was randomized.

Study phase

Each run started with a study phase, during which the 12 stimuli of a given category were randomly presented. A fixation cross appeared on the screen for 1sec., followed by the category name and an exemplar (e.g. ANIMAL-Elephant) for 2sec. Participants were instructed to study all of the exemplars and to try to memorize them the best they could, since they would be asked about them later.

Retrieval practice/ Relearning phase

On the second part of each run, 6 of the 12 studied items underwent either retrieval practice or relearning.

During retrieval practice blocks, participants saw a fixation cross (900ms), followed by a word stem (e.g. El____) for 3 sec. and were asked to covertly retrieve the corresponding word from the studied list (in this case, Elephant). Relearning blocks were identical, apart from the fact that instead of seeing the word stem, subjects saw the whole word written on the screen (Elephant) and were instructed to rehearse each of them. On both types of blocks, each word was presented twice.

Test phase

After a 30sec. distracter task, where participants were asked to order digits presented on the screen in ascending order, the test phase took place. In this phase, participants again saw a fixation cross for 1sec. and were then presented with the category and the first two letters of the to-be-retrieved word (3 sec.). During this phase, subjects were asked to retrieve aloud the word that completed the two letters on the screen, from the list studied in the beginning of the run.

To control for output order effects (e.g. Anderson et al., 1994), unpracticed items were always shown before practiced ones. After each run, participants were given a few seconds to rest, before moving on to the next list.

Participants performed the whole task while inside a Siemens 3T MRI scanner, so all the stimuli were presented on a screen placed at the rear of the magnet bore, and visualized by the subjects on a mirror attached to the head coil. Scanning occurred only during the second phase of each run (retrieval practice/relearning).

fMRI Data Acquisition and Processing

Structural and functional images were collected in a 3T Siemens Magneton TrioTrim scanner. Participants were instructed to avoid movement as much as possible, and head motion was restricted using foam inserts. High-resolution T1-weighted (MPRAGE) anatomical images were acquired for each participant, prior to the start of the behavioural task.

Functional images were obtained using T2*-weighted EPI sequence, with a TR of 2000msec, a TE of 25msec and a 90º flip angle. 24 volumes were acquired in each run (for a total of 288 volumes *per* subject) and each volume was comprised of 36 axial slices, acquired in an interleaved fashion, with a resolution of 3x3mm.

Data processing was done using SPM8 software (Wellcome Trust Centre for Neuroimaging, London, UK; http://www.fil.ion.ucl.ac.uk/spm/software/spm8/). EPI images were unwarped and spatially realigned to the first image. The structural image was co-registered with a mean functional one and segmented into grey and white matter and cerebro-spinal fluid. The parameters obtained from segmentation were then applied in the next step, where all images were normalized to a T1-weighted template provided by SPM. Finally all images were smoothed with an 8mm FWHM isotropic Gaussian kernel.

Statistical Analyses

Behavioural

A mixed factorial ANOVA was conducted to assess forgetting effect (considered as the difference in recall performance between unpracticed items in the retrieval practice and relearning blocks). Item type (practiced and unpracticed) and block type (retrieval and relearning) were taken as within subject variables, whereas age group (young and older) as a between subjects variable.

fMRI

For first level analysis, box-car functions were convolved with a canonical hemodynamic response function, over the periods of interest, creating “retrieval” and “relearning” regressors. A fixed effects model was constructed for each subject, with two linear contrasts being estimated to investigate differences between blocks (retrieval>relearning and the opposite contrast). Session-specific effects and low frequency components (>128 sec) were treated as confounds.

The estimated contrasts were entered in a second-level analysis, with subject considered as a random factor. A 2x2 ANOVA was used to establish comparisons between groups with age group (young vs. older) and block type (retrieval vs. relearning) as factors. Subsequently, within group comparisons were acessed with one sample *t*-tests. To further investigate the contribution of age to the neural response, we conducted a multiple regression analysis on brain activation during retrieval practice, introducing each participant’s age as a covariate. Note that performing this analysis allows to test for correlations between a variable of interest (such as age) and the changes in BOLD signal across subjects, in a given contrast. Furthermore, we extracted beta values from these areas and from areas activated during retrieval (retrieval>relearning) and correlated these values with an inhibitory index (difference between unpracticed items in retrieval and relearning blocks). We report significant values measured by Spearman-rho correlations (2-tailed).

All reported effects survive a statistical threshold of $p<.001$, uncorrected for multiple comparisons, and comprising at least 10 adjacent voxels. Images for visualization were constructed using Caret software (version 5.65; http://brainvis.wustl.edu/wiki/index.php/). Anatomical labelling and assignment of Broadmann's areas to peak location were done using Talairach Deamon (Lancaster et al., 1997, 2000).

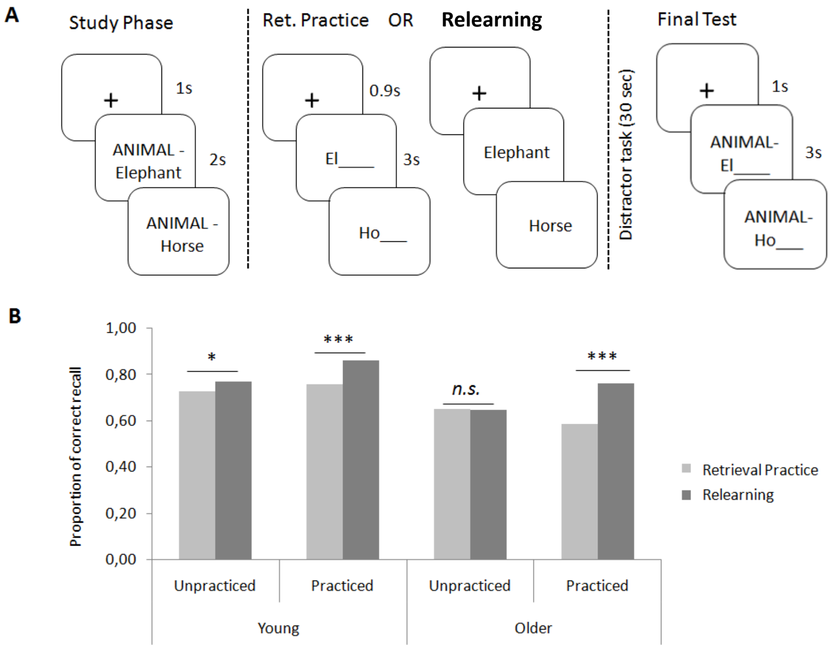

Figure 16. (A) Experimental procedure in this study. The experiment consisted of three phases: During study phase, participants studied pairsof associated items (category-exemplar). During the intermediate phase, participants either performed retrieval practice, where participants were instructed to retrieve a given item, or relearningd, where the full item was presented again for the participants to study it again. Finally, a final memory test took place, where participants were tested for all items of the category, using a cued recall test. This was repeated for 12 runs (with a new category presented in each one). **(B)** Behavioural results of this study. Whereas younger adults show both, a forgetting effect (revealed by the significant difference found in unpracticed items in the retrieval vs. relearning condition), older participants did not.

Results

Behavioural

Behavioural results are depicted in Figure 16B. A significant item type x block type x group interaction was found [$F(1,33)=5.13$, $p<.05$, $\eta_p^2=.14$]. Moreover, significant main effects of item type [$F(1,33)=6.60$, $p<.05$, $\eta_p^2=.17$], block type [$F(1,33)=56.85$, $p<.001$, $\eta_p^2=.63$] and group [$F(1,33)=17.28$, $p<.001$, $\eta_p^2=.34$] were found. Regarding the type of item, practiced items were recalled significantly better than unpracticed ones ($M_{\text{practiced}}=75\%$; SD=15% and $M_{\text{unpracticed}}=70\%$; SD=11%). For the main effect of block type, items in the re-exposure block were recalled better than those belonging to retrieval blocks ($M_{\text{re-exp}}=76\%$; SD=14% and $M_{\text{ret-practice}}=69\%$; SD=13%). Finally, the main effect of age group revealed that younger adults recalled overall more items than older adults ($M_{\text{younger}}=78\%$; SD=9% and $M_{\text{older}}=66\%$; SD=14%)

Planned comparisons revealed that young participants recalled unpracticed items in the retrieval practice runs significantly worse than in the relearning runs ($M_{\text{ret-practice}}=73\%$, SD=.09 and $M_{\text{re-exp}}77\%$, SD=.07; $t(18)=-2.47$, $p<.05$). Such difference did not emerge, however, for older adults ($M_{\text{ret-practice}}=65\%$, SD=.11 and $M_{\text{re-exp}}65\%$, SD=.11; $t(15)<1$).

Regarding practiced items, both age groups recalled items in the relearning condition significantly better than those in the retrieval practice condition. For young adults, mean recall in retrieval practice runs was of 76% (SD=.09) and 86% in relearning runs (SD=.06; $t(18)=-4.32$, $p<.001$). For older participants, mean recall of practiced items was of 59% (SD=.16) in the retrieval practice runs and of 76% (SD=.13) in relearning ones [$t(15)=-6.21$, $p<.001$].

fMRI

Young vs. Older

To assess differences between groups a 2x2 ANOVA was conducted with the factors block type (retrieval vs. relearning) and age group (young vs. older). No interaction between these factors arose, but the analysis revealed a main effect of block type, as well as a main effect of age (see Table 1). The main effect of block revealed that retrieval led to greater activation of three frontal clusters in cingulate gyrus (-6 20 43, ~BA 32) and inferior frontal gyrus (-39 5 31, ~BA 9 and 33 26 -5, ~BA 47; see Figure 17A).

A main effect of age group was also found, with younger adults showing greater activation in several clusters, especially in frontal areas, in comparison to older ones, as depicted in Figure 17A. These included middle (-27 20 58, ~BA 6; 54, 17, 40 and 3 26 43, both ~BA 8), superior (30, 62, 1 and -18 65 19, both ~BA 10; 24 26 58, ~BA 6 and 3 47 49 ~BA 8) and inferior

(-42 14 -11, ~BA 47; -54 20 25, ~BA 9) frontal gyrus. Frontal activations also included a cluster in cingulate gyrus (9 -19 28, ~BA 23). Additionally, two parietal clusters (-57 -28 49 and 45 -46 52, both ~BA 40) and two bilateral clusters in the caudate (-9 2 19 and 9 8 16) were more active in young than old adults (see Figures 17A and B).

This effect, however, reveals age differences found regardless of the type of block performed. Thus, since one of our main goals was to assess the specific effect of age in brain activation while performing retrieval practice, a multiple regression analysis was conducted, introducing participants' age as a covariate. Only one cluster in posterior lobe showed a positive correlation between brain activity during retrieval practice and age (33 -61 -17), but several areas showed a negative correlation with age, that is, these areas were less active during retrieval practice as participants' age increased (see Figure 17C). Most of the clusters were found in frontal areas, namely mid (60 17 31, ~BA 9), superior (30 62 4, ~BA 10) and inferior (-42 14 -11, ~BA 47) frontal gyrus. Additionally, there was also a negative correlation between age and brain activity in two clusters in inferior parietal lobe (45 -46 52 and -45 -43 55, both ~BA 40) and in a cluster in the precuneus (-30 -79 43, ~BA 19; see Table 2).

Young adults

For young adults, retrieval blocks led to increased activation in frontal and posterior regions when compared to relearning ones. Posterior clusters showing increased BOLD signal in retrieval blocks included middle occipital gyrus (-24 -97 7, ~BA 18) and temporal pole. Temporal pole clusters were located in the superior temporal gyrus (45 20 -17, ~BA 38) and fusiform gyrus (45 20 -17, ~BA 37). Frontal activation was found to increase in the cingulate gyrus (-3 23 40, ~BA 32), inferior frontal gyrus (-33 29 7, ~BA 45) and precentral gyrus (-29 2 31, ~BA 6). On the other hand, the contrary contrast (relearning > retrieval) did not yield any significant results (see Table 3).

Older adults

The same contrasts were tested in older adults. In this sample, the comparison between retrieval and relearning blocks only showed increased activation in retrieval in one mid frontal cluster (-54 5 43, ~BA 6), as mentioned in Table 3. Similarly to the young sample, the opposite contrast did not yield significant results.

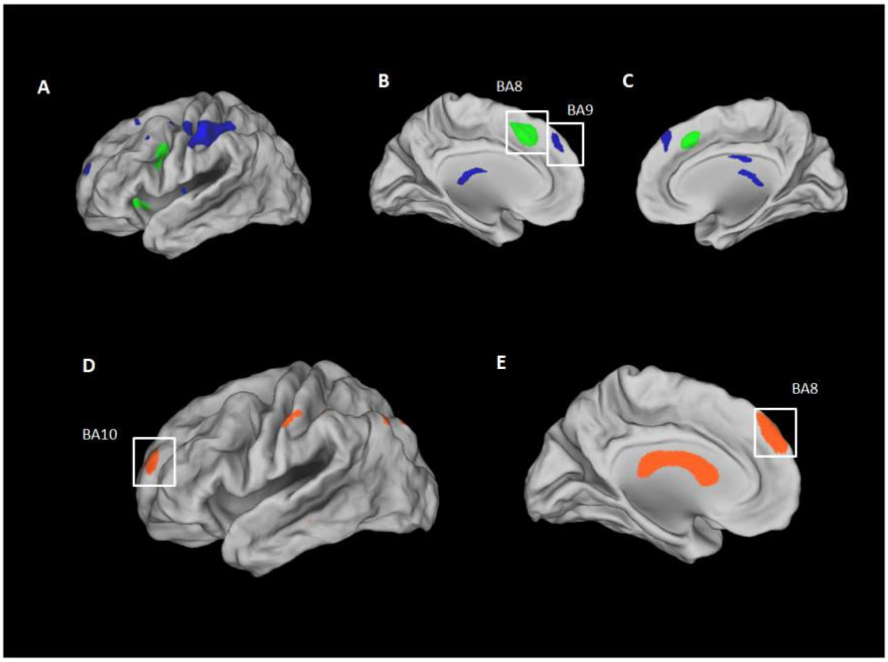

Figure 17. **(A, B, C)** Areas showing significant differences in activation between retrieval practice and relearning (green) and between older and younger adults (blue) in lateral left (A) and medial left (B) and right brain (C). **(D, E)** Areas that significantly correlated with aging (depicted in orange), in a negative direction in lateral (D) and medial (E) and left hemisphere.

Table 1. Areas showing a significant main effect of condition (retrieval>relearning) and a significant main effect of age group (younger >older)

				MNI coordinates			
Anatomic label	*BA*	*HS*	*Size*	*x*	*y*	*z*	*t*
Retrieval>Relearning							
Cingulate Gyrus	32	L	107	-6	20	43	4.08
Inferior Frontal Gyrus	9	L	50	-39	5	31	3.91
Inferior Frontal Gyrus	47	R	22	33	26	-5	3.51
Younger>Older							
Frontal Lobe							
Superior Frontal	10	R	103	30	62	1	5.54
Superior Frontal	6	R	37	24	26	58	4.53
Superior Frontal	10	L	26	−18	65	19	4.42
Superior Frontal	8	R	77	3	47	49	4.11
Middle Frontal	6	L	30	-27	20	58	6.80
Middle Frontal	8	R	192	54	17	40	6.78
Medial Frontal	8	R	17	3	26	43	3.86
Inferior Frontal	47	L	48	−42	14	−11	5.02
Inferior Frontal	9	L	59	-54	20	25	4.14
Cingulate	23	R	41	9	−19	28	4.64
Parietal Lobe							
Postcentral Gyrus	40	L	327	−57	−28	49	6.77
Inferior Parietal Lobe	40	R	182	45	−46	52	6.30
Caudate	----	L	143	−9	2	19	4.41
Caudate	----	R	39	9	8	16	4.21

HS = hemisphere; L = left; R = right; BA = (approximate) Brodmann's area;
Size = number of adjacent voxels surviving a threshold of p_{uncorr}<.001.

Table 2. Peak coordinates showing a significant correlation between BOLD signal activation and aging

				MNI coordinates			
Anatomic label	*BA*	*HS*	*Size*	*x*	*y*	*z*	*t*
Positive Correlation							
Posterior Lobe	---	R	54	33	-61	-17	4.18
Negative Correlation							
Frontal Lobe							
Superior Frontal	10	R	46	30	62	4	5.18
Middle Frontal	9	R	42	60	17	31	5.40
Inferior Frontal	47	L	28	-42	14	-11	4.51
Parietal Lobe							
Inferior Parietal	40	R	18	45	-46	52	4.73
Inferior Parietal	40	L	21	-45	-43	55	4.07
Precuneus	19	L	11	-30	-79	43	4.21

HS = hemisphere; L = left; R = right; BA = (approximate) Brodmann's area; Size = number of adjacent voxels surviving a threshold of p_{uncorr}<.001.

Table 3. Peak Coordinates showing a positive main effect of condition (retrieval>relearning) in younger and older adults separately

				MNI coordinates			
Anatomic label	*BA*	*HS*	*Size*	*x*	*y*	*z*	*t*
Young adults Rp>Rl							
Frontal Lobe							
Cingulate Gyrus	32	L	86	-3	23,	40	5.12
Precentral Gyrus	6	L	14	-39	2	31	3.92
Inferior Frontal	47	L	28	-33	29	-5	4.22
Temporal Lobe							
Superior Temporal	38	R	12	45	20	-17	4.12
Fusiform Gyrus	37	L	17	-51	-61	-11	4.08
Middle Occipital Gyrus	18	L	26	-24	-97	7	4.82
Older adults Rp>Rl							
Middle Frontal Gyrus	6	L	-54	5	43	12	5.18

HS = hemisphere; L = left; R = right; BA = (approximate) Brodmann's area;
Size = number of adjacent voxels surviving a threshold of p_{uncorr}<.001.

Brain behaviour correlations

In order to explore whether regions active during retrieval practice were in fact predictive of participants' behaviour, beta values from clusters that showed a positive effect of condition (retrieval>relearning) were extracted and correlated with an inhibitory index, calculated as the difference between unpracticed items in the retrieval condition and the unpracticed items in the relearning one. Positive correlations were found between the activation of two clusters during retrieval practice and the inhibitory index, namely the inferior frontal gyrus cluster (-39 5 31, ~BA 9; r=.35, p<.05) and the cingulate gyrus (-6 20 43, ~BA 32; r=.34, p<.05); differences in activity during retrieval and relearning in inferior frontal gyrus also predicted later behaviour (33 26 -5, ~BA 47; r=.33, p<.05). In all cases, more activation correlated with greater posterior forgetting (see Figure 18).

Furthermore, we wanted to assess if regions that were less active as people age were involved too in later forgetting. Hence, we extracted activity from the clusters negatively correlated with age in the multiple regression analysis and correlated their beta values with the inhibitory index. Two clusters showed a positive correlation with behaviour: a superior frontal cluster (30 62 4, ~BA 10; r=.28, p<.05) and a right parietal one (45 -46 52, ~BA 40; r=.32, p<.05).

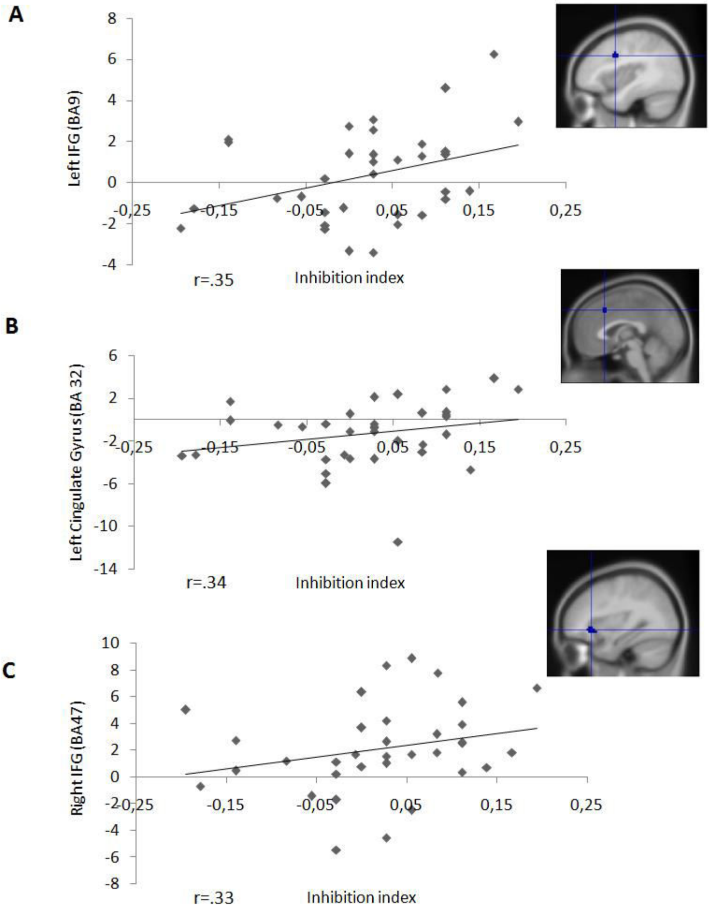

Figure 18. Regions that yielded a significant correlation between subject's activation during selective retrieval, and forgetting on the final test. These included clusters in **(A)** left cingulate gyrus (-6 20 43, ~BA 39) and **(B)** left (-39 5 31, ~BA 9) and **(C)** right inferior frontal gyrus (33 26 -5, ~BA 47). The *y*-axis in the scatterplots show beta values from the difference between retrieval and relearning blocks (C), whereas *x*-axis show the subjects' inhibitory index, computed as the difference between unpracticed items in retrieval and relearning.

Discussion

The main aim of this study was to assess age-related changes in inhibitory mechanisms, as those involved in the retrieval practice paradigm, both at a behavioural and at a neural level. In fact, age related differences in performance become apparent already at a behavioural level. As expected, in the young sample recall of unpracticed items in retrieval blocks was significantly lower than recall of unpracticed items from relearning blocks. Our results then show that young adults suppress information in a selective retrieval condition to a greater extent than in a relearning condition, thus replicating Wimber et al.'s (2009) results, amongst others. This pattern of results has previously been explained as a difference in competition between conditions. Concretely, during retrieval practice blocks, participants are asked to retrieve one particular item and, when attempting to do so, all of the other previously studied ones will come into mind and compete for retrieval. Participants then need to push these items away from memory resulting in their later forgetting. During relearning blocks, however, since there is no need for participants to retrieve any information, unpracticed items do not interfere and do not need to be suppressed, hence being remembered better than those in the retrieval blocks (Anderson et al., 2000; Hanslmayr et al., 2010).

A different pattern of results was found, however, for older participants. Older adults showed no difference in mean recall of unpracticed items from one or other type of block. This result comes in accordance with previous literature that found this effect to be hindered in older adults (e.g. Aslan et al., 2012; Marful et al., 2014; Ortega et al., 2012), with RIF effect disappearing gradually as people age, as well as when their cognitive resources become less available.

These previous studies however, did not inform how brain activity relates to the impairment in performance associated to retrieval practice. To investigate this question, the present study looked at brain activity in a group of young and older adults, to compare which neural substrates were implicated in this task. Predictions for the young adults sample were clear, as we aimed to replicate results found in previous literature (e.g. Kuhl et al., 2007; Wimber et al., 2009), that showed greater engagement of frontal structures (namely ventro-lateral prefrontal cortex and cingulate cortex) during retrieval practice and, importantly, that the involvement of these regions predicted performance on the final memory test.

Regarding the older adults, predictions were not as clear cut. On one hand, according to the IDT (e.g. Hasher & Zacks, 1988; Lustig, Hasher, & Zacks, 2007) and to brain research showing how age affects prefrontal areas (e.g. Raz, 2000), one would expect these areas to be less engaged by older adults and for this lesser engagement to be a correlate of impaired behaviour. On the other hand, some research has put in evidence that older adults often show patterns of activation that are actually more extended than that of young adults and this extended activation could reflect compensatory mechanisms that enable elders to maintain performance (e.g. Cabeza, 2002; Park & Reuter-Lorenz, 2009). The idea is that extra areas, adjacent to those normally used by young adults, are recruited by elders to aid the main ones and help maintaining a good level of performance, even though research has shown that extended patterns of activation can still be found even with no benefit to the behavioural outcome. If this is the case, one could expect older adults to actually show greater activation of frontal areas in comparison to young, regardless of the behaviour results.

Our results do in fact replicate to a great degree previous findings with young adults. Specifically, when comparing selective retrieval to relearning, young adults showed increased BOLD signal in frontal areas such as the cingulate cortex and left ventrolateral prefrontal cortex (VLPFC). Cingulate cortex has often been related to interference detection (e.g. Botvinick et al, 2001; Ferreira et al., 2014; Kuhl et al., 2007; Staudigl et al., 2010) and it is thought to track its rise and fall over time. Additionally, VLPFC has been shown to underlie inhibitory mechanisms in motor actions (e.g. Aron, Robins, & Poldrack, 2004; Levy & Wagner, 2011) and in memory processes (Wimber et al., 2009). Thus, it seems reasonable to assume that these areas are in charge of exerting inhibition and so, the more active they are the more suppressed items should be in the final memory test. Agreeing with this idea, activity in frontal clusters during retrieval practice predicted later forgetting, such that the more these areas were activated, the more forgetting participants exhibited in the final test.

Crucially these frontal areas seemed to be less active in the elderly. Concretely, a main effect of age revealed that younger adults activated these areas to a much greater extent than older adults, regardless of the task in hand. Also, even though the interaction analysis did not yield significant results, the comparision between the two types of blocks in elders revealed only one significant cluster in pre-motor area. This clearly contrasts with the results obtained in the same comparison with young adults. Moreover, multiple regression analysis showed that these areas correlated negatively with age, so that older participants showed less engagement of these areas than younger ones. Moreover, these same areas correlated with forgetting in the final test. This suggests that as people get older, frontal areas are less engaged in the face of competition. By being less engaged, they cannot effectively solve competition which is shown by impairment in performance.

These results then suggest that, at least our participants, were not capable of engaging additional brain areas to maintain performance. This speaks against compensation hypotheses (Cabeza, 2002; Park & Reuter-Lorenz, 2009), though it could be a result specific to our task, since our it was a rather demanding one (participants were required to memorize a great number of lists in a potentially stressful context as the MRI scanner). Given that RIF has been found to be dependent on available cognitive resources (Ortega et al., 2012), we hypothesize that our participants may not have had the available resources to call additional areas into play; an idea that agrees with the CRUNCH (Compensation Related Utilization of Neuro Circuits Hypothesis) model, put forth by Reuter-Lorenz and Cappel (2008). These authors propose that compensatory activation is only effective at lower levels of task demand. At these lower levels, seniors over activate prefrontal cortex to achieve similar performance as that of younger adults. However, as demand increases, a resource ceiling is reached and prefrontal cortex becomes underactivated in the elders and performance is hindered.

Our results do agree quite well though with the IDT (e.g. Hasher and Zacks, 1988; Lustig, Hasher, & Zacks, 2007). The

IDT proposes that inhibitory mechanisms are impaired in older adults and that this impairment should be underlay by changes in the brain, namely in prefrontal structures. Both our behavioural and our fMRI results corroborate this idea and agree with previous research showing that seniors have impaired performance in inhibitory tasks (e.g. Stop Signal and Go/No go: Bedard, Nichols, Barbosa, Schachar, Logan, y Tannock, 2002; Think/No Think: Anderson, Reinholz, Kuhl, y Mayr, 2011; Murray, Anderson y Kesinger, 2015), as well as with studies showing underactivation of brain areas during inhibition. Gazzaley, Cooney, Rissman and D'Esposito (2005) for instance, showed that though older participants had no problem in activating brain areas to a greater extent when asked to attend *vs.* passively viewing a stimulus, they could not regulate brain activation in order to diminish it when comparing ignoring to passive viewing instructions, like younger participants did. Thus, it seems that cognitive deficits evidenced by older adults could be dependent on a lack of inhibitory capacity.

It must be stressed though that there are some limitations to our study, and that accordingly, our results should be taken with care. Namely, our samples are somewhat small, specially the older adults'. We believe that our results would hold or become even stronger by enlarging this sample, though that has yet to be tested. Moreover, aging studies that use neuroimaging techniques should always take into account the fact that older adults' brains are much more variable in their structure than young adults', positing potential problems for the comparison between the two.

In sum, in the current study we replicate previous findings with young adults, showing that, in contrast to a relearning condition, retrieval practice leads to inhibition of competing items and that control related areas, such as the cingulate cortex and the left VLPFC are in charge of dealing with competition and triggering the necessary inhibitory mechanisms. More importantly, we find that older adults are not capable of engaging these structures to the same extent which is reflected in their hindered behavioural RIF effect. These results strongly agree with the IDT, that is, the hypothesis that aging entails a decline in cognitive function that is underlay by anatomical and functional changes in the brain, namely in prefrontal cortex. Future work could potentially focus on how to prevent these regions to suffer so abruptly from aging, or on how to stimulate them in order for behavioural performance to be maintained.

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6. CONCLUSION

The present work aimed to investigate age differences in inhibitory mechanisms during memory retrieval, focusing on one of the memory problems more frequently reported by older people, i.e., their difficulty in retrieving personal information such as faces and names. In order to know whether an inhibitory deficit could underlie naming difficulties in aging, we first needed to know whether personal representations, such as faces or names, would be subjected to inhibitory mechanisms of a controlled nature (Experimental Series I). Once we had established this, we wanted to assess the neural correlates of these mechanisms in young adults, to pin point the neural substrates involved in suppressing competing personal representations (Experimental Series II to IV). Finally, with the last research question we tackled the key subject of how inhibitory mechanisms are affected by aging, both at a behavioral level as well as at a neural one (Experimental Series III and IV).

We next discuss how the results obtained in each experimental series answer these questions and the theoretical implications of these results, as well as future work that can be developed within this framework.

6.1. Are personal representations vulnerable to controlled inhibitory mechanisms?

In order to know whether inhibitory failures associated with age could help explaining naming difficulties in old age, we first needed to investigate whether faces and other personal representations were subject to the same type of inhibitory mechanisms as other types of representations.

Literature has often considered faces to enjoy a special status on cognition and to depend on different mechanisms and processes than other objects (e.g. Farah, 1996; Haxby, Hoffman, & Gobbini, 2000; McKone, Kanwisher, & Duchaine, 2006). Moreover, there is some debate about whether personal representations are equally vulnerable to interference mechanisms than other objects (Marful, Ortega, & Bajo, 2010; Vitkovitch, Potton, Bakogianni, & Kinch., 2006) and even though models of face recognition do consider that interference between representations may arise they either do not propose a solution to solve it (Bruce & Young, 1986) or posit automatic, non-controlled mechanisms to overcome competition (Burton, Bruce & Johnston, 1990).

In four experiments (Experimental Series I), we tested whether faces could indeed depend on inhibitory mechanisms of a more controlled nature, as those arguably underlying the RIF effect. We found that competing facial features (Exp. 1a) and competing names (Exp. 2a) were recalled significantly worse in the final memory test, as a result of being suppressed during retrieval practice phase. To further test the hypothesis that our results were due to inhibitory mechanisms, Experiments 1b and 2b replicated the previous ones, but instead of actively retrieving information during the intermediate phase, participants were simply re-exposed to the stimuli. As hypothesized, this led to the disappearance of the RIF effect. In Experimental Series II, we found similar results at a behavioral level, and these effects were traced by mid frontal theta oscillations, probably generated in the anterior cingulate cortex (ACC), as discussed ahead.

Interference and inhibition play a role in retrieving personal representations

There are several theoretical implications that come from these series of experiments. First, the fact that RIF effect occurred when participants were asked to retrieve part of the information during the intermediate phase but not when they were required to just passively review the stimuli, suggests that personal representations are prone to interference and inhibition, just like other types of representations.

Especially relevant is the fact that, as our second experimental series suggests, this interference is tracked by mid frontal theta oscillations. Theta oscillations have been associated with interference, since mid-frontal theta power has been shown to increase in several interference-related tasks such as Stroop (Hanslmayr, Pastötter, Bäuml, Gruber, Wimber, & Klimesch, 2008) or Flanker (Cavanagh, Cohen & Allen, 2009) tasks. Congruent with this idea, theta activity in our experiments seems to have been originated in the ACC, a brain structure responsible for detecting interference situations (e.g. Botvinick, Braver, Barch, Carter, & Cohen, 2001).

Taken together, these findings extend both RIF effect and mid-frontal theta oscillations that were previously found with semantic materials (e.g. Anderson, Bjork, & Bjork, 2000; Hanslmayr, Staudigl, Aslan, & Bäuml, 2010) to other type of stimuli, i.e., personal respresentations. Furthermore, it gives empirical support to the claim made by face recognition models that personal representations are vulnerable to competition (Brèdart, Valentine, Calder, & Gassi, 1995; Bruce & Young, 1986; Burton et al., 1990, 1999). Crucially, competition seems to be solved by means of inhibition, since recall of unpracticed (competitor) items, is impaired on the final memory test across several of our experiments.

The idea that controlled inhibition could play a role in face recognition had been posited before by Ciranni and Shimamura (1999) and by Anderson (2003). Namely, these authors proposed that the Verbal Overshadowing phenomenon

(Dodson, Johnson, & Schooler, 1997; Kinlen, Adams-Price, & Henley, 2007; Schooler & Engster-Schooler, 1990) could depend on an inhibitory mechanism akin to that underlying RIF. Verbal Overshadowing makes reference to the counterintuitive finding that partially describing a face impairs the recall of those facial features that were not described. From this perspective, it could be that non-retrieved features compete for retrieval while participants are describing a particular face and again, this competition could potentially be solved by the inhibition of the competitor features that would consequently impair the later face recognition (Ciranni & Shimamura, 1999; Anderson, 2003).

Interestingly, these inhibitory mechanisms seem to act at different stages of the recognition process. Experiment 1a indicates that inhibition is acting at a very early stage of recognition, namely at the FRU (Face Recognition Unit) level, whereas Experiment 2a, as well as Experiments 3 and 4, indicate that inhibition acts upon lexical-semantic representations (the famous people's names), that is, at the SIU (Semantic Information Unit) level. It could be argued however, that in Experiment 1a inhibition is acting on suppressing the actual representation of the studied people instead of their facial features. To test this hypothesis we conducted an experiment similar to Experiment 1a, apart from the test phase. In this experiment, the memory test consisted on a recognition test where participants were asked whether a particular face had been presented before. If inhibition was acting at the PIN (Person Identity Node) level, access to the identity of previously presented people should be impaired and RIF should still occur when participants are asked to focus on the whole face instead of particular features. Results failed to find the RIF effect, which indicates that the people's identities were not suppressed, but rather a very specific feature – their eye color - thus supporting the idea that the impairment in recall found in Experiment 1a was occurring at the FRU level.

Implications for face recognition models

Overall, the data from the first and second experimental series indicate that inhibitory mechanisms of a controlled nature are engaged in solving interference between personal representations. Not only do these results disagree with the more traditional view that faces are special (see section 1.3), by showing that the same sort of mechanisms can act upon both personal and object representations, but they also posit a problem to face recognition models, that cannot fully explain these data.

As mentioned earlier, Bruce and Young's model (1986) does not explain how interference between representations is overcome. On the other hand, Burton et al.'s model (1990) does assume the action of inhibitory mechanisms; however, the nature of these mechanisms is notably different than that thought to underlie RIF. The mechanisms proposed by face recognition models are rather quick and automatic, resembling a sort of lateral inhibition (Burton et al., 1990). According to this idea, one would expect that the more a unit is activated, the more it should inhibit competing ones, which, in the retrieval practice paradigm would mean that the more Rp+ items are strengthened, the more Rp- should be suppress. Several studies have shown that this is not the case, that is, that there is no connection between the strengthening of Rp+ and the inhibition of Rp- (e.g. Anderson & Spellman, 1995; Storm, Bjork, Bjork, & Nestojko, 2006). Accordingly, the type of inhibition proposed by face recognition models could not explain our results.

Another prediction these models make, is that, within the self-regulation mechanism proposed by Burton et al. (1990), inhibited items should go back to their initial level of activation, but not fall below it. This self-regulatory mechanism, cannot explain then the fact that Rp- are recalled significantly worse than baseline items. Thus, we argue that face recognition models should take into account controlled inhibitory mechanisms to solve interference between representations.

In sum, Experimental Series I and II show that personal representations, just as other types of representations, can be vulnerable to inhibitory mechanisms of a controlled nature, that act throughout all stages of face recognition, from a more perceptual one (Experiment 1a) to a lexical-semantic stage (Experiments 2a, 3 and 4). These experiments start pointing in the direction that a deficit in inhibitory mechanisms, as that proposed by Hasher and Zacks (1988), could help explaining naming difficulties in elders. In order to explore that question in a more precise fashion, we first needed to know if RIF's neural correlates reported in the literature are maintained when using personal representations as stimuli. We discuss our results related to this question over the next sections.

6.2. What are the neural correlates of RIF effect?

In Experimental Series II to IV we focused on the neural correlates of RIF, in order to pin point brain activity related to interference and its resolution. In Experimental Series II and III we used electrophysiological techniques to assess how brain oscillations may reflect the cognitive processes working during retrieval practice and their precise temporal dynamics. In Experimental Series IV, we used fMRI to better determine the spatial location of neural substrates implicated in retrieval practice.

Briefly, in Experimental Series II and III we found theta oscillations with a mid-frontal topography to underlie selective retrieval under competitive conditions. These oscillations were source localized to the ACC, a structure related to interference detection that we also found to be more active during retrieval than during relearning in Experimental Series IV. Additionally, in this series we found other prefrontal areas to be more engaged during retrieval, namely the ventrolateral prefrontal cortex (VLPFC) which has been said to be involved in inhibitory behavior (e.g. Aron, Robins, & Poldrack, 2004; Levy & Wagner, 2011).

We now discuss in more depth the results obtained in these experiments with the samples of young adults.

Role of mid-frontal theta

In Experimental Series II and III we found in two experiments that competition between stimuli led to an increment in mid-frontal theta power. In Experiment 3, we compared a condition that led to interference between stimuli against another that did not. Presentation of a category cue in the first condition yielded greater theta power in comparison to the second. This is exactly what one would expect if, upon presentation of the cue, all associated items become active and compete for retrieval in the competitive condition, since participants know beforehand that they will need to retrieve some information. In the relearning condition, however, this should not happen given that participants are simply asked to retrieve a category and do not need to recall any particular information about the items (such as a name). We argue that differences in theta power between these two conditions arise due to this key distinction.

An alternate explanation for these results would be that theta oscillations are reflecting task effort or difficulty rather than interference, since one condition (the competitive one) could be rendered more demanding than the other. However, studies have shown that difficulty at retrieval is actually related to theta oscillation in a negative fashion, that is, the more difficult items are to retrieve, the more theta power decreases (e.g. Spitzer, Hanslmayr, Opitz, Mecklinger, & Bäuml, 2009; Klimesch et al., 2006), which makes this explanation rather implausible for our data.

In addition, in Experiment 4, difficulty levels were kept constant, since we compared performance within the exact same task and a similar pattern of results was obtained. Concretely, in Experiment 4, we looked into how the dynamics of interference changed over time, comparing theta oscillations in the first cycle of retrieval practice to the subsequent ones. We found that theta power was reduced from the first to the third cycle, which is what one would expect if participants were gradually solving interference from one cycle to the next. Thus, in broad strokes, it seems that theta oscillations should be tracking the temporal dynamics of interference, that is, its rise and fall over time.

In fact, these results agree with previous research showing that mid-frontal theta oscillations are associated with an increase of activated information in memory (e.g. Khader & Rösler, 2011; Mecklinger, Kramer, & Strayer, 1992) and with response conflict tasks, such as Flankers or Stroop (e.g. Cavanagh et al., 2009; Hanslmayr et al., 2008). Our data also replicate prior RIF studies that find a similar pattern of results (e.g. Hanslmayr et al., 2010; Staudigl, Hanslmayr, & Bäuml, 2010). Notice however, that our experiments go one step beyond these studies, by using a procedure that separates the category and the retrieval cue in time. Specifically, this procedure allowed us to disentangle the moments when interference arises and when inhibition comes into play. The underlying assumption is that when participants see the category cue, all of the studied items become active in memory, generating interference between them. This interference should then be overcome upon presentation of the retrieval cue, since participants need to choose one response. In order to promote retrieval of the correct response, competing items have to be inhibited.

Hence, using this pre-cuing procedure, allowed us to eliminate a possible confound in previous studies, and attribute the increase in theta oscillations specifically to interference, rather than its resolution. Further support to this claim comes from the fact that theta activity was source localized to the ACC. This structure has been consistently associated with interference detection and mediation (e.g. Botvinick et al., 2001). We argue then that theta oscillations trace the fine grained temporal dynamics of interference: how it increases when representations become active in memory and compete for retrieval and how it decreases when interference is solved.

To support this late idea, we found in Experiment 3 that theta power is reduced upon presentation of retrieval cue (when interference needs to be solved) and that this decrease correlates with behavior in the final memory test. Moreover, in Experiment 4 theta power also decreased from the first to the third cycle of retrieval practice, which other researchers have interpreted as an indication of interference resolution (e.g. Kuhl, Dudukovic, Kahn, & Wagner, 2007; Staudigl et al., 2010). So, it seems that mid-frontal theta oscillations can work as a direct marker of interference and an indirect marker of inhibitory mechanisms, getting reduced when they act upon competing stimuli to suppress them.

In sum, Experiments 3 and 4, point to theta oscillations as tracers of the temporal dynamics of interference during competitive memory retrieval with the source of this activity being localized to the ACC. Importantly for the scope of this work, these experiments also show that previously found neural correlates of inhibition hold even when personal representations are used as stimuli.

Role of frontal brain regions

In Experimental Series II and IV, we found cingulate cortex to be active to a greater extent in competitive conditions than in non competitive ones. As briefly mentioned before, the cingulate cortex (and especially the ACC) has been closely linked to the detection and mediation of interference (e.g. Botvinick et al., 2001). In Experiment 3, we found that theta oscillations were generated by the ACC. The involvement of the ACC was further supported by the results from Experiment 5, where using fMRI, a technique of greater spatial precision that the EEG, we found again that, compared to relearning, retrieval practice led to greater activation of a cluster in left cingulate cortex. Moreover, theta power during the presentation of the category cue in the first retrieval practice cycle (Experiment 4) and activity in cingulate cortex (Experiment 5) correlated with later forgetting. This correlation corroborates the inhibitory account that claims that interference is a necessary condition for inhibitory mechanisms to act.

The ACC is not only involved in response conflict (e.g. Aron & Poldrack, 2006; Aron et al., 2004; Menon, Adleman, White, Glover, & Reiss, 2001), but in conflict in general (Cavanagh et al., 2009; Hanslmayr et al., 2008). Thus, we argue that in the present work, upon presentation of the category cue, several memory representations compete for retrieval and that this conflict is monitored by the ACC.

As Botvinick et al. (2001) point out, though the ACC is responsible for detecting interference, it is not responsible for reducing it. For that, there are other plausible candidates who might be in charge of suppressing irrelevant representations in order to deal with competition. Previous studies using the retrieval practice paradigm (e.g. Kuhl et al., 2007; Wimber et al., 2009) have shown an engagement of left VLPFC in this task, and results from our Experiment 5 replicate this finding. The authors interpreted the increase in BOLD signal as a correlate of inhibition itself and this brain region has actually been associated with inhibition in domains other than memory, such as in the motor domain (e.g. Aron et al., 2004; Levy & Wagner, 2012), where activity in this brain region has been shown to increase in Stop or No/Go trials in comparison to Go ones. Importantly, it has been argued before that mnemonic and motor inhibition might share some neural substrates (Levy &

Anderson, 2002), and the VLPFC could be a core structure underlying inhibition across domains.

Another possible structure associated with inhibitory behavior is the dorsolateral prefrontal cortex (mainly right DLPFC). The role of this area has been discussed in the classical paper by Botvinick et al. (2001). In the memory field this area has been shown to underlie results in the Think/No-Think (TNT) paradigm (e.g. Anderson et al., 2004; Benoit & Anderson, 2012) and has also been said to be responsible for triggering inhibitory mechanisms. Note however, that the type of forgetting responsible for the TNT effect is motivated (participants are actively trying to suppress information), whereas forgetting in RIF is incidental. In fact, this same distinction is made by Benoit and Anderson (2012) who find that directed suppression is related with an increase in right DLPFC activity, whereas VLPFC gets more activated in a thought substitution condition, that would be more akin to RIF. In any case, prefrontal structures seem to be actively engaged during selective retrieval under competitive conditions. Specifically, whereas cingulate cortex seems to be associated with the detection of interference, left VLPFC appears to be responsible for dealing with competition and reducing it, arguably by suppressing interfering mnemonic representations.

Implications for the inhibitory account

Our results greatly support the inhibitory account for RIF. Firstly, behavioral results from our experiments confirm predictions made by inhibitory account that whereas retrieval practice should lead to impairment of competitor items, mere relearning of stimuli should not (e.g. Anderson et al., 2000). This is precisely what we find in Experimental Series I, II and IV. What should happen is that when participants are asked to actively retrieve specific information associated to a category cue, all of the previously studied items associated to that same cue should compete for retrieval (and hence the need of an inhibitory mechanism to act). In contrast, when subjects are merely re-exposed to the stimuli, without the need for retrieval, even if items do become active in memory, they should not create competition since none of them will be retrieved. Thus, as the inhibitory account predicts, RIF is dependent of interference.

Our electrophysiological results further support this claim. Theta oscillations with a mid-frontal topography, which have been related to the detection of conflict, increased when comparing a competitive to a non competitive condition (Experiment 3) and the source of this activity seems to be the ACC (Experiments 3 and 5). Moreover, theta (Experiment 3 and 4) and ACC activity (Experiments 3 and 5) positively correlated with later forgetting, which is exactly what one would expect according to this account: the more interference there is, the more competing items will be inhibited.

Regarding inhibition itself, though we did not find a direct marker of it in our EEG experiments, we did find an indirect one, namely theta reduction from category cue to item-specific cue (Experiment 3), and the reduction of theta from one cycle of retrieval practice to the next (Experiment 4). As mentioned above, theta should be tracing interference and its decrease would reflect a reduction in interference. We argue that this reduction is achieved by means of inhibitory mechanisms. To further support this claim, in Experiment 5 we found regions previously related with inhibitory behavior to become more engaged in competitive selective retrieval than in relearning, namely the VLPFC. VLPFC should be underlying the resolution of interference and is, thus, somewhat of a more direct marker of inhibition. In fact, activity in this area predicted later forgetting.

To add to this, alternative accounts of RIF could not explain our results. Blocking theories (e.g. McGeoch, 1942; Mensink & Raaijmakers, 1988), for instance, would not be able to explain why we find RIF in a competitive but not in a non competitive condition. Moreover, the context hypothesis (Jonker, Seli, & MacLeod, 2013) could not account for our results either, since at least in Experiments 2 to 4 one of the core premises of this theory - that during test the retrieval practice context is reinstated - is not complied with. In these experiments, test phase resembles the study phase to a much greater extent, and thus the context theory would predict that no RIF effect should be found.

A final implication for the inhibitory account is that our data extends traditional RIF findings to complex and more ecological stimuli. As far as we are aware, no RIF experiments had been done using personal representations. In the present work, not only do we show that the behavioral effect of RIF is maintained when using more complex stimuli, but also that the neural correlates of this effect are very similar to those reported in the literature with semantic stimuli.

6.3. How do inhibitory mechanisms change with normal aging?

By this point, we have established that i) faces and other personal representations are vulnerable to RIF and that ii) RIF depends on inhibitory mechanisms of a controlled nature. We can now turn to tackle our main question of whether a failure in inhibitory ability could explain naming difficulties in old aging. Experiments 4 and 5 tried to answer this question by looking at age-related changes in the behavioral effect of RIF and in its neural correlates.

In two experiments (Experiments 4 and 5), we found RIF effect to be hindered in older adults, since no significant difference was found between unpracticed items in a competitive condition (retrieval practice) and control items. Concretely, in Experiment 4, participants were instructed to name a face given a category cue (e.g. Actors) followed by a specific retrieval cue (e.g. Bandera's face). Analysis of theta oscillations indicated that older adults did not suffer from interference when presented with the category cue (e.g. Actors) and, consequently, had no need to engage inhibitory mechanisms. We believe this result might be due to the fact that in this experiment, the category cue was not necessary to correctly complete the task, that is, participants would still be able to name Banderas upon presentation of its face, even if they had not paid attention to the cue "Actors". Thus, it is possible that older adults were just not processing the category cue, which is an idea backed up by studies showing that older adults have impaired context processing (Braver et al., 2001; Rajah, Languay, & Valiquette, 2010; Rush, Barch, & Braver, 2006). Another related, but somewhat more intentional possibility is that rather than having a deficit in context processing, older adults simply do not employ the same retrieval strategies. According to this hypothesis, whereas younger adults use the category cue to answer quickly upon presentation of the photo, the elderly chose to ignore the category cue and do not engage searching processes until the face is presented. Thus, younger adults would suffer from forgetting to a greater extent than their older counterparts, since they would be attending to the category cue, while elders would ignore it (see Bajo, Gómez-Ariza, Fernández, & Marful, 2006, for an example on a larger RIF effect when a pre-cuing procedure is used during the retrieval practice phase in comparison to a standard procedure). Similar differences in retrieval strategies between young and older adults were found by Sahakyan, Delaney, and Goodmon (2008) using the Directed Forgetting paradigm and by Murray, Anderson, and Kesinger (2015), using the Think/No-Think paradigm.

Because of this pattern in our data, in Experiment 5 we decided to use semantic material instead of faces. Using pairs of words as stimuli instead of faces, we forced participants to actually focus on the category cue, since in order to retrieve Apple when given Ap___, one needs more information than just the word stem to promote successful retrieval. This necessary information is given precisely by the category cue (Fruit), and thus participants would need to process this cue in order to respond correctly.

As expected, in Experiment 5, RIF effect again disappeared for elders and this impairment correlated with a lesser engagement of frontal areas. Namely, whereas younger participants activated a fronto-parietal network when comparing retrieval practice to relearning, older participants only activated a cluster in pre-motor cortex. More importantly, a multiple regression analysis showed that several frontal regions, namely the cingulate cortex, correlated negatively with aging, so that the older the participants were, the less these areas were activated. Furthermore, prefrontal areas other than cingulate cortex correlate negatively with aging, and are active in young but not in elder participants. Importantly, these regions that seniors did not activate have been consistently linked with inhibitory behavior (e.g. Aron et al., 2004; Levy & Wagner, 2012). Thus, results from Experiment 5 point towards the idea that older adults might be vulnerable to interference at similar levels as younger ones (given that ACC activity did not depend on aging), but not be capable of dealing with this interference due to an incapacity to engage the appropriate brain areas that will trigger the necessary inhibitory mechanisms to solve competition.

As far as our knowledge goes, this is the first set of experiments that disentangles interference and inhibition related activity in seniors, and the implications of our results to different theories of aging are discussed next.

Implications for aging theories

As briefly mentioned before, our work greatly supports the Inhibitory Deficit Theory (IDT) put forth by Hasher and Zacks (1988), since we found no evidence of RIF effect in a group of old adults in both Experiments 4 and 5. Since RIF has been shown to depend on inhibitory mechanisms (e.g. Anderson & Spellman, 1995; Anderson et al., 1994; Bajo, et al., 2006; Hicks & Starns, 2004; Johansson, Aslan, Bäuml, Gäbel, & Mecklinger, 2007; Kuhl, et al., 2007; Román, Soriano, Gómez-Ariza, & Bajo, 2009; Staudigl, et al., 2010; Storm, et al., 2006; Veling & van Knippenberg, 2004; Wimber et al., 2009), the fact that the effect disappears in an older sample, gives empirical evidence to support this hypothesis.

Also, this inhibitory deficit is supposed to be dependent on brain regions located in prefrontal cortex. In agreement to this, in Experiments 4 and 5, older adults showed reduced activation of cingulate cortex and other inhibition related areas, such as VLPFC and DLPFC. These findings corroborate a study by Solesio-Jofre et al. (2012), who showed that age-related deficits in inhibitory mechanisms increase vulnerability to retroactive interference (in the case of their study), and are associated with neural under-recruitment of prefrontal areas in high interference tasks. This makes it the whole more reasonable to assume that our behavioral results were due to a lack in inhibitory capacity. Importantly, we argue that this failure in inhibitory capacity could be responsible, in part, for naming difficulties in older adults.

Another hypothesis that tries to account for naming difficulties in aging is the Transmission Deficit Hypothesis (TDH; Cross & Burke, 2004; MacKay & Burke, 1990). This hypothesis posits that naming difficulties arise due to the weak connections between phonological nodes that impair retrieval of the complete phonology of the word (Burke & MacKay, 1997; Burke, MacKay, Worthley, & Wade, 1991; MacKay & Burke, 1990). Then, whereas semantic representations receive converging activation from the semantic system, phonological nodes may be linked by unique connections, especially in the case of proper names, and thus, naming difficulties would be located at the word's phonology. Since connections are weakened in aging, the phonological system becomes more vulnerable and that should lead to a deficit in transmission in elders. Though this hypothesis can account for differences between young and older adults, it cannot fully explain why recall of Rp- is impaired in comparison to Nrp in young adults, nor why this pattern changes with aging.

Finally, in our study we did not find any evidence for functional compensation in older adults. Previous work by Reuter-Lorenz and col. (e.g. 2005, 2008) or Cabeza (2002) would predict that older participants could activate some frontal regions to a greater extent than their younger counterparts. However, this is usually found as a correlate of a maintenance in performance (in comparison to young adults), and in our experiments, older adults performance was not preserved, which could explain why we did not find any evidence of compensation. This could be due, according to the CRUNCH (Compensation Related Utilization of Neural Circuits Hypothesis; e.g. Reuter-Lorenz and Cappell, 2008) model to our tasks being too demanding for participants. Concretely, this hypothesis states that compensatory activity can be effective at lower levels of task demand, but that as demand increases, a ceiling level is reached, that is, areas in the brain cannot become more active and this leads to insufficient processing and age-related impairments in performance. Thus, our tasks might simply have been too demanding, not allowing participants to engage compensatory mechanisms to maintain performance. This idea is supported by the fact that RIF has been shown to be dependent on the amount of cognitive resources available (Ortega et al., 2012) in aging.

In conclusion, across four experimental series we found that personal representations are vulnerable to controlled inhibitory mechanisms, as those presumably underlying the RIF effect; that this effect is dependent of frontal brin regions that become more active under circumstances of competitive selective retrieval, similar to what had previously been found with semantic materials, and that this same regions are less engaged in old age, leading to diminished RIF effect. Thus, it seems that an inhibitory deficit, as that proposed by the IDT (Hasher and Zacks, 1988) could explain naming difficulties that come about with normal healthy aging, and that have significant consequences on elders well-being and perception of linguistic competence (Light, 1991; Burke & Shafto, 2004; Gauthier et al., 2006; Pike et al., 2012).

6.4. Future work

More work can still be developed within this line of research. On the one hand, when it comes to the role of interference and inhibition in personal representations, future experiments could try to manipulate suppression of other facial features. It would be especially interesting to know what results would be obtained when the general configuration of the face is manipulated, given that previous research has pointed out that faces might be perceived in a more holistic, configurational way (e.g. McKone et al., 2006), so we wonder whether interference would still play a role when the general configuration of the face is manipulated.

Regarding our electrophysiological experiments, it would be interesting to find a more direct marker of inhibition. Using the pre-cuing procedure we managed to selectively attribute theta oscillations as a marker of interference, but only indirectly of inhibibition (first *vs.* third retrieval practice trial; retrieval practice *vs.* relearning). A procedure as that used by Waldhauser et al. (2012) seems appropriate to look at inhibition itself, but did not disentangle the two processes. Note that because we were using more complex stimuli than those used by Waldhauser, we could not do a similar manipulation of laterally encoding the information. Thus, a combination of these two procedures could potentially provide further insight about the specific temporal dynamics of interference and its resolution.

In addition, given that results from Experiment 4 seemed to show that older participants did not suffer from interference when presented with the category cue, we would like to test the effect of either changing instructions or material type, to have a clearer picture of the effect of these changes in elders' performance. We hypothesize that if senior participants manage to rely more on the context (the category cue) the pattern of results would be somewhat more similar to that of young adults.

Finally, future work on RIF using the fMRI technique seems a promising line of research, for instance, comparing how the different age groups solve interference from one retrieval practice cycle to the next. We hypothesize we would find results parallel to that of Experiment 4 and to Staudigl et al. (2010) and Kuhl et al. (2007) with the young adults sample and that perhaps interference would not be resolved across cycles for the older participant. Moreover, it could be especially relevant to define differences between groups, to analyse Difusion Tension Imaging (DTI) data, since the volume of white matter, especially in prefrontal regions, declines abruptly in aging (Raz et al., 2005) and an age-related decrease in anisotropy, a measure of fiber integrity, has been reported in frontal vs. temporal, parietal and occipital white matter (Salat et al., 2005). Another possibility would be to adapt the pre-cuing procedure to fMRI, since combining the temporal precision obtained in EEG with the spatial precision given by MRI, we could potentially disentangle the specific activity related to interference and inhibition, both their temporal dynamics and their spatial distribution, as well as better understanding their changes across aging.

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