Disentangling OlderAdults' Difficulties in Person Memory

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Neurophysiological Studies on Face and Name Processing

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Preface

From a statistical point of view, life expectancy is steadily increasing: two and a half year per decade, three month per year, six hours a day – a trend which has been and will be continuing due to, for instance, society's increasing life quality and medical progress. Low birth rates, together with a steady increase in life expectancy, give rise to dramatic demographic changes. Society grows older – an issue beyond controversy. This issue has also already triggered a growing body of research on aging in various domains, and up to now emphasizes the need to study aging, its effects, and trajectories.

Findings from developmental and cognitive psychology reveal that (normal) aging is not necessarily a story of major loss. Whereas performance in older age decreases in measures of fluid intelligence, such as perceptual speed, older adults often outperform younger adults on tasks of crystallized intelligence, such as verbal knowledge. Similarly, older adults perform better than their younger counterparts on prospective memory tasks in every-day life situations. Related to that, it is a matter of debate, whether there is a discrepancy between 'aging in the laboratory' and 'aging in the wild', given that healthy older adults, despite the well-documented decline in a number of cognitive functions, are usually not very restricted in their real-life functioning. That 'brighter' perspective on aging notwithstanding, a very common self-reported age-related concern is, in fact, cognitive frailty. It has been documented that especially memory failures in the domain of person recognition and memory, i.e. naming a familiar person, are particularly upsetting and alarming for healthy older adults.

This thesis aims at elucidating the basis for such difficulties by separately investigating age effects on different abilities which likely contribute to failures in person identification. First, the thesis will address age-related changes in the neuro-cognitive mechanisms involved in face perception and memory (Experiments 1 and 2). Faces are the most important source for information about a person's identity; even unfamiliar faces can convey diverse information about a person and foster social interactions. Yet, effects of aging on face processing are rather far from being completely understood. The thesis then shifts the focus towards age effects when remembering the context of familiar names. Familiar names, as faces, provide information about an individual and indirectly entail all the personal history of that person. However, familiar names have been largely neglected in the field of source memory. A subsequent series of experiments in this thesis thus examines neuro-cognitive processes involved in source memory for familiar names in both younger (Experiments 3 and 4) and older adults (Experiment 5).

I would like to cordially thank the people who supported me, while I worked on this thesis. First, I would like to deeply thank Holger Wiese for being such a great advisor from whom I learned an awful lot about experimental setup, EEGs and how to make sense of these data. Many thanks also for the opportunity to pursue my own research ideas.

Furthermore, I would like to express my gratitude to Stefan Schweinberger for his motivating supervision and support during my PhD period, and for staying enthusiastic about my work and a potential future in science, even in moments in which I was not.

I am much obliged to Roberto Cabeza who kindly agreed to be my second reviewer. Some time ago he also agreed to have me visiting his lab for a couple of months – an experience which I still benefit from today and his work has been always very inspiring to me.

I am also very grateful to all the people from the Department and the PPRU. To Kathrin R. for her excellent support with data collection and her way of taking care of our older participants, and to the other PhD students and Post-docs who were also always supportive. Special thanks to Sven, who shares his office with me and still manages to like me, although I created an indescribable mess (not only on my desk) with all the papers cited in this thesis. I am incredibly thankful to Helene as she proofread most part of this thesis (on her holiday!!!), for her encouragement and for always oozing good mood. Many many thanks to Kristin who was also always there when I needed advice or just a person I could faithfully turn to when I felt that things were not going well.

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“The future is not some place we are going, but one we are creating. The paths are not to be found, but made. And the activity of making them changes both the maker and the destination.”

John H. Schaar (1928 – 2011)

2. General Introduction

2.1 Cognitive Aging

Human development is considered as a multi-dimensional, multi-directional and multi-factorial process (Lindenberger, 2007) - inherently representing a rich and interesting field for psychological research. Across the entire life span, we are not only subject to biological or environmental changes, but we also seek or avoid certain activities and decide which relationships or behaviors to pursue or to end, which certainly both enables and constrains developmental dynamics (Asendorpf, 2007). Hence, we are often apt and able to actively create our personal trajectory, our development (Brandstaedter, 2007; Brandtstaedter, 2009; Brandtstaedter & Rothermund, 2002). However, whereas younger adults see their future as manifold in options and designs, older adults perceive their lives as less open and controllable, but more confined by impairments or functional losses (see Brandtstaedter, 2009; Lachman, 2006), such as cognitive decline.

Demographic changes with an increasing percentage of older adults in the general popoulation underscore the need for research on aging and the effects that come with it (Grady, 2012). Although development is plastic and the consequences of aging can be diverse (Cabeza, 2002; Salthouse, 2013), a very common and grave age-related concern is cognitive frailty (Bishop, Lu, & Yankner, 2010). Such concern is legitimate, since cognitive decline affects our quality of life, our (perceived) well-being and even whether we are able to live independently or not (Salthouse, 2004). A vast amount of studies illustrates that aging can indeed have strong effects on various domains of cognitive functioning and performance, such as processing speed, inhibitory control, reasoning and memory (e.g. Baltes & Lindenberger, 1997; D. C. Park & Reuter-Lorenz, 2009; Salthouse, 1996). Such age-related alterations certainly covary and may be caused by mechanisms in the aging brain (Cabeza, Nyberg, & Park, 2004) related to changes in function, structure and neural transmission (Davis, Dennis, Daselaar, Fleck, & Cabeza, 2007; Davis, Kragel, Madden, & Cabeza, 2012; Persson et al., 2006).

Cognitive decline in general and memory decline in particular are very important functional domains to examine not only with respect to age-associated pathologies, such as dementia (Pires et al., 2012), but also because memory complaints are very common in healthy older adults (Ossher, Flegal, & Lustig, 2013). Interestingly, it seems that deficits in the domain of person recognition are among the greatest hassles in older adults' every-day life. For example, older adults report difficulties to retrieve the names of friends and family members (Cohen & Faulkner, 1986) – an issue which has recently been shown to be perceived as particularly alarming, prompting older adults to seek clinical support (Pires et al., 2012). In addition, older adults also report that learning new names and recognizing a person who was recently encountered for the first time causes great difficulties (Naveh-Benjamin, Guez, Kilb, & Reedy, 2004; Ossher et al., 2013; Rendell, Castel, & Craik, 2005).

Importantly, such difficulties most likely entail several different processes that may be disturbed in isolation (for similar argument, see James, Fogler, & Tauber, 2008) and hence may greatly benefit from being examined seperately to prevent a mix-up of effects or confound of results. First, face recognition abilities may be the constraint that determines failures of person identification (see also James et al., 2008). Though age-related differences in face perception and memory have recently been documented independently of declines in general cognition (Hildebrandt, Wilhelm, Schmiedek, Herzmann, & Sommer, 2011), research determining specific age-related decrements in this area still seems less common than in other domains of cognitive functioning. Second, as episodic and especially associative memory seems to be particularly affected by aging (Light, 1991; Old & Naveh-Benjamin, 2008), problems such as name retrieval or remembering the context in which a person was encountered may reflect age-related deficits in the formation and retrieval of new associations (see James et al., 2008). Although other processes may additionally explain older adults' difficulties involved in person recognition (such as problems in retrieval and production of phonological sequences of proper names), these will not be considered here.

Hence, the present thesis focuses on the two aforementioned aspects relevant for person recognition which have not yet attracted much consideration: First, face recognition will be examined in both younger and older adults using pre-experimentally unfamiliar faces (section 3 to 6.3). The aim is to elucidate age-related changes in face perception and memory as well as the relationship between the two. Next, the thesis considers older adults' difficulties to retrieve item-context associations and uses familiar names in a source memory paradigm (section 7 to 11.3). Critically, source memory for person-related information has been tested only rarely. The use of familiar names may make it possible to examine a potential interplay between explicit episodic memory which is largely reduced in older adults and implicit effects (priming) which are relatively preserved in older age (see below). As behavioral data merely captures the outcome of a number of processes underlying an effect in performance, other methods provide the opportunity to more directly assess and potentially disentangle the mechanisms that contribute to a specific result. Event-related brain potentials (ERPs) seemed particularly promising for this purpose and a number of related studies have already taken advantage of this method. ERPs directly measure (task-related) neural activity with high temporal resolution in the range of milliseconds and hence provide an on-line window to neural processes that covary with cognitive processes. Consequently, the following sections also entail decriptions of neuroscientific findings in the domains of face processing and memory, with a particular focus on electrophysiological studies.

As the core questions of this thesis relate to memory, I begin by providing a broad overview of general aspects of age effects on memory, related to present purposes (section 2.2). Subsequently, section 3 decribes relevant models of face memory and perception, as well as more specific phenomena of face memory (i.e. face memory biases) and perception, which the present experiments build on. The potential mechanisms underlying these memory biases are outlined, followed by an overview of relevant findings from brain imaging and electrophysiological studies in face procesing in section 3.4. Finally, the most important aspects regarding age effects on face processing are summarized, leading to the main research questions (section 3.5). Two large-scale studies are then decribed (section 4 and 5) and discussed integratively in section 6.

The thesis then turns towards its second main part which adresses source memory, as a form of associative memory, for familiar names. First, relevant characteristics and effects of aging on person memory and associative memory for names are introduced, and related to the role of source information (section 7.1 - 7.2). Subsequently, the main features of source memory and their neural correlates in young and older adults are described (section 7.3) with respect to the outline of the research questions regarding potential benefical fluency effects on source memory for familiar names (section 7.4). Three experiments are then described (section 8-10) and discussed comprehensively in section 11. Finally in section 12, I provide a brief integrative discussion of the main findings obtained in this thesis, as well as a short (re-) classification of those into the broader context of human development and aging.

2.2 Effects of Aging on (Face) Memory

As stated above, within the memory domain, episodic memory is presumably affected most strongly by increasing age (Light, 1991). It may be argued that many studies of age effects on episodic memory have used artifical material (unrelated word pairs, geometric figures) and that performance differs in the lab as opposed to every-day situations (Salthouse, 2012; see also Verhaeghen, Martin, & Sedek, 2012, for a discussion of a potential disconnect between laboratory studies and real life). Nonetheless, several studies revealed that effects of episodic memory decline are also prevalent with relatively realistic material as the Rivermead Behavioral Memory Test (Wilson, Cockburn, Baddeley, & Hiorns, 1989), which was designed to reflect everyday memory situations, and with respect to real life activities (see e.g. Salthouse, 1991). Though age effects are clearly more pronounced in free recall relative to recognition (e.g. Craik & Mcdowd, 1987; Spencer & Raz, 1995), recognition memory may not necessarily be spared in the old - older adults' performance rather depends on the exact task. If a recognition task requires recollection of the previous episode, recognition performance would be expected to be much lower relative to a task in which familiarity may be sufficient for a correct recognition decision (for similar arguments, see Baddeley, 2009; Yonelinas, 1999). Many models of recognition memory (e.g. Mandler, 1980) consider familiarity and recollection as two different styles of retrieval (Yonelinas, 2002). Whereas recollection entails remembering study phase details or context information and is assumed to be a relatively slow, controlled and cognitively demanding process, familiarity is considered a fast-acting and automatic process providing a 'feeling of knowing' for recognition of an item or an episode. Several studies using the so-called remember/know-procedure (Tulving, 1985) could show that remember-responses (indicative of recollection) decrease, while know-responses (indicative of familiarity) are stable or increase with age (Gardiner & Richardson-Klavehn, 2000; Mantyla, 1993). Participants in this procedure are instructed to indicate every instance of a stimulus that evokes recollection of the specific episode in which it was encountered previously (i.e. information about the source) by a remember-judgement. For those stimuli that are thought to have been experienced previously, but for which recollection of a specific episode is lacking, participants are instructed to make know-judgements. Hence, as opposed to remember-judgements, know-judgements typically entail a feeling that a stimulus is familiar, in the absence of information about the source of this sense of familiarity (for similar description, see Henson, Rugg, Shallice, Josephs, & Dolan, 1999).

While aging has stronger effects on explicit and more strategic memory processes, it leaves familiarity (and other fluency-based processes) unaffected or relatively spared (Anderson et al., 2008; Duarte, Ranganath, Trujillo, & Knight, 2006; Prull, Dawes, Martin, Rosenberg, & Light, 2006). In line with this idea, fluency-based processes such as priming are also largely unaffected by age (Balota, Dolan, & Duchek, 2000). Fluency is defined as a feeling of ease associated with a cognitive operation and has been shown to influence a variety of judgments based on, for instance, conceptual or perceptual similiarity (for overview, see Oppenheimer, 2008). Of relevance for current purposes is the assumption that fluency is linked to implicit processes and that the same fluency signals that give rise to priming may also guide explicit forms of recognition, i.e. familiarity (for a similar line of argument, see Lucas, Taylor, Henson, & Paller, 2012). Of note, it is often assumed that memory failure and false remembering in older adults results from the conjunction of reduced recollection and spared fluency processes, that enable an over-reliance on gist-based representations in the absence of recollection – making older adults more suceptible to false memories (Jacoby, 1999; Jacoby & Rhodes, 2006).

Sometimes it is argued that older adults' performance on pure old/new item recognition, relative to source or associative memory, is comparable to the perfomance in younger adults (Chalfonte & Johnson, 1996; Old & Naveh-Benjamin, 2008). With respect to face recognition, however, it should be kept in mind that faces (and familiar names) represent unique individuals and that distinctions have to be made within a specific category (i.e. at a sub-ordinate level) as opposed to between-category distinctions (i.e. at the basic level) when remembering concrete or abstract nouns or objects (see also Tanaka & Taylor, 1991). Hence, a correct old/new decision in face recognition might actually entail recollection-based processes to a greater extent than such a decision in recognition paradigms using wordlists, for which familiarity-based retrieval is often argued to be sufficient (Yonelinas, 1997). In line with this idea, Boutet and Faubert (2006) found no performance differences in object recognition between younger and older adults, whereas face recognition was impaired in the older group. This finding held when within-category variations of object stimuli were used. Hence, the authors concluded that age affects mechanisms that are tied to or even specialized for face recognition (Hildebrandt et al., 2011). Moreover, as addressed in more detail below, it has been proposed that age-related differences in face processing efficiency may relate to decreases in face recognition abilities in older age (see e.g. Chaby, Narme, & George, 2011; Obermeyer, Kolling, Schaich, & Knopf, 2012). However, before examining whether and how aging affects specific processing stages, e.g. early perceptual versus later representational stages, it is important to explain how face processing is assumed to operate in general. Hence, a short overview of relevant models is provided in the next section.

3. Models of Face Perception and Memory

Several models have been developed to describe the mechanisms involved in face recognition. Of these, Bruce and Young's (1986) cognitive model is probably the most influential one (see Figure 1). Crucially, their model describes several consecutive processing stages involved in the recognition of a *familiar* face. Information about gender, age, ethnic membership, emotional expression or even intention as inferred from gaze – so called visually-derivable semantics – can be extracted for both familiar and unfamiliar faces. Importantly, however, familiar but not unfamiliar faces are recognized on the basis of robust representations stored in long-term memory (termed face recognition units [FRU] by Bruce and Young, see next paragraph) and provide identity-specific information, such as the person's occupation.

According to Bruce and Young (1986), at the first stage of recognition, faces are structurally encoded, a process which entails both a view-centred pictorial analysis potentially important for the perception of facial expression and speech (variant aspects of a face) as well as a viewpoint- and picture-independent analysis of the face physiognomy for processing relatively stable aspects of the face (i.e. identity).

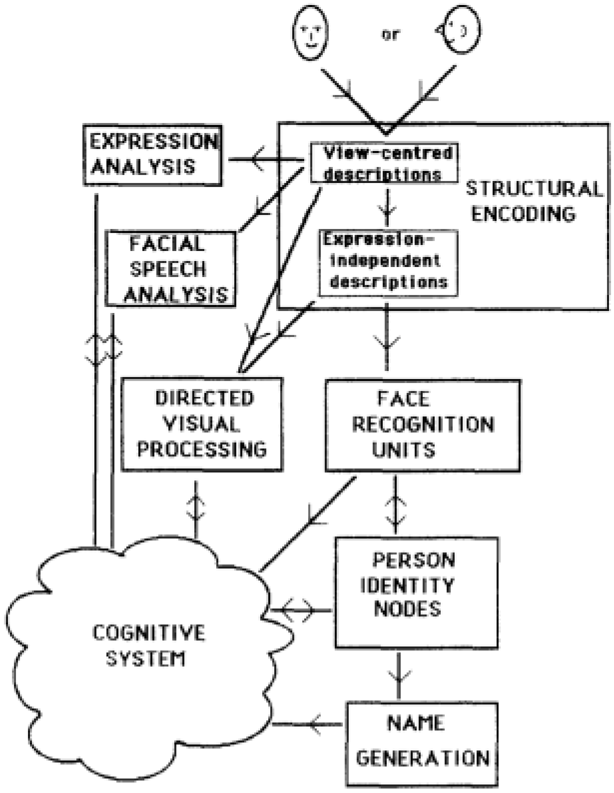

Figure 1. Schematic illustration of the model of face recognition proposed by Bruce and Young (1986).

The products of structural encoding are subsequently compared to stored perceptual representations, i.e. FRUs.In case of a match between information obtained from structural encoding and a familiar face (stored as a FRU), a corresponding person-identity node (PIN) will be activated and semantic information about the person becomes accessible. This, in turn, may enable the access to a person's name, which is thought to be stored separately from other semantic informtion.

Inspired by this model and integrating empirical evidence from human neuroimaging and evoked-potentials on face procesing, Haxby and colleagues (Haxby, Hoffman, & Gobbini, 2000) devised a neural model with a core system responsible for perceptual stages of face processing and an extended network for extracting meaning from processed faces (see Figure 2). The core system of face processing entails the bilateral fusiform gyri (FG) – when functionally defined often referred to as fusiform face area (FFA; e.g. Kanwisher, McDermott, & Chun, 1997), the bilateral superior temporal sulci (STS), and the bilateral inferior occipital gyri (IOG) – often referred to as occipital face area (OFA; Gauthier et al., 2000) when functionally defined.

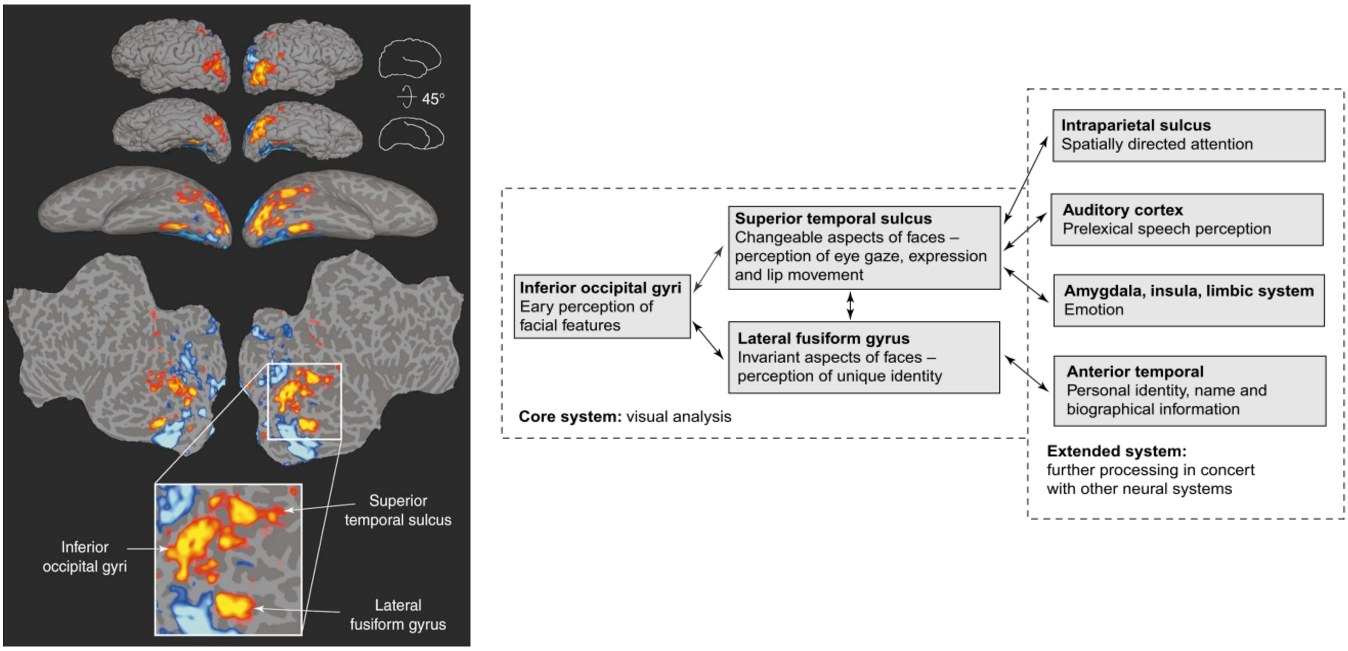

Figure 2. Left panel: Cortical regions (from a single subject) comprising the core system in the distributed network of human face perception (Haxby, Hofmann, & Gobbini, 2000). Right Panel: Illustration of the neural model of face perception proposed by Haxby et al. (2000), consisting of a core and an extended system.

It is assumed that initial processing of facial features takes place in the IOG. The results of this analysis are passed on in parallel to both STS and lateral FG areas. Variant aspects of a face (e.g. expression, facial movement) are thought to be processed by the STS, whereas invariant aspects related to identity perception are tied to the lateral FG areas. Moreover, the extended neural system consists of a variety of areas in the brain and is responsible for processing the meaning of the information obtained from visual analysis in the core system. For instance, it engages in processing emotional content via the amygdala and insula, and in the activation of person-related semantic information via regions in the anterior temporal lobes (Haxby et al., 2000).

For the present purpose, however, the Multidimensional Face Space Model (MFDS, see Figure 3) is the most important theoretical account as it explains processing and storing of *unfamiliar* faces (Valentine, 1991). The model rather vaguely assumes that physiognomic aspects (such as the shape of the eyes, nose and mouth, but also configural characteristics) of a face are represented as parameter values on multiple dimensions. Of note, more recent principal component analysis (PCA)-based approaches (see Burton, Jenkins, Hancock, & White, 2005; Burton, Jenkins, & Schweinberger, 2011) allow to extract specific dimensions, not only taking into account variation on dimensions *across* faces of different individuals, but also dimensions of variation *within* a single person. Importantly, these dimensions do not reflect isolated features or facial configurations, but rather reflect complex image characteristics which may not only vary due to short- or long-term changes (such as expression or age), but may be tied to superficial or low-level variations as well (e.g. camera position, lighting).

The norm-based coding model (based on the multidimensional space framework) assumes that faces are coded in an n-dimensional space as the deviation from a prototype or norm face located at the origin. A specific face is hence defined by the vector from the origin to the point at which the n-dimensional values for that face converge. With respect to recognition it is important to note that encoding is associated with some error or noise (e.g. due to difficult viewing conditions) which may result in attenuated confidence during recognition decisions, and hence lead to false recognition of a particular face. Thus, when a face is (re-)encountered, the model suggests that this face is compared to representations of previously encountered faces via the vectors that define the new and the known faces. Ultimate recognition success depends on the encoding error associated with a vector, and on the proximity of the vectors between the perceived face and an already stored face (i.e. the similarity of the two faces).

An exemplar-based model also described by Valentine (1991) differs from the norm-based model (Valentine, 1991) in two aspects: first, faces are considered to be coded as points/dots rather than vectors, and secondly, the exemplar-based model does not contain a face norm; instead, its origin is defined as the point of maximal exemplar density. Similarly to the norm-based model, recognition of a face is influenced by the error occurring during encoding, and the similarity between a perceived face and a stored representation. Both models claim to account for the effects of facial distinctiveness. Whereas the norm-based model explains superior recognition for distinct faces via the greater distances from the prototype (norm) of distinct versus typical faces, the exemplar-based model posits that distinct faces as opposed to typical faces are located in regions in which the density of dots representing faces is rather low (but see also Burton & Vokey, 1998, for critical considerations on arguments about densities and distances from the norm/prototype).

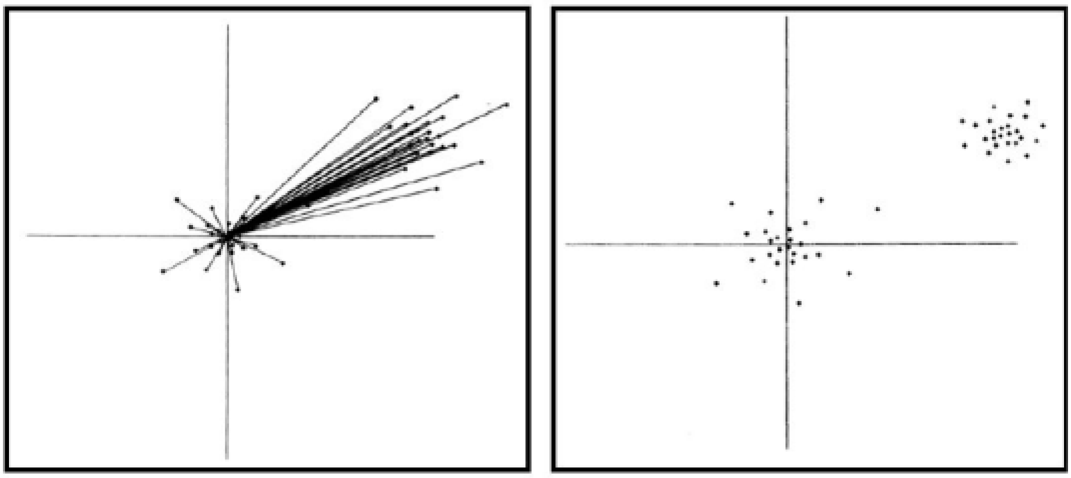

Figure 3. Schematic illustration of the norm-based (left panel) and exemplar-based (right panel) Multidimensional Face Space (Valentine & Endo, 1992).

Hence, distinct faces are easier and more accurate to recognize. Crucially for present purposes, it has been claimed that the MDFS serves to explain phenomena such as the own-race bias (ORB) and related phenomena, such as the own-age bias (OAB; Valentine & Endo, 1992). These phenomena, which are assumed to index expertise with different classes of faces and hence may be understood as reflecting the degree of specialization of our face processing system, are described in the following section.

3.1 The Own-Race and the Own-Age Bias in Face Recognition Memory – Role of Expertise

Visually-derivable semantics (see Bruce & Young, 1986), such as a person's race or age, have been found to influence recognition memory. The finding of more accurate memory for own- relative to other-race faces (own-race bias) was first described by Malpass and Kravitz (1969) and has since been addressed by a number of behavioral (for review, see

Meissner & Brigham, 2001), ERP (e.g. Herzmann, Willenbockel, Tanaka, & Curran, 2011; Lucas, Chiao, & Paller, 2011; Stahl, Wiese, & Schweinberger, 2008, 2010) and neuroimaging studies (Golby, Gabrieli, Chiao, & Eberhardt, 2001).

The ORB has been shown to develop during childhood, and in view of evidence that face processing becomes species-specific only after 6-12 month of age (Pascalis, de Haan, & Nelson, 2002), may reflect gradually increasing specialization of the face processing system during further development. While school-aged children show recognition advantages for own-race faces, younger children do not (Chance, Turner, & Goldstein, 1982). This developmental course of the ORB is in line with a perceptual learning account, stressing the importance of expertise with different classes of faces, as suggested by the MDFS (Valentine, 1991; Valentine & Endo, 1992). The space's dimensions are assumed result from personal experience, and are consequently optimized to represent those faces most often encountered, which in most cases will be own-race faces. Due to the lack of perceptual expertise with other-race faces, the face space's dimensions are not optimal to represent these other-group faces. Such faces are clustered more densely in the periphery of the face space (see Figure 3), resulting in less accurate recognition (Valentine & Endo, 1992).

Expertise-based accounts are supported by a study in which Asian adult participants who were adopted into French Caucasian families as children showed a memory bias for Caucasian but not for Asian faces, unlike a Korean control group which exhibited a memory advantage for Asian relative to Caucasian faces (Sangrigoli, Pallier, Argenti, Ventureyra, & de Schonen, 2005). A more recent study tested Asian children who had been adopted into Belgian families and had been living there for several years (6-14 years). Whereas age-matched controls showed a clear ORB, the adopted children did not exhibit a complete 'reversal' of the ORB, but recognition performance was comparable for Asian and Caucasian faces (de Heering, de Liedekerke, Deboni, & Rossion, 2010). These findings suggest that the face representational system can be shaped by multiple encounters or substantial experience with faces, at least when the face processing system has not yet fully evolved. This interpretation is in line with studies using multi-dimensional scaling approaches, yielding empirical evidence for separate and more densely clustered other- relative to own-race faces (Byatt & Rhodes, 2004; Papesh & Goldinger, 2010). Still, several years of expertise are apparently not sufficient for an entire reorganization of a face space which was initially tuned towards Asian faces. However, training babies between 6 and 9 months of age with other-race faces seems to prevent the emergence of the ORB. This was revealed by fixation preferences, which are thought to reflect recognition (Heron-Delaney et al., 2011). Of note, and as a qualification, the authors did not test a control group of babies without training; this, to some extent at least, limits their interpretation.

Data from training studies with adults suggests that the ORB may also be modifiable later in life. In a learning study over a few days (Tanaka & Pierce, 2009), recognition memory for other-race faces increased (numerically) from pre- to post-testing to a greater extent after training on the individual level (i.e. label other-race faces with names) compared to categorization training (categorization task: Hispanic vs. African American) . In a very similar study, this increase was additionally paralleled by a reduction in a measure of an implicit racial bias (Lebrecht, Pierce, Tarr, & Tanaka, 2009). The authors concluded that both perceptual and socio-cognitive factors (see below) shape the ORB in the first place.

The interplay of plasticity and stability of the face representational system also becomes apparent when addressing the own-age bias (OAB) – a potentially related phenomenon (Schweinberger & Wiese, 2011) which is less extensively investigated than the ORB (Wiese, Komes & Schweinberger, in press). In young adult participants, more accurate memory for own- than for other-age faces has been found relative consistently (e.g. Backman, 1991; Bartlett & Leslie, 1986; Harrison & Hole, 2009; Wolff, Wiese, & Schweinberger, 2012). Importantly, discrepant results exist regarding the occurrence of such an OAB in older adults. Some studies detected more accurate recognition of older relative to younger faces in older participants (e.g. Anastasi & Rhodes, 2005; Lamont, Stewart-Williams, & Podd, 2005), but others did not (Backman, 1991; Wiese, Schweinberger, & Hansen, 2008; for reviews, see also M. G. Rhodes & Anastasi, 2012; Wiese, Komes, & Schweinberger, in press). These findings, which may appear contradictory at first glance, have been explained with the MDFS model. Typically, in those studies in which no OAB was detected in older adults, it has been argued that, since older adults have been young in their past, their life-time experience gained with faces of different ages has shaped the face representational system. Dimensions are, thus, finely tuned for both young and older faces, resulting in no particular (dis-)advantage for younger or older faces (see e.g. Fulton & Bartlett, 1991; Valentine & Endo, 1992; Wiese et al., 2008; Wolff et al., 2012). Opposed to this explanation, studies that revealed an OAB in older participants stress the notion of face space plasticity, suggesting that more recent daily-life experience might substantially influence the dimensions of the face space. More specifically, in these studies it is usually argued that older adults' face spaces are optimized for older faces, since older adults preferentially tend to spend more time with people from their own- relative than other age groups (see He, Ebner, & Johnson, 2011). Hence, older adults encounter older faces more frequently than younger adults, which might lead to optimized coding and representation of older relative to younger faces, and consequently to an OAB. Evidence for an influence of daily-life contact that may shape the face space in young adults comes from a study that revealed a reversed bias, in terms of numerically better recognition memory for child- relative to own-age faces in a population of trainee teachers (Harrison & Hole, 2009). In a more recent study, geriatric nurses were reported to lack an OAB when tested with own- and older age faces (Wiese, Wolff, Steffens, & Schweinberger, 2013).

In sum, perceptual expertise seems a valid account for the emergence of face memory biases. Furthermore, it may also explain the presumably (limited) convertibility of the ORB and OAB due to training or differences in life-styles that bring about increased levels of contact to different categories of faces. However, it remains unclear as yet whether expertise may still shape the representational system in older adults and outweigh effects of aging. As outlined earlier, the cognitive architecture changes as a consequence of aging, and specific deficits seem to occur with respect to face processing (Boutet & Faubert, 2006) and face cognition (Hildebrandt et al., 2011). A generally reduced efficiency in face recognition may result in near-floor performance for both same- and other- age faces, thus prohibiting the occurrence of biases.

Expertise-based accounts do not exclusively explain memory biases with respect to differences in representation. Memory differences emerging from differential *perceptual processing* of other-group faces due to different degrees of expertise are considered in the next section.

3.2 Perceptual Processing Accounts and Own- versus Other-Group Faces

Perceptual processing accounts as a second sub-group of expertise-based models suggest that different degrees of experience with own- relative to other-group faces might affect the perceptual processing (rather than the representation) of these faces. Importantly, such differences in perceptual processing can explain later differences in memory performance. More specifically, holistic processing, which denotes the integration of facial features into a Gestalt, is considered a hallmark of human expertise with faces (Gauthier, Curran, Curby, & Collins, 2003) and has been found to be less efficient for other- relative to own-race faces. For instance, using the so-called part/whole task, Tanaka and colleagues (2004) demonstrated that the processing of facial parts when presented in the context of a whole face was more disrupted for Caucasian relative to Asian faces in Caucasian participants. The Asian participants tested in this study were living in North America and had gained life-long perceptual expertise with Caucasian faces. They exhibited no differences in measures of holistic processing between Asian and Caucasian faces (Tanaka, Kiefer, & Bukach, 2004). In a subsequent study (Michel, Rossion, Han, Chung, & Caldara, 2006), Asian and Caucasian participants were tested using the so-called composite face task (Young, Hellawell, & Hay, 1987) for unfamiliar faces. In this task, a probe face is composed of an upper and a lower part, which are either horizontally aligned or misaligned, and the participants are asked whether either the bottom or top half of a face (while ignoring the respective other part) matches the top or bottom part of a previously presented target face. Importantly, the other half of the probe face is always different from the target. This decision is more difficult, as indicated by decreased accuracies and/or longer mean response times, if the lower and upper parts of the probe face are aligned; in this case, the two parts are immediately merged into a Gestalt-like representation, and hence processed holistically. This hampers processing and matching of face parts, while misalignment of the two parts facilitates face part processing and matching, resulting in faster decisions. Michel and colleagues (2006) found that the decrease in accuracy in the aligned condition was apparent for own- but not for other-race faces in Caucasian participants, largely confirming the hypothesis of reduced holistic processing for other-race faces. In line with this finding, a significant relationship (r = .3) between holistic processing and the ORB was recently found using regression analysis (DeGutis, Mercado, Wilmer, & Rosenblatt, 2013). However, in the study by Michel and colleagues (2006), Asian participants showed a comparable misalignment effect for Asian and Caucasian faces, although the effect was numerically larger for own-race faces (for similar and related findings, see also Mondloch et al., 2010; Tanaka et al., 2004). The finding of overall differences in the extent of holistic processing in Asian versus Caucasian participants was addressed in a very recent study by Crookes and colleagues (2013). Their investigation on whether Chinese as opposed to Caucasian participants would generally rely more strongly on feature information indeed found showed a stronger reliance on holistic processing in Caucasian relative to Asian participants (Crookes, Favelle, & Hayward, 2013).

Furthermore, configural processing (often defined as the analysis of the metric distances between facial features) has been suggested to be more pronounced for faces of expertise, i.e. own-race faces. This was tested using face inversion, i.e. 180° rotation of a face, which is often assumed to disrupt configural processing and thus impede the recognition of inverted relative to upright faces (Maurer, Grand, & Mondloch, 2002; Yin, 1969). Inversion effects have been variably reported to be larger for own-race faces (e.g. Hancock & Rhodes, 2008), similar between own- and other-race faces (Buckout & Regan, 1988 cited after Michel et al., 2006), or even larger for other- relative to own-race faces (Valentine & Bruce, 1986). Similarly, feature-based processing has also been reported to be increased for own- relative to other-race faces (Hayward, Rhodes, & Schwaninger, 2008). In an extensive review of findings from different paradigms, Hayward and colleagues (in press) claim that greater expertise with own-race faces results in general benefits in face processing (configural, holistic, and feature-based).

The relationship between the OAB and holistic or configural processing has been less well investigated. Evidence for more pronounced holistic processing for faces of expertise comes from a study in which pre-school teachers (experts for child faces) were compared to child novices (non-expert group) on the composite face task (Kuefner, Cassia, Vescovo, & Picozzi, 2010). Whereas RTs (but not accuracies) yielded a misalignment advantage for adult versus child faces in non-experts, this composite effect was larger for child faces in the expert group. Of high relevance for the present thesis, younger and older adults were investigated with the composite face task using young and older adult composite faces in a very recent study (Wiese, Kachel, & Schweinberger, 2013). Both in younger and older adults, a composite face effect was revealed in accuracy and efficiency scores (but not in RTs) for young face stimuli only. This indicates a processing advantage for young faces irrespective of participant age and hence yields no support for the hypothesis that differences in holistic processing might underlie the OAB in recognition memory – at least in the adult age range.

With respect to configural processing, face inversion effects in delayed matching tasks have been shown to occur in young adult participants with very little or no experience with children when tested with own-age but not when tested with new-born faces (Kuefner, Cassia, Picozzi, & Bricolo, 2008, Experiment 1). This again suggests that configural processing for other-age faces is decreased. However, Kuefner and colleagues (2008) found a different pattern for child faces used as stimuli in a subsequent experiment (Experiment 2). Here, an inversion effect for both adult and child faces was clearly apparent in young adults both in accuracy and in RTs, though the accuracy effect was numerically larger for adult faces. Importantly, in a third experiment with pre-school teachers, no differences were found in measures of the inversion effect, once more supporting the role of expertise for the tuning of face processing mechanisms. In addition, and in line with this interpretation, accuracies in the matching task with upright faces were increased for young adult faces in both Experiment 1 and 2. Pre-school teachers, on the contrary, did not exhibit such a matching advantage for own-age relative to child faces. Measures of configural processing comparing younger and older faces in young and older observers have, to the best of my knowledge, not been published. Nonetheless, as described in the next paragraph, some studies have revealed age-related differences in holistic and configural processing.

Paralleling the developmental trajectory of fluid cognitive abilities, an increase in configural processing from childhood to young adulthood, followed by a decrease towards older age has been described (Schwarzer, Kretzer, Wimmer, & Jovanovic, 2010). Chaby and colleagues (2011) reported older adults' difficulties in processing configural information to be particularly related to the eye region (i.e. distance between eyes but not distance between eyes and mouth, for instance). Following up on this finding, Slessor, Riby, and Finnerty (2013) more directly tested whether decrements in the use of configural information might be related to specific face parts only. The authors argue that their findings suggest that decline in configural processing is specifically tied to the eye-region. However, this interpretation is limited in the sense that comparisons were made only between processing the eye and the mouth region. Studies addressing configural processing via behavioral measurements in older adults have been relatively scarce, although it has often been suggested that impairments in face recognition result from impaired perceptual processing of faces (for similar argument, see Daniel & Bentin, 2012).

In sum, the results suggest that decreased holistic and/or configural processing of other-group faces presumably relates to decreases in memory for these faces. From the studies reviewed above, this conclusion seems primarily based on the ORB, as less studies have examined perceptual processing for own- versus other-age faces. Importantly for present purposes, it seems that research is lacking on perceptual processing in participants of higher age. Age-related deficits in perceptual processing might interact with memory biases, given the evidence that such biases are influenced by the degree of holistic/configural processing of own- versus other-group faces. In other words: If the occurrence of a bias in face memory is related to the integrity of holistic/configural processing, age-related disruption of such processing may result in attenuated or absent memory biases in older adults. To my knowledge, no study has addressed this relationship systematically.

For the sake of completeness, an alternate class of accounts which claim to be able to explain the ORB and the OAB will be outlined in the next section. These are socio-cognitive approaches which have become more and more popular. However, for present purposes they are considered as less important than expertise accounts, since they are not mainly concerned with basic face processing mechanisms and therefore do not offer a straightforward account for age-related changes of such processes.

3.3 Socio-Cognitive Accounts and Own- versus Other-Group Faces

Initial socio-cognitive models assumed that an early categorization mechanism would determine the way own- and other-group faces are processed. The race-feature theory/feature selection hypothesis (Levin, 1996, 2000) and similarly the In-group/Out-group model (Sporer, 2001) proposed that, based on the presence versus absence of facial features diagnostic for ethnic group membership (e.g. eye shape for race, wrinkles for age information), faces are categorized as belonging to an in- or and out-group. Faces with features that are associated with an out-group can be subject to cognitive disregard. More precisely, for out-group faces, group-defining features are assumed to be coded at the expense of individuating, identity-diagnostic information, which in turn leads to less accurate memory representations for out-group faces (or increased recognition of own-group faces due to the processing of individuating information). Interestingly, this mechanism is assumed to manifest in higher accuracies and faster response times for out-group faces in visual search and categorization tasks. Of note, socio-cognitive accounts explicitly state that the lack of processing out-group faces in an individuating manner is not due to inability, but that categorical processing based on facial features simply represents the default mode for other-group faces (see also Levin, 2000).

More recently, Hugenberg, Young, Bernstein, and Sacco (2010) enunciated the Categorization- Individuation Model (CIM) and suggested that different co-active cues drive selective attention processing of category- versus identity-diagnostic facial features, causing memory biases. At the initial stage when a face is encountered, social category information is spontaneously activated, leading to stronger processing of category-diagnostic facial characteristics of other-group faces. The focus on those characteristics shared by different exemplars of a certain out-group makes confusions among target faces more prevalent and is a contributing factor to memory biases, such as the ORB/OAB. In addition, the CIM assumes that motivation to individuate faces is generally higher for in- versus out-group faces. This motivation is an additional factor potentially affecting memory. Moreover, situational cues may alter the processing, or at least redirect attention to identity information, of a specific out-group face when that face is of high social relevance for the observer. The latter two points may also serve as a starting point to modify processing of other-group faces by manipulating the motivation of the viewer and/or the social relevance of the face (which are presumably per se interacting factors), hence modifying memory biases. Finally, the model explicitly states that expertise in individuating out-group faces is an additional factor that plays a role for the occurrence of memory biases. Nonetheless, individuation highly depends on the viewer's motivation.

The CIM originated from findings in studies in which own-race and own-age face stimuli were arbitrarily assigned to a social in- or out-group, for instance according to university affiliation or via a minimal group design based on fake personality types (Bernstein, Young, & Hugenberg, 2007). Participants exhibited increased memory for the respective in- relative to out-group faces. Based on these findings, the Hugenberg group initially claimed that the Categorization/Individuation Model would account for memory differences between own- and other-race faces and defined the ORB as a mere in-group bias.

The hypothesis that memory biases should be reduced or even abolished if participants were sufficiently motivated to individualize out-group faces was supported in a subsequent study on the ORB. Participants were informed about the ORB prior to the experiment, and were instructed to avoid categorical processing by focusing on unique characteristics in the faces. As predicted, the ORB was reduced in the informed condition (Hugenberg, Miller, & Claypool, 2007; Experiment 1a and b). Interestingly, however, in a subsequent experiment in which participants were again informed about the ORB and instructed to try very hard to remember the faces but not told to individualize them, they clearly exhibited an ORB (numerically even larger relative to the control condition in which participants were only instructed to memorize the faces for later testing). Similarly, G. Rhodes, Locke, Ewing, and Evangelista (2009) found that encoding instructions related to race membership or race typicality did increase rather than abolish the ORB. Elimination of the effect was again only successful when instructing participants to individuate other-race faces. Based on these findings it seems somewhat inadequate to postulate that motivation per se can abolish the ORB – rather, the instruction to rely on individualization when processing other-race faces acts as a critical parameter influencing the effect.

Socio-cognitive accounts could be transferred to the OAB. However, the inconsistent occurrence of the OAB in older adults is hard to reconcile with the core assumptions of these accounts, which would suggest that older adults should generally recognize older versus younger faces more accurately (provided that older adults perceive younger adults as an out-group). Moreover, even regarding young adult participants, a recent study suggested that the

OAB is no pure in-group bias: Young adult participants (18-30 years of age) remembered young middle-age faces (30-45 years of age), formally out-group faces, just as well as faces of their own-age group (Wolff et al., 2012). However, it merits comment that sometimes the learning phase data, and more specifically the finding of faster age categorization of older faces in young adults (Wiese et al., 2008), is in line with the assumption of categorical processing of other-group faces (see also Levin, 2000).

In sum, the behavioral results reviewed so far support both a representation and a processing account of the perceptual learning hypothesis to explain the ORB and the OAB. Besides, although research from socio-cognitive approaches claims to point towards a role of motivational aspects for memory biases in general, there is relatively weak supporting evidence, especially with respect to the OAB, in part due to a lack of studies.

3.4 Neurophysiological and Brain Imaging Correlates of Face Processing

As noted earlier, in contrast to behavioral results, ERPs provide the opportunity to more directly assess and potentially disentangle sub-processes that mediate effects such as the OAB and ORB, as well as age-related changes in processing facial race or age. Before I turn to the ERP section, a brief, non-exhaustive overview of findings from related neuroimaging studies will be provided in the next paragraph.

3.4.1 Brain Imaging Studies on the ORB and OAB

Golby and co-workers (2001) published a seminal fMRI study reporting brain imaging results on the own-race bias. The authors examined European-American and African-American participants in a face recognition paradigm using European-American and African-American stimuli. Increased activation for own-race faces in the FFA was found during encoding in both groups of participants. Moreover, greater activation in the *left* FFA for own-race faces during encoding was correlated with the subsequent behavioral own-race bias. The authors suggested that these results reflect the interplay of individualization and categorization processes within FFA, as a result of differences in perceptual expertise due to long-term exposure differences to own- versus other-race faces.

No corresponding study exists on the OAB – however, other fMRI work has investigated processing differences between own-age and other-age faces, but did not assess memory correlates (Ebner, Gluth, et al., 2011; Ebner et al., 2013; Wright et al., 2008). Greater activity in medial prefrontal cortex (anterior cingulate) for own-age faces was reported in both young and older adults and interpreted as reflecting greater similarity to the self, and personal interest in those faces (Ebner, Gluth, et al., 2011). This finding was replicated in a very recent study (Ebner et al., 2013) in which enhanced activation for own-age faces was further reported in insular regions, suggestive of positive affinitive feelings while processing own-age faces. In that same study, similar to a previous investigation by Wright and colleagues (2008), stronger amygdala responses for own-age faces were observed in older adults. This finding was interpreted to reflect increased importance of own-age faces (Ebner et al., 2013; Wright et al., 2008), with age being a particular salient feature for older adults (Ebner et al., 2013). In sum, it remains unclear as yet whether the ORB and OAB rely on similar patterns of brain activation.

3.4.2 Brain Imaging Studies on Age-Related Changes of Face Processing

Regarding the question which neural mechanisms determine differences in face perception between young and older adults, it has been proposed that activations in occipital cortex (Grady et al., 1994) and ventral visual cortex (D. C. Park & Reuter-Lorenz, 2009) become less specific with older age. Lee, Grady, Habak, Wilson, and Moscovitch (2011) used fMRI adaptation and revealed the strongest adaptation effect in FFA during blocks of same-view repetitions of the same face in younger adults - this effect was absent in the older adults. Further analysis, however, revealed greater activation in left FFA and left middle occipital, frontal and parietal areas for older as compared to younger adults, indicating notable differences in neural processing. Furthermore, face-matching performance correlated with activations in a network of left occipital, parietal and frontal areas in older but not in younger adults. This was interpreted as a mechanism directed at compensating for neural decline in face-sensitive occipital areas (Lee et al., 2011), in line with studies reporting shifts in functional activity towards more bilateral (for review, see Cabeza, 2002) or anterior activation (Davis, Dennis, Daselaar, Fleck, & Cabeza, 2008). A recent study (Burianova, Lee, Grady, & Moscovitch, in press) replicated the finding of age-related reductions in face specific brain regions. Further the results revealed age-related differences in functional connectivity of the neural face processing network. Right and left FG were functionally connected in young, but not in older adults. Instead older adults showed functional connectivity between right FG and the left orbitofrontal cortex. Activity in this latter region was also positively correlated with face-matching performance (outside the scanner) in older but not in younger adults.

Burianova and colleagues (in press) concluded that this frontotemporal connection might compensate for the loss of functional connectivity between fusiform gyri in older adults.

3.4.3 ERP Findings on Face Processing

The section contains descriptions of different ERP components relevant for face processing. More specifically, I will outline how the components are tied to processing of facial race and age, followed by a discussion of age-related alterations on the respective components.

P1. The first ERP component of interest in face processing is usually the P1 or P100 – a positive deflection peaking around 100 ms after stimulus onset over occipital areas. The P1 has been shown to be sensitive to low-level stimulus characteristics such as contrast, luminance or spatial frequency and to reflect early visual processing (see Luck, 2005). However, the P1 may also be influenced by top-down processes, such as spatial attention (Hillyard, Vogel, & Luck, 1998). Although the P1 reflects early visual processing, its generators are clearly not in the primary visual cortex (striate cortex, V1 or Brodmann´s area 17). Rather, the P1 is generated in extrastriate visual cortex, with a prominent contribution of areas 18 and 19 (e.g. Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2002; see also Di Russo et al., 2012).

Although it has been argued that P1 might possess a particular role for face compared to object processing (Itier & Taylor, 2002) involving even early configural processing (Itier & Taylor, 2004), modulations of P1 amplitude or latency are most probably elicited by uncontrolled low-level characteristics (see e.g. Jacques & Rossion, 2007, 2009; Rossion & Jacques, 2008). This latter point may be a reason for a number of inconsistent results in the literature. With respect to facial ethnicity or age, P1 seems inconsistently affected by these factors. Some studies have detected amplitude modulations by facial race (e.g. Stahl et al., 2010; Wiese, 2012), but others have not (e.g. Montalan et al., 2013; Stahl et al., 2008). Moreover, larger P1 amplitudes have been observed in response to child faces as compared to adult and older adult faces (Melinder, Gredeback, Westerlund, & Nelson, 2010), but no such difference was found between young adult and older adult faces (Melinder et al., 2010; Wiese et al., 2008; see also Wolff et al., 2012).

When P1 elicited by face stimuli was compared comparatively in participant groups of different age, P1 was decreased but not delayed in older adults (Pfütze, Sommer, &

Schweinberger, 2002; Wiese et al., 2008; Wolff et al., 2012). Of note, when tested with flicker fields, checker board patterns or sinusoidal grating patterns, older adults yielded modulations, typically in terms of decreased and delayed P1 amplitudes (e.g. Bobak, Bodiswollner, Guillory, & Anderson, 1989; Celesia, Kaufman, & Cone, 1987; Porciatti, Burr, Morrone, & Fiorentini, 1992) most likely due to decrements in primary visual cortex. These are suggested to at least partially account for visual deficits that cannot be explained by changes in the optical system alone (for review, see Spear, 1993).

N170. This negative deflection peaking over occipito-temporal areas around 170 ms after stimulus onset is probably the most extensively investigated ERP component in the area of face processing. Although visual stimuli in general elicit an N170-like response (also referred to as N1), its amplitude is reduced for non-face stimuli relative to faces (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Schweinberger & Burton, 2003). Some researchers claim that the N170 is face-specific (e.g. Carmel & Bentin, 2002) while others relate differences in N170 responses to enhanced expertise with faces compared to other objects (e.g. Gauthier et al., 2003). Thierry and colleagues (2007) suggested that N170 merely reflects the larger perceptual homogeneity typically found in sets of face stimuli relative to greater variance in sets of other object categories (Thierry, Martin, Downing, & Pegna, 2007), but this claim has been convincingly refuted (Bentin et al., 2007).

Several studies using the inversion and composite face effect revealed that the disruption of holistic and configural processing manifests in increased and/or delayed N170s (e.g. Eimer, 2000; Itier & Taylor, 2002; Jacques & Rossion, 2010; but see Vizioli, Foreman, Rousselet, & Caldara, 2010). Hence, N170 is generally thought to reflect structural encoding of a face (Bentin et al., 1996; Eimer, 2011), which may include the detection of a face-like pattern, and holistic and configural processing (for a more detailed description of these processes, see Maurer et al., 2002). At this point, the inconsistency of interpretations regarding N170 appear noteworthy: as yet it is not completely clear how the possible conflict between relating a large N170 response (to upright faces compared to objects) to configural processing in structural encoding, and relating an even larger N170 (to inverted compared to upright faces) to a disruption of configural processing can be reconciled (for a possible resolution of this conflict, see Itier, Alain, Sedore, & McIntosh, 2007).

Importantly in the light of current purposes, increased N170 amplitudes have also been observed for other-race faces (e.g. Caharel et al., 2011; Stahl et al., 2010) suggesting reduced configural/holistic processing of these faces. Furthermore, in a recent study with European and Asian participants (Wiese, Kaufmann, & Schweinberger, 2013), this N170 ethnicity effect was observed in both groups. Importantly, N170 differences during learning significantly correlated with a later memory advantage for own-race faces at test. Consequently, the authors interpreted this finding as hinting at a direct relationship between less efficient encoding of other-race faces and a lack of experience resulting in decreased memory for these faces.

With respect to facial age, the situation is different: Older faces generally elicit larger N170 amplitudes than young adult faces (Ebner, He, Fichtenholtz, McCarthy, & Johnson, 2011; Wiese et al., 2008) in both young and older participants (Wiese et al., 2008). Similarly, a larger N170 misalignment effect for young relative to older faces was recently reported in both younger and older adults (Wiese, Kachel, et al., 2013). These findings argue for less efficient processing of older faces independent of participant age. Hence, increases in N170 for old faces cannot be directly related to the OAB in face recognition (see also Wiese, Komes, et al., in press).

In accordance with the neuroimaging data of decreased specificity of the face processing system mentioned above, Rousselet et al. (2009) varied the extent of face information embedded in noise and found a significantly larger N170 response to pure noise in older relative to younger adults. The authors conclude that older adults' face processing system becomes less finely tuned towards faces than the system in younger adults. At variance with this finding, two studies found N170 to be similarly sensitive towards faces when compared to other objects in young and older adults (Daniel & Bentin, 2012; Gao et al., 2009; see Fig. 4 below). These studies also investigated age effects on configural and holistic processing. Effects of face inversion were reported in terms of a delayed (Gao et al., 2009) but not increased N170 in older adults (Daniel & Bentin, 2012; Gao et al., 2009), which may prompt the idea of less efficient configural/holistic processing in the elderly. Moreover, these reports stress a difference regarding the lateralization of N170 between groups: whereas in younger adults the component was clearly right-lateralized, a more bilatral N170 was found in the older participants (Daniel & Bentin, 2012; Gao et al., 2009; see Figure 4). Daniel and Bentin (2012) speculated that this finding might result from neuro-cognitive re-organization, presumably directed at counteracting age-related decline (see also Cabeza, 2002; Reuter-Lorenz & Park, 2010).

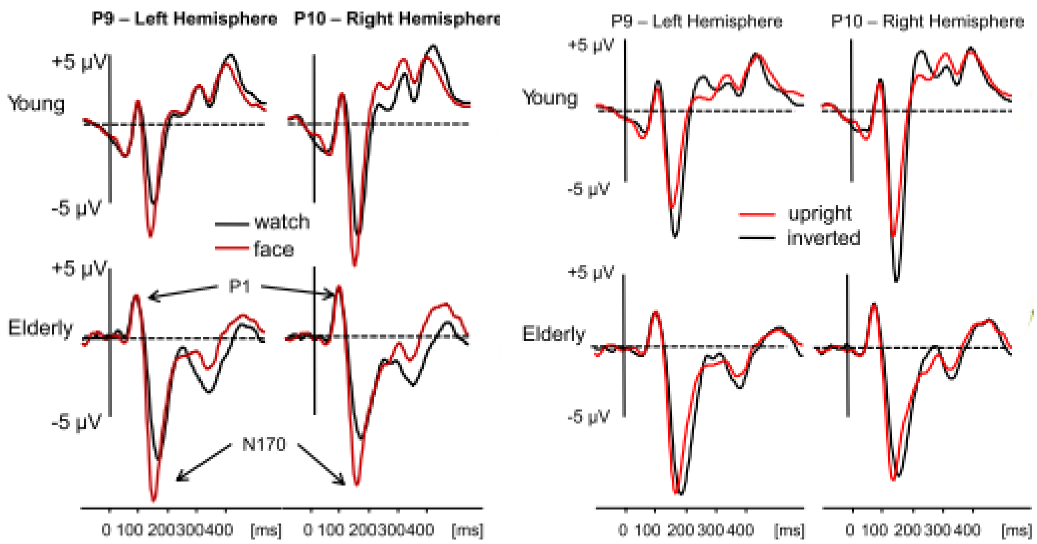

Figure 4. Left panel: N170-category effects (watch vs. face) in younger and older adults. Right panel: Inversion effects in young adults and lack of such effect in older adults. Note the more bilateral pattern of N170 in the elderly (Daniel and Bentin, 2010).

In sum, the N170 is of great interest for the current thesis, as it was previously related to the ORB in face recognition in young participants, implying that the ORB is strongly tied to early perceptual processing. However, as relatively little is known about the influence of facial race on older adults' memory, it is unclear whether similar effects would be found in the N170 of older adults. Moreover, and as outlined before, if configural/holistic processing is decreased in older adults, but necessary to elicit memory biases in general and the ORB in particular, this would prompt the hypothesis that the effect may be attenuated or even absent in older adults. To date, no published ERP study has directly tested the relationship of age-related changes on N170 and the own-race bias in older participants. Besides, our knowledge regarding the mechanisms underlying age-related changes in face perception and memory is relatively scarce and the (functional) significance of a more bilateral N170 in older adults remains unaddressed.

P2/P200. This positive-going deflection at occipito-temporal sites following N170 and peaking 200-250 ms after stimulus onset has received relatively little attention so far. Face researchers suggest P2 to be sensitive to (second-order) configural information and to reflect later stages of structural encoding (Latinus & Taylor, 2006). For instance, increased P2 amplitudes have been reported for vertically stretched as compared to normal faces (Halit, de Haan, & Johnson, 2000) and for changes in metric distances between facial features compared to changes in facial features themselves (Mercure, Dick, & Johnson, 2008).

With respect to stimulus modulations, Stahl and colleagues (2008) tested a group of experts for other-race (Asian) faces and a non-expert control group. Although the two groups did not differ with respect to performance (both groups exhibited an equivalent behavioral ORB), expertise-related differences were detected in the occipito-temporal P2 component at test. Caucasian faces elicited more positive amplitudes than Asian faces in controls but not in experts. These results were interpreted as revealing differential processing of own-versus other-race faces in non-experts. P2 has also been shown to be more positive for own-race faces in two subsequent studies (Stahl et al., 2008, 2010; Wiese, Kaufmann, & Schweinberger, in press) and for young faces in both young and old participants (Wiese et al., 2008). Furthermore, veridical relative to spatially caricatured faces elicit more positive P2 amplitudes (Kaufmann & Schweinberger, 2008), whereas spatially anti-caricatured faces elicited even larger P2 responses (Schulz, Kaufmann, Walther, & Schweinberger, 2012). This suggests that P2 may reflect the perceived typicality of a face (see also Wolff et al., 2012). With respect to effects of aging on this component, Wiese and colleagues (2008) observed generally reduced P2 amplitudes in older as compared to younger adults, and Wolff and colleagues (2012) reported smaller amplitudes in middle-aged as compared to young adults. However, the functional significance of these changes remains unclear.

In sum, the P2 could be a promising component for understanding how memory biases may be affected by differences in later stages of perceptual processing, and perhaps in the encoding of second-order configural information in particular. Based on the described findings, P2 seems more closely related to the ORB than to the OAB.

N250/N250r. Following P2, the N250(r) usually peaks around 230-330 ms at inferior temporal regions and yields more negative amplitudes for repeated as compared to non-repeated faces (e.g. Henson et al., 2003; Schweinberger, Pfütze, & Sommer, 1995). The N250r (r for repetition) is usually tested in immediate repetition paradigms and may be related to the activation of facial representations (FRUs, see above; Schweinberger et al., 1995; Schweinberger, Pickering, Burton, & Kaufmann, 2002). Of note, whereas FRUs have been suggested to be image-independent representations of a person, N250r modulations are reduced when different images of a face are used (Schweinberger, Pickering, Jentzsch, Burton, & Kaufmann, 2002)

In addition, N250 effects may be involved in face learning (Tanaka, Curran, Porterfield, & Collins, 2006). Importantly, N250 has been shown to build up over blocks along with improved perceptual representations due to face learning, even when tested with novel images of the learned identities (Kaufmann, Schweinberger, & Burton, 2009). Tanaka and Pierce (2009) reported N250 effects for other-race faces after training participants to individuate these faces, while no such effects were apparent after categorization training. Importantly, N250 effects accompanied improved recognition of novel (untrained) other-race faces, leading the authors to conclude that N250 at least partially indexes the degree of expertise with a class of faces. Potentially related to this, effects of face category have been found to correlate with the behavioral ORB in both Caucasian and Asian participants, with more negative amplitudes for other-race compared to own-race faces (Wiese et al., in press). Notably, N250 effects in these two latter studies are somewhat contradictory. Tanaka and Pierce (2009) reported more negative amplitudes for those faces with which participants had more (experimentally induced) individuating experience, whereas Wiese and colleagues (in press) found those faces of (natural) expertise to elicit more positive amplitudes.

In a study examining episodic memory, more negative amplitudes for hits (correctly remembered items) relative to correctly rejected new items (CRs) were observed only for own-age faces in young participants, but no corresponding effect was found in older adults (Wiese et al., 2008). Interestingly, in this latter study, the pattern in N250 paralleled the behavioral effects: whereas older adults did not show an OAB, enhanced recognition for own-age faces was clearly exhibited in the younger group. The authors argued that the effect in the N250 time range might be a neural correlate of the OAB, presumably reflecting facilitated access of perceptual representations of newly learned own-age faces during retrieval from memory. Recently, Wiese and colleagues (2013) also reported a larger misalignment effect for own- relative to other-age faces in young but not in older adults. The authors suggested that this is an indication of more efficient holistic processing for own-age faces in young adults which may underlie their OAB in recognition memory.

In sum, the N250 time range presumably entails a number of different and yet related processes that are of high relevance for present purposes. For instance, N250 category effects (i.e. differences between own- and other-group faces) are well in line with a perceptual learning account. N250 effects may reflect more efficient coding of own- vs. other- group faces, in line with the idea of a processing or representational advantage due to perceptual learning (Tanaka & Pierce, 2009; Wiese, Kaufmann, et al., in press). It may also be related to learning and memory, e.g. the difference between hits and CRs. Here, N250 might index enhanced access to representations and more accurate memory retrieval for own- vs. other-age faces (Wiese et al., 2008), suggesting that the OAB is tied to representational stages. In older relative to younger adult participants, N250 has been reported to be delayed in an immediate repetition paradigm (Pfütze et al., 2002). Apart from these studies, very little is known to date about N250 effects in older adults.

LPC and Old/New Effects. A positive-going deflection at about 400 ms with a centro-parietal scalp distribution often referred to as late positive complex (LPC) is thought to index post-perceptual processes. In an odd-ball paradigm, Ito and Urland (2003) reported more positive amplitudes for own-race relative to other-race faces, but a reversed effect in a subsequent study (Ito, Thompson, & Cacioppo, 2004). Similarly to the latter finding, Stahl and colleagues (2010) reported more positive amplitudes for other-race faces (in a categorization but not in an individuation task), and Ebner and co-workers (2011) found older faces to elicit more positive amplitudes than young faces in young participants. These findings were interpreted as reflecting either intentional or spontaneous activation of stimulus-related evaluations (e.g. stereotypes) or more controlled processing of other-group faces (Ebner, He, et al., 2011).

More important for this thesis are episodic memory effects. Whereas an LPC occurs during memory encoding in learning phases of a recognition memory paradigm, old/new effects emerge during retrieval from memory in the test phases. A large number of studies consistently found that hits evoke more positive amplitudes than CRs or misses between approximately 500 ms and 800 ms with a left parietal scalp distribution, at least for verbal material (for review, see Rugg & Curran, 2007). This (late) left parietal old/new effect is relatively uniformly assumed to index recollection, rather than familiarity (Rugg & Curran, 2007; Hayes & Verfaellie, 2012). As described above (section 2.2), most dual-process models of recognition memory (see e.g. Mandler, 2008; Yonelinas, 1999) assume that recollection is a controlled, relatively slow and conscious process which involves remembering the study phase or contextual details. Vilberg, Moosavi, and Rugg (2006) could show that the amount of additional information retrieved (e.g. when or where an item was encountered) is positively associated with greater and more widespread old/new effects. In contrast to recollection, familiarity is a rather fast-acting automatic process resulting in a 'feeling of knowing', without recall of source or context details of an episode (Mandler, 1980; Yonelinas, 2002). Familiarity is assumed to manifest in an earlier old/new effect with a mid-frontal maximum around 300-500 ms (e.g. Curran, 2000), sometimes also referred to as FN400 (Paller, Voss, & Boehm, 2007). However, others suggested that the early old/new effect is not related to familiarity in general, but only when conceptual implicit memory co-varies with familiarity (Paller, Lucas, & Voss, 2012). Hence, stimuli that are conceptually similar (or sometimes perceptually similar, see e.g. Groh-Bordin, Zimmer, & Ecker, 2006) to an item which has been previously encountered - without explicitly recognizing it - are supposed to elicit an FN400 effect (Paller et al., 2007). Incidentally, this effect is often also paralleled by perceived enhanced familiarity of these items. However, the authors (Paller et al., 2012; Paller et al., 2007) clearly argue that the FN400 is a marker of conceptual priming processes and not of explicit familiarity.

Although interpretations of old/new effects in terms of reflecting recollection and familiarity have recently been challenged for face stimuli (MacKenzie & Donaldson, 2007), more pronounced old/new effects in a time window from 400 ms to 800 ms for own- relative to other-race faces have also been found in an individuation learning condition, but not during categorization (Stahl et al., 2010). This finding was interpreted as indexing a larger amount of information retrieved from the study phase for own-age faces in this group, though a behavioral bias was apparent in both conditions. Hence, the later old/new effect in this study most probably cannot underlie the ORB reflecting different numbers of remembered versus forgotten own- and other-race faces. At some variance with this result, a more recent study reported very typical parietal old/new effects for own-race faces in both Caucasian and Chinese participants, whereas old/new effects for corresponding other-race faces were found in a prolonged late frontal effect that was believed to index stronger engagement in retrieval monitoring (Herzmann et al., 2011).

Old/new effects may also underlie the OAB. Enhanced parietal old/new effects for young relative to old faces (presumably recollection-based) were observed in young participants who exhibited a behavioral OAB, but not in older adults who did not show a corresponding effect (Wiese, 2012; Wiese et al., 2008). However, it remains unclear whether the lack of greater old/new effects for own-age faces in older participants is indeed related to similar memory for young and old faces, since parietal old/new effects are often decreased or diminished in older adults (which might be related to an overall trend towards more frontal scalp topographies for late parietal components, see Friedman, Kazmerski, & Fabiani, 1997), paralleling general overall memory decline and recollection deficits in particular (Friedman, 2003, 2013; Friedman, de Chastelaine, Nessler, & Malcolm, 2010).

In sum, memory biases may co-vary with episodic memory effects in ERPs, at least in younger participants. Due to the severe decline in episodic memory in older adults, differential effects on the relationship between old/new effects and memory biases merit further examination.

3.5 Summary and Aim of the Present Studies

To summarize, there is strong evidence that face memory biases are related to expertise, and hence to the fine-tuning of the face perception system. It seems that compared to the OAB, the ORB is more strongly related to specialized mechanisms in early stages of face processing, given the relatively consistent findings of ethnicity effects in N170 amplitudes (Caharel et al., 2011; Stahl et al., 2010; Wiese, Kaufmann, et al., in press). By contrast, larger N170 amplitudes for old faces have only been found independent of participant age (Ebner, He, et al., 2011; Wiese, Kachel, et al., 2013; Wiese et al., 2008), which suggests that the OAB is not related to early perceptual processing stages. The effect might rather be tied to representational tuning, as indexed by more pronounced repetition or old/new effects for own- relative to other-age faces in the N250 time window (Wiese, Kachel, et al., 2013; Wiese et al., 2008). These findings are indicative of more efficient access to own-age facial representations than to those of other age groups (Wiese et al., 2008; Wolff et al., 2012). Analogous findings have not been reported in studies on the ORB.

Based on those insights, face memory biases seem a promising tool for investigating age-related changes in the fine-tuning of face perception and memory. Previous research clearly argues for specific face processing deficits independent of general cognitive decline, (Hildebrandt et al., 2011), but only little is known about the exact locus of those deficits.

Furthermore, the literature presented above suggests a lack of investigations about the occurrence of the ORB in older adults (for an initial behavioral demonstration of an ORB in older adults, see Wallis, Lipp, & Vanman, 2012). Importantly, the lack of an effect that is thought to develop as an index of perceptual specialization for own- versus other-race faces could be interpreted as indicating less differentiated processing mechanisms in older adults. There is some evidence that face processing inefficiency might be the cause of reduced face memory in older adults (e.g. Chaby et al., 2011), and this might be related to the finding that the N170 is often larger in older as compared to younger adults (e.g. Gao et al., 2009; Wiese et al., 2008). However, to the best of my knowledge, no study has systematically tested the link between face memory and early face processing in older adults. Moreover, although two studies have speculated about the functional significance of a less lateralized N170 in older adults as indexing a compensatory mechanism (Daniel & Bentin, 2012; Gao et al., 2009), again there is no study that has directly tested this assumption. The first experiment described in this thesis (Experiment 1) is designed to close these gaps: This study will address effects of aging on early stages of face processing by examining the ORB using event-related potentials in older participants who differ with respect to memory performance.

As the OAB appears to primarily depend on the tuning of the face representational system, this effect can be exploited to determine whether this system becomes less flexible with increasing age or whether it can adapt to environmental demands due to more recent contact to own-age persons. As stated above, older adults inconsistently exhibit an OAB (for review, see Wiese, Komes, et al., in press), which may relate to differences in contact to own- versus other-age persons. However, no study has directly tested whether differences in life-long perceptual learning versus recent contact shape the OAB. Effects of recent contact would be in line with the idea of a more flexible face representation system even in older age. Evidence for this idea so far comes only from studies on young or young middle-aged experts who display reduced own-age biases (Harrison & Hole, 2009; Wiese, Wolff, et al., 2013). No study has taken age-related differences in face recognition into account, despite the fact that such differences could have implications for a potential plasticity of the face space. Furthermore, it is unclear which neural mechanisms would underlie a behavioral OAB in older adults, or how cognitive and brain aging would interact with potential differences in neural representations of own- versus other-age faces. Hence, Experiment 2 sets out to close this gap and focuses on the OAB as a potential index of representational specialization. It compares ERPs in two groups of older adults who differed in the amount of contact towards own-age persons.

In the following chapters 4 and 5, Experiments 1 and 2 will be described, which were conducted to examine

(1a) whether poor face memory in older age is accompanied by reduced expertise-based specialization of face processing, manifested in a reduced or absent behavioral ORB and/or in modulations of the N170 ethnicity effect;

(1b) whether differential memory performance in older adults is associated with differences in efficiency of early perceptual processing, indexed by group differences in N170 amplitude;

(1c) whether a more bilateral pattern of N170 occurs in aging, due to neuro-cognitive compensation, dedifferentiation, or both;

(2a) whether the face representational system exhibits age-preserved plasticity, manifested in a behavioral OAB shaped by more recent contact with own-age individuals;

(2b) whether effects of more recent contact affect neural correlates of face memory differentially for older adults with high amounts of contact with own-age persons (potentially exhibiting a behavioral OAB) and for low contact participants (potentially lacking a behavioral OAB);

(2c) whether a (potential) OAB is differentially reflected in neural correlates related to face representations and face memory for young participants and for those older participants who show a behavioral effect due to cognitive and brain aging.

4. Experiment 1: The ORB in High- and Low-Performing Older Adults

Abstract

Humans more accurately remember faces of their own-ethnic group, when compared to other-race faces. Event-related brain potential correlates of this own-race bias were assessed in two groups of high- and low performing older adults (mean age = 69 years; N = 24 per group), to investigate whether poor face memory in older age is accompanied by reduced expertise-based specialization of face processing. Intriguingly, both older groups demonstrated an equivalent pattern of a behavioral own-race bias, and a parallel increase in N170 for other-race faces. Group differences only emerged independent of face ethnicity: whereas low-performers exhibited a right-lateralized N170, high-performers showed a more bilateral response, suggestive of a neural mechanism compensating for age-related decline by recruiting additional resources. Overall, the results demonstrate that even a less efficient face processing system in older adults can exhibit preserved expertise-related specialization towards own-race faces.

4.1 Introduction

During aging, the human brain undergoes various changes in structure, function and neural transmission (e.g. Raz et al., 2005; Sowell et al., 2003). These alterations most probably underlie, and certainly covary with cognitive functioning (Cabeza et al., 2004; Dennis & Cabeza, 2008; Nyberg, Lovden, Riklund, Lindenberger, & Backman, 2012). During childhood, the interaction of maturation, experience and learning results in cortical differentiation (for review, see M. H. Johnson, 2001; Scherf, Behrmann, Humphreys, & Luna, 2007), which is paralleled by more fine-grained cognitive abilities (S. C. Li et al., 2004; Werkle-Bergner, Shing, Mueller, Li, & Lindenberger, 2009) This pattern reverses during older age, when senescent changes include cognitive and sensorimotor dedifferentiation (Baltes & Lindenberger, 1997; Lindenberger & Baltes, 1994; Lindenberger, Scherer, & Baltes, 2001) and diminished cortical specialization (D. C. Park et al., 2004; J. Park et al., 2012).

Notably, age-related alterations and their putative consequences can be very diverse, and within-cohort differences can be similarly pronounced as between-cohort differences

(Salthouse, 2013). More specifically, while some older adults show decreased performance in memory and executive processes (Anderson & Craik, 2000), others maintain high levels of functioning, and match (Cabeza, Anderson, Locantore, & McIntosh, 2002; Duarte et al., 2006; Friedman et al., 2010) or even outperform their younger counterparts (Christensen et al., 1999; Federmeier, Kutas, & Schul, 2010; Henry, MacLeod, Phillips, & Crawford, 2004). Results from functional brain imaging suggest that different processes in the aging brain could mediate such performance differences: First, reduced activations of memory-related brain regions were found in older adults with poor performance (for overview, see Grady, 2008). Second, increased activations in older participants were observed in prefrontal areas contralateral to those usually activated in younger adults (for review, see Cabeza, 2002; D. C. Park & Reuter-Lorenz, 2009; Reuter-Lorenz & Park, 2010). Importantly, these latter findings were interpreted as indexing either dedifferentiation or compensation (see D. C. Park & Reuter-Lorenz, 2009; Reuter-Lorenz & Cappell, 2008). While dedifferentiation connotes "negative plasticity" in terms of loss in specialization of neuro-cognitive structures, compensation connotes "positive plasticity", allowing additional resource recruitment to optimize performance (Reuter-Lorenz & Park, 2010). This debate remains largely unresolved (Davis et al., 2012).

In line with the dedifferentiation view, several studies on object and face processing suggested the fading of distinctive neural representations with increasing age in ventral visual cortex. Activation in category-sensitive brain regions (e.g. faces, houses) was less selective in older than younger adults (Burianova et al., in press; Chee et al., 2006; D. C. Park et al., 2004; J. Park et al., 2012). In addition, a number of event-related potential (ERP) studies examined the face-sensitive N170. At potential variance with the above-described neuroimaging results, N170 category-selectivity (with larger N170 to faces than objects) was similar across age groups (Daniel & Bentin, 2012; Gao et al., 2009), suggesting preserved neural sensitivity for faces in older adults. However, the N170 is generally increased in older adults (see e.g. Rousselet et al., 2009), and is also larger for inverted relative to upright faces, which is commonly interpreted as reflecting disrupted configural processing. A larger N170 in older adults may therefore reflect reduced configural processing. In line with this interpretation, smaller N170 inversion effects were observed in older participants (Daniel & Bentin, 2012; Gao et al., 2009)

Moreover, whereas N170 is typically lateralized to the right hemisphere in young participants, this asymmetry is less pronounced in older adults (Daniel & Bentin, 2012; Gao et al., 2009). As neuroimaging studies documented reduced hemispheric asymmetries in aging populations to covary with performance, a less lateralized N170 might hint at neuro-cognitive re-organization. This idea is supported by a study on the processing of alphanumeric stimuli (De Sanctis et al., 2008), in which a clear left-lateralization of occipito-temporal N1 in young adults was in contrast to a bilateral N1 in older participants. However, even when reduced lateralization of the face-sensitive N170 reflects age-related plasticity, it remains unclear whether this indicates beneficial recruitment of additional brain regions (i.e., compensation) or reduced specialization of face-sensitive areas (i.e., dedifferentiation). To distinguish between these accounts, the relationship between performance in a face recognition task and lateralization of N170 in older adults was directly tested.

Differentiation in the ability to discriminate individual faces develops early, with a specialization towards own species faces from around six months of age (Pascalis et al., 2002) and subsequent further tuning towards own-race faces during childhood (Scherf & Scott, 2012). In younger adults, the ORB reflects the consistent finding of better memory for own- relative to other-race faces (for overview, see Meissner & Brigham, 2001). Beyond about 60 years of age, decline in face memory accelerates (Hildebrandt et al., 2011). This could reflect dedifferentiation in the context of a general broadening of cognitive architecture with age (see e.g. S. C. Li et al., 2004), possibly related to a decline in perceptual face processing (Chaby et al., 2011).

Importantly, such dedifferentiation should result in a less specialized face processing system, and therefore in a reduced own-race bias. Research on the ORB in older adults is scarce, and to my knowledge the only previous study revealed a behavioral ORB in face recognition memory for young faces (Wallis et al., 2012). Here, memory for own- and other-race faces was examined in two groups of high- and low-performing older adults to test whether poor face memory in low-performers reflects advancing dedifferentiation (as indexed by a reduced or absent ORB), a lack of compensatory neural plasticity (as indexed by a different pattern of N170 lateralization), or both.

Notably, several recent studies have identified neural correlates of the ORB using ERPs. Suggestive of reduced configural processing, other-race faces elicited a larger N170 than own-race faces (Balas & Nelson, 2010; Caharel et al., 2011; Stahl et al., 2010; but see Vizioli et al., 2010). Larger N170 to other-race faces during the learning phases of a recognition memory paradigm were reported in both young Asian and Caucasian participants (Wiese et al., in press). Importantly, this effect during encoding significantly correlated with the recognition advantage for own-race faces during test.

Apart from the ORB, an own-age bias (OAB) in terms of better memory for own-age relative to other-age faces has also been described (for review, see M. G. Rhodes & Anastasi, 2012) although the exact conditions for an OAB in older adults remain unclear. To avoid underestimating older adults' performance, it was decided to examine their face recognition memory in a full-factorial design by using young and old own- and other-race faces (Wiese, 2012). In addition, the sample of older participants was divided into a high-performing and a low-performing subgroup. Three hypotheses were tested in particular: First, it was reasoned that a reduced (or even absent) behavioral ORB in low- relative to high-performing participants would argue for a (incipiently) dedifferentiated face processing system in this participant group. Second, it was tested whether an increased N170 would be associated with reduced memory, which would suggest less efficient early face perception in low-performers. Finally, it was examined whether high- and low performers would show different degrees of N170 lateralization. Specifically, while a reduction or absence of the right lateralization of the N170 in high-performers would argue for a compensatory account, the analogous pattern in low-performers would point to dedifferentiation.

4.2 Method

Participants

Forty-eight older adults (27 female, mean age = 69.0, *SD* = 4.7), recruited in senior citizen groups and via a press release in a local newspaper, participated in the study and were reimbursed with 7.50 Euro per hour. All participants reported to reside in independent living conditions and were right handed according to a modified version of the Edinburgh Handedness Inventory (Oldfield, 1971). None reported psychiatric or neurological disorders or received central-acting medication. All participants gave written informed consent, and the study was approved by the local ethics committee.

The participant group was post-hoc subdivided via a median-split with respect to performance in the main recognition experiment into 24 high-performing (14 female, mean age = 68.4, SD = 5.2) and 24 low-performing (13 female, mean age = 69.6, SD = 4.4) older adults. The groups did not differ with respect to age, $F < 1$, or education, Mann-Whitney-U = 234.50, p (asymptotic) = .240.

Stimuli

Stimuli were identical to those used in Wiese (2012) and consisted of 480 pictures showing 120 older Caucasian, 120 older eastern Asian, 120 young Caucasian and 120 young Asian faces (50 % female respectively, see Figure 5), which were collected from different internet sources. Due to this stimulus selection procedure, the exact age of the persons depicted is unknown. However, stimuli have been rated for age by young participants in a previous study from our group (rated age of young Caucasian faces = 28.61; SD = 0.42, young Asian faces = 29.28, SD = 0.41, older Caucasian faces = 66.16; SD = 0.57, older Asian faces = 72.29, SD = 0.94). All of the pictures displayed front views of neutral or moderately happy faces and were edited using Adobe Photoshop™ removing all information (clothing, background, etc.) apart from the face which was subsequently pasted in front of a black background. All stimuli were framed within an area of 170 x 216 pixels (6.0 x 7.6 cm), corresponding to a visual angle of 3.8° x 4.8° at a viewing distance of 90 cm.

Luminance (i.e., pixel intensities) and contrast (i.e., standard deviations of pixel intensities) for each stimulus was determined via Adobe Photoshop™. For older Asian and Caucasian faces, mean pixel intensity was 71.0 and 74.6, mean SD was 60.6 and 57.6, respectively. For young Asian and Caucasian faces mean pixel intensity was 61.3 and 61.6 and mean SD was 67.3 and 57.7, respectively (where = = black and 255 = white).

Procedure

Prior to the recognition memory experiment, visual acuity and contrast sensitivity were measured for each participant via a computer-based test (FrACT, Version 3.5.5, Bach, 1996) at 90 cm viewing distance.

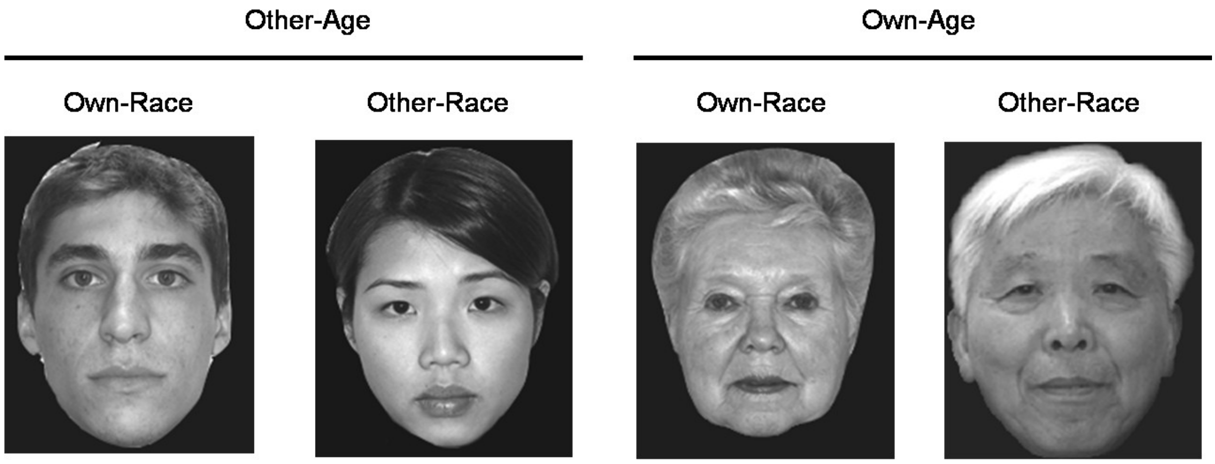

Figure 5. Stimuli examples used in the recognition memory paradigm of Experiment 1.

Participants were asked to indicate the positions of Landolt's C gaps presented in different sizes (test for visual acuity) and grey-scales (contrast sensitivity). Visual acuity was determined by the logarithm of the minimum angle of resolution (logMAR). Contrast sensitivity was measured by Michelson Contrast scores, which refer to the difference between highest and lowest luminance values divided by the sum of the two values.

The procedure of the main experiment was identical to Wiese (2012). Participants were seated in a dimly lit, electrically shielded, and sound–attenuated chamber (400A-CT_Special, Industrial Acoustics, Niederkrüchten, Germany) with their heads in a chin rest. Approximate distance between eyes and computer screen was 90 cm. Each experimental session began with a series of practice trials on different stimuli, which were excluded from data analysis. On each trial, a face stimulus was presented for various durations (depending on study vs. test phases, see below), preceded by a fixation cross for 500 ms and followed by a blank screen for 500 ms indicating the end of a trial.

The main experiment consisted of twelve blocks, each divided into a study and a test phase. In each study phase 10 young and 10 older faces, 50% Caucasian and 50% Asian, respectively, were presented for 5000 ms each (see Figure 6). Half of the participants were asked to categorize the face on the screen as fast and correctly as possible according to age

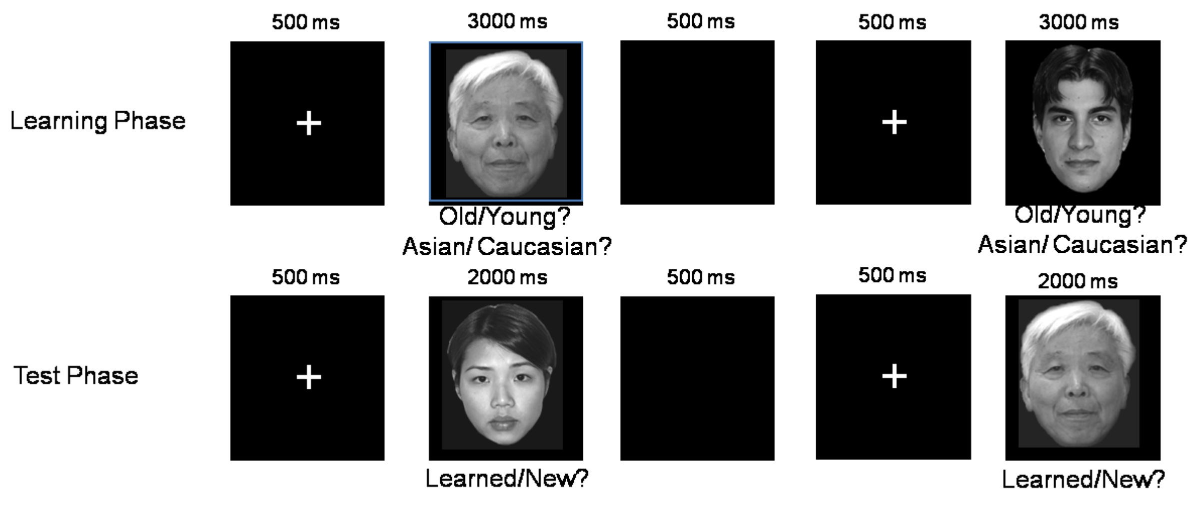

Figure 6. Illustration of study and test phases in the recognition memory paradigm of Experiment 1.

(elderly vs. young), whereas the other half was asked to categorize the face on the screen as fast and correctly as possible according to ethnicity (Asian vs. Caucasian). Furthermore, participants were instructed to memorize the faces. Between learning and test phases a fixed break of 30s duration was inserted. During each test phase all of the 20 faces from the directly preceding study phase and 20 new faces (50% older, 50 % Asian) were presented for 2000 ms each. Participants were instructed to indicate as fast as possible and without compromising accuracy whether the faces have been encountered in the preceding study phase. Between each block, participants were allowed a self-timed period of rest. During study and test, stimuli were presented in a randomized order, and key assignment and allocation of stimuli to learned and non-learned conditions were counterbalanced across participants. During study phases, mean reaction time (RT, correct responses only) and accuracy was analyzed for old and young faces separately. Data from the test phases were sorted into hits (correctly identified studied faces), misses (studied faces incorrectly classified as new), correct rejections (CR, new faces correctly classified as new), and false alarms (FA, new faces incorrectly classified as studied) for old and young faces, respectively. Measures of sensitivity (d') and response bias (C) were calculated (Green & Swets, 1966).

ERP Recording and Analysis

32-channel EEG was recorded using a BioSemi Active II system (BioSemi, Amsterdam, Netherlands). The active sintered Ag/Ag-Cl-electrodes were mounted in an elastic cap. EEG was recorded continuously from Fz, Cz, Pz, Iz, FP1, FP2, F3, F4, C3, C4, P3, P4, O1, O2, F7, F8, T7, T8, P7, P8, F9, F10, FT9, FT10, TP9, TP10, P9, P10, PO9, PO10, I1, I2, with a 512-Hz sample rate from DC to 155 Hz. Please note that BioSemi systems work with a “zero-Ref” set-up with ground and reference electrodes replaced by a CMS/DRL circuit (for further information, see www.biosemi.com/faq/cms&drl.htm).

Contributions of blink artifacts were corrected using the algorithm implemented in BESA 5.1 (MEGIS Software GmbH, Graefelfing, Germany). EEG was segmented from -200 until 1000 ms relative to stimulus onset, with the first 200 ms as baseline. Trials contaminated by non-ocular artifacts and saccades were rejected from further analysis. Artifact rejection was carried out using the BESA 5.1 tool, with an amplitude threshold of 100 µV, as well as a gradient criterion of 75 µV. Remaining trials were recalculated to average reference, digitally low-pass filtered at 40 Hz (12 db/oct, zero phase shift), and averaged according to the following four experimental conditions during learning for the first six study blocks (see below): young Asian, young Caucasian, elderly Asian, elderly Caucasian. The mean number of trials contributing to an individual averaged ERP for these conditions was 27, 27, 26 and 27, respectively. The minimum number of trials contributing to an individual waveform was 16.

In the resulting waveforms, mean amplitudes for P1 were determined at O1/O2 and between 110 and 160 ms and for N170 at TP9/P9/PO9 and TP10/P10/PO10 between 180 and 220 ms. Although not of primary interest for Experiment 1, but for the sake of completeness, P2 (between 260 and 400 ms), N2 (between 400 and 600 ms) and the late positive slow wave (between 600 and 1000 ms) were analyzed at the same electrode sites. Statistical analyses were performed by calculating mixed-model analyses of variance (ANOVA), with degrees of freedom corrected according to the Greenhouse-Geisser procedure where appropriate.

4.3. Results

4.3.1 Behavioral Results

Visual Acuity/Contrast Vision. An ANOVA on the logMAR measure of visual acuity with the between-subjects factor group (high- vs. low-performers) revealed no significant difference, $F(1, 46) = 1.73$, $p = .195$, $\eta^2_p = .04$. Similarly, an ANOVA on the Michelson Contrast indicated no group difference, $F < 1$.

Performance. Given the length of the experiment (> 70 min plus preparation times for EEG) and frequent reports of exhaustion towards the end of the session, an initial ANOVA on d’ was conducted entailing the factor “block” (1-6 versus 7-12) to test for potential effects of fatigue. A significant block effect, $F = 6.85$, $p = .012$; $\eta^2_p = .13$, indicated decreased performance in the second half of the experiment. As overall performance was a critical aspect, it was decided to analyze data in the first six blocks only, to avoid contamination of any effects by fatigue.

A mixed-model ANOVA on study phase accuracy with the within-subject factors face ethnicity (Asian vs. Caucasian) and face age (older vs. young) and the factor group yielded a main effect of task, $F(1,44) = 27.82$, $p < .001$, $\eta^2_p = .39$, indicating more accurate classifications according to age versus ethnicity. Similarly, a corresponding ANOVA on mean reaction times (RTs) during study resulted in a significant effect of task, $F(1,44) = 14.14$, $p < .001$, $\eta^2_p = .24$, indicating faster RTs for correct age versus ethnicity classifications.

Analysis of d’ at test revealed main effects of group, $F(1,46) = 55.42$, $p < .001$, $\eta^2_p = .55$, face ethnicity, $F(1,46) = 11.06$, $p = .002$, $\eta^2_p = .19$, face age $F(1,46) = 11.62$, $p = .001$, $\eta^2_p = .20$, and a significant interaction of Face Ethnicity x Face Age, $F(1,46) = 19.85$, $p < .001$, $\eta^2_p = .30$. Post hoc tests indicated better recognition for young Caucasian versus young Asian faces, $t(48) = 6.86$, $p < .001$, $d = 1.05$, but no difference between older Caucasian and Asian faces, $t(48) = 1.18$, $p = .245$, $d = 0.20$. Furthermore, recognition was more accurate for older Asian as compared to young Asian faces, $t(48) = 5.66$, $p < .001$, $d = 0.98$, whereas there was no difference between older Caucasian and young Caucasian faces, $t(48) = 1.20$, $p = .237$, $d = 0.19$. Importantly, these effects were not modulated by group, $F < 1$ (see Figure 7).

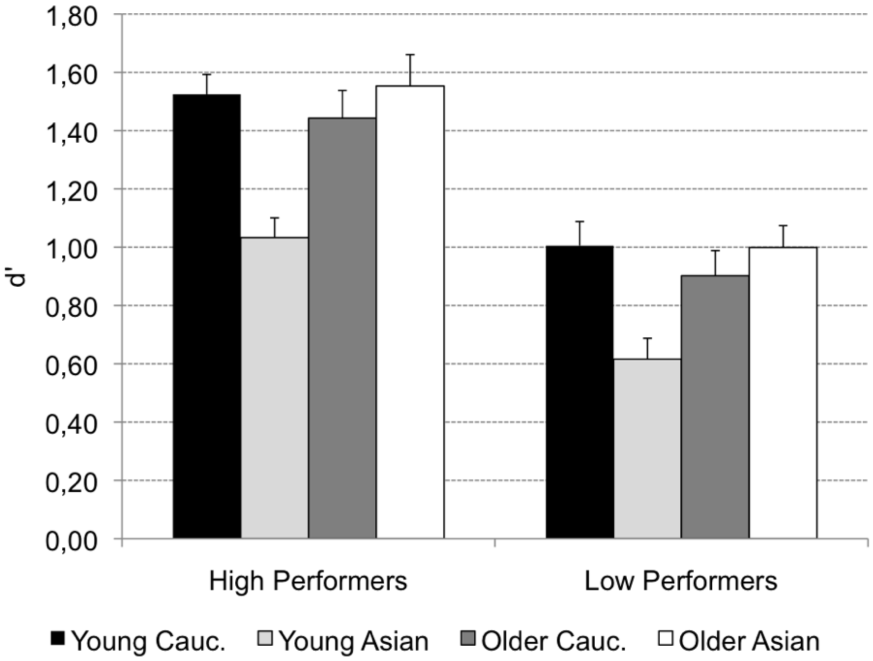

Figure 7. Recognition memory performance measured in d' for high- and low-performers during test phases of Experiment 1.

A corresponding ANOVA on C (response bias, see Table 1) revealed an interaction of Group x Face Ethnicity, $F(1,46) = 4.95$, $p = .031$, $\eta^2_p = .10$. Post-hoc tests yielded an effect of race with more conservative responses for Caucasian as compared to Asian faces in the high performing group $F(1,23) = 5.04$, $p = .035$, $\eta^2_p = .18$, but not in the low-performing group, $F < 1$. In addition ethnicity interacted with age, $F(1,46) = 48.63$, $p < .001$, $\eta^2_p = .52$. Follow-up testing indicated that responses were more conservative for young Asian as compared to young Caucasian faces, $t(47) = 2.83$, $p = .007$, $d = 2.58$, for older Caucasian as compared to

Table 1. Response Bias (C) from Experiment 1; Mean (*SD*).

	High Performers		Low Performers	
	Asian Faces	Caucasian Faces	Asian Faces	Caucasian Faces
Young Faces	-.21 (.34)	-.11 (.38)	-.28 (.41)	-.07 (.46)
Old Faces	.19 (.31)	-.20 (.38)	.10 (.39)	-.05 (.41)

older Asian faces, $t(47) = 4.70$, $p < .001$, $d = 2.88$, for young Asian as compared to older Asian faces, $t(47) = 5.90$, $p < .001$, $d = 0.63$ and for older Caucasian as compared to younger Caucasian faces, $t(47) = -2.58$, $p = .020$, $d = 0.33$ (see Table 1).

4.3.2 Event-Related Potentials

Study phase ERPs were analyzed, as previous research suggested the study phase N170 as a neural correlate of the ORB (Wiese et al, in press). Note that, effects involving topographic factors (hemisphere, laterality, site) are only reported when interacting with experimental factors.

P1. A mixed-model ANOVA on P1 with the within-subject factors hemisphere (left, right), face ethnicity and face age, and the factor group resulted in no significant effects, $0.05 < F < 3.62$, $.886 > p > .064$, $.000 < \eta^2_p < .07$.

N170. An ANOVA with the within-subject factors hemisphere, site (TP/P/PO), face ethnicity and face age and the factor group resulted in effects of face ethnicity, $F(1, 46) = 5.77$, $p = .020$, $\eta^2_p = .11$, with larger N170 for Asian faces, and face age, $F(1, 46) = 8.88$, $p = .005$, $\eta^2_p = .16$, with larger N170 for old faces, as well as in an interaction of Face ethnicity x Face age x Site, $F(1.59, 73.01) = 3.61$ $p = .042$, $\eta^2_p = .073$. Separate post-hoc analyses for each site and ethnicity yielded larger amplitudes for young Asian as compared to young Caucasian faces at P9/P10, $F(1, 47) = 4.46$, $p = .040$, $\eta^2_p = .09$ and PO9/PO10, $F(1, 47) = 15.45$, $p < .001$, $\eta^2_p = .25$, but not at TP9/TP10, $F < 1$. No corresponding effects were detected for older faces, all $F < 1$ (see Figure 8).

Additionally, the three-way interaction of Site x Hemisphere x Group, $F(1.44, 66.12) = 3.56$, $p = .048$, $\eta^2_p = .072$, was significant (see Figure 9). Separate ANOVAs at each site and for high- and low-performers were suggestive of a right-lateralized N170 in the low-performers at TP9/TP10, $F(1, 23) = 3.27$, $p = .084$, $\eta^2_p = .13$, and at P9/P10, $F(1, 23) = 2.86$, $p = .104$, $\eta^2_p = .11$. By contrast, there was no evidence of right lateralization in high-performers, $F(1, 23) = 2.05$, $p = .166$, $\eta^2_p = .08$, who even exhibited numerically larger N170 over the left hemisphere at the more anterior electrode sites (e.g. for TP9/TP10; see Figure 9).

P2 (260 -400 ms)[1]. A corresponding mixed-model ANOVA resulted in a main effect of face age, $F(1, 46) = 14.84$, $p < .001$, $\eta^2_p = .24$, indicating more positive amplitudes for young as compared to old faces. Interestingly, an interaction of Hemisphere x Ethnicity, F(1,

[1] Please note that analyses of P2 and subsequent later time windows will not be discussed in section 4.4., since these were not of primary interest for Experiment 1. Nonetheless, effects in these time ranges will be addressed and discussed integratively with the results from Experiment 2 in section 6.

46) = 8.02, p = .007, η^2_p = .15, was detected. Further testing via ANOVAs for the left and right hemisphere separately revealed more positive amplitudes for Caucasian as compared to Asian faces at left hemispheric sites, $F(1, 46) = 7.07$, p = .011, η^2_p = .13. No corresponding effect was found over the right hemisphere, $F(1, 46) = 1.06$, p = .308, η^2_p = .02 (see Figure 8).

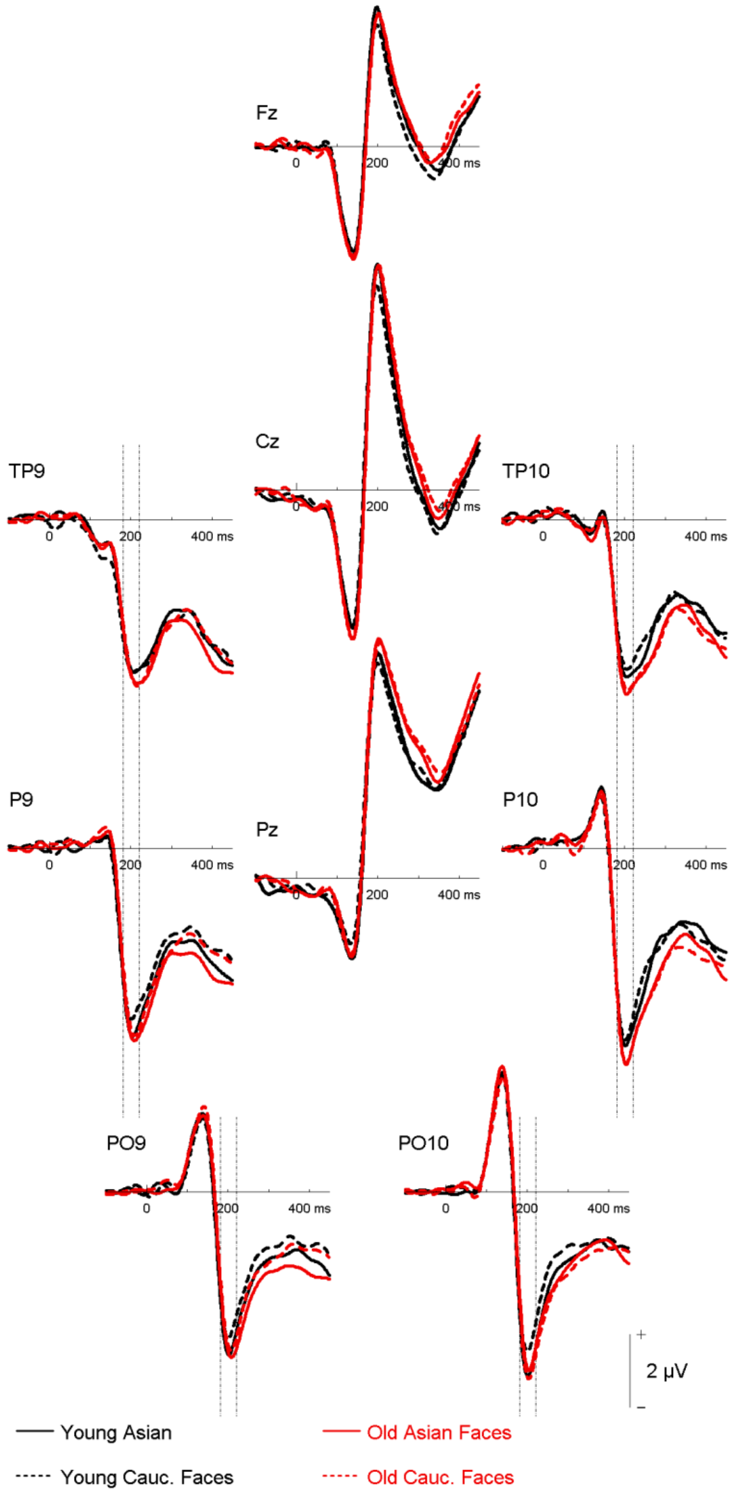

Figure 8. Grand Mean waveforms collapsed across all participants for young and older Asian and Caucasian faces from the learning phases of Experiment 1. Dashed lines depict the 180-220 ms (N170) time window.

N2 (400-600 ms). A corresponding ANOVA detected main effects of ethnicity, $F(1, 46) = 11.58$, $p = .001$, $\eta^2_p = .20$, and age, $F(1, 46) = 7.62$, $p = .008$, $\eta^2_p = .14$, which were further

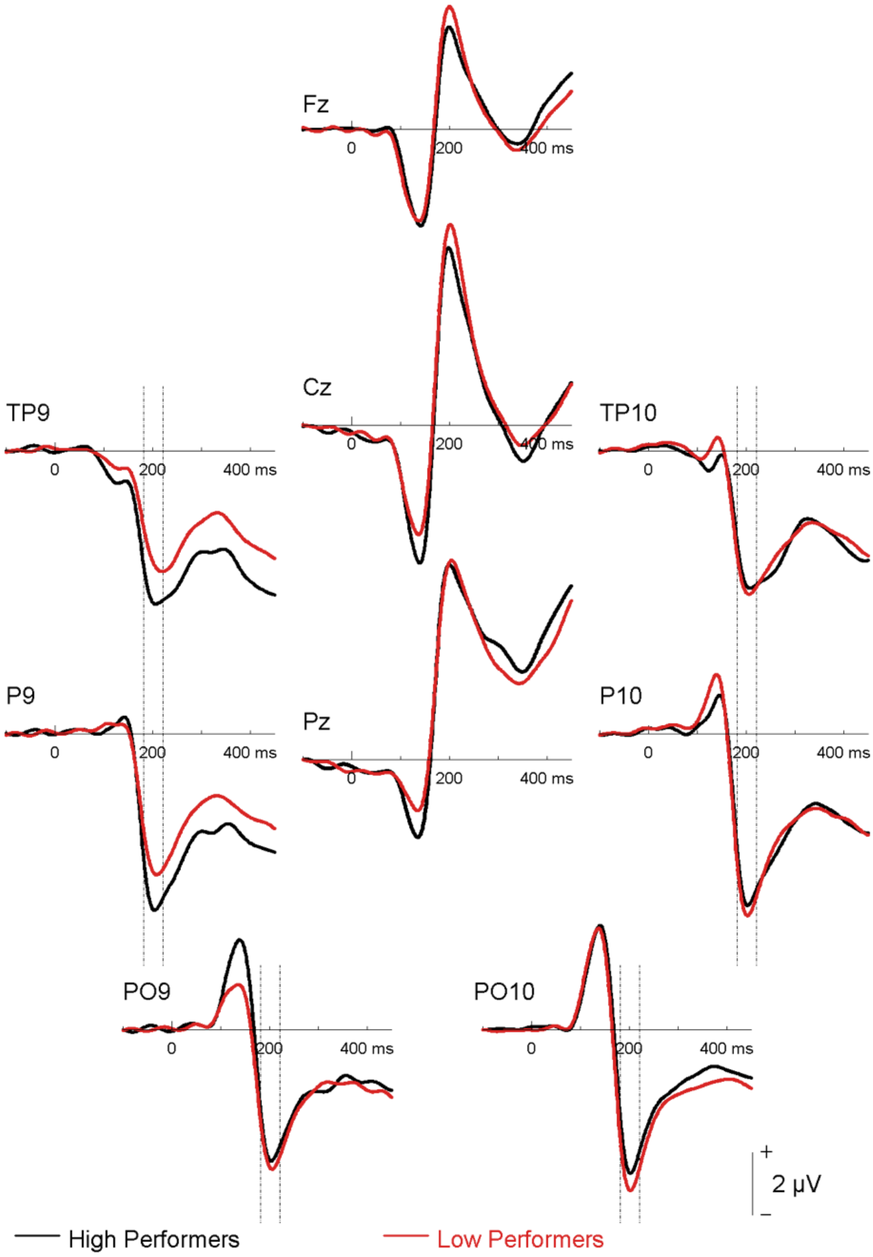

Figure 9. Grand Mean waveforms of high- and low-performing participants from the learning phases of Experiment 1. Dashed lines depict the 180-220 ms (N170) time window.

qualified by several interactions. First, a three-way interaction of Face Ethnicity x Face Age x Hemisphere, $F(1, 46) = 9.64$, $p=.003$, $\eta^2_p = .17$, was observed, and follow-up testing again revealed more positive amplitudes for Caucasian as compared to Asian faces over the left, $F(1, 46) = 19.88$, $p < .001$, $\eta^2_p = .30$ but not over the right hemisphere, $F < 1$. Conversely, young faces elicited less negative amplitudes as compared to old faces over the right hemisphere only, $F(1, 46) = 13.19$, $p = .001$, $\eta^2_p = .22$, whereas no such effect was detected over left hemispheric electrode sites, $F < 1$ (see Figure 10).

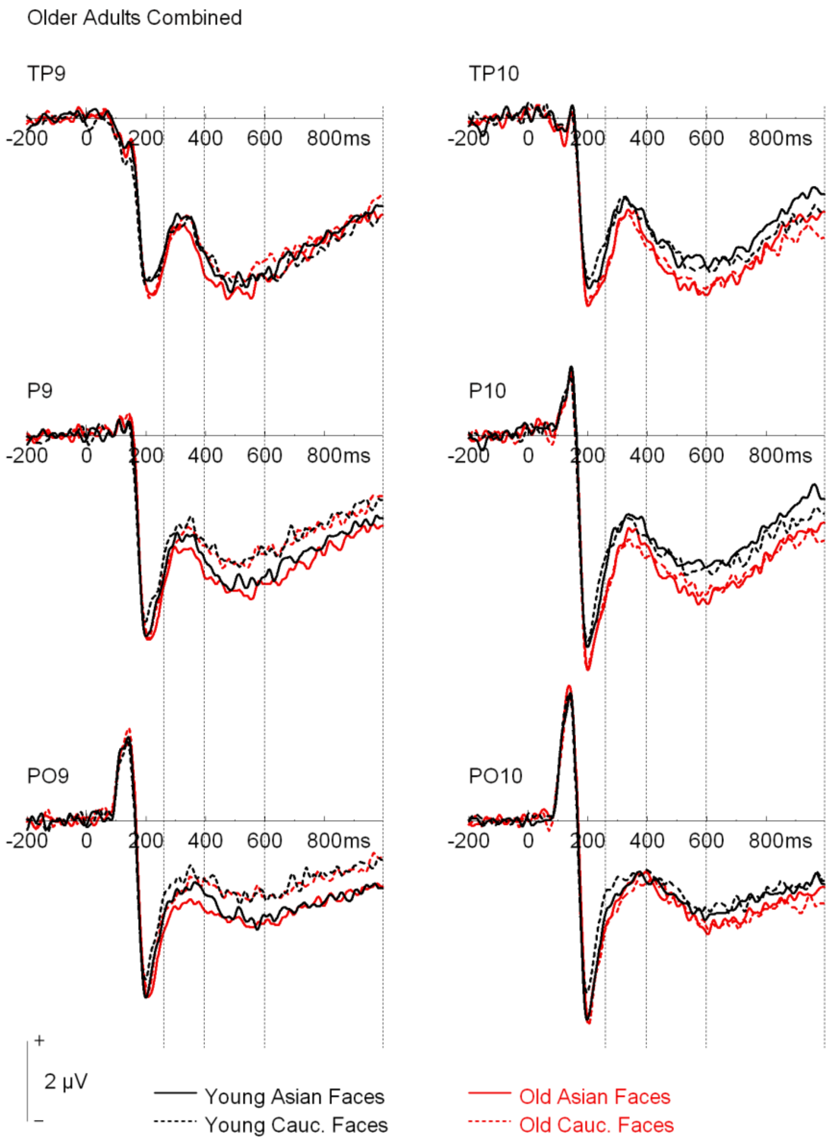

Figure 10. Grand Mean waveforms collapsed across older participants for young and older Asian and Caucasian faces from the learning phases of Experiment 1. Dashed lines depict the 260-400 ms (P2), 400-600 ms (N2), and 600-1000 ms (positive slow-wave) time window.

Second, an interaction of Site x Ethnicity x Group was found, $F(1.74,79.98) = 3.64$, $p = .036$, $\eta^2_p = .07$. Follow-up ANOVAs conducted at the three electrode positions, and for high- and low-performers separately, indicated an effect of ethnicity at TP-electrodes in the low-performing group, $F(1, 23) = 13.19$, $p = .001$, $\eta^2_p = .22$, with more negative amplitudes for Asian as compared to Caucasian faces. No such effect was apparent in the high-performing group, $F < 1$. At P-electrodes, Asian elicited more negative amplitudes than Caucasian faces in both low-, $F(1, 23) = 10.43$, $p = .004$, $\eta^2_p = .31$, and high-performing groups, $F(1, 23) = 4.62$, $p = .042$, $\eta^2_p = .17$. Similarly, at PO-electrodes Asian faces elicited more negative amplitudes as compared to Caucasian faces in both the low- , $F(1, 23) = 5.95$, $p = .023$, $\eta^2_p = .206$ and high-performing group, $F(1, 23) = 6.15$, $p = .021$, $\eta^2_p = .21$, see Figures 11 and 12.

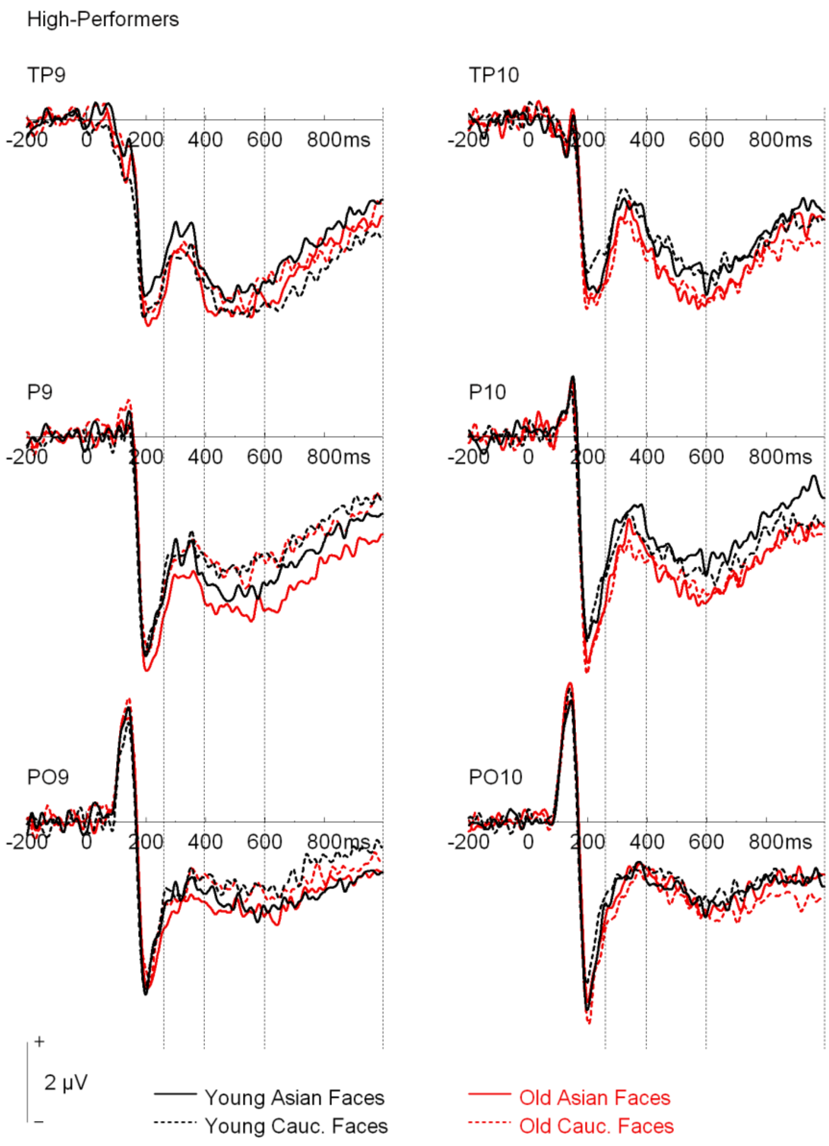

Figure 11. Grand Mean waveforms of high-performing older participants for young and older Asian and Caucasian faces from the learning phases of Experiment 1. Dashed lines depict the 260-400 ms (P2), 400-600 ms (N2), and 600-1000 ms (positive slow-wave) time window.

Additionally, at TP- sites a trend for an effect of group, $F(1, 46) = 3.06$, $p = .087$, $\eta^2_p = .06$, pointed towards more negative amplitudes for Asian faces in the low-performing relative to the high-performing group. Corresponding effects were neither detected for Asian faces at P- or PO- electrode sites, nor for Caucasian faces at any electrode position, all $F < 1$.

(Positive) Slow-Wave (600-1000 ms). A corresponding ANOVA revealed a main effect of age, $F(1, 46) = 6.52$, $p = .014$, $\eta^2_p = .12$, pointing towards more negative amplitudes

for old as compared to young faces. Interestingly, age interacted with hemisphere, $F(1, 46) = 6.97$, $p = .011$, $\eta^2_p = .13$. Follow-up ANOVAs revealed that old faces elicited more

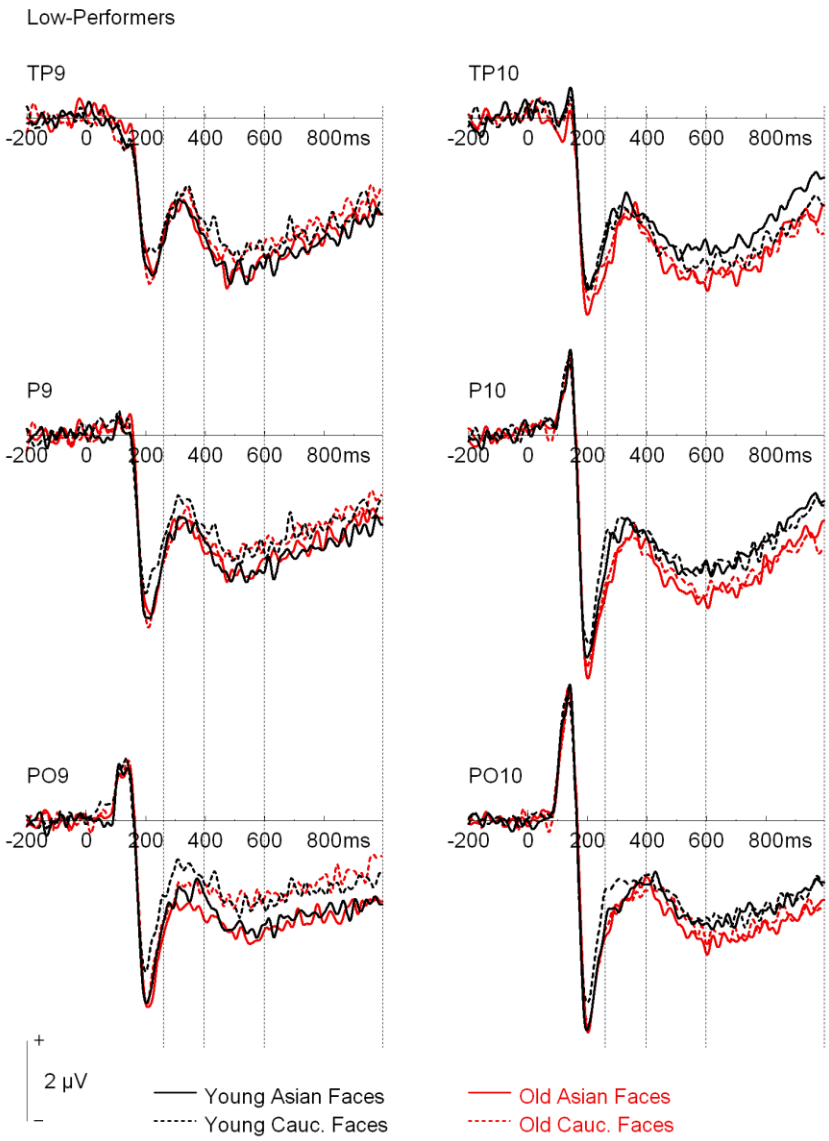

Figure 12. Grand Mean waveforms of low-performing older participants for young and older Asian and Caucasian faces from the learning phases of Experiment 1. Dashed lines depict the 260-400 ms (P2), 400-600 ms (N2), and 600-1000 ms (positive slow-wave) time window.

negative amplitudes than young faces over the right hemisphere $F(1, 47) = 16.08$, $p < .001$, $\eta^2_p = .26$, while no such effect was apparent over the left hemisphere, $F < 1$. Additionally, ethnicity interacted with hemisphere, $F(1, 46) = 8.95$, $p = .004$, $\eta^2_p = .16$. Subsidiary ANOVAs revealed more negative waveforms for Asian as compared to Caucasian faces over the left, $F(1, 47) = 8.06$, $p = .007$, $\eta^2_p = .15$, but not over the right hemisphere, $F(1, 47) = 1.37$, $p = .248$, $\eta^2_p = .23$, see Figure 10.

The analysis also resulted in an interaction of Site x Ethnicity, $F(1, 46) = 4.26$, $p = .017$, $\eta^2_p = .09$. Post-hoc tests showed that Asian faces elicited clearly more negative amplitudes as compared to Caucasian faces at PO9/PO10, $F(1, 47) = 4.61$, $p = .037$, $\eta^2_p = .09$, while only a trend for a corresponding ethnicity effect was observed at electrodes P9/P10, $F(1, 47) = 3.22$, $p = .079$, $\eta^2_p = .06$. No ethnicity effect was apparent at TP9/TP10, $F < 1$. Finally, there was an interaction of Ethnicity x Age x Group, $F(1, 46) = 4.77$, $p = .034$, $\eta^2_p = .09$. ANOVAs carried out for the high- and low- performing groups and for young and old faces separately revealed more positive amplitudes for old Caucasian faces as compared to old Asian faces, $F(1, 23) = 11.17$, $p = .003$, $\eta^2_p = .32$, in the high-, but not in the low-performers, $F < 1$. No such effect was apparent for young faces neither in the high-performing nor in the low-performing group, both $F < 1$, see Figure 11 & 12.

4.4. Discussion

The present study examined the ORB in face recognition memory in high- and low-performing older adults. Despite prominent overall performance differences, both groups demonstrated an equivalent magnitude of the ORB. Paralleling behavioral results, ERP effects of face ethnicity first showed up in a larger N170 to young Asian versus Caucasian faces in both groups alike[2]. Crucially, performance-related group differences were also observed: While low-performing older adults showed evidence of a right-lateralization of N170, this was clearly not the case in high-performers. These findings are discussed in more detail below.

The first aim was to test whether poor overall performance would be accompanied by dedifferentiation of processing within the category of faces, in terms of a reduced ORB in low-performers. Such a finding would complement previous reports of attenuated between-category (faces vs. objects) neural distinctiveness in older adults (D. C. Park et al., 2004; J. Park et al., 2012), by indicating a degree of loss in the fine-tuning of the face processing system. A clear ORB for young faces was observed, which was virtually identical in both high- and low-performing participants. Therefore it is concluded that the fine-tuning of the face processing system of low-performers was not compromised when compared to high-

[2] Although it cannot be completely ruled out that differences in overall contrast between young Asian and Caucasian face images contributed to this pattern of results, this explanation seems unlikely given that a larger N170 for other-race faces was observed in both Asian and Caucasian participants in a further study (Wiese et al., in press).

performers, despite their reduced overall face memory. This conclusion is also in line with the present finding of similar N170 ethnicity effects in the two older groups, which further suggests similar encoding of facial race in the older groups.

At a more specific level it is notable that ethnicity effects were prominent for young but not old faces, both in the N170 component and in the behavioral ORB. The absence of an ORB for old faces replicates two recent studies (Wallis et al., 2012; Wiese, 2012). This consistent absence of an ORB for old faces may be attributed to decreased perceptual salience of ethnicity information in these faces, along with an increased salience of general age-related changes in facial shape and skin texture.

The second aim was to examine whether the previously observed larger N170 amplitude (e.g. Wiese et al., 2012) in older as compared to young adults was related to a decrease in configural processing, and consequently reduced face memory, in older adults. This idea was based on the N170 inversion effect, reflecting an increased N170 amplitude for inverted, less configurally processed faces (Jacques, d'Arripe, & Rossion, 2007), an effect which is reduced in older participants (Daniel & Bentin, 2012; Gao et al., 2009; Saavedra, Olivares, & Iglesias, 2012). In the present study, a decrease in face memory was not associated with larger N170 amplitudes, arguing against the idea of decreased configural processing as the basis for reduced memory. If anything, N170 was larger in high- relative to low-performing participants, which, however, was apparent only over the left hemisphere.

Finally, the third aim of the present study was to examine whether the previously described reduced lateralization of N170 amplitude in older adults (Daniel & Bentin, 2012; Gao et al., 2009) was related to performance. In the present study, a reduced laterality of N170 in high- relative to low-performing older adults was observed. On the one hand, this finding is generally in line with the idea of reduced hemispheric asymmetry as a function of compensation rather than dedifferentiation (for review, see Cabeza, 2002) , which may not only occur for higher-order cognitive processes, but also for (early) perceptual processes (De Sanctis et al., 2008). Importantly, the present findings extend this idea to the domain of face processing.

Although the more bilateral N170 in high-performers clearly argues for a compensatory mechanism, the specific interpretation of their enhanced left-hemispheric N170 is subject to debate. One possibility considers that the left hemisphere may be more involved in feature-based than configural or holistic face processing (Rossion, Dricot, et al., 2000; Scott & Nelson, 2006). Accordingly, high-performers may engage in more feature-based processing during encoding, enabling them to exhibit better memory performance than low-performers at test. While such a strategy could provide more effective encoding fostering clearer subsequent representations, it is noteworthy that even high-performers in the present study perform at levels clearly below those of young participants in an identical experiment (Wiese, 2012). Accordingly, even high-performers may not be able to fully compensate for age-related decline in face memory.

The present study is, to my knowledge, the first to examine ERP correlates of the ORB in older adult participants. The finding of an ORB independent of overall performance indicates that the fine-tuning of the face processing system towards faces of particular expertise is preserved in older adults. In line with this interpretation, the specific pattern of N170 ethnicity effects was found to parallel the behavioral own-race bias. In addition, a more bilateral N170 response in high-performing older adults suggests a partial compensation for general age-related decline in face processing by recruiting additional neural resources in the left hemisphere. In conclusion, the present results indicate that the older adults' face processing system, even when working less efficiently, may still exhibit preserved expertise-related specialization towards own-race faces.

Experiment 2: The OAB in Old/High and Old/Low Contact Participants

Abstract

Previous studies revealed consistently enhanced recognition memory for own- as compared to other-age faces (own-age bias, OAB) in young adults, but inconsistent results in elderly participants. To resolve these discrepancies, and to see whether the presence or absence of the OAB in older adults results from differential environmental demands on the face representational system, I examined recognition memory and event-related potentials (ERPs) for young and old faces in young participants and two elderly groups, who either reported high or low degrees of daily contact with older relative to younger persons. As expected, young adults showed more accurate memory for young versus old faces. While no OAB was found in old/low contact participants, old/high contact participants were more accurate with old versus young faces. ERPs in young adults revealed a parietal old/new effect from 500-800 ms (hits > correct rejections) for young but not old faces. Whereas no old/new effect was seen in the old/low contact group, the old/high contact participants exhibited a prominent reversed old/new effect (hits < correct rejections) for old faces. These results suggest that a behavioral OAB in elderly participants may depend on high degrees of contact towards old people. The finding of ERP old/new effects specific to own-age faces suggests enhanced recollection of study phase detail in young participants, whereas it may reflect increased engagement in processes aiming at compensating for a deficit in recollection in elderly participants. In sum, the study reveals that despite age-related overall changes in face memory, the face representational system remains flexible and adapts to environmental demands even in higher age.

5.1 Introduction

Experiment 1 addressed effects of aging on early (perceptual) processes involved in face processing examining the ORB, Experiment 2 uses the OAB to examine whether the face representational system would be affected by aging. As described in the introduction, several studies suggest better memory for faces of the viewer's own age group, a finding consistently reported in young adults (Bartlett & Leslie, 1986; Fulton & Bartlett, 1991; Wiese et al., 2008;

for review, see Wiese, Komes, et al., in press). Discrepant results were reported with respect to an OAB in elderly participants. While some studies did not detect this effect (Bartlett & Leslie, 1986; Fulton & Bartlett, 1991; Mason, 1986), others reported a significant OAB in the elderly. Specifically, Backman (1991) reported more accurate memory for old as compared to young adult faces in participants aged between 63 and 70 years. In this very same experiment, however, two older groups (aged 76 and 85 years, respectively) did not show an OAB. More recently, Anastasi and Rhodes (2005) reported superior memory for old as compared to children's faces in elderly participants. Others, using young and old adult faces as stimuli, also reported corresponding effects (Lamont et al., 2005).

With respect to the ORB, it has been proposed that increased contact and/or perceptual expertise with faces of one's own relative to other group results in better recognition memory (see e.g. Chiroro & Valentine, 1995; Furl, Phillips, & O'Toole, 2002; Tanaka & Pierce, 2009) – an assumption that can be analogously applied to the OAB (Valentine & Endo, 1992). Accordingly, a relatively small degree of lifetime experience with other-age faces may be responsible for less accurate representations. Thus, it has been suggested that the face representational system (often referred to as Multidimensional Face Space, see Figure 3) is optimized to discriminate between individual own- but not other-group faces, due to limited perceptual expertise with this latter face category (Byatt & Rhodes, 2004; Papesh & Goldinger, 2010; Valentine & Endo, 1992). Of note, a perceptual expertise account of the OAB may be interpreted in two different variations, i.e. long-term expertise versus more recent contact, which most importantly entail different predictions regarding the occurrence of an OAB in older participants.

First, if lifetime perceptual expertise or contact over long periods of time (i.e., in the range of decades) is crucial, one would predict an OAB in young, but not in elderly participants (Fulton & Bartlett, 1991). According to this view, young participants likely have preferential contact to, and thus more expertise with young faces. By contrast, elderly participants have been young in the course of their lifetime, and thus have accumulated substantial expertise with different age groups. Second, amount or quality of recent daily-life contact, rather than lifetime expertise, may be crucial. If so, an OAB should occur in both young and elderly participants alike, provided that both groups exhibit preferential contact towards own-age people (see also He et al., 2011). Similarly, recent research suggests an OAB in terms of less accurate memory for children's compared to young adult faces in young adult observers (Harrison & Hole, 2009; Hills & Lewis, 2011), although the interpretation of those results may be complicated by developmental factors influencing face encoding in the first two decades of life (see Crookes & McKone, 2009).

Independent of facial age, cognitive aging may substantially affect face memory (Backman, 1991; Bartlett, Leslie, Tubbs, & Fulton, 1989). Critically, lower levels of overall performance pose a methodological problem for studies examining the OAB, because its absence in elderly participants may be related to near-floor performance (but see Experiment1 for an example of memory biases in low-performing older adults). As a possible example, Bäckman (1991) reported both decreasing overall performance across three consecutive age groups, and a significant OAB in the youngest group of elderly participants only. One solution for studies investigating the OAB in young and elderly participants may thus be to utilize a measure that is corrected for overall performance differences between groups.

Moreover, studies revealing a crucial role of daily-life contact for the occurrence or absence of an OAB have examined young or middle-aged participants only. For instance, whilst undergraduate students ($M = 23$ years of age) showed a clear recognition advantage for faces of their own-age as compared to child faces, young adult trainee teachers ($M = 24$ years of age) were found to exhibit a reversed effect with more accurate recognition for child versus own-age faces (Harrison & Hole, 2009). A very recent study examined young middle-aged geriatric nurses ($M = 33$ years of age) and a middle-aged control group ($M = 31$ years of age) with young and old faces and reported a clear OAB in the controls, but no such effect in the experts for old faces (Wiese, Wolff, et al., 2013). Paralleling this pattern of behavioral results, differential N250 repetition effects for own- vs. other age faces, possibly reflecting more efficient re-activation of own-age facial representations, were only observed in controls, not in experts. It remains unclear whether (more recent) contact may similar affect face memory in older participants. Such a prominent role of recent expertise for the OAB over and above potential detrimental effects of cognitive aging, would argue for preserved integrity of the face representational system plastically adapting to environmental demands in older age.

In the context of studies on face memory biases, ERPs have provided important information about the mechanisms underlying the own-race bias (Herzmann et al., 2011; Lucas et al., 2011; Stahl et al., 2010) and the OAB (Ebner, He, et al., 2011; Wiese, 2012; Wiese et al., 2008). In general, as described in section 3.4.3, this research has provided evidence for modulations by face group (i) of perceptual processing (indicated by amplitude effects on early occipito-temporal N170 and P2 components), (ii) of the access to facial representations for repeated faces (indicated by enhanced occipito-temporal N250 responses), and (iii) for a modulation of episodic memory retrieval (indicated by later centro-parietal ERP old/new effects, for a detailed description of relevant ERP components and interpretation of effects, please see Section 3.4.3). In the present study, these ERP responses were assessed in order to understand the mechanisms mediating any memory differences between young and old faces.

Based on the literature discussed above, the present study aimed at testing the effect of daily-life contact towards young and old people on the OAB in a relatively large group of elderly participants. For that purpose, the elderly group was divided into two subgroups via a median split on a self-report measure of relative contact towards old versus young people. A group of young adult participants was additionally tested. Note that the young participants group was not divided into contact-based subgroups, because in contrast to findings in elderly participants (i) previous research suggested a consistent OAB in young participants (Wiese, 2012; Wiese et al., 2008), and (ii) relative contact is homogenously biased towards young people in this group. Crucially, to ensure that potentially reduced or absent age biases in elderly participants were not related to low overall performance levels, and thus to potential floor effects, memory biases towards young or old faces were additionally corrected for individual performance level.

The following assumptions were derived from the considerations described above: if neither of the two old groups would show an OAB, such a pattern of results would argue for lifetime perceptual expertise playing a crucial role for the occurrence of the OAB, (since both subgroups have been young in the course of their lifetime and should have accumulated experience with all adult age groups). By contrast, a contact-based account, emphasizing the importance of more recent daily-life interactions, would predict an OAB for those elderly participants only who report relatively more contact towards own-age as compared to other-age people. Importantly, such latter pattern of results would inform about the potential flexibility of the face space adapting to (self-created) environmental demands with older age.

In ERPs, it was expected to replicate earlier results, namely a smaller N170 and larger P2 for young faces in young participants and in those elderly participants who do not show a behavioral OAB (Wiese et al., 2008)[3]. Related to stages of facial representations, larger effects of stimulus repetition (N250) and recollection-based episodic memory (parietal old/new effect) for own-age faces were expected in the young participants. Similarly, if one

[3] For the sake of completeness, but not primarily related to present purposes, the configural/holistic processing variant of the perceptual expertise account assumes more in-depth analysis of own-age faces at the level of early perceptual processing. The investigation of N170 and P2 in different groups of elderly participants allowed an examination of this account. More precisely, if either one or both elderly groups demonstrated a memory advantage for own-age faces, *and* if N170 and/or P2 reflected processing stages relevant for the OAB, a reversed effect, namely a smaller N170 and larger P2 for *old* relative to young faces may be detected in those groups.

(or both) of the elderly groups demonstrated a behavioral OAB, a larger N250 repetition effect for own-age faces would be expected for this group, since this component likely reflects processes of implicit memory, commonly assumed to be relatively spared by cognitive aging (Balota et al., 2000). By contrast, the late old/new effect presumably reflects conscious recollection, usually assumed to be reduced in the elderly (Anderson & Craik, 2000). Accordingly, a behavioral OAB would not necessarily be predicted to be accompanied by larger late old/new effects for own-age faces in old participants.

5.2 Method

Participants

The studied population consisted of 20 younger (18-29 years, $M = 22$; $SD = 3.3$; 8 male) and 40 older participants (60-81 years, $M = 68$; $SD = 4.4$; 16 male). All of the older participants, who were recruited in senior citizen groups and via a press release in a local newspaper, reported to reside in independent living conditions and received monetary reward for participation. Younger adults were undergraduate students at the Friedrich Schiller University and either received course credit or monetary rewards. All participants were right-handed according to a modified version of the Edinburgh Handedness Inventory (Oldfield, 1971) and none reported neurological or psychiatric disorders or received central-acting medication. The groups of young and old participants did not differ with respect to level of education (measured as the highest degree of formal education; Kruskal-Wallis test; $p > .05$). All participants gave written informed consent and the study was approved by the local faculty ethics committee.

The group of older adults was subdivided via a median-split with respect to the difference in amount of contact (as measured in hours/week; see below) towards older versus younger persons. This procedure resulted in two elderly subgroups consisting of 20 high contact participants (old/high contact group, with substantially increased contact to old as compared to young people, see below; 62-81 years, $M = 69$, $SD = 4.2$) and 20 low contact participants (old/low contact group, with more similar amounts of contact towards young and old people; 60-74 years, $M = 68$, $SD = 4.6$), respectively.

Stimuli

Stimuli were identical to those used in Wiese et al. (2008) and consisted of 240 natural images showing 120 old (mean age 69 years; *SD* = 7.2; 50% female) and 120 young faces (mean age 22 years; *SD* = 3.0; 50% female). Pictures were taken from the CAL/PAL face database (Minear & Park, 2004) and edited using Adobe Photoshop^{TM}. They were converted to grey-scale with black background so that all information apart from the face (clothing, etc.) was deleted, and were framed within an area of 255 x 324 pixels (9 x 11 cm), corresponding to a visual angle of approximately 5.7° x 6.9° at a viewing distance of 90 cm. Old and young faces were similar in luminance (8-bit pixel value; $M = 67.4$, $SD = 12.3$ and $M = 63.3$, $SD = 14.4$, respectively) and contrast ($M = 53.2$, $SD = 7.3$ and $M = 54.9$, $SD = 8.7$, respectively). All stimuli were presented on a computer monitor using E-Prime^{TM}.

Procedure and Experimental Design

Prior to the recognition memory experiment, measures of visual acuity and contrast sensitivity were obtained for each participant via a computer-based test (FrACT, Version 3.5.5; Bach, 1996) at 90 cm viewing distance. Participants were to indicate the positions of Landolt's C gaps presented in different sizes (test for visual acuity) and grey-scales (contrast sensitivity). Visual acuity was measured by determining the logarithm of the minimum angle of resolution (logMAR). Contrast sensitivity was measured by obtaining Michelson Contrast scores, which refer to the difference between highest and lowest luminance values divided by the sum of the two values.

The procedure of the main experiment was identical to Wiese et al. (2008). Participants were seated in an electrically shielded, sound-attenuated and dimly lit cabin (400-A-CT-Special, Industrial Acoustics, Niederkrüchten, Germany) with their heads in a chin rest and an approximate eye-screen distance of 90 cm. Each trial consisted of the presentation of a face for various durations depending on experimental condition (see below). Each face was preceded by a fixation cross presented for 500 ms. The trial ended with a blank screen for 500 ms. Participants had to respond via button presses within 2000 ms after face onset. The experiment consisted of a practice block (excluded from the analysis) and six experimental blocks, each divided into a study and a test phase. During the study phases, 10 young and 10 elderly faces (50% female, respectively) were presented for 5 s each. The participants were instructed to decide as fast as possible without compromising accuracy whether the current face was old or young. In addition, they were asked to memorize the faces for later test. Study and test phases were separated by breaks of 30 s. During each test phase the 20 studied faces from the directly preceding study phase were presented with 20 new faces (50% old; 50% female) for 2000 ms each. Participants were instructed to decide as quickly and accurately as possible whether the current face had been presented in the directly preceding study phase (see Figure 13). Order of stimuli during study and test phase was randomized. Between each block, participants were allowed a self-timed period of rest. Assignment of faces to studied versus non-studied conditions, as well as button assignments, were balanced across participants.

During study phases, mean reaction time (RT; correct responses only) and accuracy was analyzed for old and young faces separately. Data from the test phases were sorted into hits (correctly identified studied faces), misses (studied faces incorrectly classified as new), correct rejections (CR, new faces correctly classified as new), and false alarms (FA, new faces incorrectly classified as studied) for old and young faces, respectively. Measures of sensitivity (d') and response bias (C) were calculated (Green & Swets, 1966). In order to test differences

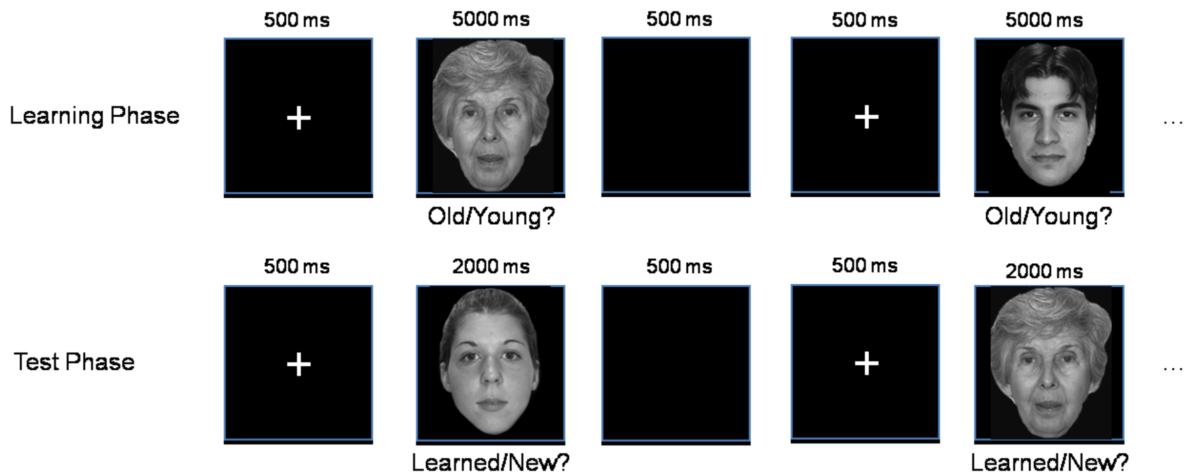

Figure 13. Illustration of study and test phases from Experiment 2.

in memory towards own- and other-age faces independent of overall performance levels (which are often decreased in elderly participants), additional measures of memory biases, corrected for performance levels, were calculated for each participant separately. For that purpose, d' for old faces was subtracted from d' for young faces, and this difference was divided by the sum of the two scores. A positive score on this measure thus represents a memory bias towards young faces, whereas a negative score depicts a memory bias towards old faces.

Finally, after the recognition memory experiment, all participants filled in a questionnaire, which asked for the amount of contact towards young (18 to 29 years) and old

(60 to 79 years) people in different daily-life situations (job/university, meeting friends/spare time activities, family, domestic circumstances). Both hours of contact per week as well as the number of different contact persons per age group were recorded. Participants were asked to avoid multiple allocation of time spent with identical people. Total scores were calculated for each participant by adding contact data from the different situations. Finally, participants were asked to rate the quality of contact towards the two different age groups (from 1 = very superficial to 4 = very intense).

EEG Recording and Analysis

EEG recording and analysis was identical to Experiment 1, except for the following changes. Trials were averaged according to four experimental conditions during test (young faces – hits, young faces – correct rejections [CR], old faces – hits, old faces - CR) for each of the three groups separately. In order to be able to assess both potential repetition effects on early visual ERPs (see e.g., Wiese, Schweinberger, & Neumann, 2008) and memory effects on later ERP components, the study focused on ERPs from the test phases in the present experiment.

For statistical analysis, peak amplitude and latency for two early ERP components (P1, N170) were analyzed at the electrodes of their respective maximum amplitudes and at the corresponding contralateral homologue. Peak analyses were carried out for the P1 component between 80 and 160 ms relatively to a 200 ms baseline at O1, O2 and I1 and I2. Due to the fact that P1 was maximal at O-electrodes in the younger adults and at I-electrodes in both of the older groups, analyses of this component required the inclusion of all four electrodes. Peak measures for the N170 component were determined in a time window between 150 and 230 ms relative to a 200 ms baseline at P9 and P10. To analyze the subsequent P2 component, time windows were chosen on the basis of the P2 peaks at P9/P10 in the grand average waveforms of young and elderly participants. Mean amplitudes relative to a 200 ms baseline were calculated in time windows ranging 80 ms around these peaks (from 200 – 280 ms in young participants, and from 260 – 340 ms in the two elderly groups). N250 was analyzed in 120 ms time windows following the P2 range (from 280 – 400 ms in young participants, and from 340 – 460 ms in elderly participants) at electrodes P9/P10. Mean amplitudes between 300 and 500 ms (early old/new effect) as well as between 500 and 800 ms (later old/new effect) were analyzed at frontal, central, and parietal electrodes (F3, Fz, F4, C3, Cz, C4, P3, Pz, P4). Statistical analyses were performed by calculating mixed-model analyses of variance

(ANOVA), with degrees of freedom corrected according to the Greenhouse-Geisser procedure where appropriate.

5.3. Results

5.3.1 Behavioral Results

Visual Acuity/Contrast Sensitivity. A univariate ANOVA on the logMAR measure of visual acuity with the between-subjects factor group (young participants, old/high contact participants, old/low contact participants) revealed a significant main effect, $F(2,57) = 8.70$, $p = .001$; $\eta^2 = .23$, with better visual acuity for young ($M = 0.10$; $SD = .17$) as compared to both old/low contact ($M = 0.30$; $SD = .16$; $F[1,38] = 15.27$; $p < .001$; $\eta^2 = .29$) and old/high contact participants ($M = .29$; $SD = .19$; $F[1,38] = 11.45$; $p = .002$; $\eta^2 = .23$). Importantly, the two older groups did not differ significantly, $F < 1$. Similarly, an ANOVA on the Michelson contrast measure yielded a significant group effect, $F(2,57) = 3.63$; $p = .033$; $\eta^2 =.11$, again reflecting higher contrast sensitivity for young ($M = .63$; $SD = .17$) as compared to both old/low contact ($M = 3.50$; $SD = 5.6$; $F[1,38] = 5.34$; $p = .026$; $\eta^2 = .12$) and old/high contact participants ($M = 3.84$; $SD = 4.5$; $F[1,38] = 10.15$; $p = .003$; $\eta^2 = .21$). Again, the older groups did not differ significantly, $F < 1$.

Contact measures (see Table 2). A mixed-model ANOVA on contact as measured in hours per week with the between-subjects factor group and the within-subjects factor old versus young contact persons yielded a significant main effect of group, $F(1,57) = 54.01$; $p < .001$; $\eta^2_p = .66$, and, as expected, a significant interaction, $F(2,57) = 161.30$; $p < .001$; $\eta^2_p = .85$. Paired t-tests revealed that young participants spent significantly more time with young as compared to older adults, $t(19) = 8.81$; $p < .001$; $d = 1.97$, while older participants spent significantly more time with elderly adults, which was found for both the old/high contact, $t(19)= -21.25$; $p < .001$; $d = .85$, and the old/low contact group, $t(19)= -3.81$; $p = .001$; $d = .51$.

Importantly, the old/high contact group reported more contact towards older people as compared to the old/low contact group, $t(38)= -16.90$, $p < .001$; $d = 5.34$, while there was no significant difference between the two older groups with respect to the amount of contact to younger people, $t(38)= .20$, $p = .841$; $d =.06$. Please note that the analysis reported in this paragraph is not redundant, given the procedure to allocate elderly participants to high and low contact groups, since this assignment was based on the *difference* between contact towards old and young people.

Table 2. Means and Standard deviations: *M* (*SD*) of self reported contact towards younger (YA; 18-29 years) and older adults (OA; 60-79 years) from Experiment 2.

	Younger Adults		Old/Low Contact Group		Old/High Contact Group	
Contact	YA	OA	YA	OA	YA	OA
Hours/week	80.2 (37.1)	4.9 (9.9)	1.6 (2.5)	6.8 (6.3)	1.5 (2.0)	57.7 (11.9)
Persons/week	47.3 (50.7)	1.4 (1.4)	1.4 (2.5)	22.0 (27.3)	4.7 (8.0)	15.5 (19.7)
Quality	3.0 (0.8)	1.8 (1.5)	1.4 (1.5)	2.4 (1.2)	1.6 (1.6)	3.2 (0.6)

A corresponding mixed-model ANOVA on number of contact persons revealed a significant interaction, $F(2,56) = 20.49$; $p < .001$; $\eta^2_p = .42$.[4] Subsequent paired t-tests revealed significantly more contact towards young people in the young participants group, $t(19) = 4.09$; $p = .001$; $d = .91$ and significantly more contact towards elderly people for both the old/low contact, $t(18) = -3.26$; p=.004; $d = -.75$, and the old high-contact group, $t(19)$= -2.37; $p = .029$; $d = -.53$. No significant differences were obtained between the two older groups with respect to the number of young adult, $t(37)$= 1.68; $p = .101$; d =.55, or older adult contact persons, $t(37)$= .85; $p = .399$; d =.27.

Finally, an ANOVA on quality of contact resulted in a significant interaction, $F(2,56) = 17.71$; $p < .001$; $\eta^2_p = .39$. Further testing revealed higher quality of contact with younger adults perceived by young participants, $t(19) = 3.06$; p =.007; $d = .68$, and higher quality of contact with older adults perceived by both groups of older participants (old/low contact: $t[18] = -3.06$; $p = .007$; $d = -.70$; old/high contact: $t[19] = -4.85$; $p < .001$; $d = 1.09$). In addition, higher quality of contact towards old people was reported by old/high contact as compared to old/low contact participants, $t(38)$= -2.59; $p = .013$; $d = .58$, whereas no difference regarding perceived quality of contact with younger adults was observed, $t(38)$= -.32; $p = .75$; $d = -.10$.

Performance (see Table 3)

Study phases. A mixed-model ANOVA on accuracy data with the between-subjects factor group and the within-subjects factor face age yielded a significant main effect of group, $F(2,57) = 3.59$; p =.034; $\eta^2_p = .11$, indicating more accurate responses in younger adults as compared to old/low, $F(1,38) = 5.94$; p =.020; $\eta^2_p = .14$, but not to old/high contact participants, $F(1,38) = 3.28$; p =.078; $\eta^2_p = .08$. The two older groups did not differ significantly, $F(1,38) = 1.73$; p =.196; $\eta^2_p = .04$.

[4] One participant in the old/low contact group did not complete this questionnaire, and thus is missing from the analyses of contact persons and quality of contact.

Table 3. Behavioral data of study and test phases from Experiment 2: *M* (*SEM*).

	Younger Adults		Old/Low Contact Group		Old/High Contact Group	
Study Phases	YF	OF	YF	OF	YF	OF
Accuracy	.98 (0.01)	.99 (0.03)	.94 (0.02)	.95 (0.02)	.97 (0.01)	.96 (0.01)
RT (ms)	909.08 (50.06)	840.90 (43.15)	1029.99 (45.01)	1001.47 (45.25)	1085.47 (43.75)	1117.48 (43.08)
Test Phases						
Hits	.81 (0.03)	.74 (0.03)	.73 (0.03)	.76 (0.03)	.71 (0.03)	.79 (0.02)
CR	.86 (0.02)	.78 (0.02)	.67 (0.03)	.64 (0.03)	.60 (0.03)	.58 (0.040)
d'	2.01 (0.11)	1.63 (0.11)	1.18 (0.10)	1.18 (0.14)	.87 (0.10)	1.14 (0.13)
C	0.15 (0.06)	0.99 (0.08)	-0.11 (0.08)	-0.22 (0.07)	-0.16 (0.08)	-0.31 (0.09)

*YF = young faces; OF = old faces

A corresponding ANOVA on RTs resulted in a significant main effect of group, $F(2,57) = 6.88$; $p = .002$; $\eta^2_p = .19$, reflecting shorter RTs in younger adults as compared to both old/high contact, $F(1,38) = 13.74$; $p = .001$; $\eta^2_p = .27$, and old/low contact participants, $F(1,38) = 4.91$; $p = .033$; $\eta^2_p = .11$. Again, the two older groups did not differ, $F(1,38) = 2.02$; $p = .163$; $\eta^2_p = .051$. Further, a significant interaction, $F(2,57) = 4.70$; $p = .013$; $\eta^2_p = .14$ was detected. Subsequent separate ANOVAs revealed significantly shorter RTs to old as compared to young faces in young participants, $F(1,19) = 9.86$; $p = .005$; $\eta^2_p = .34$. RTs for old as compared to young faces did not differ significantly in neither of the elderly participant groups (old/low contact group: $F[1,19] = 2.84$; $p = .108$; $\eta^2_p = .13$; old/high contact group: $F[1,19] = 1.81$; $p = .291$; $\eta^2_p = .06$).

Test phases. A mixed-model ANOVA on d' with the between-subjects factor group and the within-subjects factor face age yielded a significant main effect of group, $F(2,57) = 15.24$; $p < .001$; $\eta^2_p = .35$, with higher d' scores for younger adults as compared to both old/high contact, $F(1,38) = 34.49$; $p < .001$; $\eta^2_p = .48$, and old/low contact participants, $F(1,38) = 16.64$; $p < .001$; $\eta^2_p = .31$. Importantly, the older groups did not differ significantly overall, $F(1,38) = 1.07$; $p = .307$; $\eta^2_p = .03$. Critically, an interaction of Face age x Group, $F(2,57) = 11.87$; $p < .001$; $\eta^2_p = .29$, reflected higher d' scores for young as compared to old faces in younger adults, $F(1,19) = 9.62$; $p = .006$; $\eta^2_p = .34$, no difference in the old/low contact group, $F < 1$, but higher d' for old as compared to young faces in the old/high contact group, $F(1,19) = 9.15$; $p = .007$; $\eta^2_p = .33$.

A univariate ANOVA on the corrected memory bias score (see Figure 14) resulted in a significant effect of group, $F(1,57) = 8.36$; $p = .001$; $\eta^2 = .23$. Post-hoc tests revealed a significantly more positive memory bias (i.e., towards young faces) for young as compared to old/low contact participants, $F(1,38) = 5.51$; $p = .024$; $\eta^2 = .13$, and a significantly more negative bias (i.e., towards old faces) in old/high contact as compared to old/low contact elderly participants, $F(1,38) = 4.37$; $p = .043$; $\eta^2 = .10$. Finally, t-tests were performed to test whether memory biases in the three groups were significantly different from zero. This analysis revealed a positive memory bias in younger adults, $t(19) = 3.09$; $p = .006$; $d = .71$, a negative bias in old/high contact participants, $t(19) = -2.38$; $p = .028$; $d = .54$, and no bias in old/low contact participants, $t(19) = .009$; $p = .993$; $d = .004$.

A mixed-model ANOVA on C resulted in a significant main effect of face age $F(2,57 = 6.23$; $p = .015$, $\eta^2_p = .10$), indicating more liberal responses to old faces. Further, a significant main effect of group, $F(2,57) = 7.90$; $p = .001$, $\eta^2_p = .22$, reflected more conservative responses in young adults as compared to both old/low contact, $F(1,38) = 9.21$; $p = .004$; $\eta^2_p = .20$, and old/high contact participants, $F(1,38) = 14.51$; $p < .001$; $\eta^2_p = .28$. No significant interaction was found and the two older groups did not differ from one another (all $Fs < 1$).

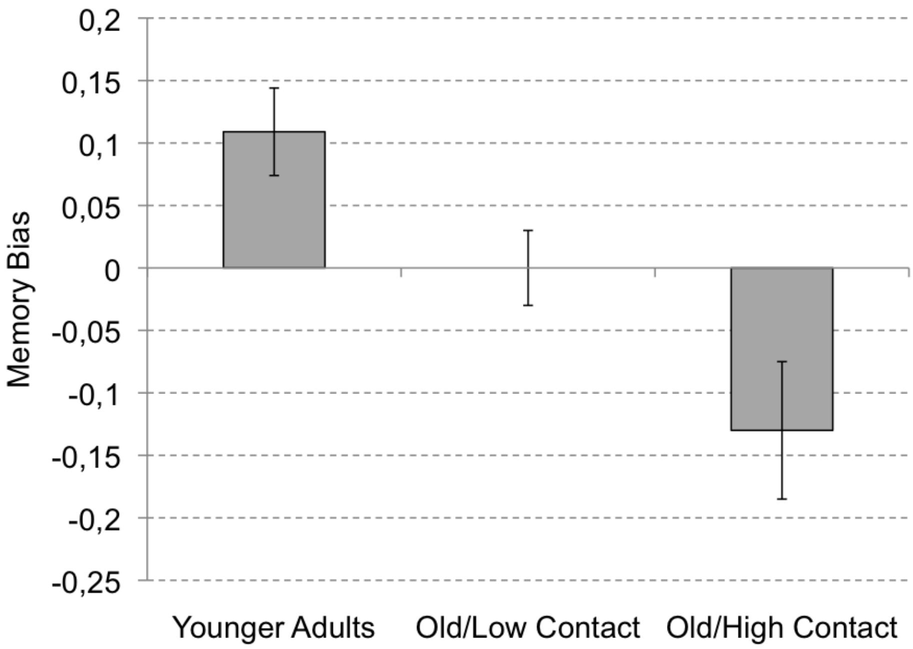

Figure 14. Memory bias (d'[YF]-d'[OF]/d'[YF]+d'[OF]) for the three participant groups from Experiment 2. Please note the own-age bias in young and old/high contact, but not in old/low contact participants.

5.3.2 Event-Related Potentials (test phases)

The descriptions of the ERP analyses provided in the following paragraphs focus on effects of facial age, memory and interactions of these factors with participant group, which were of primary interest for present purposes. Therefore, main effects of group, hemisphere, laterality or site, as well as interactions containing only these factors are not reported.

P1 (peak analysis; see Figures 15-17). A mixed-model ANOVA on peak latency with the between-subjects factor group and the within-subject factors hemisphere (left vs. right), site (occipital vs. inferior occipital), face age and response (hits vs. CR) resulted in a significant main effect face age, $F(1,57) = 4.12$; $p = .047$; $\eta^2_p = .07$, with longer P1 latencies for old as compared to young faces.[5] No group differences were detected, $F < 1$.

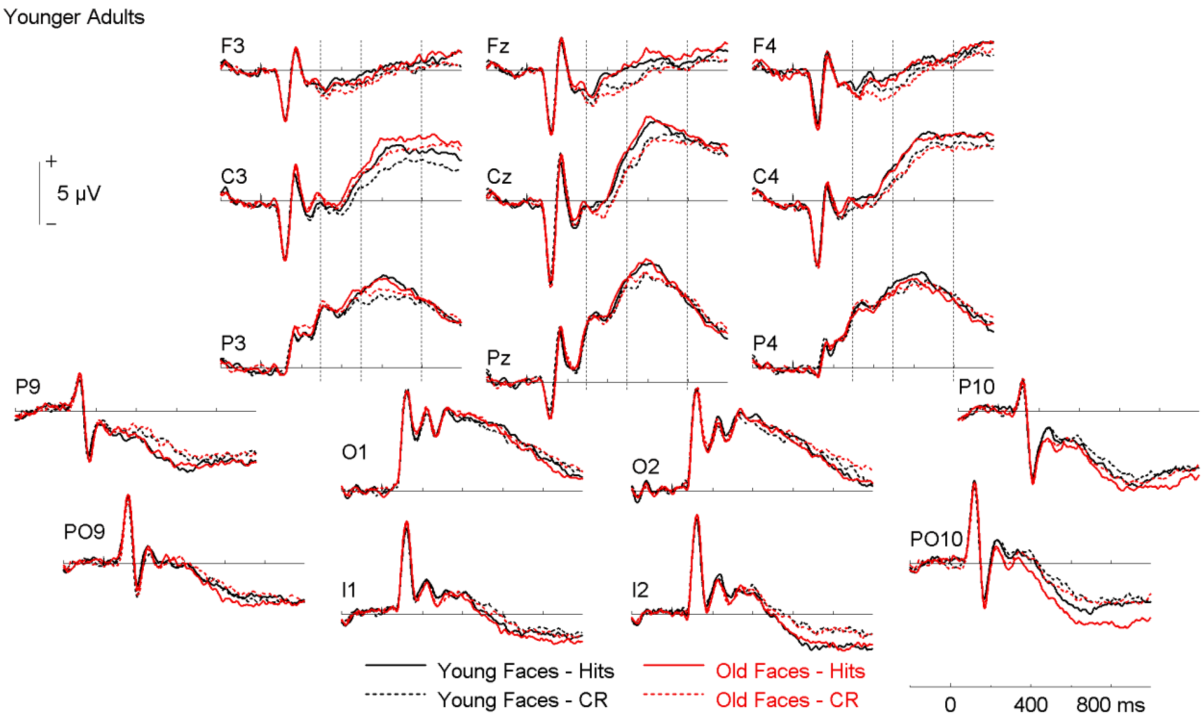

Figure15. Grand Mean waveforms from the test phases of Experiment 2 in the young participant group. CR = correct rejections. Dashed lines depict early and late old/new effect time windows.

N170 (peak analysis). An ANOVA on N170 latency yielded a significant effect of face age, $F(1,57) = 11.76$; $p = .001$; $\eta^2_p = .17$, reflecting longer latencies for old as compared to young faces. An ANOVA on N170 peak amplitude revealed a main effect of face age, $F(1,57)$

[5] Note that it does not normally make sense to analyze the latency of the same component at different sites, and that analysis of peak latencies is usually performed at the site of maximum amplitude. In the present data set, however, we decided to include both sites, because of age-related differences in the topographical maxima of P1, which was largest at O1/O2 in young participants but at I1/I2 in older participants.

= 7.50; p =.008; η^2_p = .12, with larger N170 to old than young faces. There was no interaction involving face age and group, $F < 1$.

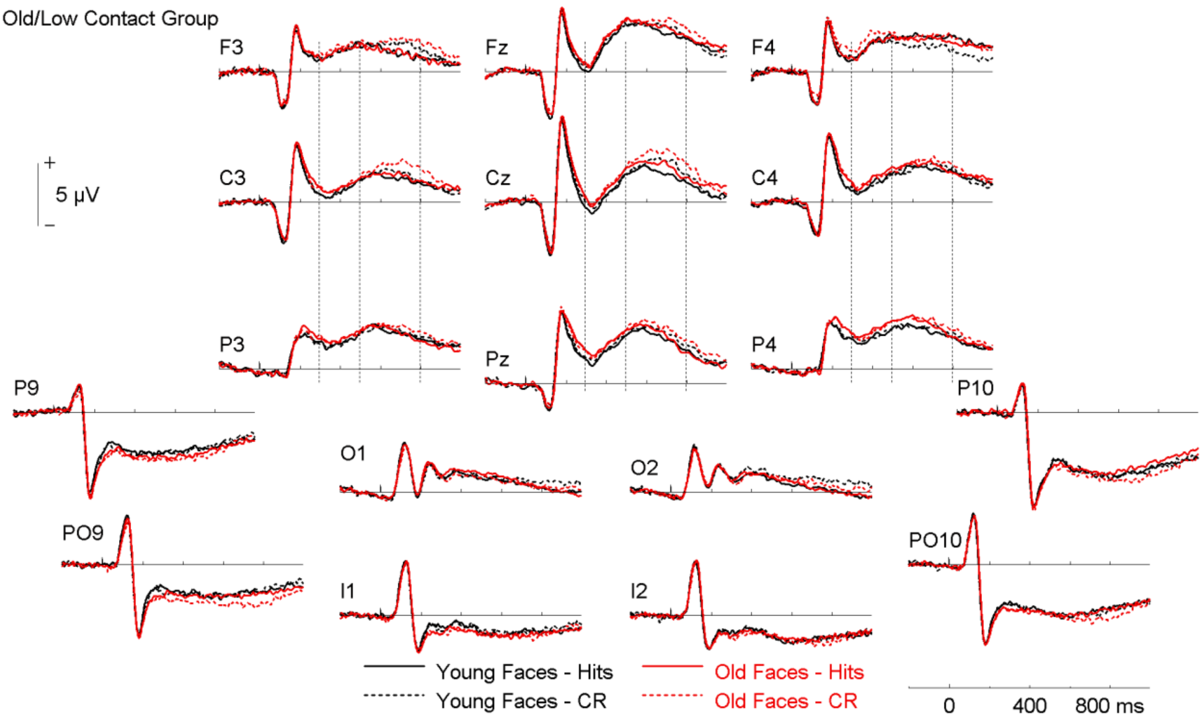

Figure 16. Grand Mean waveforms from the test phases of Experiment 2 in the old/low contact group. CR = correct rejections. Dashed lines depict early and late old/new effect time windows.

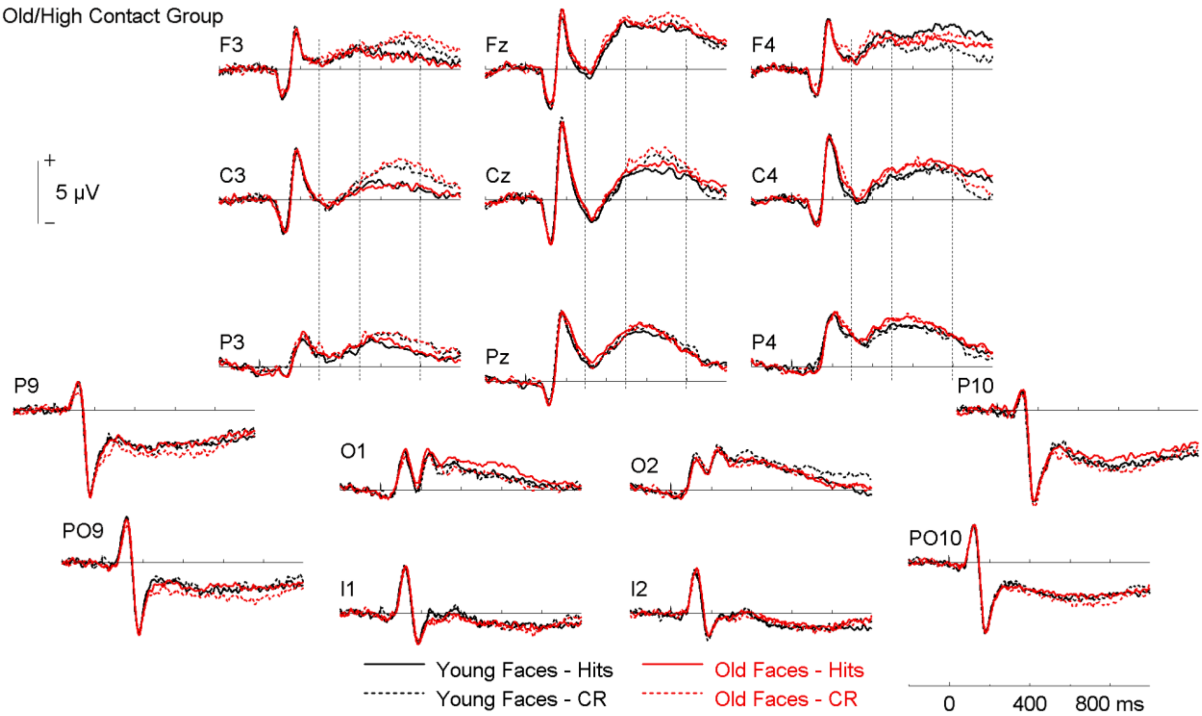

Figure 17. Grand Mean waveforms from the test phases of Experiment 2 in the old/high contact group. CR = correct rejections. Dashed lines depict early and late old/new effect time windows.

P2 (200 - 280 ms in young participants, 260 – 340 ms in elderly participants; see Figure 18). An ANOVA on P2 mean amplitudes yielded a significant main effect of face age, $F(1,57) = 19.72$; $p < .001$; $\eta^2_p = .26$, reflecting more positive amplitudes for young relative to old faces. In addition, there was a significant three-way interaction of Face age x Response x Group, $F(2,57) = 4.21$; $p = .020$; $\eta^2_p = .13$. Separate ANOVAs carried out for the three groups and for old and young faces revealed a significant effect of response for old faces in the old/high contact group, $F(1,19) = 13.71$; $p = .002$; $\eta^2_p = .42$, with more negative amplitudes for CRs as compared to hits, but no significant effect for young faces, $F < 1$. In addition, no significant effects were found in the two other groups (younger adults –young and old faces: both $F < 1$; old/low contact group – young faces: $F[1,19] = 2.50$; $p = .130$; $\eta^2_p = .12$; old/low contact group – old faces: $F[1,19] = 1.46$; $p = .242$; $\eta^2_p = .07$).

N250 (280 – 400 ms in young participants, 340 – 460 ms in elderly participants, see Figure 18). A corresponding ANOVA on N250 mean amplitudes revealed a significant main effect of face age, with more negative amplitudes for old relative to young faces, $F(1,57) = 5.03$; $p = .029$; $\eta^2_p = .08$. Similar to the results in the P2 time range, a significant interaction of Face age x Response x Group, $F(2,57) = 3.34$; $p = .043$; $\eta^2_p = .11$, was detected. Post-hoc analyses in the old/high contact group yielded a significant effect of response for old faces, $F(1,19) = 10.83$; $p = .004$; $\eta^2_p = .36$, reflecting more negative amplitudes for CRs relative to hits, but no corresponding effect for young faces, $F(1,19) = 1.81$; $p = .194$; $\eta^2_p = .09$. Again, no significant effects were detected in the two other groups (younger adults, young faces: $F < 1$, old faces: $F[1,19] = 1.87$; $p = .188$; $\eta^2_p = .09$; old/low contact: both $F < 1$).[6]

Early old/new effect (300-500 ms; see Figures 15-17). Mean amplitudes of the early old/new effect were analyzed via a mixed-model ANOVA with the between-subjects factor group and the within-subjects factors laterality (left, middle, right), site (frontal, central, parietal), face age and response. Several main effects and two-way interactions were all further qualified by two three-way interactions. The interaction of Laterality x Face age x Group', $F(4,57) = 2.56$; $p = .042$; $\eta^2_p = .08$, revealed more positive amplitudes for old as compared to young faces over the right hemisphere in elderly, but not in younger participants (cf. Figures 15-17).

[6] In P1 amplitude, minor differences were obtained, since the previously detected "face age x group" interaction failed to reach significance ($F[2, 57] = 2.00$; $p = .145$; $\eta^2 p = .065$), perhaps due to the smaller statistical power with only half of the original data. In addition, an interaction of "site x face age" ($F[1, 57] = 4.92$; $p = .031$; $\eta^2_p = .079$) was observed, reflecting very slightly larger amplitudes for young faces at O1/O2 (by 0.1 µV) and slightly larger amplitudes for old faces at I1/I2 (by 0.22 µV). No additional effects of face age or interactions of face age x group were detected in any of these analyses.

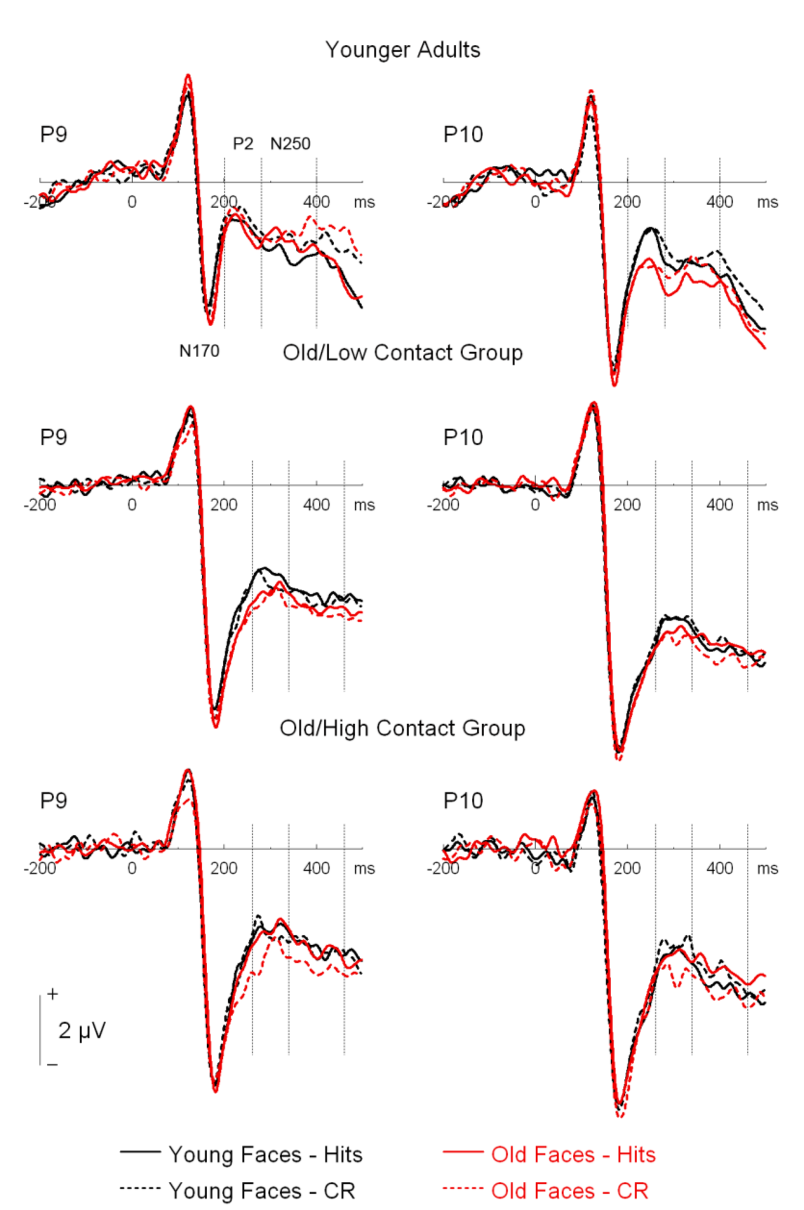

Figure 18. Grand Mean waveforms from the test phases of Experiment 2 at electrodes P9 and P10 for all three participant groups. CR = correct rejections. Dashed lines depict P2 and N250 time ranges.

More importantly for present purposes, an interaction of Site x Response x Group', $F(4,57) = 3.20$; $p = .016$; $\eta^2_p = .10$, reflected old/new effects (with more positive waveforms for hits as compared to CRs) in younger participants only, at frontal, $F(1,19) = 15.75$; $p = .001$; $\eta^2_p = .53$, and central, $F(1,19) = 20.06$; $p < .001$; $\eta^2_p = .51$, but not at parietal sites, $F < 1$; see Figure 19. No corresponding effects were detected in both groups of elderly participants (old/low contact group at frontal sites: $F[1,19]) = 1.63$; $p = .22$; $\eta^2_p = .08$; at central and parietal sites: all $F < 1$; old/high contact group at frontal sites: $F[1,19]) = 1.84$; $p = .190$; $\eta^2_p = .09$; at central and parietal sites: all $F < 1$).

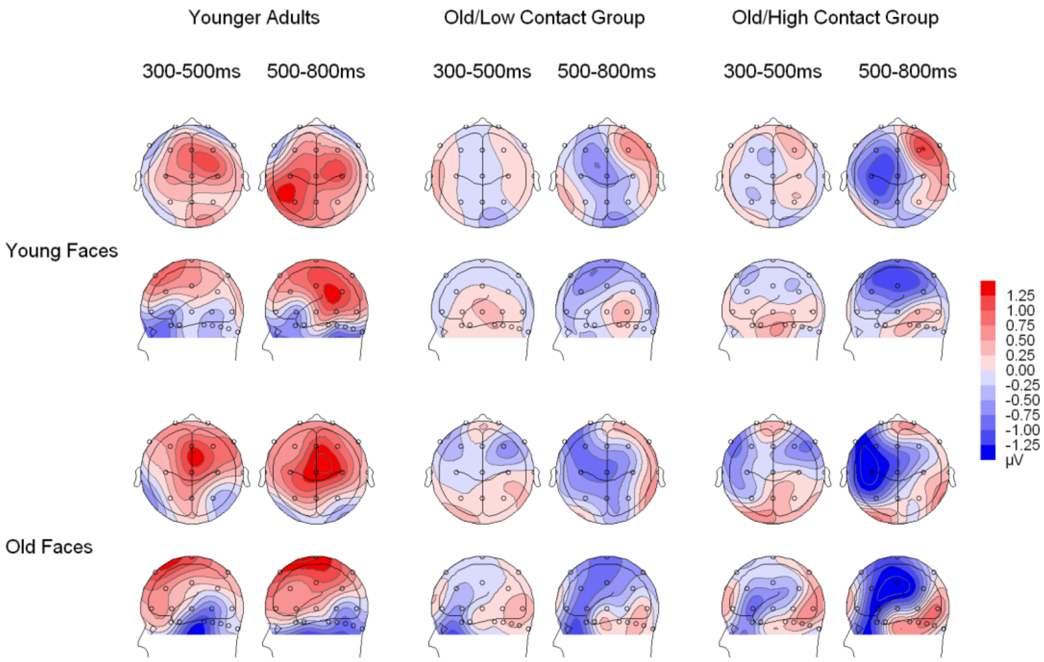

Figure 19. Scalp topographical voltage maps (spherical spline interpolation, 90° equidistant projection) of the old/new effect (hits minus correct rejections) from Experiment 2.

Late old/new effect (500-800 ms; see Figures 15-17). An ANOVA on mean amplitudes between 500-800 ms resulted in a main effect of face age, $F(1, 57) = 7.02$; $p = .010$; $\eta^2_p = .11$. In addition, significant interactions Response x Group, $F(2,57) = 19.48$; $p < .001$; $\eta^2_p = .41$, Laterality x Response x Group, $F(4, 57) = 3.46$; $p = .010$; $\eta^2_p = .11$, and Laterality x Site x Face age x Group, $F(8, 57) = 2.38$; $p = .018$, $\eta^2_p = .08$, were observed.

Crucially for the present study, a significant four-way interaction of Site x Face age x Response x Group, $F(4,57) = 3.01$; $p = .021$; $\eta^2_p = .10$, was detected. To test for differences between participant groups in the scalp distribution of old/new effects for young and old faces, separate analyses for effects of response were carried out for each of the three groups, for old and young faces, and at frontal, central and parietal electrodes. For younger adults, a significant old/new effect, indicating more positive amplitudes for hits as compared to CRs, was found at frontal electrode sites for old faces, $F(1,19) = 19.81$; $p < .001$; $\eta^2_p = .51$, at central electrode sites for both old, $F(1,19) = 11.40$; $p = .003$, $\eta^2_p = .38$, and young faces, $F(1,19) = 15.21$; $p = .001$; $\eta^2_p = .45$, and at parietal electrode sites for young faces only, $F[1,19] = 8.39$; $p = .009$; $\eta^2_p = .31$). In the old/low contact group, no significant old/new effects were found (at parietal sites for old faces: $F[1,19] = 2.46$; $p = .133$; $\eta^2_p = .16$; all other comparisons: $F < 1$). Intriguingly, in the old/high contact group a reversed old/new effect, with more negative amplitudes for hits than CRs, was detected at frontal electrodes for old faces, $F(1,19) = 5.15$; $p = .035$; $\eta^2_p = .21$, and at central electrodes for both young, $F(1,19) =$

4.61; $p = .045$; $\eta^2_p = .20$, and old faces, $F(1,19) = 7.71$; $p = .012$, $\eta^2_p = .29$. No corresponding effect was found at parietal sites (young faces: $F[1,19] = 2.92$; $p = .104$, $\eta^2_p = .13$; old faces: $F < 1$). In summary, in *young* participants, a parietal old/new effect was only detected for own-age *young* faces, whereas *old*/high contact participants demonstrated a more widespread reversed old/new effect for own-age *old* faces, see Figure 19.

5.4 Discussion

Experiment 2 examined whether daily-life contact would affect the occurrence of an OAB in face recognition memory of elderly participants and hence informed about age-preserved flexibility of the face representational system. For that purpose, both younger controls and a sample of elderly participants was tested, and the latter were subdivided into an old/high contact group (with clearly more contact to old as compared to young people) and an old/low contact group (with more similar contact towards old and young people). While young participants clearly demonstrated more accurate memory for young versus old faces, old/low contact participants demonstrated no corresponding bias for own-age faces. Crucially, old/high contact participants yielded more accurate memory for old as compared to young faces, and thus an OAB. These results did not depend on differences in overall performance levels between young adults and the two elderly subgroups. Please also note that the absence of an OAB in old/low contact participants did not seem to result from a general deprivation in contact, as overall memory performance was clearly not reduced when compared to the old/high contact participants.

The present behavioral findings in young participants are clearly in line with the majority of previous studies, depicting an OAB for comparable young adult groups (Backman, 1991; Bartlett & Leslie, 1986; Fulton & Bartlett, 1991; He et al., 2011; Wiese et al., 2008). More importantly, some previous studies reported an OAB in elderly participants (Anastasi & Rhodes, 2005; Backman, 1991; Lamont et al., 2005), while others did not (Bartlett & Leslie, 1986; Fulton & Bartlett, 1991; Wiese et al., 2008). An OAB in elderly participants is of considerable theoretical interest for two reasons: First, since two different interpretations can be inferred from variations of the perceptual expertise account, the examination of two elderly groups differing mainly with respect to daily-life contact towards own-age and young adult people aimed at deciding between those. If lifetime expertise with different age groups dominated face recognition memory, neither of the two elderly groups should have shown an OAB, since both were young in the past and had substantial experience with all adult age groups. At variance with this prediction, only the old/high contact group demonstrated an OAB. The present results therefore support those accounts emphasizing a dominant role of daily-life contact, relative to contributions of lifetime expertise. Secondly and even more crucial for present purposes, it had remained unclear up to now, whether a shaping of the face representational system towards faces of more recent expertise would still occur in older adults. Studies revealing strong modulations of a memory bias in experts for certain groups of faces versus controls exclusively tested young (Harrison & Hole, 2009) or young middle-age adults (Wiese, Wolff, et al., 2013). Importantly, the finding of an OAB in older adults with high levels of daily-life contact to older persons, and the lack of such an effect in older individuals with relatively low levels of contact to their age group, suggests that the face representation system flexibly adapts to environmental or life-style conditions, even with advanced age.

Interestingly, and in line with the above arguments, several previous studies that *did* detect an OAB in elderly participants recruited in retirement communities (e.g. Anastasi & Rhodes, 2005), which suggests increased daily-life contact towards old as compared to young people in these participants. A very recent study (He et al., 2011) tested the effect of contact on the OAB in young (19-29 years of age) and elderly participants (63-92 years). Using regression analysis *across* both groups, these authors reported a significant relationship between the difference of self-reported contact to old versus young persons and a measure of the OAB. Unfortunately, it is not clear whether separate regression analyses for young and elderly participants would have resulted in significant effects. Importantly, when unconfounding age and contact, the present study observed an effect of contact *within* an age-homogeneous group of elderly participants, thus more directly demonstrating the influence of environmental factors on recognition memory. Interestingly, in the study of He et al. (2011), a mixed-model ANOVA revealed no significant memory bias for elderly participants, but a clear effect in the younger participants. With respect to this finding, it should be noted that (1) it is well possible, that, similar to the present study, a high-contact subgroup of elderly participants would have demonstrated a significant memory effect with more accurate memory for old versus young faces, and that (2) this OAB in the elderly participants may have been underestimated in this study, since authors did not correct their measure of the OAB for overall performance levels. Similar to a previous study from our group (Wiese et al., 2008), an uncorrected measure introduces the possibility of a non-significant effect due to reduced sensitivity in lower performance ranges. By contrast, the presence or absence of an

OAB in the present study did not depend on overall performance, excluding the possibility that near floor performance is responsible for the absence of an OAB in the old/low contact participants.

The subgroups in the present study were divided via the amount of time (in hours per week) spent with old as compared to young people. Of note, old/low and old/high contact participants reported a comparable *number of old contact persons*, but old/high contact participants rated the *quality* of contact as more intense. Thus, it seems probable that both time and quality of contact are important.

In addition to the behavioral results discussed above, analysis of ERPs revealed a number of important findings. Replicating results from a previous study (Wiese et al., 2008), old relative to young faces elicited a more negative N170 and less positive amplitudes in the P2 (and in the subsequent N250) in all participant groups. Similar results have been observed in studies on the own-race bias, which yielded both larger N170 (e.g. Caharel et al., 2011; Herrmann et al., 2007; Stahl et al., 2008, 2010) and less positive P2 amplitudes (Stahl et al., 2008, 2010) for other-race as compared to own-race faces. N170 has been associated with early stages of structural encoding and face detection, and an enhanced N170 may be associated with more difficult processing (as, e.g., demonstrated in effects of face inversion on N170; see Bentin et al., 1996; Rossion, Gauthier, et al., 2000a; Wiese, Stahl, & Schweinberger, 2009). Accordingly, structural encoding and/or face detection may be more difficult for old faces. Alternatively, N170 amplitude is strongly related to the processing of the eye region in faces (see e.g. Itier et al., 2007). Reduced contrast in the eye region of old relative to young faces (for instance, due to a more cloudy sclera) may contribute to the N170 increase. The occipito-temporal P2 has been suggested to reflect later stages of structural encoding, such as the processing of metric distances between facial features (see e.g. Latinus & Taylor, 2006) which may be more difficult for old faces. Alternatively, the P2 may reflect the perceived typicality of faces, and young faces may be perceived as being more typical than old faces both by young and elderly participants (who, however, showed somewhat smaller P2 effects both in a previous and in the present study). This interpretation is consistent with recent results, demonstrating increased P2 amplitudes for veridical as compared to caricatured faces (Kaufmann & Schweinberger, 2012), as well as for same- as compared to other-race faces (Stahl et al., 2008, 2010).

Importantly, the above-described effects of face age on the N170 and P2 clearly did not reflect an OAB, as they did not interact with participant group[7]. ERP effects that can be related to the OAB were observed in time windows associated with representational stages of face processing - more specifically in the P2, N250 and old/new effect time ranges. First, in the P2 (and very similarly in the subsequent N250) time range, significantly less negative waveforms for hits (i.e., repeated stimuli) as compared to correct rejections (i.e., non-repeated or new stimuli) were detected for old faces in the old/high contact group only. Previous studies detected *more negative* amplitudes for repeated as compared to non-repeated faces from approximately 200 – 400 ms in immediate repetition priming paradigms (Begleiter, Porjesz, & Wang, 1995; Neumann & Schweinberger, 2008; Schweinberger et al., 1995; Schweinberger, Pickering, Jentzsch, et al., 2002). This effect is known as N250r, and has been related to the access of facial representations for repeated faces. A previous study observed an N250r effect in elderly participants (Pfütze et al., 2002), which was delayed in comparison to the corresponding effect observed in young participants. In a previous study on the OAB, examining explicit recognition memory over longer time intervals, a comparable repetition effect for elderly participants was not detected (Wiese et al., 2008). Interestingly, however, the present reversed repetition effect (which only occurred for old faces) in the old/high contact participants may represent a neural correlate of the behavioral OAB in this group. If so, this may be initial evidence for more efficient access to perceptual representations, and thus presumably implicit memory processes, for own- versus other-age faces in this group. While the mechanisms underlying this finding are not entirely clear at present, it should be noted that reversed effects for hits as compared to correct rejections were also observed in later time ranges in this group (see below).

The young participants in the present study further demonstrated a late old/new effect at parietal sites for own- but not for other-age faces. This finding resembles previous reports of similar effects for either age- or ethnic "in-group" faces (Herzmann et al., 2011; Stahl et al., 2010; Wiese, 2012; Wiese et al., 2008), and thus increased recollection-based recognition memory. These findings are also generally in line with a recent study, which demonstrated enhanced old/new effects for objects of expertise (such as car stimuli for "car experts") as

[7] If N170 and/or P2 reflected processing stages relevant for the behavioral OAB, one would have expected those elderly participants who demonstrated this effect, i.e., the old/high contact group in the present study, to show an opposite pattern of face age effects in N170/P2 amplitude relative to young participants. Consequently, the present results provide no evidence for the idea that early perceptual processes modulate the OAB, and are thus not easy to integrate with a configural/holistic processing account, which assumes more in-depth perceptual processing for own-age faces.

compared to control stimuli (Herzmann & Curran, 2011). However, this interpretation of the left parietal effect as reflecting recollection remains somewhat preliminary, since recollection versus familiarity-based recognition memory were not directly examined (but see discussion below), and some previous results point to a more frontally distributed effect of recollection in face memory (see MacKenzie & Donaldson, 2007)

Most importantly, a reversed old/new effect with more positive amplitudes for correct rejections as compared to hits was detected in the old/high contact group, but not in the old/low contact group. Please note that this group difference cannot be due to differences in overall memory performance between those two groups (see Table 3). Importantly, the reversed old/new effect in the old/high contact group (who also showed a behavioral OAB) was more widespread for own- versus other-age faces. Although such effects are comparatively rarely reported, available evidence can be taken to suggest that the present reversed old/new effect in old/high contact as compared to young participants may reflect qualitatively different processes directed at the recovery of information from study episodes, and presumably an attempt to compensate for reduced recollection (see Friedman et al., 2010; Nessler, Friedman, Johnson, & Bersick, 2007), which may be related to enhanced attentional control (Nessler et al., 2007) and may be successful in some, but not all cases.

Specifically, reversed ERP old/new effects in elderly participants have been reported in tasks that emphasize source memory (Duarte et al., 2006; Li, Morcom, & Rugg, 2004; Swick, Senkfor, & Van Petten, 2006), in which recollection of study phase detail is crucial for succesful performance. In the present experiment, item (rather than source) memory was investigated for unfamiliar faces. Although participants were not explicitly asked to remember study phase information, memory for large numbers of unfamiliar faces may pose considerable demands on recollective processes, given the relatively homogenous stimulus material in the present study. In contrast to studies using verbal material or pictures of objects, participants had to make within-category decisions (i.e., it was not sufficient to remember having seen, e.g., “an old man” or “a blonde woman”). Crucially, as noted above, the ERP effect in the old/high contact group was more widespread for own- as compared to other-age faces. Taken together, the results suggest that the OAB is accompanied by increased recollection and thus more detailed memory for own- as compared to other-age faces in young participants, and a stronger tendency to engage in compensatory processes directed at recollecting study phase detail for own-age faces in elderly participants.

Of note, a number of studies observed more positive amplitudes for correct rejections versus hits in young adult participants in source memory tasks and conditions with high response conflict (see e.g. Johansson & Mecklinger, 2003), an effect termed late posterior negativity (LPN). Interestingly, LPN in source memory tasks has been interpreted as reflecting the prolonged search for and/or retrieval of study episode detail (Herron, 2007). Thus, if one assumed a similar mechanism underlying the LPN in young and the reversed old/new effect in elderly participants, this interpretation is in line with the suggestion of increased effort to retrieve study phase detail for own-age faces in the old/high contact group. It should be noted, however, that the reversed old/new effect in elderly participants both in the present and previous studies (Duarte et al., 2006; J. Li et al., 2004) has a different scalp distribution compared to the LPN, with a more frontal and left lateralized maximum for the former relative to the latter effect.[8] As a qualification (although this limitation is not specific to the present experiment alone), interpretations of reversed old/new effects remain somewhat speculative at present.

To sum up, an own-age bias was observed in young adults and in a subgroup of elderly participants, both reporting substantially more contact towards their own- as compared to the respective other-age group. A corresponding effect was not detected in an elderly subgroup reporting more similar contact towards old versus young people. Thus, time (and presumably also quality) of daily-life contact towards people of different age groups, rather than experience accumulated over the lifespan, predominates the OAB. Importantly, the data thus suggest that the face representation system exhibits substantial plasticity and flexibly adapts to environmental demands, even in higher age. ERP old/new effects specific to own-age faces suggest enhanced recollection of study phase detail in young participants, whereas it may reflect increased engagement in processes aiming at compensating for a deficit in recollection in elderly participants. Moreover, results from the P2 and N250 time ranges may indicate that fluency-based memory processes accompany the OAB in high contact elderly participants.

[8] For the sake of completeness, it should be noted that reversed old/new effects may relate to strategically enhanced encoding of new as compared to old items. This seems less likely for the current study as participants were instructed to respond on the basis of whether the specific items at test were presented in the *directly preceding* learning phase. Deliberately encoding new items is not particularly useful when new items from the test phases do not reappear in the course of the experiment.

6. Discussion of Experiments 1 and 2: Effects of Aging on Early Perceptual and Later Representational Stages of Face Processing

Two studies were conducted to systematically examine selected aspects of face processing in older adults. Whereas Experiment 1 sought to capture age-related effects on the interplay of face perception and memory, Experiment 2 focused on changes of facial representations that were proposed to occur with higher age.

Experiment 1 examined the ORB in a group of high- and low-performing older adults to test whether a potential reduction or lack of this expertise-related bias might index dedifferentiation of the face processing system (Research Question 1a in section 3.5). In addition, it investigated whether decreases in processing efficiency, i.e. impaired configural/holistic processing, indexed by increases in N170, would relate to poor face memory (Research Question 1b). Furthermore, the study addressed the functional significance of the previously reported less lateralized N170 in older as compared to younger adults (Research Question 1c).

Experiment 2 examined the OAB in older adults differing with respect to the amount of contact to older and younger people. The central question was whether the face representational system would exhibit age-preserved plasticity and manifest in a behavioral OAB in older high-contact individuals (Research Question 2a). In addition, the study sought to find corresponding ERP effects indicative of differences in the representation of own-age relative to other-age faces, resulting from differential amounts of daily-life contact (Research Question 2b). Finally, it addressed potential age-related differences in neural correlates between young adults and those older participants who exhibited an OAB (Research Question 2c).

6.1 Behavioral Findings

The main behavioral findings from both experiments reveal the occurrence of memory biases in older participants. In Experiment 1, an ORB for young faces was detected in both high- and low-performing older adults. An equivalent pattern was reported in the only previous study which examined effects of facial race in an older population (Wallis et al., 2012). In the present study, the occurrence of an ORB for young but not old faces could potentially be related to the higher salience of age information in older faces eclipsing ethnicity information. Although this explanation is somewhat speculative, it has been shown that perceptually salient relative to non-salient inputs can capture attentional processing more easily (e.g. Theeuwes, 1994) - in both younger and older adults (Passow et al., in press). In turn, this could have resulted in more efficient processing of ethnicity information in younger (own-race) as opposed to older (own-race) faces and consequently in increased recognition rates for young own-race faces. Moreover, in the present study, diagnostic information related to ethnic group membership may be primarily tied to the eye-region (Asian versus Caucasian faces). Substantial differences in the eye region with respect to altered shape and size (Albert, Ricanek, & Patterson, 2007), a cloudier sclera and reduced contrast (Porcheron, Mauger, & Russell, 2013) are typically more prevalent in older as compared to younger faces. These changes might well conceal ethnicity-related characteristics in the older faces[9]. However, older adults' study phase data does not fully support this idea: No interaction was found between face age and face race, which would have indicated faster ethnicity categorizations for young relative to old faces. Still, it could be argued that the main effect of faster and more accurate categorization according to age indicates that age information was easier to access than ethnicity information, suggesting overall increased salience of facial age cues.

Most importantly, the finding of a behavioral ORB in older adults indicates that expertise-related specialization of the face processing system remains preserved, even if face memory is reduced in older age. High- and low-performers exhibited an equivalent pattern of behavioral results, which was also similar to younger controls in a previous study (Wiese, 2012). Put differently, although face memory was, per definition, poor in low-performing older adults, they reliably exhibited memory differences between young own- and young other-race faces, arguing against the idea of dedifferentiation of the face processing system. This is clearly in line with a perceptual expertise account suggesting that processing is tuned towards those classes of faces most often encountered, i.e. own-race faces. Less finely-tuned processing results in decreased recognition for faces less frequently encountered. If this line of argument is accepted, the lack of an ORB for old faces may at first glance appear somewhat surprising, because older and younger Asian faces are similarly uncommon. Most probably, this is due to the lack or reduction of saliency of ethnic aspects in older faces. A recent study (Bukach, Cottle, Ubiwa, & Miller, 2012) found further support for the notion of perceptual expertise. That study yielded moderate to strong correlations between individuating experience (considered as a measure of quality rather than quantity) with other-

[9] For future studies the systematic comparison of eye region size and its contrast among different sets of stimuli varying in age and ethnicity appears promising.

race persons and holistic processing of such faces in both African American and Caucasian young adult participants. Furthermore, Experiment 1 yields strong evidence that - unlike other cognitive functions (for overviews, see e.g. Baltes & Lindenberger, 1997; Reuter-Lorenz & Park, 2010) - expertise-related face processing mechanisms remain relatively spared, even when overall face memory performance is taken into account.

The idea that deficits in face processing are not necessarily face-specific appears at variance with previous results reporting distinguishable constructs of face perception and memory when compared with general cognitive functioning assessed as e.g. working memory, figural reasoning and mental speed (Hildebrandt et al., 2011). A very recent study, however, examined the specificity of face versus object cognition at the level of latent constructs across the adult life span (Hildebrandt, Wilhelm, Herzmann, & Sommer, 2013). The authors reported a perfect overlap in the relative speeds of object and face cognition (including both perception and memory) in both younger and older adults, arguing against face specificity. In addition, and potentially at odds with the present behavioral results, the accuracy of face and object perception became less distinguishable in older age, which Hildebrandt and colleagues (2013) interpreted as a weak form of dedifferentiation due to neuro-cognitive and not sensory factors (i.e. visual acuity and contrast vision). Further studies using ERPs should aim at contrasting face and object processing (in younger and older age) on representational and mnemonic stages. Previous studies mainly focused on differences in perception between face and non-face categories (e.g. Itier & Taylor, 2004).

Experiment 2 additionally corroborates the idea of a preserved impact of perceptual expertise on face processing in older age. More specifically, levels of recent contact strongly affected the occurrence of the OAB in older participants: Only those participants with significantly higher contact to their own-age group than to younger adult persons exhibited an OAB. Strikingly, there was virtually no difference in the recognition of own- relative to other-age faces in the old/low contact group. The fact that this latter group reported a numerically higher number of persons encountered per week may indicate that an OAB does not depend on exposure per se, but on the quality (and not just on the amount) of social interactions. In line with this idea, the intensity of contact towards own-age persons was also rated reliably higher in the old/high versus old/low contact group. These results to some degree parallel the patterns reported in training studies on the ORB, in which individuation but not more shallow processing (i.e. categorization) was found to influence face memory (Tanaka & Pierce, 2009).

This second study yields evidence for the suggested plasticity in older adults' face processing system. It extends Experiment 1 by showing that the degree of specialization can be strongly modified by self-created environmental demands tied to more recent contact to own-age persons. Although it is more likely that the lack of life-time experience rather than differences in recent contact underlie the ORB in the first study, no definite conclusion can be drawn on the effects of these sub-accounts of the perceptual expertise hypothesis on the ORB. In contrast, Experiment 2 yields strong evidence that more recent contact rather than life-time expertise contributes to the OAB. Besides the fact that this study suggests that differences in contact may account for discrepant results in the literature, this is the first demonstration that expertise can shape the face processing system in older adults. Previous studies supporting contact-based explanations for the OAB showed that work-related expertise influences face processing and memory in pre-school teachers (Harrison & Hole, 2009), maternity ward staff (Cassia, Picozzi, Kuefner, & Casati, 2009) and geriatric nurses (Wiese, Wolff, et al., 2013). Crucially, in those studies participants were of young adult or (young) middle age. Hence, the present study is the first to show that the effects of more recent perceptual expertise appear to override detrimental effects of aging on face processing, i.e. dedifferentiation, and become evident in older adults differing in levels of recent expertise with older faces.

Memory biases are often discussed with reference to socio-cognitive factors. As a brief reminder to the reader, categorization is at the core of these accounts and should be faster for out-group faces. Although faster categorization during learning was detected in the young controls in Experiment 2 - which would be in line with socio-cognitive accounts (Hugenberg et al., 2010; Levin, 1996, 2000) - no corresponding effect was found in older participants across both studies. Hence, the study phase data from age/ethnicity categorization do not support the view that memory biases evolve from selective encoding of category-diagnostic facial features in out-group faces. More importantly, the second study directly contradicts predictions derived from socio-cognitive models, which would have proposed analogous patterns of results in both groups of older adults independent of recent contact. It should be conceded that the CIM clearly suggests a role of motivational factors underlying *enhanced* memory for same- as compared to other-group faces, and similarly that a lack of motivation to process faces individually might result in *decreased* memory even for in-group faces (Hugenberg et al., 2010, p. 1172). This line of argument might be interpreted as reflected in the older adult data in Experiment 2, assuming that the old/low versus old/high contact group was less motivated to process older faces. Clearly however, CIM does not represent the most parsimonious account to explain these results due to several additional specifications, such as perceiver motives and individuation experience. In addition, the validity of socio-cognitive explanations with respect to the findings on both the ORB and on the OAB might be more convincing if additional measurement of implicit or explicit motives were tested concomitantly.

A potential concern regarding the present experiments might be that face memory is examined using the same images during study and test, and it could be argued that picture memory rather than face memory was tested. However, the occurrence of face memory biases in both Experiment 1 and 2, and the finding that these biases can be modulated by contact (as shown in Experiment 2) clearly argues against this objection, and bears evidence that the present results do not (exclusively) reflect picture memory.

In sum, and with regard to Research Questions 1a and 2a, the behavioral results from both experiments show that face processing remains specialized to faces of expertise in older age and may even exhibit substantial plasticity due to (potentially self-created) differences in environmental conditions or demands. Since the ORB seems more closely related to early perceptual processing, whereas the OAB is linked to facial representations, it may be concluded that the findings from the first study argue for preserved integrity of the fine-tuning of face perception, even if general recognition abilities may be differentially affected in older adults. Preserved integrity in older age may be similarly inferred from the second study with respect to the plasticity of representational processes, even if face memory is substantially reduced for older compared to younger participants. Further conclusions should incorporate the ERP data, especially with regard to distinguishing between sub-processes of face processing.

6.2 Findings from Event-Related Potentials

The following section attempts an integrative discussion of the ERP findings from the two studies. It should be noted that ERP results focus on the test phase in Experiment 2 (OAB study) but on the learning phase in Experiment 1 (ORB study).[10]

P1. Modulations of P1, the earliest component examined for present purposes, were only observed in the second study: Latency was increased for old faces independent of participant age, and no main effect or interaction of the factor group was detected (a different pattern emerged for P1 amplitude, see below). This stimulus effect in latency most probably

[10] Furthermore, regarding early components (P1 and N170), Study 1 provides data from peak analyses, while Study 2 analyzed mean amplitudes.

occurred due to differences in low-level characteristics (contrast, frequency) in the pictures of young and old faces. In line with this idea, a recent study suggests reduced contrast in older faces (Porcheron et al., 2013), and hence decreased contrast might have elicited delayed P1 amplitudes. Of note, several other studies have observed age-related increases in P1 latency (e.g. Ceponiene, Westerfield, Torki, & Townsend, 2008; Rousselet et al., 2010; Wiese et al., 2008; Yordanova, Kolev, Hohnsbein, & Falkenstein, 2004) with both an optical and cortical origin (Bieniek, Frei, & Rousselet, 2013; Celesia et al., 1987). Interestingly, modulations in early visual processing ERPs have recently been shown to strongly depend on age-related decline in visual acuity (Daffner et al., 2013). After controlling for visual acuity, differential effects of age for P1 latency between a group of younger adults (18-32 years of age) and two groups of older adults (young-old: 65-79 years of age; old-old: 80+ years of age) no longer reached significance (Daffner et al., 2013). Although in the present study older adults differed with respect to visual acuity from younger adults, these optical effects were presumably not large enough to cause a delay in P1. In addition or alternatively, it could be speculated that cortical rather than optical factors may more strongly modulate P1[11] (see also Bieniek et al., 2013). Related to this, although shifts in neural activity from posterior to more anterior brain regions have been observed in older adults (e.g. Davis et al., 2008), primary visual cortex has not been found to be affected by structural and functional deterioration as much as prefrontal areas (Raz, Ghisletta, Rodrigue, Kennedy, & Lindenberger, 2010; Raz et al., 2005). Hence, preservation of respective brain areas may account for the lack of age-related differences in P1 in the current and in a number of previous studies (e.g. De Sanctis et al., 2008; Pfütze et al., 2002; Zanto, Toy, & Gazzaley, 2010).

In Experiment 2, increased P1 amplitudes for old faces were apparent in young but not in the two groups of older adults, probably due to age-related differences in contrast sensitivity. Older adults are suggested to be particularly impaired in contrast sensitivity for middle and high spatial frequencies (Spear, 1993). Whereas younger and older faces are presumably similar in low spatial frequencies, older faces hold enhanced spatial frequencies (for similar assumptions, see Wiese et al., 2008), thus explaining the lack of P1 modulation by face age in older adults. At this point, it should be noted that differences between younger and older adults were only detected due to the use of older versus younger faces, indicating a benefit of this experimental manipulation for examining group effects. Generally, reports on

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11 If this were the case, a delayed P1 may index age-related changes in extrastriate visual cortex. Further studies could test this idea by comparing older adults with and without delayed P1 components with respect to structural integrity of this brain region (for instance by applying voxel-based morphometry).

age effects on P1 amplitude have been inconsistent. Analogous to the results from Study 2, amplitudes were not modulated as a function of age in some studies (e.g. De Sanctis et al., 2008; Zanto et al., 2010), but were either increased or decreased in older adults in other studies (e.g. Ceponiene et al., 2008; Falkenstein, Yordanova, & Kolev, 2006; Kolev, Falkenstein, & Yordanova, 2006; Wiese et al., 2008). Interestingly, the study by Daffner et al. (2013), suggested influences of visual acuity on P1 amplitude age differences: When visual acuity was controlled for, larger amplitudes were observed in young-old and old-old participants as compared to younger adults.[12]

Modulations in P1 might also have been expected in the ORB study (Experiment 1) although no younger controls were tested and thus no direct age group comparison can be drawn. Yet impairments in cognitive tasks and sensory-motor operations are thought to be strongly connected in older adults (for sensory deficit and common cause hypothesis, see Baltes & Lindenberger, 1997; Christensen, Mackinnon, Korten, & Jorm, 2001; Lindenberger & Baltes, 1994), and differences within an age group can be as large as between age groups (Salthouse, 2013). According to this hypothesis, differences in memory performance for sensory and early perceptual processes would have seemed likely to occur. However, neither visual acuity, nor contrast vision, nor P1 differed between high- and low-performing older adults. This contradicts the sensory-deficit hypothesis in the sense that no clear relationship between loss in sensory and higher-order cognitive functions could be established on the basis of the present results.

N170. Whereas Experiment 1 yielded evidence for relevant N170 modulations most probably contributing to a behavioral ORB, no equivalent effect was observed in Experiment 2 for the OAB. In Experiment 1, larger amplitudes were found for young Asian relative to young Caucasian faces (but not for old Asian versus old Caucasian faces) in both high- and low performing older adults. Crucially, this finding paralleled the behavioral ORB, which was also found for young but not for old faces. As similar results have been reported in an experiment with both Asian and Caucasian younger adults (Wiese et al, in press), the occurrence of the behavioral effect and an equivalent pattern in ERPs argues for a preserved fine-tuning of the face processing system in older adults, in particular with respect to early

[12] For the sake of completeness: Sometimes P1 has been found to be larger in women, both in young and older adulthood (Celesia & Daly, 1977; Celesia et al., 1987; Fein & Brown, 1987; Langrova, Kremlacek, Kuba, Kubova, & Szanyi, 2012). Please note that in Study 2 younger and older groups were gender-matched, but not the two elderly groups.

perceptual stages captured by N170. Hence, the findings from Experiment 1 corroborate reports on younger adults and support the idea that the ORB is a phenomenon linked to early perceptual processing rather than to representational mechanisms[13] (see below). Furthermore, with respect to Research Question 1b the group-invariant N170 ethnicity effect clearly argues against a strong association between efficiency in face perception and poor face memory.

Although decrements in configural processing have been inferred from reduced or absent inversion effects in N170 in older participants (Daniel & Bentin, 2012; Gao et al., 2009), the current findings argue for preserved sensitivity to configural information in early face perception at least with respect to own- versus other-race (Asian) faces. The reason for these somewhat discrepant results, however, remains open to speculation. One possibility is that different tasks take advantage of configural information to differential extents in older adults[14]. Whereas the studies revealing absent face inversion effects in older adults required passive viewing and target detection (butterfly vs. flower) (Exp. 1 in Daniel & Bentin, 2012; Gao et al., 2009), the present experiment asked participants to memorize (and subsequently) recognize faces. Consequently, younger adults may engage more in in-depth perceptual processes per default when encountering a face, whereas older adults might make this effort only on demand (for a similar idea, see Gao et al., 2009). In addition, participants in the current experiment were slightly younger (Mean age = 69.0; ranging from 60-78 years) than those in the study by Gao and colleagues (Mean age = 72.1; ranging from 61-85 years) and substantially younger than the participants of Daniel and Bentin (2012; Mean age = 77.1; ranging from 70-90 years). It cannot therefore be ruled out that deficits in configural processing efficiency become evident at a higher age.

The sensitivity of N170 to different classes of faces (e.g., Asian versus Caucasian) in older adults seems at variance with findings from neuroimaging studies that show fading of neural specialization in the visual system with older age, particularly in FFA (Burianova et al., in press; D. C. Park et al., 2004; J. Park et al., 2012). Although the current studies cannot resolve these potential discrepancies, it remains an interesting issue why findings from ERP studies argue for similar sensitivity in younger and older adults for both between-category, i.e. face versus object (Gao et al., 2009), and within-category discriminations (in the present study). An explanation for the divergence of fMRI results and the present EEG findings

[13] As a potential qualification, it should be noted that the ORB might indeed be tied to representational stages in a recognition memory paradigm, in which different images are used during study and test.

[14] In this context, it appears noteworthy that the concept of configural processing is often underspecified and only very few researchers exactly define (1) the processes which they refer to with this term and (2) what the exact processes are that the different tasks meant to measure configural processing actually tap into (personal communication with Stefan R. Schweinberger and A. Mike Burton, and see also Burton, 2013).

relates to the fact that the N250 or N250r (discussed below), in contrast to N170, has been consistently localized within the fusiform gyrus (for N250r, see Schweinberger, Huddy, & Burton, 2004; Schweinberger, Pickering, Jentzsch, et al., 2002; for N250, see Kaufmann et al., 2009). Hence, deficits in face processing due to neural dedifferentiation in the fusiform gyrus (or FFA), as reported in the above cited studies (Burianova et al., in press; D. C. Park et al., 2004; J. Park et al., 2012), most probably do not relate to the early perceptual mechanisms captured by N170, but are more likely linked to processes reflected in N250. This, in turn, would be perfectly in line with the age-related alterations in N250 discussed below.

Across both studies, old faces generally elicited larger N170 amplitudes than young faces. Experiment 2 also revealed longer latencies for old faces – although latency analyses were not performed in Study 1, visual inspection of the data did not suggest a corresponding effect. The finding of a larger N170 to old faces is well in line with the literature (Ebner, He, et al., 2011; Wiese et al., 2008) and may (similar to P1) be related to spatial frequency information (see also Halit, De Haan, Schyns, & Johnson, 2006). Besides, others (Wiese et al., 2008) have argued that older adult faces elicit larger N170 amplitudes similar to inverted faces because they may either be more difficult to structurally encode (for similar reasoning on inverted faces, see Rossion et al., 1999), or processed less holistically and in a more feature-based fashion (for similar reasoning on inverted faces, see Sagiv & Bentin, 2001). As pointed out above, the larger N170 amplitudes for old as opposed to young faces may also index differences in the eye region, such as reduced contrast due to a more cloudy sclera in older age (for effects of N170 in response to eye region, see Itier et al., 2007). However, and as argued above (section 5.4), the N170 age effect may, if anything, only account for the OAB in young adult participants but not in older participants. Thus, early perceptual stages of face processing seem unlikely to be linked to the OAB, but, in concert with the findings from Experiment 1, they exhibit similar sensitivity for different classes of faces in young and older adults.

Findings on general age-related changes on the N170 or N1 component are rather discrepant and, similar to P1, have been discussed recently with respect to visual acuity (Daffner et al., 2013). Some studies detected age-related increases in latency of N1 (e.g. Curran, Hills, Patterson, & Strauss, 2001; De Sanctis et al., 2008) or N170 (Gazzaley et al., 2008; Wiese et al., 2008), but others did not (Ceponiene et al., 2008; Pfütze et al., 2002; Yordanova et al., 2004). Indeed, Daffner and colleagues (2013) showed that age-related latency effects may vanish if visual acuity is controlled for. Similarly, N1 or N170 has sometimes been reported to be increased (De Sanctis et al., 2008; Yordanova et al., 2004), decreased (Ceponiene et al., 2008; Saavedra et al., 2012; Zanto et al., 2010) or not to differ between younger and older adults (Curran et al., 2001; Kolev et al., 2006). Daffner and colleagues (2013) did not detect differences between young and young-old adults, but N170 was attenuated in old-old subjects compared to both younger groups, and these findings held even when controlling for visual acuity. This prompted the interpretation that age-related modulations of the N170 primarily originates from cortical changes. Hence, against the background of the diversity of findings on early visual processing components, differential results regarding the absence of age-related N170 group effects in Experiment 2 and the presence of such effects in a similar former experiment (Wiese et al., 2008) become somewhat less surprising. In addition, it merits comment that overall group effects in the absence of interactions with experimental variables may always be difficult to interpret, as the underlying cause often cannot be sufficiently clarified, and group differences in waveforms may emerge due to anatomical factors such as cranial bone or skull thickness and related variations in conductivity (Chauveau et al., 2004; Law, 1993). This clearly argues in favor of examining systematic variations of effects arising from experimental manipulations in different (age) groups, as implemented in the current studies, instead of testing for mere group effects.

Study 1 found an interesting effect regarding performance-related N170 lateralization. Whereas low-performers yielded a more right-lateralization of N170 amplitude, the component was more bilaterally pronounced in high-performers. Two previous study reported more bilateral distributions of N170 for older as compared to young adult participants (Daniel & Bentin, 2012; Gao et al., 2009), and interpreted this age-related inter-hemispheric difference as a potential compensatory mechanism for age-related deficits in perception. Asymmetry reductions with age are well-documented (Cabeza, 2002) and have been reported in previous ERP studies for perceptual processes in the visual (De Sanctis et al., 2008) and in the auditory domain (Bellis, Nicol, & Kraus, 2000). Importantly, the current study systematically examined the functional significance of a less lateralized N170 and the results suggest that the effect more likely reflects a compensatory mechanism, rather than neuro-cognitive dedifferentiation (Cabeza & Dennis, 2012; D. C. Park & Reuter-Lorenz, 2009; Reuter-Lorenz & Cappell, 2008; Reuter-Lorenz & Park, 2010) - hence answering Research Question 1c. This conclusion is based on the fact that the effect was exhibited by high- but not by low-performers, providing a strong hint for beneficial plasticity in the aging brain. Although the effect is rather small in size, it should be noted that inter-individual variability increases as a function of age (Christensen et al., 1999) a factor that may exacerbate the detection of effects. Of note, visual inspection of the data from Experiment 2 yields no indication of inter-hemispheric differences between young controls and older adults who were not sorted into groups based on performance. Similarly, others have not detected age-related shifts in N170 lateralization, as reported by Daniel & Bentin (2012) or Gao and colleagues (2009), in highly similar paradigms (Wiese et al., 2008; Wolff et al., 2012). As a first overall conclusion that can be drawn from the results so far: Face perception mechanisms as indexed by N170 age and ethnicity effects seem to remain largely intact with older age.

P2. Across both studies, young faces elicited more positive amplitudes than old faces independent of group (for similar results, see also Ebner, He, et al., 2011; Wiese et al., 2008), despite the mentioned differences (comparison of study phase vs. test phase) and slightly different time-windows. As the occipito-temporal P2 has been suggested to reflect later stages of structural encoding (e.g. Mercure et al., 2008), the results may indicate that these processes are more difficult for old faces. Although this is somewhat speculative, it seems probable that the processing of metric distances in older faces might be hindered, as the precise processing of facial features in older faces is more difficult (in line with enlarged N170 components): Age-related changes occur in color and skin texture (Burt & Perrett, 1995), including enhanced wrinkling, and are also apparent in drooping of less pronounced facial features (for review, see Albert et al., 2007), for instance by the apparent shrinking of eye and mouth region (see also Fu, Guo, & Huang, 2010; Porcheron et al., 2013). As such, older faces exhibit fundamental characteristics that youthful faces do not, and conversely do not contain certain other aspects apparent in young faces.[15] This may be related to another interpretation of enhanced P2-amplitudes as reflecting face typicality (Kaufmann & Schweinberger, 2012)see also Ebner, He et al., 2011 for similar interpretation), to the extent that one assumes that in all participants the face prototype is a face of young adult age. A young face prototype in both young and older participants, however, appears not easy to reconcile with an OAB in older adults (as observed in the high contact group in Experiment 2).

Interestingly, besides this main effect of face age on P2 in Experiment 1 - which may be related to the idea that age dominates other features in saliency (e.g., race, see behavioral

[15] Of note, an fMRI study on processing facial age found that older adult faces elicited greater activity than younger adult faces, in right perirhinal cortex in both younger and older adult participants (Komes, Davis, Brooks, & Cabeza, in prep.). This may suggest that both older and younger adults find that elderly faces require greater processing in downstream perceptual processing regions. Moreover, it is in line with a growing body of literature which finds that the same anterior medial temporal regions (perirhinal cortex, parahippocampal cortex) are responsible for integrating multiple features into a coherent perceptual representation (e.g. Tyler et al., 2013).

results section above) - face ethnicity effects in P2 also interacted with hemisphere. Over the left (but not over the right) hemisphere more positive amplitudes were observed for Caucasian versus Asian faces[16]. The finding of more positive amplitudes for own- relative to other-race faces is generally in line with previous research in younger adults (Stahl et al., 2008, 2010; Wiese, 2012), most probably suggesting enhanced processing for these faces. However, the significance of the lateralization remains unclear. More precisely, a clearly left-lateralized P2 race effect has previously been reported in Caucasian experts for Asian faces, whereas the P2 race effect was bilateral in a non-expert Caucasian control group (Stahl et al., 2008). Stahl and colleagues interpreted the absence of the effect in the right-hemispheric P2 as reflecting similarly effective processing, i.e. efficient second-order configural processing (see also Latinus & Taylor, 2006), and/or recognition mechanisms for faces of expertise in the expert group. In a subsequent study (Stahl et al., 2010), a bilateral but numerically larger left-hemispheric pattern of the P2-ethnicity effect (see Figure 3, p. 2035) was found during learning in a task stressing categorical processing but not in an individuating condition (i.e. attractiveness rating). During test, the effect was apparent bilaterally in the categorization group, but in the right-hemispheric P2 only in the individuation condition. Although the authors interpreted the results as consistent with the findings of their earlier study (Stahl et al., 2008), it has to be noted that reductions in amplitude were evident in the experts over the right hemisphere (the ethnicity effect was only found over the left hemisphere), whereas potentially similar reductions in the later study were over the left hemisphere (the ethnicity effect was apparent over the right but not left hemisphere). Moreover, Wiese (2012) found more positive amplitudes for Caucasian faces as compared to Asian faces over the left hemisphere at test, following an age categorization task during the study phase. This may weaken the idea that expertise or in-depth processing contribute to the hemispheric differences of the effect, the extent of which remain somewhat unclear.

Of relevance for the current study, and independent of hemispheric differences, is the similarity of the effect between the young participants in the Wiese (2012) study and the older adults in the current experiment. This argues for preserved tuning of mechanisms reflected in the P2-time range in higher age. Note that whilst N170 is generally preserved (only small latency and amplitude modulations), the overall shape of P2 appears to be more strongly

[16] Of note, research has shown that topographic differences in early components can be heavily influenced by geometric neural generator orientation (Clark, Fan, & Hillyard, 1995). By extrapolating from such results, one could argue that such effects on later ERPs might be even stronger. Nonetheless, I will try to integrate the findings of hemispheric differences in both the P2 and later time-windows into the context of previous research that similarly reported hemispheric differences for ERPs in these time ranges.

affected by aging. This component and other subsequent components obviously appear later in time, are often less steep, and may be shifted in distribution. Nonetheless, the experimental effects are similar to those observed in younger adults in the P2-time range.

N2/N250/Early old/new effect. As in the P2 time range, older faces elicited more negative amplitudes in subsequent time ranges in both studies. It remains unclear whether this finding can be understood as an independent effect or merely carries over from the P2 time range. In the second study, a polarity-reversed N250 effect with more negative amplitudes for new as opposed to repeated old but not young faces was apparent only in the old/high contact group, but no corresponding effects were seen in the two other groups. N250 repetition effects in immediate repetition priming have been suggested to reflect access to facial representation of repeated faces (Schweinberger et al., 1995; Schweinberger, Pickering, Jentzsch, et al., 2002), and hence participants with higher levels of contact to older persons may be able to access facial representations of older as compared to younger adults more easily or more efficiently (for similar interpretation based on findings for young faces in younger adults, see also Ebner, He, et al., 2011). This interpretation suggests an implicit process most probably underlying the behavioral OAB in this participant group. Indeed, ERP polarity-reversals in older adults have sometimes been reported in the literature (in explicit memory tasks, see Duarte et al., 2006; Wolk et al., 2009; see also Friedman, 2013 for review). This finding is also relevant for Research Questions 2b and 2c, revealing an impact of both recent contact and of cognitive/brain aging on neural correlates of face memory. These factors resulted in a polarity-reversed N250 effect in old/high contact participants only, paralleling their behavioral OAB.

Very recently, Wiese and colleagues (2013) examined the OAB in young middle-aged geriatric nurses and controls; whereas the controls exhibited a clear OAB, the experts showed comparable recognition memory for old and younger faces (see above). Importantly, whereas in controls N250 effects were more pronounced (and more anterior) for younger versus older faces - most probably reflecting more efficient re-activation of newly learned representations for own- versus other-age faces - no corresponding effect was apparent in the expert group.

N250 effects are typically interpreted as the old/new (or repetition) effect in the N250 time range measured in the current study at occipito-temporal channels. Incidentally, the N250 may as well be related to an episodic or explicit memory effect in terms of a polarity-reversed FN400 or early old/new effect, which is typically examined at more anterior electrode sites. The FN400 or mid-frontal old/new effect is characterized by more positive amplitudes for hits versus CRs (or misses) in a time window from approximately 300 ms to 500 ms, with a fronto-central maximum. Yet in Study 2, learned faces elicited less positivity than new faces at more anterior electrode sites. Such a pattern is reversed to the expected old/new effect and might be related to cognitive aging, again alluding to research Question 2c (for polarity reversals in older adults, see also Duarte et al., 2006; Wolk et al., 2009). It should also be noted that because it is still a matter of debate (e.g. Lucas, Taylor, et al., 2012) whether or to what extent the FN400 signals implicit or explicit processes, these interpretations may not even be mutually exclusive.

However, and as a further qualification of this reasoning, an early mid-frontal old/new effect in the typical time window (only slightly later in onset and slightly earlier in offset, N250 time window for older adults: 340-460 ms; early old/new effect: 300-500 ms) at more anterior sites was not detected in the older adults but only in the young adults. This seems to contradict the assumption that familiarity is generally spared in older adults (Anderson & Craik, 2000; Jacoby & Rhodes, 2006), although ERP studies have reported deficits in familiarity- based memory before (Duarte et al., 2006). In sum, it remains open to speculation whether the (polarity-reversed) old/new effect at occipito-temporal channels is related to familiarity-based processes, and whether it may operate as a substitute for largely absent FN400 effects in a slightly later time window over more anterior scalp regions.

Other researchers postulate a direct relationship between N250 category effects and expertise. In a training study, Tanaka and Pierce (2009) reported more negative amplitudes for one group of other-race faces (African Americans) which was learned with an individuation task from pre- to post-testing (on the sub-ordinate level); the effect was not apparent for another group of other-race faces (Hispanics) that was learned through a categorization task (on the basic level). Tanaka and Pierce interpreted their findings as a neural correlate of face learning, in line with object training studies, in which participants learned to differentiate between different models of cars or exemplars of birds (Scott, Tanaka, Sheinberg, & Curran, 2006, 2008). Similarly, this interpretation is in line with face learning studies from our group (Schulz, Kaufmann, Kurt, & Schweinberger, 2012; Schulz, Kaufmann, Walther, et al., 2012). At potential variance, a face-category effect with more negative amplitudes for other-race faces was observed during both learning and test in a recognition memory study, and correlated (during test) with the memory bias towards own-race faces in both Asian and Caucasian participants (Wiese et al., in press). With respect to the two previously mentioned studies which focused on expertise effects on the ORB (Tanaka & Pierce, 2009; Wiese et al, in press) some aspects seem remarkable and merit comment. First, the findings are obviously contradictory, at least to some extent. Tanaka and Pierce (2009) reported more negative amplitudes as 'a consequence of individuation training' (Tanaka & Pierce, 2009, p. 129), hence as a result of perceptual expertise. Wiese and colleagues (in press), like Experiment 1, found more negative amplitudes for other-race faces – hence those faces that participants have gained *no or only little* expertise with. Secondly, and more generally, it seems somewhat surprising that both training in several sessions (for about a week) and life-time experiences seem to exert similar effects on face memory and to be equally related to the underlying mechanism, namely expertise. Tanaka and Pierce did not investigate own-race faces, and as a first step to resolve these discrepancies, subsequent training studies should examine own-race faces (faces of life-time expertise) and compare their neural correlates to potential training effects with other-race faces.

In the early old/new effect time window of Experiment 2, older faces elicited more positive amplitudes in older adults than younger faces specifically over the right hemisphere at anterior electrode positions; no such effect was found for the younger adults. In the ORB study (Experiment 1), old faces elicited less positive amplitudes in a similar time window (400-600 ms) at occipito-temporal channels. In Wiese (2012) this effect was not found in the late N250 or early old/new effect time window, but it was visible (though not significant), in younger adults in the earlier P2 time window (see Figure 3, p. 142 in Wiese, 2012). Typically, ERP effects in different time windows are interpreted to relate to different components and hence to different cognitive processes. Nonetheless, in this case one might argue that the P2 effect in the young reflects the same process as the later effect in the older participants, since components appear to be less separable in older adults and are sometimes delayed due to cognitive slowing (Fabiani & Gratton, 2005; Pfütze et al., 2002).

In contrast to this, a very recent study on holistic processing (Wiese, Kachel, et al., 2013) reported old faces eliciting more positive-going waveforms than young faces from 400-600 ms at occipital-temporal electrodes over the right hemisphere. Although there was no interaction with participant group, the effect seemed more pronounced in young as compared to older subjects (see Figure 2 & 3, pp. 310ff). Although direct comparisons across experiments are hard to draw, the differences in polarity for young versus old faces might be related to differential task demands in study versus test phase versus face matching, or to the use of stimuli varying on either one (age) or two (age and race) dimensions.

Interesting is the finding of hemispheric dissociations regarding the processing of facial age and ethnicity in Experiment 1. In the later N2 time-window (400 – 600 ms), effects of facial race were apparent over the left hemisphere at occipito-temporal channels, with more positive amplitudes for Caucasian as compared to Asian faces, which was similarly observed in Wiese (2012). In addition, in the current study the right hemisphere showed itself to be sensitive to the processing of facial age. This face age effect was also apparent in the waveforms for younger adults in the study by Wiese (2012), although it was not statistically significant. Besides the fact that the current (unlike the Wiese study) focused on learning and not test phase data, the implementation of a focus on *both* ethnicity and age information during learning in the present study[17] may have led to increased saliency, and thus to differential neural processing of these characteristics. This, in turn, may have caused significant hemispheric differences when encoding age and race.

One last finding from Experiment 1 that may be related to cognitive aging is a more widespread pattern of the ethnicity-effect, observed bilaterally at more anterior sites (TP-electrodes) in the low- but not in the high-performing group. The broader distribution in concert with low performance might be interpreted as a fading of specialized neural representations due to age-related dedifferentiation (see e.g. Burianova et al., in press; J. Park et al., 2012). As pointed out before, early perceptual mechanisms seem largely intact, whereas later stages involved in individual processing (and representation) of faces clearly exhibit age-related alterations.

Late positive slow wave/Old/new effects. In Study 1, the effects of face ethnicity and age continued throughout the late time window, with more positive-going amplitudes for Caucasian as compared to Asian faces over the left hemisphere, and more positive amplitudes for young as compared to old faces over the right hemisphere at occipito-temporal channels. Evidence from fMRI results from a part/whole task suggests that the left hemisphere might be more involved in feature-based processing whereas the right hemisphere more strongly engages in holistic processing (Rossion, Dricot, et al., 2000). Moreover, facial identity adaptation was observed in a divided-visual field paradigm in left and right FFA only when a face was presented to the right hemisphere. When the face was presented to the left hemisphere, no adaptation was observed in left FFA, which was interpreted as suggesting a superior role of the right hemisphere in face processing (Verosky & Turk-Browne, 2012). The left hemispheric dominance for ethnicity information in Study 1 seems to make sense from a functional perspective, when taking into account evidence indicating that other-race faces are often processed less individually or holistically (e.g. Bukach et al., 2012; Tanaka et al., 2004).

[17] During the learning phases, Wiese (2012) instructed participants to categorize the faces according to age only.

It should be noted, however, that the ERP effects discussed here appeared in later time ranges that are not involved in early perceptual mechanisms, but presumably tied to decision- or response preparation. These processes may have engaged in-depth (re-)processing of stimuli, taking advantage of the different functional potencies of the two hemispheres; alternatively, the effect may be merely carried over from earlier time ranges. Of note, a seminal fMRI study on the ORB revealed generally increased FFA activation for own- versus other-race faces, but only the activation in the left (and not in the right) FFA correlated significantly with the subsequent ORB at test (Golby et al., 2001).

Interestingly, in Study 1 more positive amplitudes were detected during this time window for old Caucasian versus old Asian faces only in the high-performing but not in the low-performing group. This differential coding of same-race/same-age faces might to some extent parallel the results regarding the old/new effect in Study 2. In Study 2, only those participants who exhibited a behavioral OAB, namely young adults and the old/high contact participants, showed an enhanced old/new effect for the respective own-age faces. To potential interpretations come to mind: first, high cognitive functioning might be related to higher amounts of contact – a relationship that has been established in the literature (Hultsch, Hertzog, Small, & Dixon, 1999; Schooler, 1990; Tun, Miller-Martinez, Lachman, & Seeman, 2013) and hence, high-performers might exhibit more contact to other older adults and thus enhanced processing of older Caucasian faces (since these are of higher social relevance). Second, but potentially related to this idea, the difference at encoding for old Asian versus old Caucasian faces might suggest a more specialized face processing system in the high-performers (revealed only by ERPs, not in behavior), similar to the argument that increased amounts of contact shaped the face space in the old/high contact participants in Experiment 2.

This latter result from Experiment 2 thus provides evidence that although face memory abilities are generally decreased in older relative to younger adults, the face processing system still exhibits substantial plasticity. The occurrence of the OAB was accompanied by more pronounced old/new effects for own-age faces in younger and older high contact adults, which were, although polarity-reversed in older adults, interpreted to reflect more recollection-based processes. As pointed out above, polarity reversals are documented in the literature and most probably index compensatory mechanisms aiming at the retrieval of study phase detail (Duarte et al., 2006; J. Li et al., 2004; Swick et al., 2006). In general, the present finding argues for a crucial role of contact affecting brain correlates of episodic face memory (Research Question 2b), which at the same time appears to be restricted by cognitive and brain aging (Research Question 2c).

In general, it should be mentioned that previous research has shown that neural correlates of episodic memory may exhibit material-specificity. When faces (and not word lists) were used as stimuli, an anterior (and not a posterior/parietal) effect was found for recollection conditions, whereas familiarity was reflected at more posterior (and not at fronto-central) sites (MacKenzie & Donaldson, 2007). Although, up to now, there has not been more incremental evidence for these patterns, material-dependent effects in general might at least partly account for some other studies in which no familiarity correlates were found in older adults (for a lack of familiarity-based ERP effects during object recognition in older adults, see Duarte et al., 2006), despite the claims of preserved familiarity in aging (e.g. Jacoby & Rhodes, 2006).

In sum, due to the fact that similar ERP effects for those groups that displayed an OAB in study 2 were not observed in components that reflect early perceptual processes (N170, P2), it seems reasonable to infer that the OAB is most likely not related to early face processing stages. Rather, and supported by the findings in later time-ranges (N250 and old/new effects) the OAB is tied to facilitated implicit (acquisition and/or) access to facial representations, as well as - presumably - to facilitated explicit (storage and) retrieval of own- relative to other-age faces.

6.3. Summary and Outlook

To sum up, the present studies replicated earlier findings on the ORB and OAB and more importantly extended the field of research to older populations. With respect to the main research question it should be noted that

(1 & 2a) Both studies revealed (expertise-related) plasticity in face processing mechanisms even in older age.

(1b) It appears that whilst the fine-tuning of early perceptual processing is largely spared in older adults, memory performance can be substantially decreased – arguing against a strong relationship between deficits in configural/holistic processing and overall age-related decline in face recognition abilities.

(1c) Differences in neuro-cognitive mechanisms during early face processing, as indexed in N170 lateralization, are most probably compensatory in nature and enable some older adults to perform better than others.

(2b) Contact affected neural correlates of facial representations and (explicit) face memory in older participants and

(2c) similarly, age-related alterations were detected in representational and mnemonic stages of face processing.

Study 1 found an ORB in both high- and low-performing older adults. This has several implications. First, on the basis of the reviewed literature and the present ERP findings, the present ORB is presumably linked to early perceptual rather than representational processing, and the tuning of such early face processing mechanisms seems intact in older adults. More precisely, I had assumed that age-related difficulties in configural processing might hinder the emergence of an ORB in older participants and – since face memory abilities are sometimes associated with difficulties in configural/holistical processing (e.g. Chaby et al., 2011), – that the older adults with low levels of face memory (as compared to high-performers) would show a mitigated or even absent ORB. However, this was not the case. Instead, these results extend the findings by Wallis and co-workers (2012) by showing that the ORB is stable even across groups of older adults that differ substantially in face memory performance (for related considerations on within- versus across age group variability in general cognitive functioning, see Salthouse, 2013). In both groups the ORB was of equal magnitude. This finding contradicts the previously postulated direct association between age-related impairments in early perceptual processing and face memory decrements (e.g. Chaby et al., 2011). The ERP results similarly do not indicate modulations directly tied to differences in configural processing, as no differences were detected between high- and low performers when processing facial race. Conversely, a sensitivity of the N170 to ethnicity was detected similarly in high- and low-performers, indicating more efficient early perceptual processing for young own- as compared to young other-race faces in both groups. In a similar vein, Experiment 2 reported larger N170 amplitudes for older faces in both younger and older adults, and independent of the occurrence of a behavioral OAB in the different groups. This can be interpreted as a second hint at preserved integrity of early perceptual processes in older adults.

In study 1, performance-related differences occurred with respect to N170 lateralization independent of processing facial race (or age). This finding extends previous research that similarly reported more bilateral N170 amplitudes for older as compared to younger participants (Daniel & Bentin, 2012; Gao et al., 2009). Previous reports only speculated about the potential compensatory nature of this finding by linking it to high performance; the present study reveals that reduced (or reversed) N170 lateralization indeed most likely reflects an attempt to counteract age-related decline via additional neural circuitry (see also Cabeza et al., 2002; Cabeza & Dennis, 2012; Reuter-Lorenz & Cappell, 2008; Reuter-Lorenz & Park, 2010). As a potential limitation, it should be noted that the face-sensitive N170 is typically reported to be right-lateralized, although several studies yielded no clear evidence for such a lateralization (Rossion, Gauthier, et al., 2000b; Wiese, 2012). The strength of the study, with its focus on variability within the older group, concomitantly compromised a direct comparison between age groups since no younger group was tested. An additional younger control group with a clear right-lateralized N170 might have served as a more solid basis comparing N170 between older groups with different performance levels[18]. At variance with results from Daniel & Bentin (2012) and Gao and colleagues (2009), several other studies (using similar paradigms as the current study) did not report shifts in N170 distribution from right to left in older versus younger adults (Wiese et al., 2008; Wolff et al., 2012). Future work might be directed at clarifying under which conditions a right-lateralized N170 occurs in younger adults and, while controlling for performance differences, examine which factors contribute to age-related differences in N170 lateralization. Related to that, it should also be noted that even though a difference in N170 lateralization between high and low performers was significant, the typical right hemispheric lateralization only approached significance. In addition, future work might also focus on why the ORB only occurs for young faces in both young and older adults (Wiese, 2012) and what exactly makes age information outweigh ethnicity information. For instance, an algorithm could be trained to recognize younger and older Caucasian faces (for a similar idea, see Furl et al., 2002). If age information is more salient than ethnicity information, old Asian faces should then be recognized more easily than young Asian faces.

Furthermore, the clear hemispheric dissociations during age and ethnicity information processing in Experiment 1 starting in the P2/N2 time range might be interesting to pursue and have not been reported so clearly in earlier research (for a left-hemispheric race effect, see Wiese, 2012; for right-hemispheric age effect, see Wiese, Kachel, et al., 2013). In general, it seems promising to report data from study phases, as effects may relate to differing task demands during study versus test, or to different tasks during encoding across different experiments.

[18] For a follow-up study with a young adult control group, it might be worthwhile to consider dividing this group into high-versus low-performers as well. This would circumvent concerns that (potential) differences are not merely related to differences in performance that could occur in any age group (see Riis et al., 2008).

The findings from Experiment 2 yield direct evidence that individual differences in contact shape the OAB and hence the face processing system in older adults. From a developmental point of view, it is very interesting to observe that in both studies the face processing system exhibited expertise-related specialization, despite age differences in recognition performance, despite general age-related neuro-cognitive decline in various domains that may modulate face memory (such as inhibitory decline, see Hasher, Zacks, & Rahhal, 1999), and despite more specific age-related decrements in face processing (Hildebrandt et al., 2011). Even if these findings suggest that expertise-based face processing is relatively spared in higher age, future (ERP) studies should incorporate comparisons to other domains, such as object processing (for relationship of latent constructs between face and object processing, see Hildebrandt et al., 2013).

With respect to later time windows, in Study 2 effects of face category were observed in the N250 time range (and in subsequent windows). Older faces elicited more negative amplitudes in both studies (only over right hemisphere in Experiment 1) and more negative-going waveforms were observed for Asian in comparison to Caucasian faces over the left hemisphere in Experiment 1. These effects have been similarly reported for younger adults (Ebner, He, et al., 2011; Stahl et al., 2008, 2010; Wiese, 2012), and might be interpreted as differential (re-)processing (possibly influencing response selection) of faces belonging to different categories. Moreover and as mentioned above, the N250 has sometimes been related to expertise resulting from individuation training with other-race faces (Tanaka & Pierce, 2009). Training effects on the OAB have not been reported and my recent (as yet unpublished) work from two large-scale training studies has not yielded any evidence that recognition for older faces can be improved in younger adults by individuating practice, even though N250 is modulated by training (Komes, Schweinberger, & Wiese, in prep.). However, if face processing can indeed be shaped through training, it would be interesting to see whether such effects can also be found in older adults, and whether, similar to expertise, they outweigh the effects of aging (at least to some extent). Based on the finding that even short training episodes may yield substantial effects on face recognition abilities in younger adults (Tanaka & Pierce, 2009), together with the evidence from Study 2 of age-preserved neuro-cognitive plasticity in face processing, it may be assumed that older adults do possess the requirements for successful training effects despite cognitive decline. Future training studies may not only be interesting with respect to memory biases, but also for improving older adults' face recognition abilities in general, especially as face recognition represents one potential source for the difficulty of putting names to faces in higher age (for similar arguments, see also James et al., 2008). Future studies should also address the concern of image-dependent picture versus face learning and examine older adults in a memory experiment in which different exemplars of faces are used at test. To my knowledge, no study has as yet addressed age effects in the acquisition of novel facial representations (for a face learning study with young adult participants, see e.g. Kaufmann et al., 2009). Such a study would certainly offer relevant information about age-related changes in the neuro-cognitive processes involved in face learning.

Furthermore, in Study 2 effects of repetition were observed in the old/high contact participants, where correct rejections elicited more negative amplitudes for new relative to previously learned old faces in N250, but not for young faces. This was interpreted as a reversed repetition effect reflecting enhanced perceptual learning, which was similarly found in younger adults for young faces (regardless of face ethnicity, see Wiese, 2012). In the current study, this effect paralleled the behavioral results, with increased recognition memory for old faces in the old/high contact group. Hence, it may be a first correlate of the behavioral OAB in this group. It should be noted that the N250 and the time window for early old/new effects, where effects were only observed in young participants at frontal sites in Experiment 2, substantially overlap in the older population. In connection with the debate on the early mid-frontal (or FN400) effect as an implicit rather than explicit memory effect (Lucas, Taylor, et al., 2012; Paller et al., 2007), this prompts the idea that, instead of a reversed N250 implicit repetition effect, the finding signals an explicit memory effect that may underlie the behavioral OAB. With precaution, it could be argued that implicit processes captured by the component may manifest in an earlier portion of the FN400, whereas explicit processes are more tied to later portions. Though this is highly speculative, this idea would account for the pattern of previous results, but might also vary in validity pending on the use of materials and tasks. In general, it is remarkable that several processes affect the N250 time range (e.g. category versus repetition/memory effects). The results obtained so far certainly offer a lot to pursue in future studies and in order to further disentangle phenomena occurring in this and in similar time ranges.

With respect to old/new effects in general, it seems sub-optimal to only speculate about the ERP effects and their relationship to familiarity and recollection; future studies may benefit from incorporating behavioral measures of those processes, such as remember/know ratings or source retrieval. A very recent study showed that the OAB occurs in younger adults in both recognition and source memory, whereas no effects were observed for the older group (Bryce & Dodson, 2013). In concert with the N250 findings, it could be that the OAB is supported by both recollection and fluency (contributing to either explicit familiarity-based or implicit processes), depending on task demands. If one assumes that familiarity is sufficient for recognition, neural and behavioral correlates of such effects might be more apparent than effects of recollection. In line with this, Wiese (2012) found an early old/new effect more pronounced for own- as compared to other-age faces, and a later parietal old/new effect only for own- versus other-race faces. However, if one accepts the proposition that face recognition relies on recollection more than word recognition does (as outlined in the Introduction, section 2.2), recollection should predominantly contribute to the OAB. These findings tie in with the late old/new effect in the young and the old/high contact group in Study 2, as well as with previous results (Wiese et al., 2008). Interestingly, it has been argued in the literature, that it may be beneficial to equalize performance across age groups and further divide both young and older adults into high- vs. low-performing participants, in order to draw conclusions about age- and not only performance-related differences in neural activity (see e.g. Riis et al., 2008). Taking this claim into account, it is not entirely clear whether the detected reversed old/new effect in older high-contact participants is related to cognitive aging or to inter-individual differences within age groups. In general, a face recognition memory experiment that tests high- and low performing older and younger adults could add to the discussion what causes the previously observed shifts in distribution, polarity reversals and/or reductions of old/new effects in older age, e.g. implementation of differential strategies or compensation counteracting neuro-cognitive decline (Duarte et al., 2006; Wang, de Chastelaine, Minton, & Rugg, 2012; for recent review, see Friedman, 2013). Furthermore, examining memory-related components in elderly participants with differential memory performance could inform about the locus of deficits that determine face memory abilities, or put differently, elucidate which mechanisms enable high performance in face recognition in older age.

As a last idea for closing a gap, to my knowledge no study has yet investigated the OAB in a Dm-Paradigm and only little research exists examining the ORB with such an approach (Herzmann et al., 2011; Lucas et al., 2011). This is remarkable as both the processing- and the representational account of the perceptual expertise model suggest a prominent role for the encoding stage of a face to explain the occurrence of biases. In line with this idea, Herzmann et al. (2011) reported a basis for the ORB both during encoding (Dm-effect), with less positive amplitudes for correctly recognized own-race faces (for Caucasian participants), and during retrieval (i.e. in old/new effects). Lucas et al. (2011) reported larger amplitudes in the N2/P2 time range for other-race faces which were subsequently remembered (and not forgotten) and hence established an association of efficient processing mechanisms and successful remembering for other-race faces, in line with implications from expertise-based processing accounts (Tanaka et al., 2004). With respect to the OAB, it seems promising to look at effects of facial age interacting with participant age, as older adults' memory problems may as well have a basis in both encoding (e.g. Gutchess et al., 2005) and retrieval (e.g. Gutchess, Ieuji, & Federmeier, 2007). Attenuations or alternations (such as polarity reversals in old/new effects) of DM-effects would thus be reasonable to assume. Furthermore, such a study would offer valuable clues about whether memory biases, and in particular the OAB, may be dominated by difficulties in encoding and retrieval, as suggested by representational accounts (Valentine & Endo, 1992).

In the following, the thesis turns towards name processing, and more specifically considers retrieval of inter-item associations between a familiar name and its source. This (sub-) domain of memory is also known to suffer from age-related impairments and therefore likely contributes to failures in person identification and memory (for similar argument, see James et al., 2008).

7. Effects of Aging on Memory for Names

7.1 Introduction to Name Processing

Memory for names is of high social utility and socializing makes up a great part of older adults' everyday life (see also Leirer, Morrow, Sheikh, & Pariante, 1990). Older adults commonly complain about their difficulties in name retrieval (as introduced in section 2.1), both for people they have recently become acquainted with and for highly familiar individuals such as family members or friends (Pires et al., 2012). When older participants are asked to indicate which specific memory skill they would like to improve, memory for people's names (as opposed to memory for dates and facts, or locations of household objects) is designated as top priority (Leirer et al., 1990).

The question arises, what makes naming so difficult, especially as we age? According to Bruce and Young's model of face recognition (1986), a name is fundamentally different from any other information we know about a certain person (for overview, see also Hanley, 2011). Semantic information that ensures recognition of a person and hence makes up a crucial part of a person's identity is stored within a PIN. Names, in contrast, are stored in a different code, and thus, are considered a different type of information. Importantly, the serial, hierarchical order of processing stages in the Bruce and Young model implies that naming can only be successful after prior retrieval of semantic information, such as a person's occupation. Evidence for this assumption was provided by a seven-week diary study in which participants were instructed to keep record of difficulties and errors in person recognition. A common reported difficulty was that despite the availability of detailed semantic information about a person, the corresponding name could not be recalled although it was felt to be on 'the tip of the tongue' (TOT;Young, Hay, & Ellis, 1985). TOT states are defined as the conscious feeling which accompanies the cognitive processes when a to- be- retrieved item is temporally inaccessible leading to failure or slowing of retrieval processes (Schwartz & Metcalfe, 2011). Burke, Mackay, Worthley, and Wade (1991) showed that during a four-week diary study older adults (*M* =71.0 years of age) experienced more TOT states than young (*M* = 19 years) and middle-aged (*M* = 39 years) participants. As compared to object names or abstract words, TOT states mostly occurred across groups for proper names infrequently used. More specifically, TOT states were more frequent in all participants groups for names of acquaintances who had not been contacted recently than for names of famous persons, places or movies/books. However, the number of TOT states for names of acquaintances was significantly larger in older than in middle-aged or young adults. A follow-up laboratory study where TOT states were experimentally induced (see also Brown & Mcneill, 1966) in both young and older adults, replicated the finding of age-related increases in the number of TOT states. Interestingly, older adults reported more TOT states for famous peoples' names than for other word types (such as object names, adjectives, places, see study 2, Burke et al., 1991). More recently, James (2006) showed an increase in TOT states for names but not for occupations with advancing age.

Further evidence suggesting increased difficulties with names versus other semantic information, comes from studies where young adult participants were instructed to learn face-surname versus face-occupation associations (McWeeny, Young, Hay, & Ellis, 1987). At test all faces were presented again, and participants were asked to recall both surname and occupation. It turned out that participants remembered the same item worse when it had been presented as a name as opposed to an occupation label (e.g. Mr. Baker vs. a baker – also referred to as the Baker-baker paradox), even though the authors controlled for potentially confounding variables, such as imageability or frequency. In addition, every single participant recalled the occupation without a name more often than the name without the occupation for a given face. These results support the idea of serial access to biographical information and name generation suggested by Bruce and Young (1986; but see also Burton, Bruce, & Johnston, 1990 for non-serial approach). Using similar paradigms, other researchers could largely replicate greater difficulties in learning names than occupations (e.g. Craigie & Hanley, 1997; Stanhope & Cohen, 1993). It has been concluded that names are learned and stored differently than other information – perhaps because nowadays names are merely perceived as purely arbitrary labels lacking semantic information (e.g. Hanley, 2011; McWeeny et al., 1987).

Cohen (1990) more directly tested this hypothesis by manipulating meaning that can be extracted from names or occupations (and possessions, see Exp. 1). She revealed that the learning advantage for occupations over names vanishes in a condition of meaningful names paired with meaningless (non-existing) occupations (e.g. Mr. Baker – ryman, see Exp. 2). It was concluded that the Baker-baker paradox arises in those cases in which name and occupational label cause potential conflicts (Mr. Baker is a lawyer) and when meaningful and meaningless names are presented intermixed, discouraging subjects from strategic meaningful encoding of proper names.

In sum, empirical evidence supports the notion that names relative to other person information pose greater difficulties for both initial learning and retrieval of familiar names (for review, see Cohen & Burke, 1993; but see also Maylor, 1997). Interestingly, older adults have been reported to show disproportional difficulties in memory for proper names. Although Cohen and Faulkner (1986) pointed out that the age-related deficits in learning new names are comparable to deficits in learning other semantic information (e.g. occupation), others obtained results indicating a special role of names for the formation of new memory associations. These studies will be outlined in the next section

7.2 Associative Memory Deficits for Names in Older Adults

With respect to age-related deficits, James (2004) investigated in detail the disproportionate learning impairments for names over other semantic information in older adults. Two experiments largely following the procedure of McWeeny et al. (1987) found higher error rates in recall for names as compared to occupations in both younger and older adults. Importantly, however, the effect was more pronounced in older adults, prompting the conclusion of increased difficulty in name learning in older adults. In addition, Experiment 2 revealed that although older adults exhibited more commission (recalling wrong information) versus omission (recalling no information) errors than their younger counterparts, commission errors were more prevalent for occupation than for name recall. Hence, the authors concluded that decreases in inhibitory control mechanisms with older age causing higher rates of commissions cannot account for a specific name learning deficit in elderly participants. In a subsequent study, James and colleagues (2008) reported a similar deficit also in recognition, indicating that naming difficulties are not necessarily tied to be more difficult forms of retrieval, such as recall where retrieval cues are entirely absent (for more detailed description, see next paragraph).

Importantly, some of the studies mentioned in section 7.1 primarily aimed at explaining age effects through differences in the architecture of semantic memory, or recall difficulties for some or all of the phonology of a target name. However, forming new face-name associations as well as retrieving existing ones may involve episodic memory components as well. As mentioned above, episodic memory is particularly affected by aging, and the decline in associative memory has been reported to be more pronounced than item recognition (Bastin & Van der Linden, 2006; Naveh-Benjamin et al., 2004; for a meta-anlysis, see; Old & Naveh-Benjamin, 2008). In two recognition experiments using a matching (Experiment 1) and multiple-choice task (Experiment 2) James and colleagues (2008) replicated a disproportionate impairment of face naming in older adults. Unlike recall, recognition does not rely on the retrieval of the phonological form of a target name, and the authors concluded that older adults' deficit is based on age-related difficulties in forming and retrieving face/name associations (James et al., 2008), strongly supporting the associative-deficit hypothesis initially proposed by Naveh-Benjamin (2000). It should be noted, however, that the associative deficit hypothesis cannot explain the specific result pattern of decreased performance for face-name versus face-occupation pairs.

A recent study addressed the question of whether a mediator item, for instance semantic information, could assist with name learning and retrieval, hence diminishing face naming difficulties in older adults (Old & Naveh-Benjamin, 2012). In Experiment 1 both younger and older adults encoded a face together with character information (good vs. bad). In cases where the participants were not able to remember the name at retrieval, they were instructed to try to think back and access the other piece of information encoded with the face. Although the character information was generally remembered better, the mediator information was found to help name memory in both younger and older adults. Interestingly, name memory did not improve accessibility of character information. This further supports the notion of serial access to a name via semantic aspects, and is hence evidence for the absence of a direct link between a name and a face (Bruce & Young, 1986). Importantly, numerically larger mediator effects were obtained for older adults, though this result failed to reach significance. Similar results were obtained in Experiment 2 in which character information was substituted by occupations. This time, mediation effects were of the same size across groups, but in line with previous reports, older adults were more impaired on name memory than on retrieval of occupations. Again, name retrieval benefitted from mediation through occupation information, but not vice versa. The authors concluded that older adults' memory for names can be improved by providing them with the mediator strategy and by actively making use of existing information (Old & Naveh-Benjamin, 2012).

In sum, the studies described above can be taken as incremental evidence for a disproportional deficit in memory for inter-item associations in older age. Importantly, item-context associations have been far less studied with this kind of stimuli – an issue addressed in the next session.

7.3 Associative Memory: The Role of Source Information

It is of great importance to examine associative memory, because the "Integration of disparate elements into a single cohesive representation constitutes the vital characteristic of episodic memory" (H. Park, Shannon, Biggan, & Spann, 2012, p. 81). Remembering details about an event provides the basis for forming unique memory representations enabling us to differentiate between (similar) events. Research in this field not only addresses inter-item associations, in which an association is built between two remembered items (e.g. a face and a name, see above). Of interest are also item-context associations, when an item is bound to its source (e.g. temporal/spatial context, physical format etc.) (Old & Naveh-Benjamin, 2008; H. Park et al., 2012).

As described above, person-related information, such as faces and names has sometimes been used in associative memory tasks, but to a lesser extent in source memory tasks. Here, participants usually learn words in different contexts (see Dywan, Segalowitz, & Arsenault, 2002). For instance, participants were asked to remember the voice in which words were spoken (Senkfor & Van Petten, 1998; Swick et al., 2006; Wilding & Rugg, 1996), the specific task during learning (Addante, Watrous, Yonelinas, Ekstrom, & Ranganath, 2011; Duarte et al., 2006; Duarte, Ranganath, Winward, Hayward, & Knight, 2004), whether items were heard or seen during encoding (Cabeza et al., 2002; Jacoby, 1999; Leynes, 2002). Yet other tasks assessed memory for spatial orientation (e.g. Mollison & Curran, 2012, Exp. 1), color (Cycowicz, Friedman, & Snodgrass, 2001; Ranganath et al., 2004), or frame color of an item (e.g. Mollison & Curran, 2012, Exp. 2). As outlined before, names play such an important role for person identification, and adequate social interactions require not only remembering that one has heard a certain name before, but also to retrieve a specific context in which the name had occurred. In addition, *familiar* names are of a special nature similar to faces (as pointed out before, see section 2.2): As opposed to word lists consisting of concrete nouns, names rely on a within-category specification and represent unique individuals, with a personal history typically available to the name user (Schweinberger, Landgrebe, Mohr, & Kaufmann, 2002). This could influence the way names are processed and remembered. Indeed, it has been shown that name and word recognition can be dissociated on the basis of word frequency effects: whilst word recognition is facilitated for words of high frequency, name recognition is superior for names of low word frequency (Valentine, Bredart, Lawson, & Ward, 1991). Neuropsychological studies on anomia observed a pattern of impaired retrieval of familiar personal (and proper) names but not common names (Fery, Vincent, &

Bredart, 1995; Semenza & Zettin, 1989). Moreover, others reported a selective sparing of personal familiar names relative to impaired retrieval of common and geographical names (Lyons, Hanley, & Kay, 2002; for reviews, see also Semenza, 2006; Semenza, Mondini, & Zettin, 1995). Furthermore, different neuro-functional systems seem to promote memory retrieval for personal (and proper) versus common names in healthy younger adults (Proverbio, Lilli, Semenza, & Zani, 2001). These findings emphasize the special status of familiar personal names and therefore call for the need to incorporate this stimulus class in research on (age-related changes in) source memory. Basic characteristics of source memory are reviewed and presented in the next section.

7.3.1 Characteristics of Source Memory

Source memory is often tested in addition to item memory, and whereas item memory is thought to be sufficiently supported by familiarity, source memory is assumed to predominantly rely on recollection (e.g. Wixted, 2007; Yonelinas, 1999). Impairments in conscious recollection with increasing age have been linked to older adults' deficits in source memory tasks (e.g. Bastin et al., 2013; Cansino, 2009). In line with this idea, Cansino and co-workers (2013) tested a large sample of 1500 participants between 21 and 80 years of age (250 per decade) to systematically examine source memory decline across the adult life span. Using a spatial source task, the authors revealed a linear decrease in performance of -0.6% per year. Age explained 30% of the variation in source memory after taking differences in background variables (such as years of education) into account.

Recent studies suggest a prominent role of familiarity for source memory decisions as well (e.g. Diana, Yonelinas, & Ranganath, 2008). More specifically, Diana and colleagues tested whether instructing participants to form a mental picture of the item with its corresponding background (e.g. red elephant for an elephant in front of a red background), and hence to unitize item and context during learning, would increase familiarity-based processes. These, in turn, were found to enable more accurate source decisions at test, relative to a non-unitized condition in which participants made animacy or size judgments of the items displayed. The findings supported the idea originally proposed by Graf and Schacter (1989) that item and source information can be bound into a single memory representation during learning, a process termed unitization. If at test the item is presented again, the whole unit is reactivated, which elicits a familiarity signal supporting the subsequent source memory judgment. In a more recent study (Bastin et al., 2013), using the paradigm by Diana and colleagues (2008), younger and older adults were tested in two experiments, which yielded evidence that a unitization instruction relative to a condition not promoting a unitization strategy can reduce older adults' source memory deficits. Importantly, measures of familiarity and recollection were calculated for older adults (via receiver operating characteristics, see e.g. Swets, 1996; Yonelinas, 1994). These revealed that recollection contributed equally to source memory under the unitization and non-unitization conditions, whereas familiarity-based processes were more apparent in the unitization condition (Bastin et al., 2013). In line with the idea of more deficient recollection versus familiarity, the authors concluded that preserved performance in the unitization condition reflected older adults' successful reliance on familiarity-based processes. Of note, others also found that familiarity (inferred from remember/know and confidence ratings) assists source memory when the spatial position (left versus right on the screen), but not when frame color was manipulated during learning (Mollison & Curran, 2012). Hence, Mollison & Curran (2012) concluded that instead of unitization, the influence of familiarity depends on more specific associated context features of an item (here spatial information versus frame color).

Importantly, not only recollection and familiarity (as explicit memory processes) have been shown to be associated with both recognition and source decisions. Research shows that source decisions can also be biased by the relative ease of stimulus (re-) processing (see also Jacoby & Dallas, 1981; Kurilla, 2011; Westerman, 2008), often referred to as (implicit) fluency (see also section 2.2).

Kurilla (2011) manipulated fluency during test by means of perceptual priming (Jacoby & Whitehouse, 1989). Initially, participants were presented with a visual and auditory word list with modality intermixed during learning. During test, participants either completed a visual recognition test, followed by a source decision if an item had been judged as old (Exp. 1A) or were asked to make a choice between a heard, seen and new option for each item (Exp. 1B). Importantly, during test, prior to the onset of each item a word was briefly presented (34 ms) between a forward and backward mask. Half of the flashed primes matched the test word (identical words), the other half was a non-match (a different word than the test word). In both experiments, test items that were processed relatively fluently due to the match between prime and test word were more likely to be judged as studied visually than non-fluent test items. Hence, fluency biased the source response in the visual learning condition. In contrast, priming had no effect on the auditory learning condition and thus did not bias the source decisions in this condition. Importantly, induced fluency in the visual condition resulted not only in a bias for the source response, but also increased the number of correct source decisions for visual as compared to auditory test items (Exp. 1A). Similar results were reported in an experiment that varied the context modality between learning and test, i.e. visual versus auditory learning and test (Leynes, Bink, Marsh, Allen, & May, 2003). Source accuracy was reliably higher when study and test modalities were kept constant than when a modality change occurred between study and test.

The Source Monitoring Framework, (SMF, M. K. Johnson, Hashtroudi, & Lindsay, 1993; Mitchell & Johnson, 2009) offers a relatively exhaustive overview of the processes involved in source monitoring and memory. According to the SMF, perceptual characteristics diagnostic for a source judgment could have led either to a fast-acting heuristic decision (i.e. fluency/familiarity-based processes) or to a more deliberate decision involving reinstatement of sensory detail (i.e. recollection-based processes), or both. Both familiarity and recollection are hence assumed to assist correct source retrieval via the same underlying mechanism namely perceptual fluency in the current example. At potential variance with this interpretation, an additional experiment in the series conducted by Kurilla (2011) used confidence ratings and a remember/know rating in the recognition paradigm. This experiment yielded evidence that the fluency manipulation via masked priming affected familiarity more than recollection. It was concluded that the detected influences of immediate perceptual priming on source memory were more likely to result from fluency-induced perceptions of item familiarity rather than experiences of illusory recollection (Kurilla, 2011).

This latter finding reflects the rather common view prevailing in the literature, of a stronger impact of fluency manipulations on familiarity as opposed to recollection (for firm overview of relevant findings, see Lucas, Taylor, et al., 2012). In turn, the potential influences on familiarity prompted the idea that fluency acts as a potential basis for both implicit processes such as priming, and explicit processes such as familiarity (Kurilla, 2011; Lucas, Taylor, et al., 2012). As a potential mechanism, some researchers have suggested that perceptual fluency can give rise to familiarity, if the ease of processing of a stimulus is attributed to its earlier occurrence in a memory experiment (e.g. Johnston, Dark & Jacoby, 1985; Kelley, Jacoby & Hollingshead, 1989). By contrast, others have claimed that perceptual fluency supports implicit perceptual memory, but not explicit familiarity-based recognition (e.g. Wagner & Gabrieli, 1998). This controversy is also reflected in the debate about the functional significance of findings obtained from event-related potentials, i.e. the mid-frontal old/new effect (described in more detail below). As mentioned previously, this ERP effect, also termed FN400, has been interpreted as either indexing (explicit) familiarity-based processes (e.g. Curran, 2000) or (implicit) processes related to conceptual priming (Paller et al., 2007). Independent of the exact functional significance of this effect, it seems reasonable to assume that influences of fluency manifest in the FN400. In concordance with this, some of the above mentioned studies have also reported ERP evidence for an influence of fluency-based processes on source memory. However, prior to a discussion of these in the next section along with age-related alterations of ERPs linked to source memory, some age-related aspects regarding familiarity and fluency should be considered – mainly pointing out that spared fluency with age is not necessarily a blessing.

For present purposes it is worth noting that older as compared to younger adults are more likely to falsely endorse familiar information. Pioneering studies on false memory applied the Deese-Roediger-McDermott paradigm (DRM; Roediger & McDermott, 1995) and revealed that under certain conditions participants show increases in false memory responses. In the DRM paradigm, participants study a list of words that converge to a common non-presented theme, e.g. hospital, injection, illness, operation. At test, participants are likely to falsely remember the non-presented theme, e.g. doctor. This tendency seems magnified in older participants (Norman & Schacter, 1997; Tun, Wingfield, Rosen, & Blanchard, 1998), and has been attributed to older adults' reliance on 'gist' (Brainerd & Reyna, 1998) and/or on deficits in source memory (see e.g. Dodson & Schacter, 2002; M. K. Johnson et al., 1993). Interestingly, study-test repetition showed decreases in false memory responses in younger, but not in older adults, who appeared to base their responses on an increasing familiarity (resulting from repetition) for both studied words and non-presented but internally generated theme words (e.g. Watson, McDermott, & Balota, 2004).

Increased false recognition is not restricted to the DRM-paradigm, which mainly exploits conceptual overlap between words. Familiarity for words has also been manipulated by means of mere repetitions during learning (Jacoby, 1999). Words were studied either visually or auditorily, but critically, were repeated only in the visual learning condition. Younger adults showed gradual decreases in false alarms from one to three word repetitions during learning when asked at test whether a word had been *heard* during learning. Interestingly, source misattributions increased as a function of repetition during learning in the older participants (similarly to a subsequent experiment in which a group of younger adults was forced to respond more quickly, see Figure 20). This was interpreted as reflecting older adults' overreliance on familiarity/fluency, paired with the incapacity to counteract this signal with conscious recollection (Jacoby, 1999; for similar idea, see Shing, Werkle-Bergner, Li, & Lindenberger, 2008). This aspect may well be related to age-related declines or alterations in strategic processes to evaluate a potential source of information, such as memory monitoring (see Mitchell & Johnson, 2009). Such monitoring or strategic processing is particularly crucial in situations when strong familiarity/fluency signals need to be transcended or adjourned to enable potential recollection-based processes and successful retrieval from memory (for similar argument, see Fandakova, Shing, & Lindenberger, 2013).

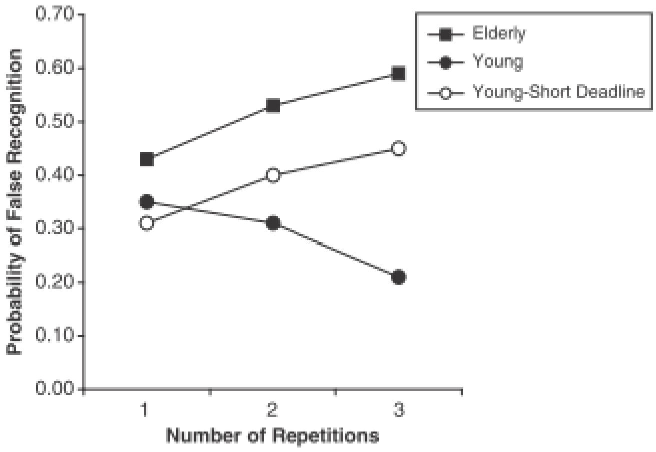

Figure 20. Data from Jacoby (1999). Probability of false recognition increases in the elderly, but decreases in the young as a function of repetition. Young adults show a similar pattern when forced to respond more quickly. Graph taken from Jacoby & Rhodes (2006).

Interestingly, the studies described above, in which fluency-based processes resulted in decreased memory performance, took advantage of the negative effects that accompanied these processes, establishing a situation in which memory monitoring and access to recollection were *particularly* necessary for correct (source) retrieval. One could suggest that older adults' intact fluency-based processes might have the opposite effect in a situation in which fluency signals can be relied on and used efficiently – and thus assist memory (just as much as they were found to hamper memory performance in those situations that brought about the downside of fluency). The second part of the present thesis will follow up on this hypothesis.

7.3.2 Neural Correlates of Source Memory

Research from fMRI studies revealed several (interacting) regions to be involved in source memory formation and retrieval (for review, see Mitchell & Johnson, 2009). Although there is some debate about the specificity of several sub-regions in the medial temporal lobe (MTL), the hippocampus is assumed to be associated with recollection, with Mitchell and Johnson (2009) concluding that greater hippocampal activity for correct versus incorrect source identifications was found in most studies. Research hence suggests that the hippocampus is involved in binding features into complex episodic memory representations. By contrast, perirhinal cortex is assumed to be tied to familiarity, and activations have often been shown to be greater for incorrect source decisions relative to misses (see Mitchell & Johnson, 2009; for a recent study on involvement of the PRC in fluency-based decisions, see Dew and Cabeza, 2013). It has been further suggested that perirhinal cortex may also contribute to contextual processing, especially when an item and its source are unitized (see Diana, Yonelinas, & Ranganath, 2007).

In addition, the prefrontal cortex (PFC) is often found to be engaged in source memory in various ways. For instance, when reviewing fMRI results from source versus item memory judgments, Mitchell and Johnson (2009) inferred that left lateral PFC seems to be more involved in monitoring specific information relevant for source identification, whereas right lateral PFC is more active during evaluation processes of less differentiated information, e.g. recency or familiarity. Furthermore, whereas ventrolateral PFC tends to be more strongly activated during the encoding of and the attention to item features, dorsolateral PFC is more involved in control processes necessary for the organization of various features from an episode (see Mitchell & Johnson, 2009).

In addition to frontal areas, parietal regions appear to be active during both encoding and retrieval, which presumably represents a directing of attention to source features (Mitchell & Johnson, 2009). Moreover, memory research focuses on understanding how activations in parietal regions interact with sub-regions in PFC and the MTL (e.g. Cabeza, 2008; Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Ciaramelli, Grady, & Moscovitch, 2008) Those findings clearly suggest that source memory generally comprises large networks, not least due to the fact that manifold details need to be integrated during encoding and later retrieved in the face of competing alternatives (Dulas & Duarte, 2013).

With respect to ERPs, retrieval of correct source information has been reported to manifest in relatively late (often right-lateralized) frontal ERP old/new effects starting at approximately 500-800 ms and lasting for several hundred milliseconds. These ERPs are assumed to index monitoring and evaluation of retrieval processes (Cruse & Wilding, 2009) including retrieval of source information (Trott, Friedman, Ritter, & Fabiani, 1997). As described above, the preceeding ERP old/new effect with an (often) left parietal maximum between approximately 500-800 ms has been linked to conscious recollection (Rugg, 1995) and has been shown to be more pronounced during remember judgments (e.g. Duarte et al., 2004; Duzel, Yonelinas, Mangun, Heinze, & Tulving, 1997) or correct source identification (e.g. Wilding & Rugg, 1996). It has also been shown to be sensitive to the amount of information retrieved, with larger effects for more abundant retrieval of study phase details (Vilberg et al., 2006). Hence, it has been argued that the parietal old/new effect (almost per definition) reflects source memory processes. An earlier effect, the mid-frontal old/new effect (or FN400), has often been linked to familiarity-based processes (e.g. Curran, 2000; Wolk et al., 2009). In many studies, the FN400 showed no modulations according to varying degrees of retrieved information, such that it was originally assumed to play a minor role in source as opposed to item memory (see Rugg & Curran, 2007).

7.3.3 Neural Correlates of Source Memory in Older Adults

Age-related attenuations of source retrieval have been commonly observed (as implied in earlier sections). For instance, older adults exhibited impaired source memory accuracy and attenuated late frontal (Trott et al., 1997; Trott, Friedman, Ritter, Fabiani, & Snodgrass, 1999; Wegesin, Friedman, Varughese, & Stern, 2002) and parietal (Swick et al., 2006) old/new effects, suggestive of impaired monitoring and/or retrieval of source information and recollection-based processes, respectively. Similarly, others found a diminished left parietal ERP effect in older adults. In addition, the effect was only sensitive to source information, with larger amplitudes for correctly remembered color of background in young but not in older participants (Schiltz et al., 2006). In this latter study, the earlier mid-frontal N400 ERP effect was interpreted to be well-preserved with increasing age, and no significant age-related differences were found. Of note, however, the voltage maps suggest a substantial reduction of the effect in older as compared to younger participants (see p. 993, Figure 1D).

Sometimes reversed ERP old/new effects are observed in older participants. In the study by Swick and colleagues (2006), correct source responses for correctly recognized old items elicited more negative amplitudes than correct rejections. Besides, this pattern was apparent in a late (600-1200 ms) frontally distributed effect lateralized to the left hemisphere. These age-related changes in polarity and scalp distribution were interpreted as a reflection of an effective compensatory mechanism in older adults, applied to maintain performance when faced with declines in more basic memory processes. Similarly, J. Li and colleagues (2004) reported that a left-lateralized and relatively widely distributed relative negativity for old items in older adults reflected old/new effects potentially analogous to parietal effects in younger adults. Referring to previous reports on source memory effects in younger adults, in which similar effects were obtained (Cycowicz et al., 2001), Li and colleagues (2004) suggested that the negative-going ERP wave more likely indicated search processes directed at the recovery of visual information from the study phase than indexing successful engagement in source retrieval. Of note, in an earlier time window between 500 ms and 700 ms a similar phenomenon seemed apparent in the study by Schiltz and co-workers (2006;

Figure 1D), but was not reported to be significant. In a study using a remember/know rating (Duarte et al., 2006), the negative going and frontally-distributed ERP component for hits relative to CRs between 600 ms and 1200 ms in low-performing older adults was suggested to be associated with recollection and was also interpreted as a compensation attempt. Based on the heterogeneity of the described findings, with respect to both differential patterns in neural activity and varying time-windows and scalp-distributions, it is difficult to draw clear conclusions about the neural mechanisms that enable retrieval of source information in older adults.

With respect to recognition studies, it has been proposed that in those tasks specifically emphasizing recollection-based processes in terms of retrieval of study phase detail, an impairment of the parietal old/new effect is typically detectable in older adults (see Wolk et al., 2009). Few studies have reported reduced or absent early mid-frontal old/new effects in older as compared to younger adults (Duarte et al., 2006; Wang et al., 2012), and it has been argued that these attenuations or lack of effects might not be attributable to mere reductions in familiarity for older adults, but to qualitatively different memory signals (Wang et al., 2012). However, as the early mid-frontal effect is associated with familiarity or fluency-based processes, it seems reasonable to assume that this should be largely preserved in older adults (Cansino et al., 2013; Friedman, 2013). In addition, age-related onset delays of old/new effects have also been reported (e.g. Cansino et al., 2013; Duarte et al., 2006) and may result from cognitive slowing (see e.g. Salthouse & Ferrer-Caja, 2003) and/or brain aging (see e.g. Davis et al., 2009).

In sum, neural correlates indexing retrieval of source information do seem to be affected by aging, yet, in a somewhat heterogeneous manner. If anything, both the later parietal and the frontal old/new effect appear to be generally reduced with older age. The mid-frontal old/new or FN400 effect, in contrast, seems more age-invariant (Friedman, 2013), which ties in with the assumption of spared fluency processes in older adults.

7.3.4 Fluency-based ERP Effects and Source memory

The view of a minor role of familiarity-based processes for source memory has been challenged by recent reports. In a study mentioned above (Diana, Van den Boom, Yonelinas, & Ranganath, 2011), a mid-frontal ERP effect for correct versus incorrect source judgments was observed in a condition emphasizing unitization, but not in a non-unitization condition. This was interpreted as reflecting familiarity-based processes assisting source memory. However, the effect was substantially later (i. e. 700 – 1000 ms) than the typical mid-frontal old/new effect described above. Independent of unitization, the early effect was significantly larger for correct relative to incorrect source retrieval, just like in an earlier study for incorrect trials relative to correct rejections of new items (Peters & Daum, 2009). This may indicate that the cognitive system distinguishes between the correct versus incorrect source manifesting in an FN400 effect. Paralleling their behavioral results, Mollison and Curran (2012) reported that a modulation in the mid-frontal old/new effect, differentiating between correct versus incorrect source responses, was only apparent when source memory for spatial information but not frame color for objects was tested. Taken together, these results reflect growing ERP evidence for a potentially important role of familiarity on source memory, though the specific conditions under which the ERP effect occurs in source memory still need to be specified.

Similarly, as noted above, the exact mechanism in terms of explicit or implicit memory, reflected in the mid/frontal old/new effect has not been fully determined. Importantly, researchers have not only claimed that the effect is tied to conceptual priming (Paller et al., 2007), but that it may also be sensitive to perceptual aspects. More specifically, the FN400 was modulated by changes in perceptual features, such as changes in object color between learning and test phases during recognition tasks (Groh-Bordin et al., 2006; for overview, see also Zimmer & Ecker, 2010). Those findings have contributed to the debate about the extent to which the FN400 is actually different from the N400 (Voss & Federmeier, 2011).

Originally proposed to index semantic processing in psycholinguistic research, the N400 has been shown to occur in response not only to words presented in different modalities but also to a variety of stimuli including faces, object pictures and symbols (Kutas & Federmeier, 2011; Kutas & Hillyard, 1980). The N400 is typically measured between 300 - 600 ms with a centro-parietal maximum at least for words in sentences, but the effect may be shifted towards more frontal areas depending on the exact type of word (abstract versus concrete), as well as for pictures of objects or face stimuli (see also Kutas & Federmeier, 2011). It is presumably the most prominent neural manifestation of relatively automatic and implicit semantic processing of a variety of meaningful stimulus categories and is even elicited when subjects show no awareness of a specific stimulus (Vogel, Luck, & Shapiro, 1998), as well as during stimulus repetition in patients with impaired explicit memory (Olichney et al., 2000). Stimulus repetition attenuates the N400, i.e. a repeated stimulus elicits more positive amplitudes than a non-repeated stimulus, and is functionally associated with greater ease or fluency of processing due to previous encounters with an item (see also Voss

& Federmeier, 2011). These similarities between the FN400 and the N400 have motivated researchers to believe that the FN400 is merely a more frontally distributed N400, and hence that it represents implicit processes linked to stimulus repetition in recognition experiments (Voss & Federmeier, 2011). Following this reasoning, and assuming this were the case, an N400 effect should be observable in source memory experiments as well.

Most importantly for the present thesis, the N400 has been examined in person recognition (Barrett & Rugg, 1989; Barrett, Rugg, & Perrett, 1988). Priming effects reflected in N400 have been shown to be larger for familiar as compared to unfamiliar faces (e.g. Henson, Mouchlianitis, Matthews, & Kouider, 2008; Schweinberger et al., 1995). Moreover, such effects can be relatively long-lasting as revealed in long-term repetition priming paradigms, for both familiar faces and names (Schweinberger, Pickering, Burton, et al., 2002). In this latter study, the authors concluded that the N400 effects observed for primed familiar faces but not for unfamiliar faces or names reflected the strengthening of the link between FRUs or NRUs (name recognition units in case of names) and the corresponding PIN: This strengthening resulted in faster and more efficient activation of the PIN with repeated presentation, as well as of related semantic information. This latter interpretation was derived from a structural model of person recognition with an interactive activation and competition architecture (Burton et al., 1990) designed to explain certain phenomena which seemed hard to reconcile with the Bruce and Young model (1986) described above. From the architecture of the Interactive Activation and Competition Model of person recognition (Burton et al., 1990), it can be inferred that different input information (e.g. a face versus a name) presents in different perceptual codes, which means that long-term repetition priming does not cross stimulus domains (e.g. a name cannot prime a face). Similarly, Schweinberger and colleagues (2002) posit that the N400 effect would be diminished in cross-domain priming conditions, reflecting attenuations in priming which occur with changes in perceptual format. Taken together, the N400, as a neural correlate of long-term repetition priming, might emerge in a source memory paradigm that is designed to elicit N400 priming effects. Behavioral (immediate) repetition priming has recently been shown to influence source memory decisions for word lists (Kurilla, 2011), but no ERP study has directly tested whether the N400 might play an important role for source memory similar to the FN400.

7.4 Summary and Aim of Present Studies

To summarize, familiar personal names play a special role in person recognition and identification. Moreover, self-reports as well as experimental research suggests that older adults experience particular difficulties in remembering names (e.g. Cohen, 1990; Cohen & Faulkner, 1986). At the same time, older adults are assumed to be generally more impaired in associative versus item memory (e.g. Old & Naveh-Benjamin, 2008), making them more prone to confuse source information (e.g. Cansino et al., 2013; Jacoby & Rhodes, 2006; Old & Naveh-Benjamin, 2008). Person-related information, such as names, has been largely neglected in source memory research (Dywan et al., 2002), although failures in remembering the specific context in which a name occurred can be detrimental for social interaction. For active older adults, social interactions are of high importance for their well-being. For instance, research has shown that social connection predicted positive changes in depressive symptoms (but not the other way around) in middle-aged and older adults (Cacioppo, Hawkley, & Thisted, 2010).

The second part of this thesis therefore aims at examining source memory for familiar names in older adults. However, since person-related information has rarely been used in investigations on source memory, Experiment 3 and 4 were tested with younger adults with the aim of developing a suitable paradigm. In addition, recent findings have shown that source decisions may not only rely on recollection-based, but on fluency-based processes as well. As it is not yet clear under which circumstances fluency can assist a source decision, the use of familiar names in younger adults in Experiment 3 and 4 made it possible to test directly whether within-modality long-term repetition priming may beneficially influence source decisions. Importantly, source memory has been shown to be strongly affected by aging contributing to memory errors due to the lack of recollection-based processes in concert with an overreliance on spared fluency-based processes. A paradigm which allows for reliance on fluency-based processes via within-modality priming could diminish age-related differences in source memory performance. This hypothesis will be tested with older adults in Experiment 5.

In the following, Experiment 3, 4 and 5 will be described which were conducted to examine

(3a) whether fluency-based processes, catalyzed through within-modality long- term repetition priming, could assist source decisions similarly in both younger and older adults. This would imply that age-related differences in source memory might be less severe if deficient processes (i.e. recollection and monitoring) can be outweighed by spared fluency-based mechanisms;

(3b) whether fluency-based processes manifest in an FN400 or N400-like priming effect associated with correct source retrieval in younger and older adults;

(3c) whether cognitive and brain aging can lead to differences in the neural correlates associated with source retrieval, e.g. in an absent or reduced later, recollection-based old/new effect and in an intact FN400 or priming effect.

8. Experiment 3: Implementing a Design to Examine Fluency Effects on Source Memory I

Abstract

A current debate in memory research is whether and how the access to source information depends not only on recollection, but on fluency-based processes as well. In three experiments, event-related brain potentials (ERPs) were used to examine influences of fluency on source memory for famous names. At test, names were presented visually throughout, whereas visual or auditory presentation was used at learning. In this first Experiment, source decisions following old/new judgments were more accurate for repeated relative to non-repeated visually and auditorily learned names. ERPs were more positive between 300 and 600 ms for visually learned as compared to both auditorily learned and new names, resembling an N400 priming effect, possibly contributing to correct source decisions.

8.1 Introduction

Memory for whether or not we have heard a certain name before is crucial for daily-life social interactions. Often, however, it is important not only to recognize that name, but also to remember in which context the name had occurred. Confusing such information can be embarrassing, and thus prejudicial to social interaction.

Typically, source memory has been examined by experimentally varying different aspects during encoding (such as whether an item was presented visually or auditorily during learning; e.g., Wilding, Doyle, & Rugg, 1995). Moreover, source memory is commonly tested in addition to item memory, and in order to determine *how* a stimulus was remembered. Until recently, there has been scant disagreement that source memory predominantly relies on recollection. However, as described in detail earlier, growing evidence suggests a prominent role of fluency for source memory, but the precise circumstances under which fluency may or may not enhance source decisions are not clear at present. Using familiar names as stimulus material is particularly promising in this context. In contrast to (abstract or concrete) nouns or objects, personal names are relatively pure referents, with little or no inherent meaning (Wittgenstein, 1922), pointing to unique mental representations for individual persons (Burton et al., 1990; Valentine et al., 1991). Fluency-based processes, such as modality-specific long-term repetition priming, easily activate these representations (Bruce & Valentine, 1985). Whereas priming has been investigated in a number of previous studies, source memory for person-related information has been examined relatively scarcely (Dywan et al., 2002; Yovel & Paller, 2004).

Previous studies on name priming yield valuable information for the present purposes. Participants are faster to indicate that a name is familiar if it has been presented previously (Bruce & Valentine, 1985; Pickering & Schweinberger, 2003). Importantly, effects of long-term repetition priming do not cross input modality (see e.g. Burton et al., 1990), which means that, e.g., the prior presentation of a written name results in a faster decision if that same written name is presented again, whereas a spoken name should not prime a familiarity decision on a written name. In an ERP study, repeated relative to non-repeated names elicited more positive amplitudes between 500 - 600 ms (Schweinberger, Pickering, Burton, et al., 2002), resembling an N400 effect (Kutas & Federmeier, 2011), interpreted as reflecting the facilitated access to person-specific representations (see also section 7.3.4). Accordingly, an influence of repetition priming on source memory judgments for person-related information may manifest in N400-like ERP effects.

The present thesis examined source memory for famous names which were either presented visually or auditorily during learning. To test for potential effects of repetition priming on source judgments, all names were presented visually at test, and accordingly half of the names were repeated within the same modality between learning and test, whereas the other half was presented in a different modality. Moreover, half of the names were presented repeatedly during learning, to test whether repetition during learning would differentially affect source memory for visually versus auditorily learned names. Experiment 3 (and 4) aimed at developing and implementing a source memory paradigm to capture fluency effects on source decisions about familiar names in younger adults. Neural correlates of the accompanying processes were examined using ERPs. It was reasoned that an effect of fluency on source memory would emerge in a relatively early time window, possibly in terms of a larger FN400 for visually than auditorily learned names. Alternatively, within-modality long-term repetition may result in an N400 priming effect, with more positive amplitudes for visually learned names as compared to both auditorily learned and new names. In addition, effects of recollection on source memory were assumed to occur in a later ERP old/new effect.

8.2 Method

Participants

The studied population consisted of 20 young undergraduate students (*M* = 23.2 years, *SD* = 2.7, 18 female) at the Friedrich Schiller University, who either received course credit or monetary reward. All participants were right-handed according to a modified version of the Edinburgh Handedness Inventory (Oldfield, 1971) and none reported neurological or psychiatric disorders or receiving central-acting medication. All participants gave written informed consent. Before the experiment, visual acuity and contrast vision (Bach, 1996), as well as cognitive covariates were assessed (see Table 6 and Participant section of Experiment 5).

Stimuli and Design

Stimuli were 400 famous names, taken from a previous rating study (see Wiese & Schweinberger, 2008). Care was taken that names were familiar to young and older adults (see Experiment 3), which was confirmed in additional familiarity ratings carried out after the main experiment. The names were either presented visually (Courier New, font size 28) or auditorily during learning. The auditory stimuli were created via audio recordings from a male speaker vocalizing each of the names. Recordings were made by means of a Beyerdynamic™ MC-930 condenser 146 microphone with pop protection and a Zoom H4n audio interface (44.1 kHz, 16 bit). By means of Adobe Audition™ software, stimuli were normalized to 70 db RMS.

During learning, of 100 spoken names, 50 were presented once and 50 were presented twice. Similarly, 50 written names were presented once and 50 were presented twice. The remaining 200 names were used as new names during test. Assignment of stimuli to each of these five conditions was counterbalanced across participants. During learning, written and spoken names were presented in a pseudo-randomized sequence, such that a minimum of 22 and a maximum of 292 (*M* = 151) intervening items occurred between any repetitions.

Procedure

Participants were seated in a dimly lit, electrically shielded, and sound-attenuated chamber (400-A-CT-Special, Industrial Acoustics, Niederkrüchten, Germany) with their heads in a chin rest approximately 90 cm from a computer monitor. The experimental session began with a series of practice trials, which were excluded from data analysis.

During the learning phase visual and auditory names were presented in an alternating sequence, in which modality changed after every stimulus (see Figure 21). Visually presented names (forename and surname) were displayed horizontally in white font in the center of a black screen. All items were presented at a stimulus onset asynchrony (SOA) of 3000 ms, including an initial fixation cross (500 ms) and a final blank screen (500 ms). Auditory names were presented in mono via Sennheiser headphones. During learning participants were asked to categorize each name via key press as male or female and to memorize the names with their respective source (visual vs. auditory presentation).

In the subsequent test phase, names were presented in white font in the center of a black screen. Each test trial started with a fixation cross (500 ms), followed by a name (2000 ms). Participants were informed that the test list would include names that they had either read or heard earlier (previously learned names) intermixed with an equal number of new names, and that the sets of read and heard names were non-overlapping. They were instructed to indicate via key presses as fast and correctly as possible whether the name was certainly old, probably old, probably new, certainly new, or whether they did not know. Key assignment was counterbalanced across participants. If a name was judged to be old, it remained on the screen (3000 ms) with the instruction to indicate as fast and correctly as possible whether the respective name was certainly heard, probably heard, probably read certainly read, or whether they could not remember the source of the name[19]. If a stimulus was judged new, the next test trial was initiated.

EEG Recording and Analysis

EEG recoding and analysis was identical to Experiment 1, except for the following changes. EEG was segmented from -200 until 2000 ms relative to stimulus onset, with the first 200 ms as baseline. Since insufficient numbers of trials (< 16) were available for conditions with incorrect responses in the majority of participants, only trials with correct responses, i.e. correct rejections or hits plus correct source judgments, entered the analysis.

Trials were averaged according to experimental conditions (correct rejections, non-repeated visually learned hits plus source correct, repeated visually learned hits plus source correct, non-repeated auditorily learned hits plus source correct, repeated auditorily learned hits

[19] Please note that it was collapsed across confidence ratings as too few subjects made use of the option to indicate that a previously studied item was probably old or new or heard or seen for an appropriate number of trials (mean number of key presses was 8 for probably old/new and 7 for probably heard/seen responses) regarding the analysis of ERPs.

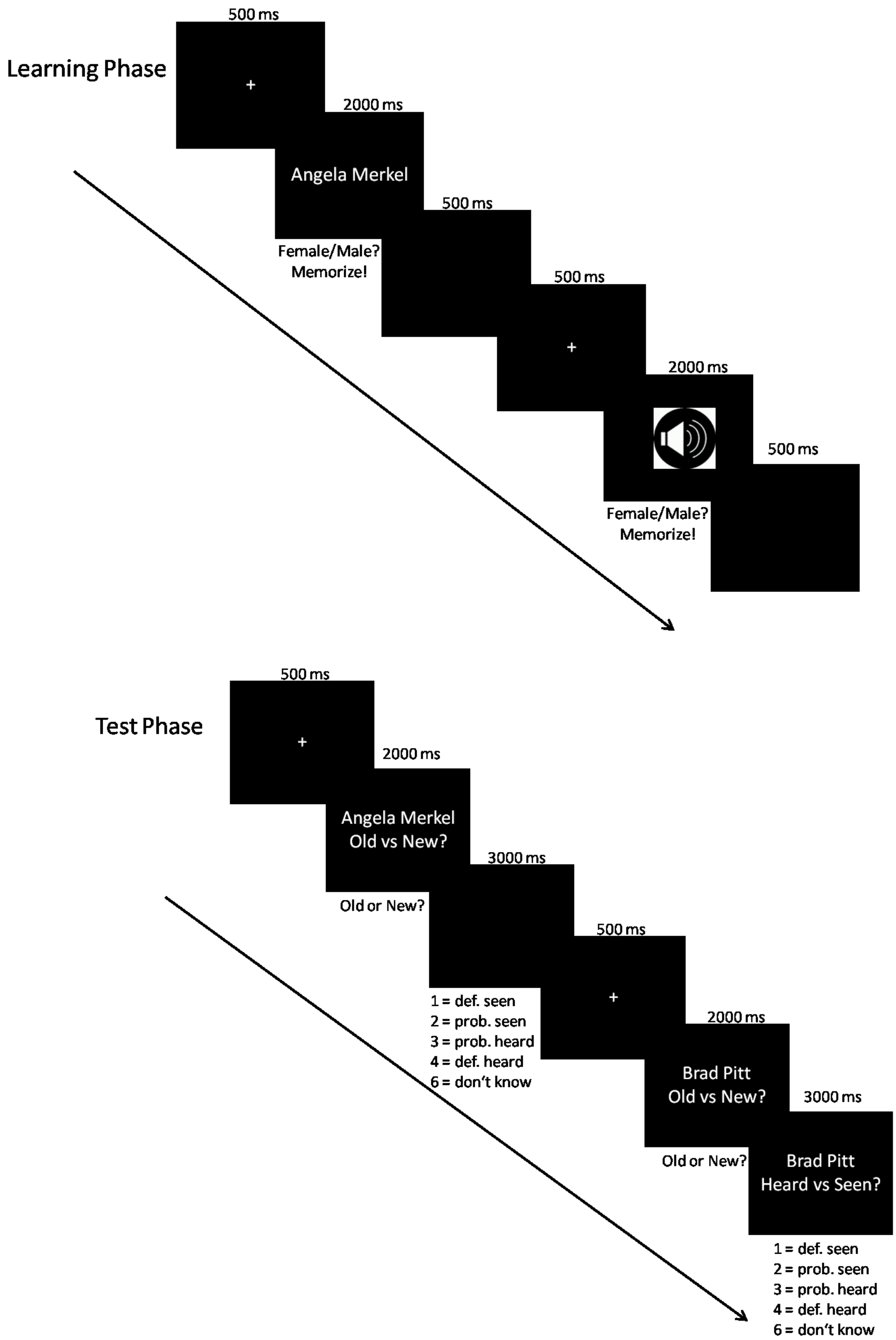

Figure 21. Illustration from learning and test phases from Experiment 3.

plus source correct)[20]. The mean number of trials contributing to an individual averaged ERP for these conditions was 148, 21, 31, 22, and 28, respectively.

[20] Additional analyses on hits including those trials with incorrect source judgments and correct rejections yielded highly similar findings as those reported in the results section. It was refrained from reporting these analyses since they were not of primary interest for the purpose of the present study.

Two time ranges from 300 to 600 and from 600 to 900 ms were analyzed, which have been related to familiarity/conceptual priming and recollection, respectively. Visual inspection of the data suggested a further analysis in a more restricted time range (400 – 500 ms). Moreover, after inspection of the scalp distribution of old/new effects it was decided to analyze the two earlier time windows at midline sites (Fz, Cz, Pz). As the later old/new effect is typically left-lateralized for verbal material, the 600 – 900 ms time window was tested in a larger grid of electrodes, additionally including lateral sites (F3/F4, C3/C4, P3/P4). Statistical analyses were performed by calculating repeated-measures analyses of variance (ANOVA), with degrees of freedom corrected according to the Greenhouse-Geisser procedure where appropriate.

8.3 Results

8.3.1 Behavioral Results

Old/new recognition accuracy. A repeated measures analysis with the factor condition (visually learned non-repeated, visually learned repeated, auditorily learned non-repeated, auditorily learned repeated and new) resulted in a significant effect, $F(1.32, 24.98) = 11.20$; $p = .001$; $\eta^2_p = .25$. Follow-up t-tests indicated higher accuracies for correct rejections as compared to both non-repeated visually, $t(19) = 2.50$; $p = .021$; $d = 0.91$, and non-repeated auditorily learned names, $t(19) = 3.21$; $p = .005$; $d = 1.02$. Furthermore, repeatedly relative to non-repeatedly learned names resulted in higher accuracies in both the visually, $t(19) = 7.32$; $p < .001$; $d = 1.29$ and auditorily learned condition, $t(19) = 7.52$; $p < = .001$; $d = 1.20$; see Table 4a. No further differences were detected, t ranging from 0.45 – 1.54; p ranging from .964 - .140.

Reaction times. A corresponding analysis on mean reaction times for correct old/new responses resulted in a trend, $F(2.43,46.17) = 2.62$; $p = .073$; $\eta^2_p = .12$, pointing towards slower responses for auditorily learned as compared to visually learned or new names; see Table 4a.

Source memory accuracy[21]. A repeated measures analysis on correct source judgments (see Table 4b) with the factors modality during learning (visual versus auditory) and repetition during learning (non-repeated versus repeated) resulted in a significant effect of

[21] We decided not to analyze mean RTs for the source decision since the respective stimulus was already on the screen during the preceding old/new task. Hence, it is not possible to clearly determine the timing of the source decision.

repetition, $F(1,19) = 14.52$; $p = .001$; $\eta^2_p = .43$, with higher source accuracies for repeated relative to non-repeatedly learned names. Although repetition during learning appeared to be more pronounced for visually learned names, the interaction of modality during learning by repetition during learning was not significant, $F(1,19) = 1.63$; $p = .217$; $\eta^2_p = .08$.

Table 4a. Means and Standard deviations (SD) of accuracies and reaction times (ms) for correct old/new responses from Experiment 3.

Condition	Accuracy	RT (ms)
New	.82 (.20)	1292.75 (187.47)
Non- Repeated Auditory	.65 (.12)	1348.37 (185.35)
Repeated Auditory	.80 (.13)	1363.75 (182.22)
Non- Repeated Visual	.66 (.16)	1256.12 (204.79)
Repeated Visual	.82 (.09)	1249.52 (153.70)

Table 4b. Means and Standard deviations (SD) of accuracies for source decisions from Experiment 3.

Condition	Accuracy
Non- Repeated Auditory	.80 (.13)
Repeated Auditory	.83 (.12)
Non- Repeated Visual	.76 (.17)
Repeated Visual	.84 (.12)

8.3.2 Event-Related Potentials

Grand Mean ERPs for each of the experimental condition of Experiment 1 are depicted in Figure 22.

300-600 ms. An ANOVA with factors site (Fz, Cz, Pz) and condition (non-repeated visually learned, repeated visually learned, non-repeated auditorily learned, repeated auditorily learned and correct rejections) revealed an effect of condition, $F(4,76) = 4.57$; $p = .002$; $\eta^2_p = .19$. Relative to correct rejections, non-repeated visually learned names, $F(1,19) = 4.98$; $p = .038$; $\eta^2_p = .21$, repeated visually learned names, $F(1,19) = 18.89$; $p < .001$; $\eta^2_p = .21$, and repeated auditorily learned names, $F(1,19) = 7.91$; $p = .011$, $\eta^2_p = .29$, elicited more positive amplitudes. No differences were detected between correct rejections and non-repeated auditorily learned names, $F < 1$.

Furthermore, among hits plus correct source judgments, an ANOVA with the factors site (Fz, Cz, Pz), modality during learning (visual, auditory), and repetition during learning (non-repeated, repeated) yielded effects of learning modality, $F(1,19) = 12.47$; $p = .002$; $\eta^2_p =$

.40, with more positive amplitudes for visually relative to auditorily learned names, and of repetition during learning, $F(1,19) = 8.54$; $p = .009$; $\eta^2_p = .31$, with more positive amplitudes for repeated relative to non-repeatedly learned names; see Figure 22.

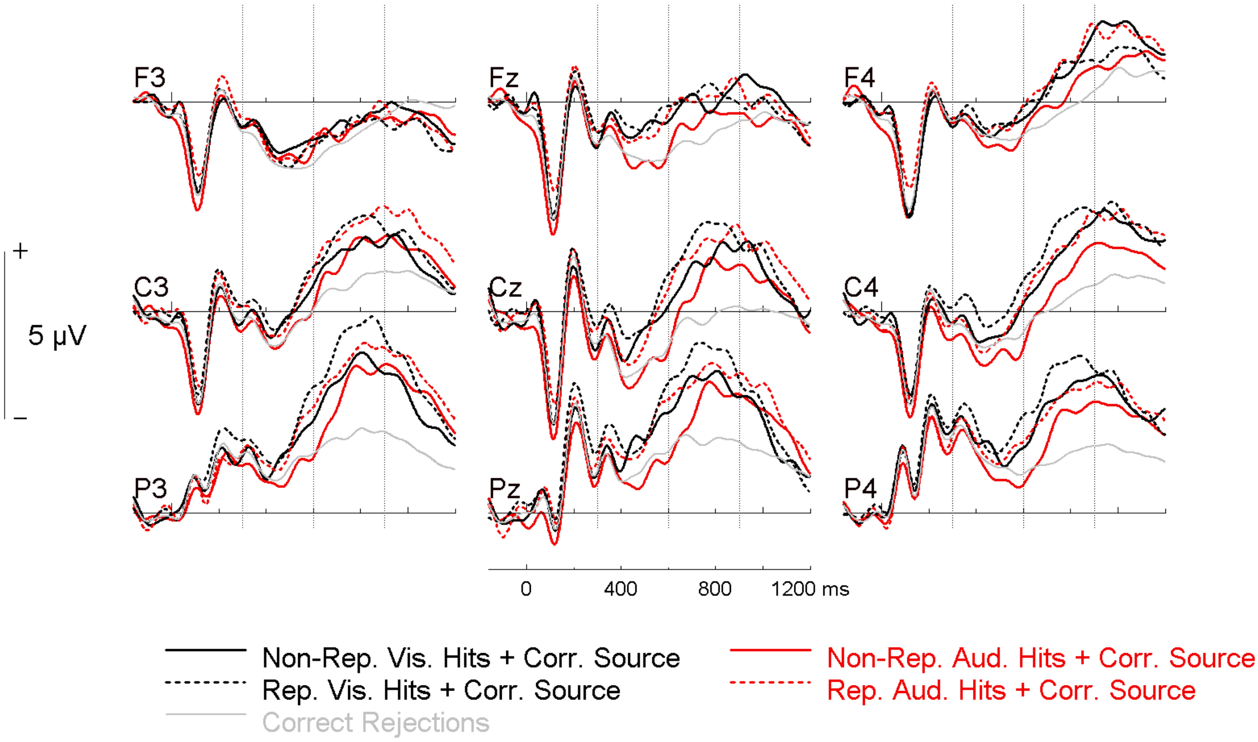

Figure 22. Grand Mean waveforms for correct source memory and correct rejections from the test phases of Experiment 3. Dashed lines depict the 300 – 600 ms and 600 – 900 ms time windows.

400-500 ms. An ANOVA with the factors site (Fz, Cz, Pz) and condition (as above) resulted in a significant effect of condition, $F(1,19) = 4.75$; $p = .002$; $\eta^2_p = .20$. Relative to correct rejections, non-repeated visually learned, $F(1,19) = 5.50$; $p = .030$; $\eta^2_p = .23$, and repeated visually learned names, $F(1,19) = 17.04$; $p = .001$; $\eta^2_p = .47$ elicited more positive amplitudes. No differences were detected between correct rejections and non-repeated auditorily learned, $F < 1$, or repeated auditorily learned names, $F(1,19) = 2.60$; $p = .12$; $\eta^2_p = .12$; see upper part of Figure 23.

As above, an analysis on hits plus correct source items was also conducted via an ANOVA with the factors site (Fz, Cz, Pz), modality during learning, and repetition during learning, which resulted in a main effect of learning modality, $F(1,19) = 12.60$; $p = .002$; $\eta^2_p = .40$, with more positive amplitudes for visually relative to auditorily learned names, see Figure 24.

600-900 ms. An ANOVA with the factors laterality (left, midline, right), site (anterior, central, posterior position), and condition yielded an effect of condition, $F(4,76) = 13.56$; $p < .001$; $\eta^2_p = .42$. Relative to correct rejections, more positive ERP were elicited by all other conditions (non-repeated visual: $F(1,19) = 17.78$; $p < .001$; $\eta^2_p = .48$, repeated visual: $F(1,19) = 43.36$; $p < .001$; $\eta^2_p = .70$, non-repeated auditory: $F(1,19) = 5.78$; $p = .027$; $\eta^2_p = .23$, repeated auditory: $F(1,19) = 46.04$; $p < .001$; $\eta^2_p = .71$; see Figure 22.

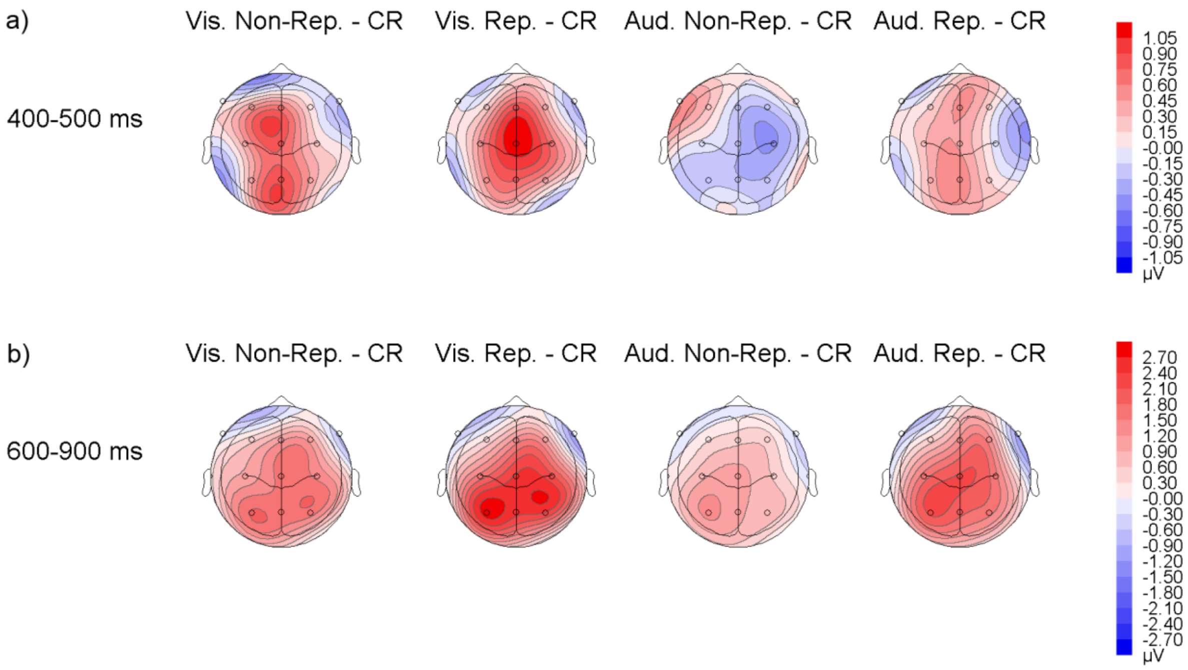

Figure 23. a) Scalp topographical voltage maps (spherical spline interpolation, 90° equidistant projection) between 400 and 500 ms displaying the difference between correct rejections and hits plus correct source for each condition in Experiment 3. *b)* Scalp topographical voltage maps (spherical spline interpolation, 90° equidistant projection) between 600 and 900 ms displaying the difference between correct rejections and hits plus correct source for each condition in Experiment 3.

Again, an analysis on hits plus correct source decisions was also conducted via an ANOVA with factors laterality, site, modality during learning and repetition during learning and revealed a main effect of learning modality, $F(1,19) = 5.51$; $p = .030$; $\eta^2_p = .23$, with more positive ERPs for visually relative to auditorily learned names and a main effect of repetition during learning, $F(1,19) = 8.30$; $p = .010$; $\eta^2_p = .30$, with more positive ERPs for repeated relative to non-repeatedly learned names; see lower part of Figure 23.

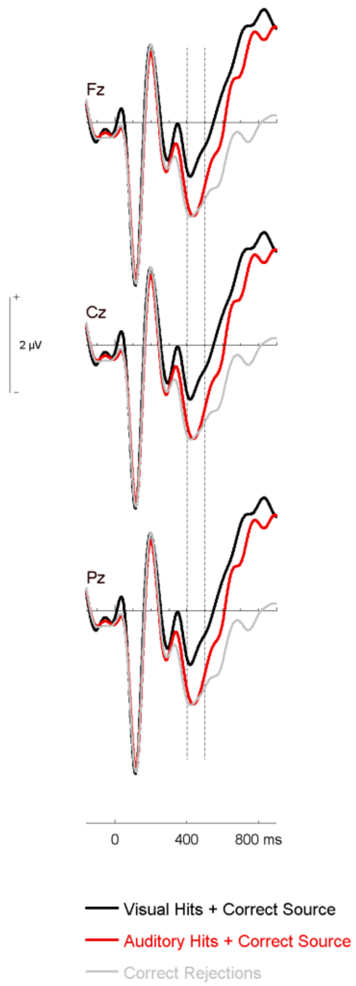

Figure 24. Grand Mean waveforms for visual and auditory hits plus correct source and correct rejections from the test phases of Experiment 3. Dashed lines depict the 400 – 500 ms time window.

8.4 Discussion

Experiment 3 tested item recognition and source memory for familiar names. Unsurprisingly, more accurate item memory was found for those items repeated during learning. Similarly, repetition during learning enhanced correct source decision, which appeared to be particularly pronounced for visually learned items (although the corresponding interaction was not significant in Experiment 3, see Table 4b).

More positive ERPs were detected from 300 – 600 ms for visually learned hits (plus correct source decisions) relative to correct rejections, while old/new effects for auditorily learned items were substantially smaller (when repeated during learning) or absent (when non-repeated). In a more restricted time range from 400 – 500 ms, no old/new effects were detected for auditorily learned names, while visually learned names elicited a substantially larger positivity, independent of repetition during learning. It is well established that within-modality repetitions lead to enhanced fluency relative to between-modality repetitions (see Kurilla, 2011; Richardson-Klavehn & Gardiner, 1996; Roediger & Blaxton, 1987). Our ERP findings may therefore either reflect an FN400 old/new effect, which is substantially larger for visually learned items, or an N400 priming effect for those items presented in the same modality during learning and test (see also Joyce, Paller, Schwartz, & Kutas, 1999). Independent of their exact interpretation, ERPs in the early time windows indicate an influence of fluency on source memory (or item memory, an issue addressed in Experiment 4).

In a subsequent time window from 600 – 900 ms, larger old/new effects were detected for repeatedly relative to non-repeatedly learned names. This finding is well in line with previous studies demonstrating larger old/new effects in this time range with increasing amounts of retrieved information (e.g. Vilberg et al., 2006). Hence, repetition during learning in the present experiment may have fostered the retrieval of more detailed study phase information. In addition, larger old/new effects for visually than auditorily learned items were observed. This finding may not be independent of the earlier effect, which was more pronounced for visually learned items, but may instead reflect a similarly pronounced later old/new effect, which builds upon an earlier difference between hits and correct rejections in the visual but not in the auditory modality.

In sum, ERP results suggest that both fluency- and recollection-related processes modulate source memory for familiar names. As a qualification, it is not clear from Experiment 3 to what degree fluency-related processes indeed were related to source memory decisions. Assuming that fluency emerges within a few hundred milliseconds, any influence of this fast-acting process on a source decision could well be diminished when that source decision is delayed by a preceding old/new judgment task, as was the case in Experiment 3. In addition, the experiment did not allow the analysis of incorrect source decisions. Those two aspects were addressed with a modified design in Experiment 4.

9. Experiment 4: Implementing a Design to Examine Fluency Effects on Source Memory II

Abstract

In this subsequent Experiment, I omitted the old/new decision to more directly test fast-acting fluency effects on source memory. More accurate source judgments for repeated versus non-repeated visually learned names were observed, but no such benefit was apparent for repeated versus non-repeated auditorily learned names. Again, an N400 effect (300-600 ms) differentiated between visually and auditorily learned names. Importantly, this effect occurred for correct source decisions only. I interpret it as indexing fluency arising from within-modality priming of visually learned names at test.

9.1 Introduction

In Experiment 4 the old/new decision was omitted to capture fast-acting neural processes related to source memory more directly. Furthermore, the design was modified to test whether ERP effects of learning modality were contingent on the *accuracy* of source decisions. I reasoned, that if this were the case, the early effect of learning modality should be absent for incorrect source decisions.

9.2 Method

Participants

The studied population consisted of 20 young adults (12 female; *M* = 23.5, *SD* = 3.2). Participant selection criteria were identical to Experiment 3. All participants gave written informed consent. Before the experiment, visual acuity and contrast vision (Bach, 1996), as well as cognitive covariates were assessed (see Table 6 and Participant section of Experiment 5).

Stimuli and Design

Stimuli were equivalent to those used in Experiment 3. In contrast to Experiment 3, all 400 names were presented during learning. Of 200 auditorily learned names, 100 were presented once and 100 were presented twice. Similarly, 100 visually learned names were presented once and 100 were presented twice. Visually and auditorily learned items were presented in a pseudo-randomized sequence, with a minimum of 156 and a maximum of 440 (*M* = 300) intervening items between repetitions.

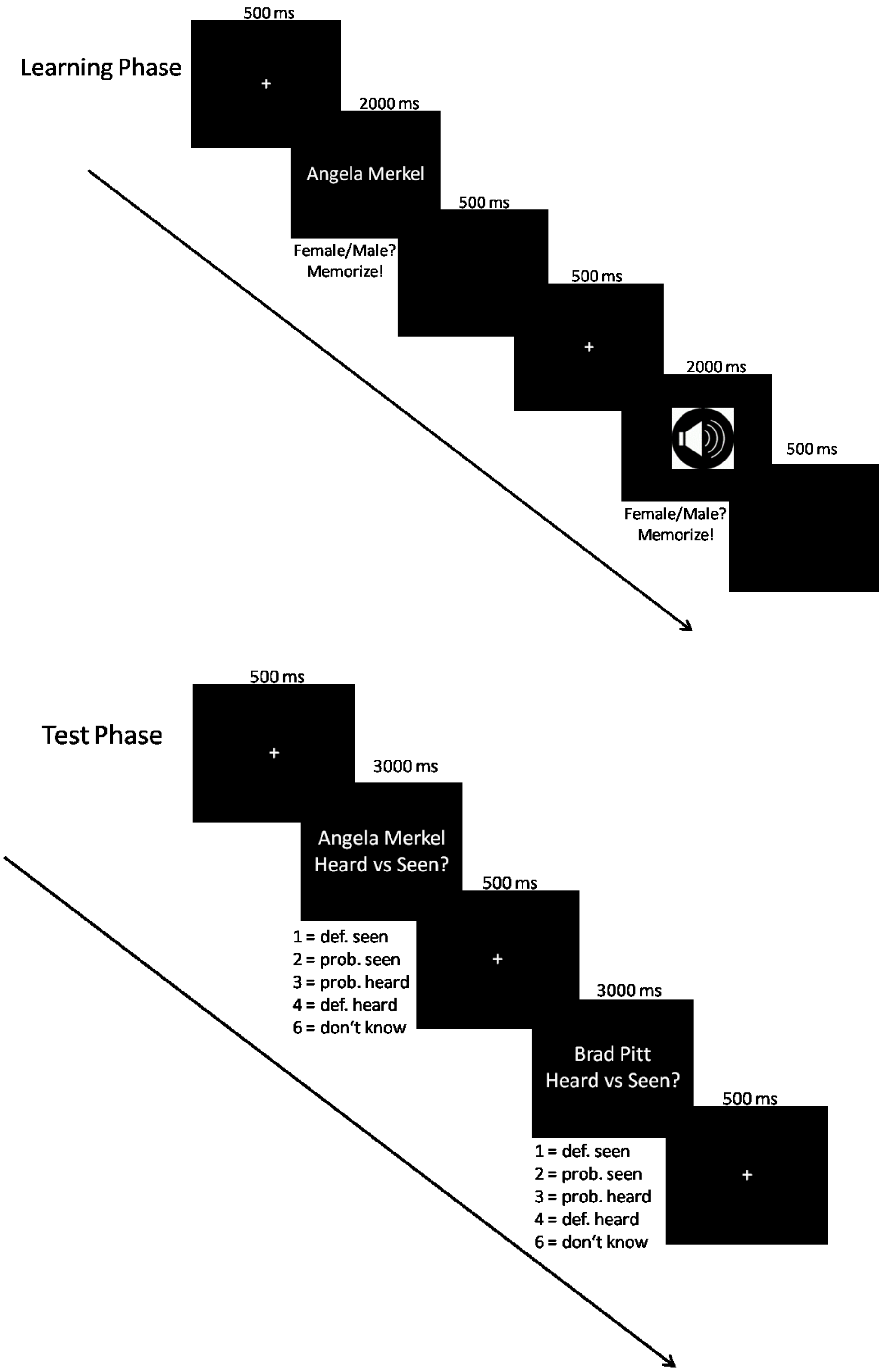

Figure 25. Illustration of learning and test phases from Experiment 4 and 5.

Procedure

The procedure was identical to Experiment 3, except that old/new decisions were omitted (see Figure 25, above). Each test trial started with a fixation cross for 500 ms, followed by a 3000 ms presentation of the name stimuli. Participants were instructed to indicate as fast and correctly as possible via key presses whether the respective name was certainly heard, probably heard, probably read, certainly read, or whether they could not remember the source of the name[22]. Participants were informed that the test list would only include names that they had either read or heard earlier and that the sets of read and heard names were non-overlapping.

EEG Recording and Analysis.

EEG recording and analysis was analogous to Experiment 3, except for the following changes. Trials were averaged according to the two experimental factors modality during learning and repetition during learning (non-repeated visually learned, repeated visually learned, non-repeated auditorily learned, repeated auditorily learned) for both correct and incorrect source memory decisions. The mean number of trials contributing to an individual averaged ERP for these conditions was 43, 57, 52, and 60 for correct trials, and 56, 41, 44, and 38 for incorrect trials, respectively.

Mean amplitudes during test were analyzed at frontal, central and parietal electrode sites (F3, Fz, F4, C3, Cz, C4, P3, Pz, P4) in a 300 - 600 ms and 600 – 900 ms time window. Visual inspection of the data further suggested analyses from 900-1200 ms at the same electrode sites.

9.3. Results

9.3.1 Behavioral Results

Performance. A repeated-measures ANOVA on accuracy (see Table 5) with the within-subject factors modality during learning (visual vs. auditory) and repetition during learning (non-repeated vs. repeated) resulted in a significant interaction, $F(1,19) = 8.34$; $p = .009$; $\eta^2_p = .19$. Paired t-tests revealed a significant effect of repetition in the visually learned

[22] Please note that it was collapsed across confidence ratings as too few subjects made use of the option to indicate that an item was *probably* heard or seen for an appropriate number of trials (mean number of key presses for *probably* heard/seen responses was 14) regarding the analysis of ERPs.

condition, $t(19) = 7.12$; $p < .001$; $d = 0.98$, but a trend only in the auditorily learned condition, $t(19) = 1.98$; $p = .063$; $d = 0.39$. Moreover, source memory for non-repeated auditorily learned names was significantly more accurate relative to the non-repeated visually learned condition, $t(19) = 3.08$; $p = .006$; $d = 1.23$, while repeated visually and auditorily learned items did not differ significantly, $t(19) = 1.20$; $p = .245$; $d = 0.35$.

A corresponding ANOVA on mean reaction times for accurate source memory decisions (see Table 5) resulted in a trend for the interaction of Modality during learning x Repetition during learning, $F(1,19) = 3.34$; $p = .083$; $\eta^2_p = .15$. Table 5 suggests a degree of repetition benefits for visually but not for auditorily learned names.

Table 5. Means and Standard deviations (SD) of accuracies and reaction times (ms) for correct responses from Experiment 4.

Condition	Accuracy	RT (ms)
Non- Repeated. Auditory	.75 (.15)	1559.66 (141.84)
Repeated Auditory	.79 (.13)	1546.42 (126.86)
Non- Repeated. Visual	.61 (.14)	1562.79 (152.45)
Repeated Visual	.74 (.13)	1486.13 (69.13)

9.3.2 Event- Related Potentials.

Grand mean ERPs for correct and incorrect source memory for Experiment 4 are depicted in the upper and lower part of Figure 26, respectively.

300-600 ms. A repeated measures ANOVA with the factors laterality, electrode site, modality during learning (visual, auditory), repetition during learning (non-repeated, repeated) and response (correct source memory decision, incorrect source memory decision) resulted in a main effect of modality during learning, $F(1,19) = 4.46$; $p = .048$; $\eta^2_p = .19$, which was further qualified by an interaction with site, $F(1.38,26.17) = 11.53$; $p < .001$; $\eta^2_p = .38$. Separate post-hoc ANOVAs at frontal, central and parietal sites revealed a main effect of learning modality, with more positive amplitudes for visual as compared to auditory names, at frontal, $F(1,19) = 7.75$; $p = .012$; $\eta^2_p = .29$, and central, $F(1,19) = 9.53$; $p = .006$; $\eta^2_p = .33$, but not parietal sites, $F < 1$.

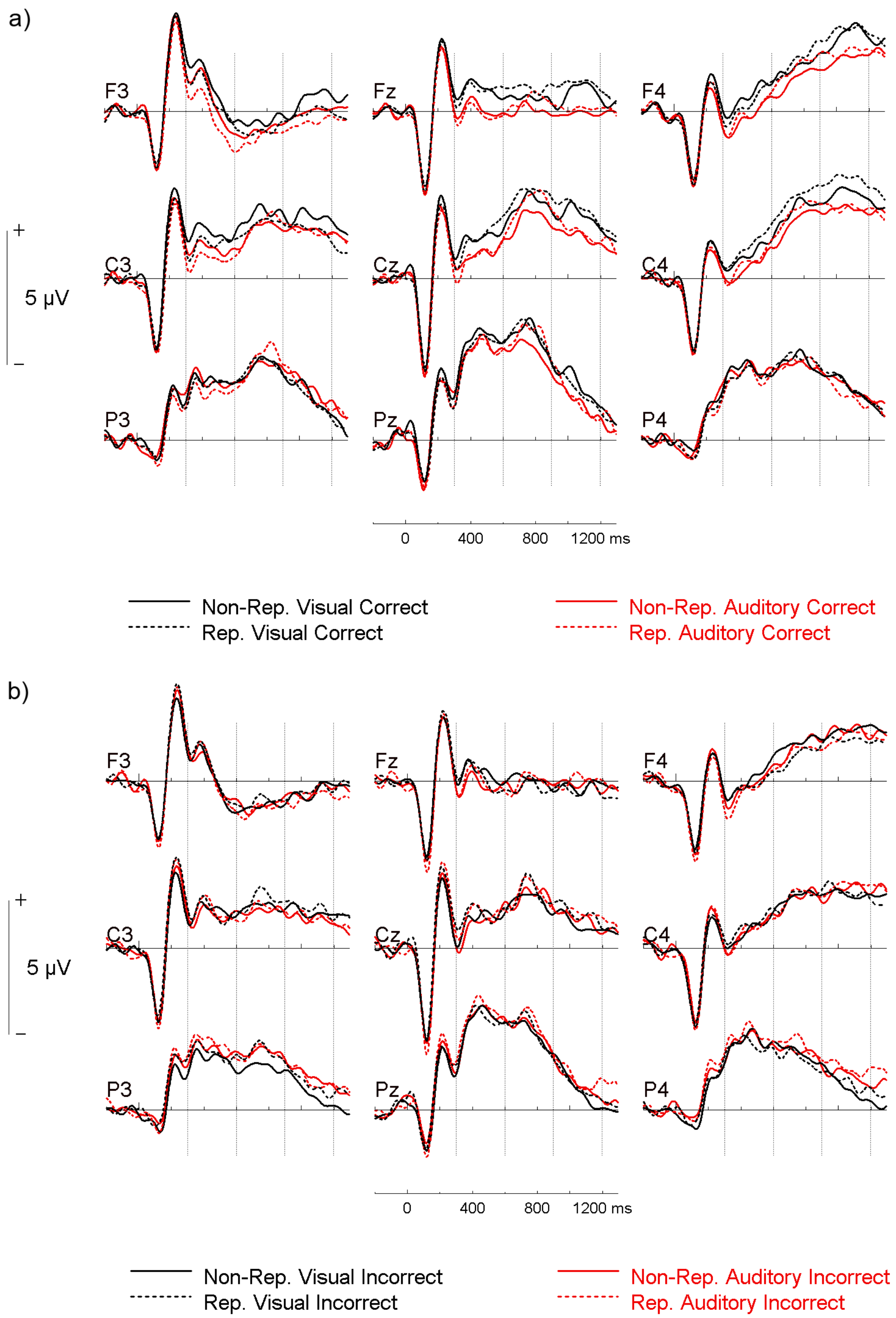

Figure 26. a) Grand Mean waveforms for correct source memory from the test phases of Experiment 4. Dashed lines depict the 300 – 600 ms, 600 – 900 ms and 900 – 1200 ms time windows. *b)* Grand Mean waveforms for incorrect source memory from the test phases of Experiment 4. Dashed lines depict the 300 – 600 ms, 600 – 900 ms and 900 – 1200 ms time windows.

In addition, there was an interaction of Modality during learning x Response, $F(1,19) = 4.66$; $p = .004$; $\eta^2_p = .20$; see upper part of Figure 27. Post-hoc ANOVAs indicated an effect of learning modality for correct trials, $F(1,19) = 8.08$; $p = .010$; $\eta^2_p = .30$, with more positive amplitudes for visual than auditory names. Importantly, no corresponding effect was detected for incorrect source memory decisions, $F < 1$. Moreover, correct relative to incorrect responses elicited more positive amplitudes for visually, $F(1,19) = 4.75$; $p = .042$; $\eta^2_p = .20$, but not auditorily learned names, $F(1,19) = 1.01$; $p = .329$; $\eta^2_p = .05$.

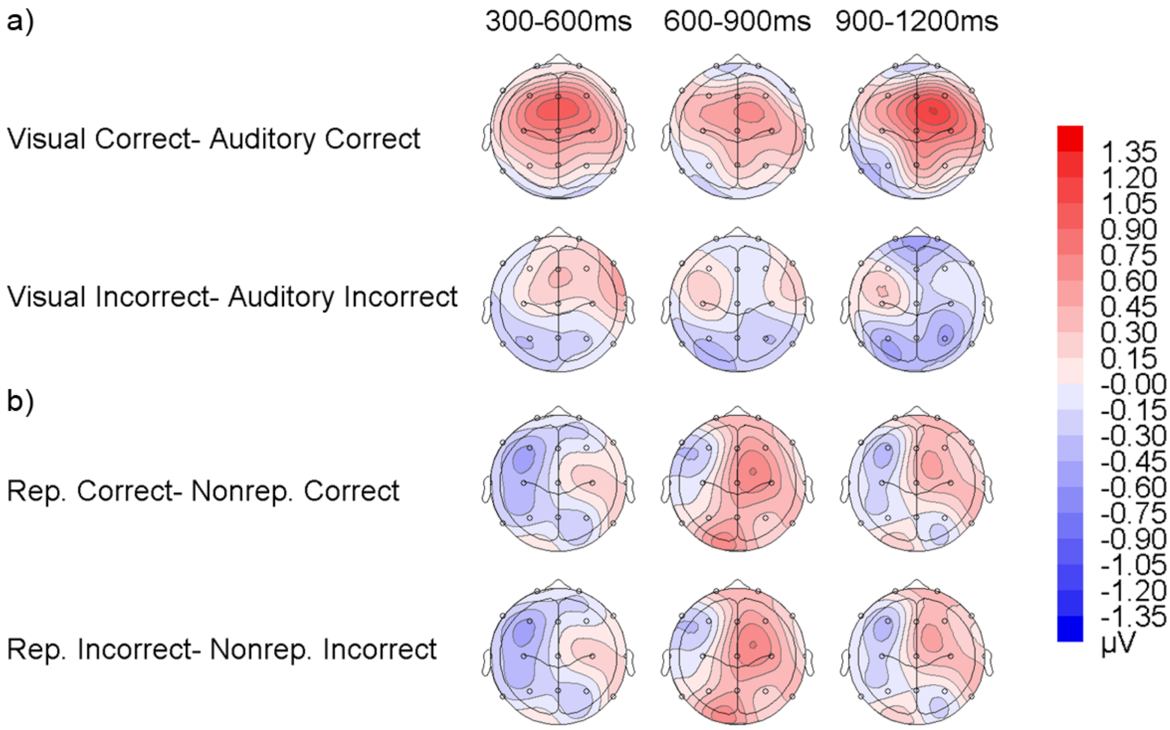

Figure 27. a) Scalp topographical voltage maps (spherical spline interpolation, 90° equidistant projection) of the learning modality effect (visually minus auditorily learned names for correct and incorrect source judgments, respectively) from Experiment 4. *b)* Scalp topographical voltage maps (spherical spline interpolation, 90° equidistant projection) of the repetition during learning effect (repeated minus non-repeated names for correct and incorrect source judgments, respectively) from Experiment 4.

600-900 ms. An ANOVA yielded a main effect of response, $F(1,19) = 9.59$; $p = .02$; $\eta^2_p = .21$, which was further qualified by an interaction of Laterality x Repetition during learning x Response, $F(1,38) = 5.01$; $p = 006$; $\eta^2_p = .21$. Subsidiary ANOVAs at left, midline and right electrodes sites and for correct and incorrect trials separately indicated an effect of repetition during learning over midline, $F(1,19) = 4.95$; $p = .038$; $\eta^2_p = .21$ and right electrode sites, $F(1,19) = 5.21$; $p = .034$; $\eta^2_p = .22$, for correct responses, with more positive amplitudes for repeatedly learned names. No such effect was detected over left hemispheric sites, $F < 1$.

For incorrect trials, there was no corresponding effect (left: $F[1,19] = 1.92$; $p = .182$; $\eta^2_p = .00$, midline and right: both $F < 1$; see lower part of Figure 27).

900-1200 ms. An ANOVA yielded a main effect of response, $F(1,19) = 12.14$; $p = .002$; $\eta^2_p = .39$, which was qualified by an interaction with modality during learning, $F(1,19) = 5.57$; $p = .029$; $\eta^2_p = .23$; see upper part of Figure 27. For correct trials, post-hoc ANOVAs revealed a trend towards more positive waveforms for visually as compared to auditorily learned names, $F(1,19) = 4.19$; $p = .055$; $\eta^2_p = .18$. Importantly, no corresponding effect was apparent for incorrect source memory decisions, $F < 1$. Moreover, more positive amplitudes for correct relative to incorrect responses were detected in the visually, $F(1,19) = 29.80$; $p < .001$; $\eta^2_p = .61$, but not in the auditorily learned condition, $F(1,19) = 2.00$; $p = .174$; $\eta^2_p = .09$.

In addition, an interaction of Site x Modality during learning, $F(1.4, 26.61) = 5.97$; $p = .006$; $\eta^2_p = .24$, was observed, suggesting a fronto-central distribution of the learning modality effect.

9.4 Discussion

In Experiment 4 larger benefits of repetition during learning were found on source memory for visually as compared to auditorily learned names. Accordingly, repetition during learning was particularly helpful when modality did not change between learning and test. However, performance measures of the present study alone may not permit a clear interpretation in terms of a fluency- or recollection-based account of this effect[23], as they do not provide separate measures of these processes.

Importantly, the ERP findings support a prominent role of long-term priming for source memory for familiar names. As in Experiment 3, more positive fronto-central ERPs were seen between 300 – 600 ms for visually as compared to auditorily learned names. This ERP effect might represent an N400 priming effect or an FN400 (for an FN400 effect in source memory studies, see also Groh-Bordin et al., 2006), thus reflecting fluency-based processes. Crucially, our finding of an early learning modality effect for correct but not

[23] Of note, in Experiment 4 source memory accuracies for non-repeated names were larger for auditorily as compared to visually learned items. It may be speculated that this may be because the default mode of language perception is auditory, or because human voices are richer in perceptual detail relative to written words. Previous research has suggested that word and voice information are stored together (Palmeri, Goldinger, & Pisoni, 1993), which may explain more accurate source judgments in the auditorily learned condition of Experiment 2. Additionally, greater saliency of the auditory relative to visual modality may have emerged due to intermixed rather than blocked presentation (Mulligan & Osborn, 2009).

incorrect source decisions strongly suggests that this fluency-based ERP effect reflects a process that is intimately related to source memory.

A substantially later effect of learning modality (900-1200 ms) was also seen for correct source decisions only. This late effect may index control processes during source retrieval (see e.g. Cansino, Hernandez-Ramos, & Trejo-Morales, 2012; Cruse & Wilding, 2009). Considering the RTs (Table 5), the processes reflected in this ERP time window may still have influenced the behavioral source decision. They could therefore also represent a re-evaluation of the earlier fluency-based signal and its match with consciously recollected source information.

It is also important to note that, in the intermediate time window from 600 – 900 ms, prominent ERP effects of repetition during learning were observed independent of learning modality. As in Experiment 3, more positive ERPs were elicited for repeatedly than non-repeatedly learned names. As noted previously, repetition during learning increases the amount of subsequently recollected information, which in turn results in more positive ERPs (Vilberg et al., 2006). In line with this idea, effects of repetition during learning were only observed for correct source decisions.

Source memory is typically impaired in older participants (Balota et al., 2000; Chalfonte & Johnson, 1996; Spencer & Raz, 1995), which has been related to diminished recollection (Anderson & Craik, 2000; Jacoby & Rhodes, 2006). By contrast, fluency-related processes are assumed to be relatively spared (Balota et al, 2000), which was shown to yield detrimental effects on memory performance when the fluency signal misled older adults to erroneous judgments (e.g. Jacoby, 1999; Watson et al., 2004). Since Experiments 3 and 4 led to the conclusion that fluency played a beneficial role in the current paradigm, Experiment 5 aimed at examining potentially adjuvant fluency- based effects in older adults.

10. Experiment 5: Fluency Effects on Source Memory in Older Adults

Abstract

In this final experiment, older adults were tested with a highly similar paradigm as younger adults in Experiment 4. Consistent with the assumption of relatively spared fluency processes in older age, an analogous pattern of results was detected: an N400 effect (300-600 ms) differentiated between visually and auditorily learned names. Again, this effect occurred for correct source decisions only. In sum, the findings suggest that fluency also assists person-related source memory via within-modality repetition priming in older adults.

10.1 Introduction

Experiment 5 addressed the question whether or not older participants would show a similar pattern of effects as younger adults in the previous experiments. More specifically, it was expected to find a similar pattern of behavioral results and of early fluency-based ERP correlates of within-modality repetitions, but weaker evidence for recollection-based ERPs. Importantly, such analogous results in younger and older adults would indicate that fluency may at least partly outweigh a lack of recollection and/or monitoring which largely determine failures of source memory with age (in situations as the current where the upcoming fluency signal is trustable).

10.2 Method

Participants

The studied population consisted of 24 older participants (15 female; Mean age = 67.2; SD = 4.2) who were recruited in senior citizen groups and via a press release in a local newspaper. All participants reported to reside in independent living conditions and received a monetary reward for participation. Participants were right-handed according to a modified version of the Edinburgh Handedness Inventory (Oldfield, 1971). None reported neurological or psychiatric disorders or received central-acting medication. All participants gave written informed consent.

Measures of educational level (years of education), visual acuity and contrast sensitivity (Bach, 1996) and cognitive covariates were assessed before the experiment. These latter variables included a marker of perceptual speed (digit symbol substitution test; Wechsler, 1981) and a marker of verbal knowledge (Spot-A-Word; Lehrl, 1977). For the sake of completeness Table 6 displays the results from Experiment 3, 4 and 5. Notably, however, since Experiment 5 was highly similar to Experiment 4, age group comparisons on cognitive covariates and on educational level were conducted only between younger participants from Experiment 4 and older participants from Experiment 5. These analyses revealed significant age-related decline for older adults in perceptual speed, $F(1,42) = 24.99$, $p < .001$, $\eta^2_p = .37$. No age difference was observed for verbal knowledge, $F(1,42) = 1.33$, $p < .256$, $\eta^2_p = .03$, but incidentally, older adults obtained numerically slightly higher raw scores (see Table 6). These results are in line with both two-component theories of life span intelligence (Baltes, 1987; Horn, 1968) and empirical evidence (S. C. Li et al., 2004; Schaie, Maitland, Willis, & Intrieri, 1998) contrasting fluid mechanics and crystallized pragmatics of cognition. This confirms the age typicality of the samples. Visual acuity and contrast sensitivity was diminished in older compared to younger adults, $F(1,42) = 22.39$, $p < .001$, $\eta^2_p = .35$ and $F(1,42) = 14.96$, $p < .001$, $\eta^2_p = .26$, respectively. Younger and older adults did not differ with respect to years of education, $F < 1$.

Table 6. Demographic variables, sensory and cognitive covariates from Experiments 3, 4, and 5; M (SD).

	Experiment 3	Experiment 4	Experiment 5
Age	23.20 (2.74)	23.20 (3.90)	67.21 (4.20)
Years of education	14.55 (1.10)	14.55 (1.19)	13.04 (3.74)
Visual Acuity	.86 (.11)	.88 (.06)	.54 (.21)
Contrast Vision	1.40(.37)	1.29 (.36)	.30 (.19)
Digit Symbol raw score	68.25 (12.20)	66.55 (8.36)	41.79 (11.32)
Spot a Word raw score	31.00 (1.92)	30.70 (3.10)	31.96 (3.98)

Stimuli and Design.

The stimuli and design were equivalent to Experiment 4.

Procedure.

The same procedure was used as in Experiment 4 except for the following changes during test: Participants were instructed to indicate as fast and correctly as possible via key presses whether the names were heard, seen, or whether the source was not remembered. I withdrew from applying the confidence rating used in Experiment 4 to create a more appropriate task for our older participants. Further encouragement to undertake this change arose from the fact that the young participants in Experiment 4 had barely used the intermediate steps of the confidence scale (see above).

EEG Recording and Analysis

EEG recording was analogous to previous experiments. Trials were averaged according to modality during learning and repetition during learning (non-repeated visual, repeated visual, non-repeated auditory, and repeated auditory) for both correct and incorrect source memory decisions, respectively. The mean number of trials contributing to an individual averaged ERP for these conditions was 44, 55, 62, and 63 for correct trials and 54, 45, 37, and 35 for incorrect trials, respectively.

10.3. Results

10.3.1 Behavioral Results

Performance. An ANOVA on accuracy of source memory decisions (see Table 7) resulted in main effects of learning modality, $F(1,23) = 18.00$; $p < .001$; $\eta^2_p = .44$, and repetition during learning, $F(1,23) = 38.95$; $p < .001$; $\eta^2_p = .63$, and in an interaction, $F(1,23) = 6.02$; $p = .022$; $\eta^2_p = .21$. Paired t-tests revealed that source memory accuracy increased with repetition in the visually, $t(23) = 4.99$; $p < .001$; $d = 0.68$, but not in the auditorily learned condition, $t(23) = .773$; $p = .447$; $d = 0.11$. Moreover, source memory for non-repeated auditorily learned names was more accurate relative to the non-repeated visually learned condition, $t(19) = 4.39$; $p < .001$; $d = 1.34$, and source memory for repeated auditorily learned items was more accurate relative to the repeated visually learned condition, $t(19) = 3.19$; $p = .004$; $d = 0.83$.

A corresponding ANOVA on mean reaction times for correct source memory decisions (see Table 6) resulted in a main effect of repetition during learning, $F(1,23) =$

28.58; $p < .001$; $\eta^2_p = .55$, indicating faster responses for repeatedly learned as compared to non-repeatedly learned names independent of learning modality.

Table 7. Means and Standard deviations (SD) of accuracies and reaction times (ms) for correct responses from Experiment 5.

Condition	Accuracy	RT (ms)
Non- Repeated. Auditory	.69 (.13)	1695.61 (234.51)
Repeated Auditory	.70 (.13)	1655.73 (209.56)
Non- Repeated. Visual	.50 (.15)	1670.07 (206.59)
Repeated Visual	.60 (.14)	1607.18 (220.52)

10.3.2 Event-Related Potentials.

Grand mean ERPs for correct and incorrect source memory for Experiment 5 are depicted in the upper and lower part of Figure 28, respectively.

300-600 ms. An interaction of Modality during learning x Response, $F(2,46) = 5.90$; $p = .023$; $\eta^2_p = .20$; see Figure 29, was detected. A follow-up ANOVA on correct responses resulted in a significant effect of modality during learning, $F(1,23) = 5.90$; $p = .023$; $\eta^2_p = .20$, with less positive amplitudes for visually learned relative to auditorily learned items. No corresponding effect was detected for incorrect source memory decisions, $F(1,23) = 2.02$; $p = .169$; $\eta^2_p = .08$. Moreover, correct relative to incorrect responses elicited less positive amplitudes in the visually learned, $F(1,23) = 7.25$; $p = .013$; $\eta^2_p = .24$, but not in the auditorily learned condition, F < 1.

*600-900 ms***.** An interaction of Modality during learning x Response, $F(1,23) = 15.76$; $p = .001$; $\eta^2_p = .41$, was further qualified by a three-way interaction of Laterality x Modality during learning x Response, $F(1.45,33.39) = 3.98$; $p = .040$; $\eta^2_p = .15$; see Figure 29. Post-hoc ANOVAs carried out separately for correct and incorrect source memory decisions at left, midline and right electrodes revealed significantly less positive amplitudes for correctly remembered visually learned versus auditorily learned names at midline, $F(1,23) = 9.34$; $p = .006$; $\eta^2_p = .29$, and right electrodes, $F(1,23) = 4.66$; $p = .042$; $\eta^2_p = .17$, but only a trend at left sites, $F(1,23) = 4.26$; $p = .050$; $\eta^2_p = .16$. Conversely, for incorrect source memory decisions, visually learned items elicited more positive amplitudes as compared to auditorily learned items at midline, $F(1,23) = 14.18$; $p = .001$; $\eta^2_p = .38$, and right electrodes, $F(1,23) = 11.16$; $p = .003$; $\eta^2_p = .33$. No such effect was detected at left electrode sites, $F < 1$. Moreover, in the visually learned condition, amplitudes for correct relative to incorrect responses were less

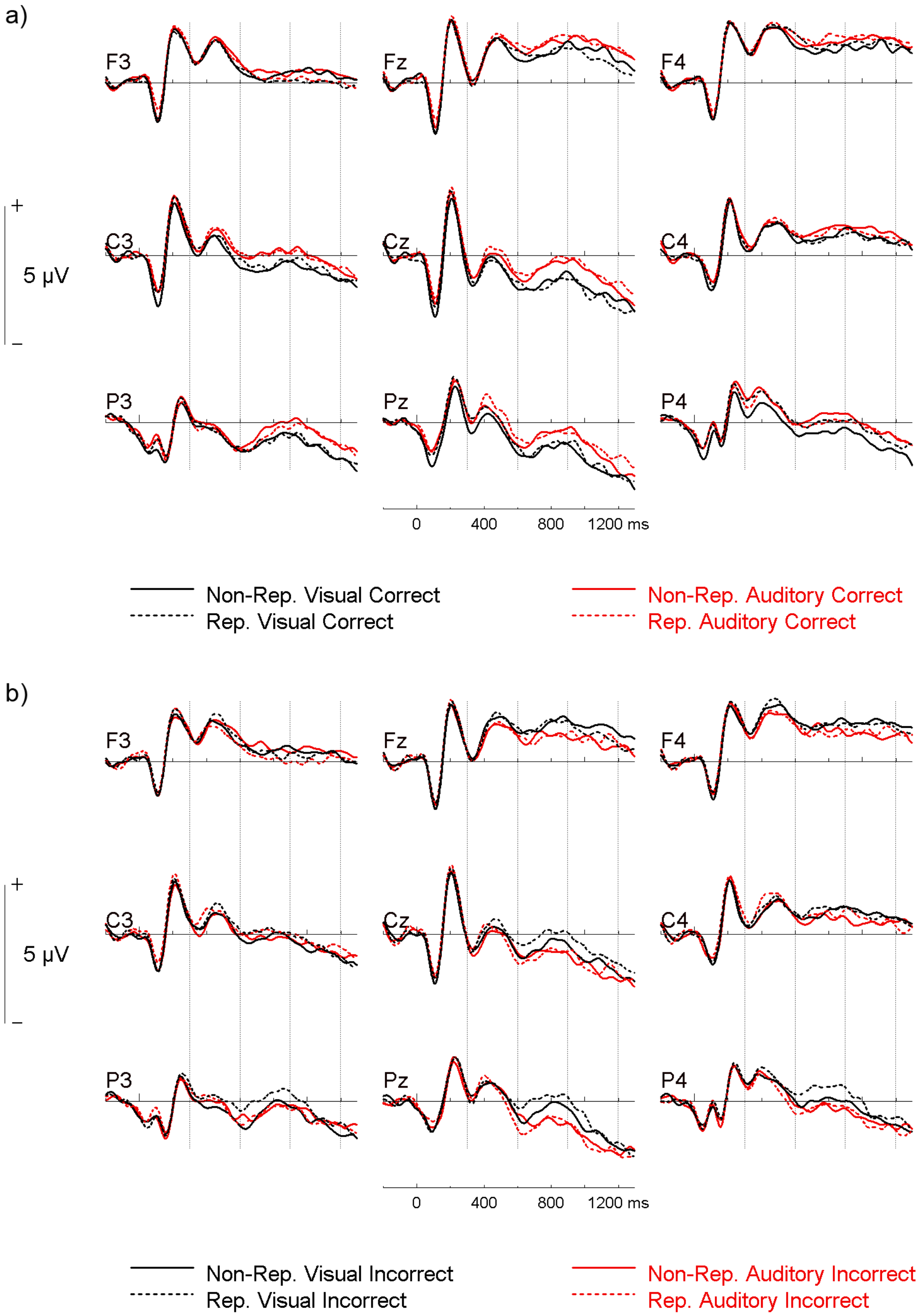

Figure 28. a) Grand Mean waveforms for correct source memory from the test phases of Experiment 5. Dashed lines depict the 300 – 600 ms, 600 – 900 ms and 900 – 1200 ms time windows. b) Grand Mean waveforms for incorrect source memory from the test phases of Experiment 5. Dashed lines depict the 300 – 600 ms, 600 – 900 ms and 900 – 1200 ms time windows.

positive at left, $F(1,23) = 9.76$; $p = .005$; $\eta^2_p = .30$, midline, $F(1,23) = 11.62$; $p = .002$; $\eta^2_p = .34$, and right sites, with the latter effect emerging as a trend only, $F(1,23) = 3.29$; $p = .083$; $\eta^2_p = .13$. In the auditorily learned condition, amplitudes for correct relative to incorrect responses were more positive at midline, $F(1,23) = 6.16$; $p = .021$; $\eta^2_p = .21$, and right, $F(1,23) = 9.65$; $p = .005$; $\eta^2_p = .30$, but not at left electrode positions, $F < 1$

900-1200 ms. An ANOVA resulted in an interaction of Modality during Learning x Response, $F(1,23) = 9.41$; $p = .005$; $\eta^2_p = .29$; see Figure 29. Separate ANOVAs for correct versus incorrect source memory decisions revealed less positive amplitudes for correct source memory decisions for visually learned as compared to auditorily learned names, $F(1,23) = 6.62$; $p = .017$; $\eta^2_p = .22$. Conversely, for incorrect trials, there was a trend towards more positive amplitudes for visually learned as compared to auditorily learned names, $F(1,23) = 3.90$; $p = .061$; $\eta^2_p = .15$. Finally, amplitudes for correct relative to incorrect responses were more positive in the auditorily learned, $F(1,23) = 12.07$; $p = .002$; $\eta^2_p = .34$, but not in the visually learned condition, $F(1,23) = 1.20$; $p = .285$; $\eta^2_p = .05$.

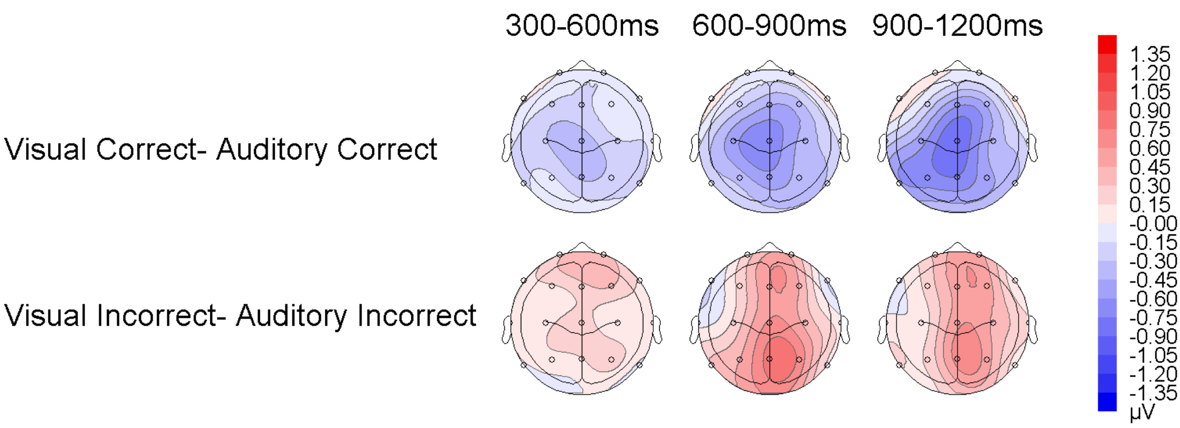

Figure 29. Scalp topographical voltage maps (spherical spline interpolation, 90° equidistant projection) of the learning modality effect (visually minus auditorily learned names for correct and incorrect source judgments, respectively) from Experiment 5.

10.4 Discussion

In Experiment 5, older participants were examined with a slightly modified version of Experiment 4. Older people are known to show reduced source memory performance (Balota et al., 2000; Spencer & Raz, 1995), which is often attributed to decreases in recollection (Anderson & Craik, 2000). As it was suggested that fluency-based processes influenced the results in the preceding experiments, a similar pattern of behavioral and ERP results as in Experiment 4 was expected for older adults.

Indeed, the behavioral results from older participants in Experiment 5 were remarkably similar to those in young adults. While repetition during learning led to more accurate source memory decisions for visually learned names, no significant benefit was observed for auditorily learned names. As noted above, it is unclear whether repetition during learning affected fluency, recollection, or both. The similar pattern in older and younger adults, however, may further argue for an influence of fluency on source memory, given that implicit relative to explicit memory processes are relatively spared in older participants (Balota et al., 2000; Jacoby & Rhodes, 2006). Furthermore, it is an indication that fluency decreased recollection, if the respective situation allows to rely on the fluency signal. Others have reported detrimental effects of older adults' reliance on fluency when this signal was misleading (e.g. Jacoby, 1999)

ERPs in older participants revealed an early effect of learning modality between 300 and 600 ms for correct but not for incorrect source decisions. While this pattern is intriguingly similar to the findings from young adults, one notable difference concerns the polarity of ERP modulations: While visually learned items elicited more positive amplitudes than auditorily learned items in young adults, they elicited less positive amplitudes in older adults. Polarity reversed ERP effects have been observed in older participants before, and have been linked to processes of age-related changes in brain function (Duarte et al., 2006; Swick et al., 2006; Wiese et al., 2012). Independent of this polarity reversal, a relatively early ERP effect again clearly distinguished between correctly assigned auditorily and visually learned items, and may therefore represent a signal supporting source memory. Thus, this finding corroborates the suggestion that source memory for familiar names is supported by fluency-based processes, both in young and older adults.

In the two following time windows (600-900 ms and 900-1200 ms) more positive amplitudes for correctly judged auditorily learned (versus visually learned) items and at the same time more positive amplitudes for incorrect visually learned (versus auditorily learned) names were observed. In other words, ERPs in these time ranges were more positive whenever the participants decided that the names had been auditorily learned, independent of whether this was correct or not. In Experiment 4, effects of modality during learning in the 900-1200 ms time window in young participants were interpreted as reflecting a re-evaluation of the earlier, presumably fluency-based signal on the basis of consciously retrieved source information. In older participants, processes reflected in the ERP effects in this time range did not additionally confirm the signal from the early 300 to 600 ms time window. The absence of this additional confirmation may be related to an overall reduction in source memory performance in older adults.

Finally, and at some variance with the results from Experiment 4, no significant effects of repetition during learning were observed in the ERPs of Experiment 5. As such effects in young participants presumably reflected recollection-based retrieval processes, their absence in older adults is in line with suggestions of age-related impairments of recollection (Friedman et al., 2010; for recent review, see Friedman, 2013).

11. Discussion of Experiments 3, 4, and 5: Effects of Fluency on Younger and Older Adult's Source Memory for Familiar Names

The previous series of experiments aimed at examining the effects of aging on name recognition in source memory. Experiments 3 and 4 were carried out with younger adults and initially served to fill the gap in this field of research on person-related source/associative memory. More importantly, these studies provided a basis for a paradigm, which made it possible to test older adults, and to subsequently compare effects of fluency (i.e. an implicit process), on explicit source judgments in both younger and older age. More precisely, the study tested the hypothesis that, in both younger and older adults, fluency might assist source memory for familiar names via within-modality priming and counteract age-related difficulties in more controlled, slow-acting processes (Research Question 3a). Furthermore, these effects were assumed to manifest in FN400 or N400-like ERP components (Research Question 3b). Finally, effects of brain aging were presumed to result in reduced or absent later old/new effects while leaving earlier fluency-based components (FN400/N400) relatively spared (Research Question 3c).

Experiment 3 examined younger adults in a paradigm using an old/new task and subsequent source recognition test. Famous names were presented either once or twice visually or auditorily during learning, but were presented only visually at test. This procedure served to capture potential effects of repetition during learning, and to test for effects of within- versus across-modality repetitions between learning and test. Using ERPs, it was hypothesized that greater influences of repetition during learning would be found on recollection-based memory processes, as reflected in later parietal old/new effects, whereas earlier FN400 or N400-like ERP effects were assumed to occur primarily for within-modality repetitions between learning and test.

Experiment 4 used a highly similar paradigm to Experiment 3. Changes were made to the test phases, where the old/new recognition test was omitted and participants were directly asked to decide about the source of a particular item. This change was implemented for two reasons: First, it was assumed that effects of fluency would be captured more directly on source (versus recognition) tests, if no intervening old/new recognition test was applied, given that fluency is a fast-acting, automatic process. Secondly, Experiment 3 did not permit clear conclusions on whether the fluency effects were beneficial for source memory. Incorrect responses were too rare to compare ERPs for correct versus incorrect source decisions. The omission of new items at test enabled this crucial comparison, and it was hypothesized that if fluency did indeed support source memory, a corresponding N400-like ERP effect should be apparent for correct but not for incorrect source decisions.

Experiment 5 tested older participants with the paradigm from Experiment 4 in a slightly modified version. It was hypothesized that similar patterns of results in older adults would lend further support to the reasoning that fluency can assist source memory via within-modality priming, given that these mechanisms, unlike recollection-based processes, are generally spared in older age (Anderson & Craik, 2000; Balota et al., 2000). More importantly, because remembering context information for a particular name is a compelling aspect in older adults' every-day life, it seems worthwhile to pursue whether older adults' memory retrieval might benefit from fluency-based mechanisms. This question is particularly relevant, since concerns have been raised that older adults might be especially vulnerable to false remembering, due to an overreliance on fluency in concert with a lack of recollection-based processes (Jacoby & Rhodes, 2006).

11.1 Behavioral Findings

In Experiment 3, repetition during learning enhanced both item recognition and source memory for familiar names. General effects of priming or fluency on old/new recognition were observed in a trend for faster correct responses for visually relative to auditorily learned names, and hence for within-modality repetitions. The benefit of repeated learning on source accuracy seemed more pronounced for visually learned names, i.e. for within-modality repetitions between learning and test. This might be interpreted as a first hint towards a beneficial role of fluency on source judgments. The fact that the effect did not reach significance weakens this interpretation, though it has to be acknowledged that the preceding old/new recognition might have attenuated effects of fluency given its fast-acting, automatic nature.

These considerations motivated the omission of a preceding old/new recognition test in Experiments 4 and 5. In these two experiments, more pronounced repetition benefits were found for source decisions with visually than auditorily learned names. While source memory decisions are often assumed to rely predominantly on recollection of study episode details (e.g.Wilding, 2000; Woroch & Gonsalves, 2010), recollection is unlikely to explain the specificity of effects of repetition during learning for visually learned items only. If enhanced recollection resulting from repetition during learning (see also Dewhurst & Anderson, 1999) affected source memory at test, it is not obvious why participants should have benefitted from such additional study phase information for visually learned items only.

Thus, a fluency-based explanation seems more likely to account for the behavioral data: When visually or auditorily learned names were repeated during learning, a modality-specific representation for the respective item was repeatedly accessed, enhancing fluency at this level of perceptual representations (see also Joyce et al., 1999; Kurilla, 2011; Roediger & Blaxton, 1987). If modality was kept constant between learning and test, the same perceptual representations were accessed in both experimental phases, resulting in enhanced fluency at test. In case of a modality change, however, a different perceptual representation was activated at test, and thus fluency was relatively smaller in this condition. Accordingly, participants may have based, at least in part[24], their source decisions on the perceived ease of name recognition at test. Of note, since the pattern of behavioral results was analogous in young and older participants, this priming mechanism may have similarly supported source memory in older participants – answering Research Question 3a.

Because performance was generally better for auditorily learned names, the data in the non-match condition between learning and test cannot be explained by modality-match effects. In studies on modality-match effects, old/new recognition tests are often applied in four study-test conditions: auditory-auditory, auditory-visual, visual-auditory and visual-visual. Higher recognition accuracy rates can sometimes be found for previously learned words when learning modality matches modality during test (see Mulligan & Osborn, 2009). Still, reports on modality-match effects have yielded inconsistent results, sometimes with higher performance in match conditions, sometimes with no such differences between conditions, and sometimes with a reversed pattern (for brief overviews of these mixed results, see Joyce et al., 1999; Mulligan & Osborn, 2009). However, to unequivocally disentangle general modality effects from modality match- versus mismatch, the present design should be extended by adding an auditory test phase (see also section 11.3 below).

An interesting aspect of the data is that source recognition for names is obviously facilitated by auditory presentation. As mentioned above, mixed (as opposed to blocked) presentation during learning and explicit modality judgments at test may have increased the saliency of the different modalities (Mulligan & Osborn, 2009). This might relate to another aspect regarding auditory presentation: It has been proposed that spoken words may benefit from a richer physical code and that words and voice information (in case of auditory

24 Note: This limitation is mentioned since overall accuracies were higher for audititorily compared to visually learned items.

presentation format) is stored together (Palmeri et al., 1993). Particularly so in the present study with long fore- and surname presentation, which may have led to more accurate decisions at test. This would also imply that auditorily learned names may have additionally benefited from re-processing whenever participants activated the physical code of the name, thus helping them to infer that they had previously heard the name. For these reasons, the advantage for auditorily learned names may have been rather explicit in nature.

Although a familiarity-based interpretation in terms of unitization rather than recollection cannot be directly supported by the present investigation and remains somewhat speculative, it might explain the pattern of results for auditorily learned names. Some studies have reported effects of more familiarity-based retrieval of source information when item and context were unitized during encoding, which was suggested to lead to a re-activation of the whole unit as a single entity when the item was presented again during test (e.g. Diana et al., 2008; Diana et al., 2011). With respect to the current study, it could be argued that name and voice information may have been merged into a single representation and that the re-occurrence of the name (though in visual format at test) automatically reactivated the whole unit, including voice information. This, in turn, resulted in a correct source decision. The results from older adults lend support to this suggestion, as similarly high source accuracies were found for both non-repeated and repeated auditorily learned names. In addition, these auditory source accuracies were significantly higher than the accuracies for both non-repeated and repeated visually learned items. In line with this idea, it has been suggested that conditions which reduce the need for recollection-based processes, such as unitization, would attenuate older adults' impairment in source or associative memory (Bastin et al., 2013). As a qualification, if unitization of voice and name was indeed apparent in the present study and was linked to familiarity effects (see Bastin et al., 2013; Diana et al., 2011; Diana et al., 2008) then this should have become apparent in the reaction times and/or in the ERPs. More specifically, correct responses for auditorily learned names should have elicited more positive going waveforms than new and correct source judgments to visually learned names. However, this was not (always) the case. Independent of the exact underlying mechanism for the apparent superiority of auditory versus visual stimuli, a next consequent step should be to conduct an experiment that uses auditory stimuli at test, with the aim to avoid confounding effects of study modality and modality match (between learning and test).

Potential fluency effects for the auditorily learned items might in principle also be attributed to cross-modal priming. Although cross-modality perceptual priming is usually weaker than within-modality priming (see Richardson-Klavehn & Gardiner, 1996; Schacter, Dobbins, & Schnyer, 2004), significant effects have been reported in both younger and older adults (Pilotti, Meade, & Gallo, 2003; Rajaram & Roediger, 1993; Richardson-Klavehn & Gardiner, 1996). Interestingly, it has been proposed that perceptual priming entails both a modality-dependent and a more abstract modality-independent component. Whereas the former lacks both voluntary retrieval and memorial awareness, the latter is likely to be associated with memorial awareness, but still lacking voluntary retrieval (Richardson-Klavehn & Gardiner, 1996). Seemingly, there are some parallels between these memory-related characterizations of within- versus cross-modality priming and the characterization of remember- and know-responses. It has been argued that remember-responses reflect awareness of what was experienced during study, whereas know-responses are based on awareness of recent encounters (but not of remembered study phase detail) (Gardiner & Richardson-Klavehn, 2000). Taken together, it might be speculated that within-modality priming should entirely relate to implicit processes that would neither elicit a remember- nor a know-response whereas cross-modality priming might manifest (at least) in a know-response - typically interpreted as a familiarity-based process. This would suggest that within-modality repetition between learning and test increases fluency on an implicit basis, whereas cross-modality repetitions contribute to more explicit familiarity-based processes, and thus to explicit memory. However, this reasoning cannot be tested on the basis of the behavioral results of the present experiments, since no remember/know rating was applied. Nevertheless, the ERP results discussed below certainly assist in disentangling different memory processes.

Perceptual priming effects have been defined as characteristics of *implicit memory* (e.g. Schacter et al., 2004). Importantly, a prominent role for perceptual information on *long-term explicit memory* and was theoretically addressed in transfer-appropriate processing (TAP) or encoding-specificity accounts (for overview of such approaches, see Roediger, Gallo, & Geraci, 2002). These accounts propose that retention is best when the mode of encoding corresponds to the mode of retrieval (TAP) or when information present at encoding is also available at retrieval. Dual-process models act on this idea by emphasizing the recapitulation of processing, and suggesting that fluent (re-)processing gives rise to familiarity-based recognition (Yonelinas, 2002). This suggestion, however, is not supported by the present data, as source information for auditorily learned names was remembered more accurately - presumably related to dominant characteristics in the voice stimuli used (see above).

At variance with these latter dual-process views of memory, recent research suggests a continuum of explicit and implicit memory processes and, more specifically, between repetition priming and recognition memory (Berry, Shanks, & Henson, 2008; Huber, Clark, Curran, & Winkielman, 2008). Results on modeling of reaction times data in both tasks prompted the idea of a single-system account of fluency, priming and recognition (Berry et al., 2008). Recent results from older adults have been claimed to support the view that explicit and implicit expressions of memory are driven by a single underlying memory system (Ward, Berry, & Shanks, 2013). This latter study reports that both priming and recognition are affected by normal aging and the authors concluded that age-related memory decline compromises a single system that supports both explicit and implicit memory manifestations. Whether the effects in the present study are tied to explicit or implicit processes, and whether they can be reconciled with a single-system account of memory cannot be entirely clarified on the basis of the behavioral results, but this question will be re-addressed when considering the ERP data.

Unsurprisingly, more accurate responses were detected for repeatedly learned names, particularly so in the visual learning condition. The overall higher accuracies for auditorily learned names might prompt the idea that near-ceiling performance could have hampered the occurrence of a repetition effect for auditory items. This objection cannot be ruled out completely, but seems unlikely given that source accuracy averaged in younger adults between .75 and .79 and in older adults between .69 and .70 for non-repeated and repeated items, respectively. Generally, repetition during learning may increase both familiarity and recollection, and repetition has been shown as being valuable for source accuracy in younger adults (Dewhurst & Anderson, 1999; Jacoby, 1999). Interestingly, and at odds with the present study, Jacoby (1999) reported opposite effects in younger and older adults. In his paradigm, words were presented either once, twice or three times visually, but only once auditorily during learning. At test participants were asked to indicate whether a word was *heard* or not during study. Crucially, source memory accuracy in older adults decreased when visual items were learned twice or three times relative to a single presentation during learning. This 'ironic effect of repetition' was interpreted to occur due to the circumstance that recollection deficits make it difficult to counteract a bias in source responses (and hence source misattribution) on the basis of increased familiarity signals of repeated names. The paradigm used in Experiments 3, 4 and 5 which resulted in more accurate source decisions for visual repeated items, may not have contained some of the core aspects responsible for the pattern of ironic repetition effects, such as repetition in the visual learning condition only, or a response format that drives a potential bias. It could also be argued that the discrepancy in results between Jacoby's (1999) study and the current one may relate to differences in stimulus material. In the current experiments, familiar names were used, representing unique individuals and within-category specifications. Jacoby (1999) used concrete nouns that rely on a between-category distinction (see section 2.2 for this argument). That notwithstanding, a second and more compelling aspect should be considered. Whilst Jacoby (1999) took advantage of the negative effects that accompany intact fluency signals, the present study allowed (older) participants to rely on this mechanism for successful source retrieval.

11.2 Findings from Event-Related Potentials

An early (300 – 600 ms) ERP effect of learning modality was observed in all three experiments. This effect clearly differentiated between visually and auditorily learned names and was interpreted to reflect the ease of name recognition, and hence increased fluency at test. As discussed above, this effect was polarity-reversed in older participants, which may reflect effects of aging. Importantly however, this effect of learning modality consistently occurred for correct source decisions only, suggesting decision-relevance of the underlying signal – thus answering Research Question 3a. Although the present experiments did not use a classical N400 paradigm, this early effect may be related to an N400-like priming effect, given its timing and its scalp-distribution (see also Kutas & Federmeier, 2011; Voss & Federmeier, 2011). Similar effects, with relatively more positive amplitudes for repeated relative to non-repeated items, have been observed in long-term repetition priming experiments using famous names and faces (Schweinberger, Pickering, Burton, et al., 2002).

The effects in Experiments 3 and 4 resemble within-modality long-term repetition priming, as names repeated in the same stimulus modality between learning and test elicited more positive amplitudes than both non-repeated new names and names learned in a different modality. At first sight, this interpretation appears to be at variance with previous studies on immediate repetition priming of famous names and faces (Pickering & Schweinberger, 2003), in which N400 priming effects were reported not to depend on a change between prime and target domain. However, unlike long-term repetition, as examined in the present study, immediate repetition effects are usually assumed to be based on a pre-activation of a target representation by the prime, which has not completely decayed by the time the target is processed. By contrast, as noted above, behavioral long-term repetition priming is domain- and modality-specific and explained by the strengthened link between a domain/modality-specific name representation and a domain/modality-independent representation of person identity (Burton et al., 1990).

More precisely, the Interactive Activation and Competition (IAC) model of person recognition (Burton et al., 1990) postulates a number of different processing units that are organized into pools. If a name is presented visually or auditorily, modality-specific mental descriptions of this name are created in an initial structural encoding step. If these visual or auditory descriptions fit with corresponding structural representations of this name stored in memory, these so-called name recognition units (NRU) become activated (Valentine et al., 1991). Importantly, recognition units are suggested to be modality-specific, and accordingly different units for written and spoken names should exist (as for words in general, see Morton, 1979). Moreover, activity is assumed to spread further to so-called person identity nodes (PINs). At this level, information from the different input modalities (e.g., written names, spoken names) is thought to converge, and if a PIN exceeds a certain threshold, the person is recognized as being familiar. Finally, semantic information is assumed to be stored in separate semantic information units (SIUs), which can be accessed once a specific PIN has been activated.

Interestingly for the present results, this architecture provides the possibility of an influence of spreading activation, or fluency-based processes, on source memory. Importantly, long-term repetition effects according to IAC do not cross input modality, which means that, e.g., the prior presentation of a written name results in a faster decision if that same written name is presented again, whereas the prior presentation of a written name should not prime a familiarity decision on a spoken name. As noted above, IAC explains this effect in terms of a strengthening of the link between the modality-specific NRU and the PIN after the first presentation. If the name is repeated in the same modality, the PIN reaches its threshold faster, resulting in faster reaction times for the familiarity decision. By contrast, in the cross-modal situation, no priming occurs because the prime will have strengthened a modality-specific link that is not used for target name processing. Critically, if a participant has to decide whether a name has been presented visually or auditorily in a previous learning phase, a particularly efficient activation of the PIN may indicate that the name was initially presented in the same modality. In a similar vein, Schweinberger and colleagues (2002) interpreted their N400 priming effect as reflecting a facilitated activation of PINs and subsequent SIUs. Accordingly, the IAC account offers a theoretical framework for potential effects of fluency on person-related source memory, providing a theoretical basis for the suggestion that influences of repetition priming on source memory judgments for person-related information may manifest in N400-like ERP effects. In the present experiments, the early ERP effect of learning modality in the 300-600 ms time window may represent a neural correlate of within-modality long-term repetition priming.

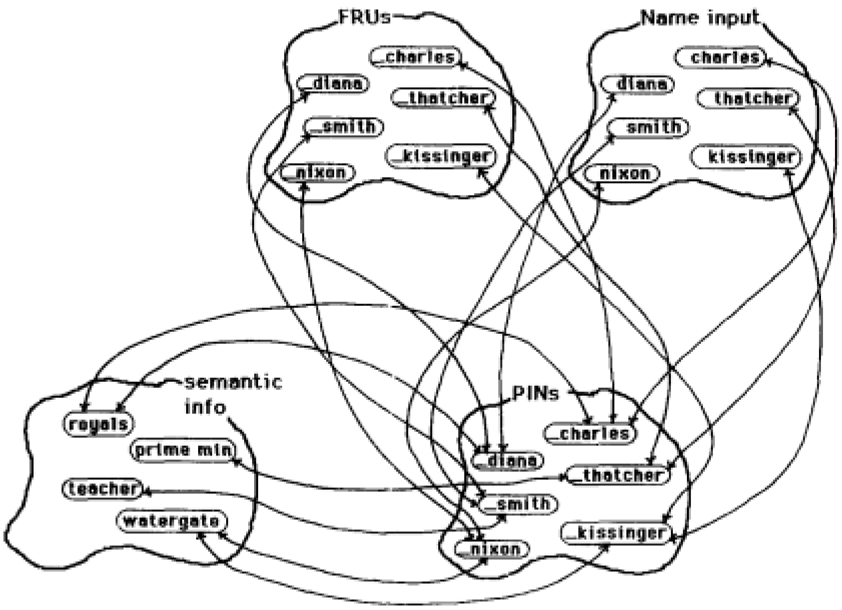

Figure 30. Schematic illustration of the IAC-model with name inputs by Burton, Bruce, & Johnson (1990).

An alternative but related interpretation would be that ERPs in the 300-600 ms time window reflect an FN400-like effect. More positive amplitudes for correct relative to incorrect source memory decisions at frontal sites and in similar time ranges have been interpreted as reflecting an FN400 (see e.g. Groh-Bordin et al., 2006; Mollison & Curran, 2012), a component which has been interpreted to indicate familiarity, and thus explicit memory (Curran, 2000). FN400 has been shown to exhibit graded effects with respect to perceptual similarity between study and test (e.g. same versus different object color) and hence was interpreted to be sensitive to and provide information about perceptual attributes (Groh-Bordin et al., 2006). In an earlier study, effects of modality-congruency between study and test were not observed in the FN400, but in a preceding 176 – 200 ms time window at frontopolar electrode sites (Curran & Dien, 2003). However, for the present experiments, an interpretation of the early ERP effect in terms of familiarity-based processes appears rather inappropriate. If this effect indeed reflected familiarity, one would have assumed more pronounced familiarity at test for auditorily learned relative to new items. A difference between these two conditions, however, was not consistently found in the 300 – 600 ms time window, and was completely absent in the 400 – 500 ms time window of Experiment 3. This finding is hard to reconcile with the aforementioned possibility that cross-modality priming might elicit an explicit familiarity-based signal. Moreover, the interpretation of the FN400 in terms of conceptual priming (Paller et al., 2007) appears inconsistent with the present finding of amplitude differences for correct versus incorrect trials in the visually learned (within-modality) condition only.

ERP effects of modality during learning were largely independent of repetition during learning, and thus did not parallel the pattern observed in performance. It is important to note that ERPs represent neural correlates of cognitive sub-routines, and the processes reflected in a specific ERP effect may or may not underlie a later behavioral decision about an item. Critically, the early ERP effect of learning modality was observed for correct trials only. This suggests that the availability of modality-specific information in this early time window might have served as a basis for a correct source decision, both in the repeated and in the non-repeated learning condition. The apparent nature of the effect appears consistent with a single-system account of memory, as recently proposed on the basis of findings in younger and older adults (Berry et al., 2008; Ward et al., 2013). The ERP finding in this time-range is apparently related to within-modality repetitions and hence to implicit memory, rather than to explicit familiarity-based processes. Nevertheless, the ERP effect only occurred for correct and not for incorrect source decisions, which in turn may reflect explicit memory manifestations. At least, this corroborates the idea that implicit memory can modulate (or even support) explicit memory under some circumstances.

In contrast to the two extremes of a rather ‘radical’ single-system view and strong claims of dissociations between fluency and explicit memory processes (Lucas, Paller, & Voss, 2012; Stark, 2012), a number of researchers (e.g. Eichenbaum, 2012; Ryan, 2012) emphasize the importance of a more integrative examination of explicit and implicit processes, their relationships to each other and how these might work in concert. Whereas Voss, Lucas, and Paller (2012) insist that (conceptual) priming presents in a neural correlate distinct from familiarity, and that the influence of implicit processes on recognition is ‘accidental’ in nature, I tend to prefer a different interpretation. More specifically, on the basis of the present results, I rather agree with researchers suggesting that enhanced fluency may manifest in priming and may be experienced as (or translated into) familiarity during recognition (Hayes & Verfaellie, 2012). Hence, in the present study, a single, identical process – fluency – might result from implicit priming, but concomitantly contribute to correct explicit remembering.

With respect to the age effects addressed in Research Question 3c, and in line with a relatively common view (Balota et al., 2000; Fleischman, 2007; Lavoie & Light, 1994), it has recently been reported that priming can result in age-invariant behavioral effects in older relative to younger adults. By contrast, neural activity related to priming as measured with both ERPs and oscillatory responses may be reduced by normal aging (Sebastian & Ballesteros, 2012). In the present study, the ERP modality effect appeared to be reduced (see Figure 29) though still significant in older adults (paralleling the effect in the young adults). The most obvious difference between age groups is the polarity reversal in old relative to young subjects. For reasons that are poorly understood as of yet, polarity reversals in old participants are sometimes reported for explicit effects of episodic memory (e.g. Duarte et al., 2006; Friedman et al., 2010). However, ERP effects related to implicit memory may also be affected by age-related polarity reversals, especially in a case of a potential overlap between implicit and explicit processes as in the current study.

It is worth noting that earlier studies yielded similar ERP effects which were interpreted differently. ERP effects of study-test compatibility starting at around 300 ms have been reported in studies that examined 'retrieval orientations'. This term refers to the cognitive states or modes, that are thought to align retrieval cue processing with the demands of a particular retrieval goal. The mechanism is assumed to maximize overlap between a cue and a memory representation (Herron & Rugg, 2003; Hornberger, Morcom, & Rugg, 2004; Robb & Rugg, 2002). In these studies, more positive amplitudes were reported broadly over the central scalp for those items that were presented in the same format during test as during study (word versus picture). Hornberger et al. (2004), for instance, interpreted their results as indexing similarity between the material in memory (as a consequence of learning modality/domain) and the retrieval cue (test format). According to this interpretation, the present ERP effects merely distinguish between match- and mismatch-processing during retrieval and are not be related to facilitated source memory. (However, if this were the case, the effect should have occurred for incorrect source responses as well.)

Hornberger and colleagues themselves concede that overall similarity between items during study and test might also increase a feeling of familiarity (or fluency), which is reflected in their ERPs. However, unlike in the present study, their ERP modulations sustained over a 600 – 900 ms and even, less pronounced, over a 900 – 1200 ms time-window with temporally relatively invariant scalp distributions and rather diffuse, broadly central maxima (Hornberger et al., 2004). Hence, their findings, unlike the present ERP results, seem hard to reconcile with a fluency- or familiarity-based account. Yet the question arises, whether such retrieval orientation effects in the case of study-test congruency might not either go hand in hand with or even be based on priming. The two processes are examined with identical experimental manipulations, because study-test congruency and within-modality (or domain) priming between learning and test are established in the same way. Thus, within-modality priming effects might yield a fluency-component on the basis of the explicit retrieval/congruency part. Interestingly, retrieval orientation effects in the papers cited above were discussed independently from priming mechanisms.

Similarly, studies that focused on within-modality priming effects have not necessarily linked their findings to retrieval orientation (e.g. Joyce et al., 1999). In Joyce et al. (1999) words were presented either visually or auditorily, followed by visual presentation during a lexical decision test, and a subsequent paper-pencil recognition test. Their ERP results are strikingly similar to the present ones: During the lexical decision test, old as compared to new items elicited more positive amplitudes between 200-500 ms. Furthermore, and more importantly, in a smaller time window from 300-400 ms the within-modality repetitions elicited greater positivity than across-modality repetitions. The authors interpreted this effect as an electrophysiological index of modality-dependent processing associated with priming.

In a later time-window from 500-800 ms more positive amplitudes were observed for auditorily studied words. Joyce et al. (1999) interpreted this effect as reflecting recollection-based processes, since auditorily learned words were recognized behaviorally with slightly higher accuracy (for low and medium, but not for high word frequencies). This effect also resembles the present behavioral data with superior accuracies for auditory names, and hence for cross-modality repetitions between learning and test. Previous findings were interpreted as indicating a benefit due to imagery of items presented auditorily during study, where participants were asked to visualize the objects represented by the word and to indicate whether these objects were smaller or larger than the monitor (see also Gonsalves & Paller, 2000). In addition, auditory presentations already provide the phonological word form, which might be advantageous compared to visually presented words which require grapheme-to phoneme-format conversion during reading. While more recollection-based processing for auditorily studied words may account for both the behavioral data and the ERPs in Joyce et al (1999), the present ERP results do not show any benefit for auditorily learned names – thus providing no evidence for increased recollection-based processes. Instead, modality-independent effects of repetition during learning were apparent in this time range (discussed below).

In young adults, starting at approximately 600 ms, names repeated during learning elicited more positive amplitudes as compared to non-repeated names. A number of ERP studies suggest that this time window reflects processes of recollection. Of particular relevance, Vilberg et al. (2006) reported that the ERP amplitude increased with the amount of recollected information. In the present study, repetition during learning may have led to the recollection of more information from the study phase at test (for behavioral evidence of such reasoning, see Dewhurst & Anderson, 1999) , and in turn to more positive ERP amplitudes. In this context, it is of interest to note that a corresponding ERP repetition effect was not observed in older participants. The lack of this effect is generally in line with the suggestion of impaired recollection in this age group (e.g. Anderson & Craik, 2000; Bastin et al., 2013; Jacoby & Rhodes, 2006). It is worth noting, though at variance with the present results (and with the apparent consent in the literature, see e.g. Friedman, 2013), that some studies have reported recollection-related old/new effects in similar time ranges in older adults (Mark & Rugg, 1998; Wang et al., 2012).

In contrast to the young participants, older adults showed a sustained learning modality effect in the later time-ranges (600-900 ms and 900-1200 ms). Yet, this effect was not longer reliable for correct source memory compared with the earlier 300-600 ms effect. In the later time ranges, more positive amplitudes were observed for auditorily learned names that were correctly classified, and for visually learned names when these were mistakenly attributed to having been learned auditorily. These effects, in concert with missing corresponding recollection and control/monitoring processes during source retrieval, might contribute to lower performance levels for visually learned names in older adults. However, the potential lack of efficient retrieval control processes most probably does not account entirely for the age-related drop in performance. Other studies that revealed decreased source memory performance reported similar frontal effects of source retrieval in late time windows in both young and older adults. However, these were somewhat shifted in distribution in the older adults (Cansino et al., 2012). More precisely, whereas in the young the right frontal effect, with more positive amplitudes for correct than incorrect source responses, was apparent from about 800 ms at anterior sites only, the effect was shifted to more central electrode sites in older adults.

In sum, the ERP findings suggests that although later more effortful processes, such as recollection or monitoring are impaired in older adults, earlier fluency-based processes are relatively spared. In the 300-600 ms time window the ERP priming effect in the older adults was associated with correct, but not incorrect source retrieval, similar to what was observed in young adults. Notably, however, the effect was polarity reversed and hence most probably exhibited some degree of age-related neural reorganization.

11.3 Summary and Outlook

Three experiments were conducted and yielded evidence that

(3a) Fluency-based processes assisting source decisions similarly in both younger and older adults most probably arise through within-modality long-term repetition priming. This suggests that age-related differences in source memory may be at least somewhat diminished in cases in which deficient processes (i.e. recollection and monitoring) are partly outweighed by spared fluency-based mechanisms. However, this interpretation should be viewed with precaution, since a direct comparison to a situation where fluency is less prominent was not provided by the present study.

(3b) Fluency-based processes manifest in N400-like priming effects associated with correct source retrieval in both younger adults and older adults.

(3c) Cognitive and brain aging leads to differences in the neural correlates associated with source retrieval in terms of an absent later, recollection-based old/new effect in older adults. Interestingly, cognitive and brain aging most likely also affected the N400 priming effect in these experiments by causing a polarity-reversed ERP effect in the elderly.

In all three experiments, converging evidence was obtained for an early (300-600 ms) ERP effect of learning modality, which was interpreted as reflecting fluency-based processes. This ERP effect was observed for correct trials only, in both young and older participants, which suggests that it reflects a signal supporting source memory decisions. Alternative interpretations have been discussed: The finding could be related to explicit familiarity-based processes, in terms of a mid-frontal old/new effect or FN400 (Curran, 2000; Paller et al., 2007), or it could be based on retrieval orientation and study-match congruency (Hornberger et al., 2004). Importantly, even when taking these alternatives into account, the effect is most likely a manifestation of within-modality priming, and hence constitutes an implicit memory processes. Nevertheless, the presumably fluency-related processes reflected by this effect seem to concomitantly affect explicit memory processes (involved in source decisions). This finding can potentially be interpreted as providing evidence for a single-system memory account (e.g. Berry et al., 2008), or at least for the view that implicit and explicit memory are not completely separate.

For future work following up on the present results, and particularly on the N400 ERP effect postulated to relate to fluency, it could be worthwhile to consider that blurred as opposed to un-blurred words diminish perceptual fluency (see Shah & Oppenheimer, 2007). This could be applied as a simple manipulation to test a perceptual fluency-account for the data. Similarly, a further option would be to change the font of the names between study and test. Both manipulations (blurring and font changes) should result in more positive amplitudes for visual than for auditorily learned names, and at the same time in relatively less positive amplitudes for blurred names or for those with altered fonts between leaning and test. As pointed out above, another reasonable next step consists in a replication of the study applying auditory testing, or both auditory and visual testing. Compared to current results, these latter variations should yield the reversed pattern of ERP results (auditorily learned and tested items more positive than visually learned items), or an interaction with test format (in case of a mixed auditory/visual test phase), respectively. In addition, this variation might shed light on the superiority in remembering spoken names, and more precisely on whether this is indeed related to a lack of fluency at test (due to visual testing in the current study) or whether it constitutes a more general phenomenon related to the human voice.

With respect to aging, it is interesting to observe a decline in source memory in older participants, which seems less pronounced than often reported in the literature. In the current study performance was only around 10% lower for older relative to younger adults, whereas others (e.g. Bastin et al., 2013; Cansino et al., 2013) reported a difference of roughly twice this magnitude in comparable age groups. The present study did not include a non-names control task to directly test the hypothesis that the nature of (familiar) names representing unique individuals may actually help source memory. But specific deficits with respect to inter-item associations (naming a face) have been reliably reported in both research and self-reports in older adults (see Introduction sections 2.1 and 7.1). On the one hand, this potential discrepancy between the present and former findings may be related to the fact that the current study involved a potentially easier task, with learning and remembering two alternative item-context associations with different names. On the other hand, it should be noted, that only two possible contexts for a multitude of names were presented, and hence interference might well have been more pronounced in the present paradigm. This, in turn, would likely increase the prevalence of errors (for potentially related findings of interference on memory processes in young and older adults, see also May, Hasher, & Kane, 1999; G.

Rowe, Hasher, & Turcotte, 2010). Increased interference in the present paradigm would argue against the idea that the present source paradigm is easier to master than an associative face-name task.

Recollection-associated effects in later time ranges were only detected in younger adults, in line with the literature on episodic memory decline in older adults (Balota et al., 2000; Friedman, 2013). However, it should be noted that a number of studies have reported intact recollection-based processes in older adults (Mark & Rugg, 1998; Wang et al., 2012). A recent study (Angel et al., 2010) showed that if retrieval support is high in a word-stem cued-recall task, performance and the left parietal old/new effect can be similarly pronounced in younger and older adults, as opposed to a low-support condition (in line with the so-called environmental support hypothesis, see Craik, 1983). This latter finding may be considered as conflicting with the current study, in which retrieval support was arguably high (the full name was presented on the screen, and in half of the trails it appeared in the same format during learning and test). However, the occurrence of a recollection-based effect might not entirely depend on the quantity of retrieval support, but also on the extent to which older adults make use of it. In a next step, it should be tested whether similar recollection-associated effects for younger and older adults would be seen when equated for performance between age groups (similar to Angel et al., 2010).

In light of the present results and for the benefit of research on associative memory in general, it should be of interest to investigate whether difficulties in memory for names is rather a problem tied primarily to encoding, retrieval or both. To my knowledge this has very rarely been studied by means of ERPs. Regarding source memory in general, only two studies have looked at Dm-effects and measured encoding differences between younger and older adults. Friedman and Trott (2000) observed no encoding differences in the source task, but in their remember/know procedure: Whereas younger adults showed a subsequent memory effect both in recollection (subsequent remember-items elicited larger amplitudes than missed judgments) and in familiarity processes (subsequent know-items elicited larger amplitudes than missed items), older adults showed a corresponding effect only in the latter case, arguing for learning processes leading to preserved familiarity, but recollection (e.g. Anderson & Craik, 2000; Cansino, 2009). A more recent study (Cansino, Trejo-Morales, & Hernandez-Ramos, 2010) found subsequent memory effects with larger amplitudes during study for those items that attracted a correct source response at test in young (21-26 years of age), middle-aged (50-55 years) and older adults (70-77 years). However, the onset was delayed as a function of age, and the scalp topography differed between young adults and the two older groups. Middle-aged and older adults showed a more posterior scalp distribution of the effect, which was interpreted to potentially reflect cerebral re-organization resulting in less efficient encoding in these age groups. Consequently, a future follow-up study with the present paradigm might hence benefit from testing for (additional) contributions of subsequent memory effects. This would make it possible to evaluate the extent of encoding and retrieval difficulties and their potential relationship. More specifically, comparable Dm-effects across age groups would suggest that source memory difficulties are primarily linked to retrieval or memory consolidation, as opposed to encoding – an issue which has been addressed before but which is still lacking a straightforward answer (see e.g. Cansino et al., 2010; Glisky, Rubin, & Davidson, 2001). Attenuations of Dm-effects, similar to absent recollection, and reversed fluency-based ERPs effects, would additionally account for age-related differences in performance. Alternatively, (and to the extent that Dm-effects reflect encoding into episodic memory) reductions in both Dm- and recollection-based effects would themselves represent evidence for a prominent role of fluency on source memory - particularly so, if these reductions occurred along with priming effects (reversed or not) for correct source judgments: in this case, fluency would be the only mechanism source memory could build on.

Finally, the use of fMRI would also be suitable for further investigating fluency-based processes and source memory in younger and older adults. Functional brain imaging correlates of priming have been observed in various brain regions related to specific stimuli and tasks, e.g. extrastriate cortex in the case of perceptual processes. Frequently, such priming correlates occur as repetition suppression (see e.g. Badgaiyan, Schacter, & Alpert, 2001; Schacter & Buckner, 1998). If long-term repetition priming effects were directly linked to explicit source retrieval, priming effects in these brain regions should be associated with correct but not with incorrect source decisions. This would provide further evidence for the proposed interplay between fluency-based processes and explicit memory and might yield valuable insights into the relationship of neural structures supporting implicit versus explicit processes in the aging brain.

12. Towards an Overall Integrative Discussion on Age-Related Effects in Person Perception and Memory

This thesis focussed on age-related changes at various stages of person recognition. The main starting point was the well-established phenomenon that older adults are particularly poor at remembering the names of faces (Leirer et al., 1990; Naveh-Benjamin et al., 2004; Old & Naveh-Benjamin, 2012). These age-related disproportional difficulties in putting names to faces were hypothesized to emerge due to several different underlying reasons, such as a decline in face processing mechanisms and deficits in the formation and retrieval of new associations in episodic memory (see also James et al., 2008). Hence, the first part of the thesis examined face processing in older adults.

More specifically, the first study focused on performance-related differences at early perceptual stages in higher age. The ORB was used as a marker of perceptual expertise (see also Wiese et al., in press) that further allowed to test for potential age-related dedifferentation in the face processing system, and to examine potential associations between decreased configural/holistic processing and impairments in face recognition abilities (see also Chaby et al., 2011). Intriguingly, both high- and low performers demonstrated an equivalent pattern of a behavioral ORB, and a parallel increase in N170 for other-race faces – similar to effects for younger adults reported in previous studies (e.g. Wiese et al., in press). Group differences emerged only independent of face ethnicity: whereas low-performers exhibited a right-lateralized N170, high-performers showed a more bilateral response, suggestive of a mechanism compensating for age-related decline by recruiting additional neuro-cognitive resources (see e.g. Cabeza, 2002; Reuter-Lorenz & Cappell, 2008). Overall, the results from Experiment 1 demonstrate that even a less efficient face processing system in older adults can exhibit preserved expertise-related specialization towards own-race faces. This finding argues for well-preserved early perceptual stages of face processing in older age.

Experiment 2 focused on age-related changes at representational stages of face processing. This study exploited the OAB as a marker of the integrity of the face representational system which has been shown to adapt to environmental demands in young and young-middle aged participants (Harrison & Hole, 2009; Wiese, Wolff, et al., 2013). Experiment 2 aimed at testing whether influences of increased contact to own-age persons would shape the face representational system even in older age. The behavioral results argue for age-preserved plasticity of the face representational system, as indexed by increased recognition memory performance for older faces in those elderly participants who reported enhanced contact with persons from their own-age group. However, age-related changes were observed in neural correlates of facial representations with polarity-reversals from the N250 time window on. Whereas a neural correlate of the behavioral OAB was observed in both younger and older participants in the later old/new effect, this finding was again accompanied by a polarity reversal in older adults. The finding of later ERP old/new effects specific to own-age faces suggests enhanced recollection of study phase detail in young participants, whereas it may reflect increased engagement in processes aiming at compensating for a deficit in recollection in older participants (see also Duarte et al., 2006; Wolk et al., 2009).

Study 1 and 2 examined face processing at the level of image-specific face learning and representation, and hence at relatively low levels of the hierarchical stages involved in person recognition according to Bruce and Young (1986). The subsequent experiments shifted the focus towards high-order mechanisms operating at the NRU and PIN level, and further aimed at testing for age effects on name-context associations in episodic memory.

A paradigm allowing the investigation of potential influences of long-term within-modality repetition priming on recognition and source memory was implemented in younger adults in Experiments 3 and 4, respectively. Both experiments revealed N400-like repetition effects presumably reflecting fluency-based processes, which most probably arose from the strengthening between an NRU and its corresponding PIN (see also Schweinberger, Pickering, Burton, et al., 2002). These effects, in a time-range from 300-600 ms appeared to beneficially affect source memory for familiar names, since they emerged for correct source responses only. Crucially, Experiment 5 found similar results for older adults. An analogous, though polarity-reversed, pattern of N400-like ERPs was shown to differentiate between within- and across modality repetitions from learning to test, and occurred for correct responses only. Thus, all three experiments yielded evidence that fluency-based implicit processes may assist retrieval of context information for a particular name via within-modality long-term repetition priming. However, the polarity reversal of the N400 effect and the lack of ERP effects of repetition during learning in older adults, which were evident in the young adults in a later recollection-related time window, indicated influences of cognitive aging on source/associative memory processes. These influences appear to occur in parallel with decreased memory performance in higher age.

A general conclusion, from the experiments conducted in this thesis, is that lower levels of person perception, such as early perceptual stages of face processing, are relatively spared in older adults (Experiment 1). In contrast, higher levels in person perception, such as representational (Experiment 2) and associative memory processes (Experiment 3, 4, and 5) are more strongly affected by aging. Of note, these more age-vulnerable higher levels of processing involve not only controlled, effortful processes, such as recollection, but fluency mechanisms as well, which are generally thought to be largely preserved in older age (Balota et al., 2000). Interestingly, the present studies relatively consistently reveal that, in fact, these mechanisms are at least to some degree affected by participant age, evident in attenuations or polarity-reversals in ERPs in the N250 (see Experiment 2) or in the N400 time window (300-600 ms; see Experiment 4 and 5).

At the very beginning of this thesis, my interest in human development was highlighted with reference to its multi-dimensional, multi-directional and multi-factorial nature – all these aspects and their interrelations played a role over the course of the current studies and therfore merit comment. Study 1 revealed that although break-downs or impairments in visual processing have been previously observed in older age (see e.g. D. C. Park et al., 2004), face processing as a sub-domain may remain specific and differentiated - as reflected in an ORB - even if face memory abilities decrease. These differential trajectories reflect on the multi-dimensionality of development. Similarly, it has been reported that fluency might have detrimental effects for older adults, prompting memory errors when tested with wordlists consisting of concrete or abstract nouns (Jacoby, 1999; Jacoby & Rhodes, 2006). This does not seem not to be case for the domain of familiar names (and presumably also for familiar faces) where benefical processes, such as within-modality priming, may be operating.

Furthermore, older adults generally showed impairments in memory performance relative to young participants across all experiments, but these were sometimes (at least partly) counteracted by neuro-cognitive plasticity indicating multi-directionality. This was reflected in more bilateral N170 components in older high-performers in Experiment 1, a behavioral bias in the old/high contact participants in Experiment 2, and reversed N400 effects in Experiment 5.

In addition, Experiments 1 and 2 revealed that aging can be diverse and influenced by multiple factors, acting on either the cognitive, or social level, or both. Finally, Experiment 2 in particular yields evidence that individuals can actively shape their own development and hence enable what is often termed sucessful or graceful aging (Abbott, 2004; J. Rowe & Kahn, 1998). A key message conveyed by this conzeptualization is that although aging is of course influenced by genetic factors, there is an essential component which is determined by life-style choices (see Abbott, 2004). For instance, twin studies show that only 25% of the variation in life expectancy (Skytthe et al., 2003) and half of the variation in cognitive function late in life can be attributed to genetic differences (McGue & Christensen, 2002). Thus, behavioral factors have considerable potential to affect cognitive abilities and the accompanying neural processes (as in the present study) contributing to one's aging trajectory (for a similar argument, see Lachman, 2006). Hence, aging is to some extent under one's own control, which also underscores the importance of self-organized, self-initiated behavior in advanced age:

"But its eminent modifiability, and its predisposition to self-initiated action, may it develop little or much, and may it differ in amount between different individuals, is among the immutable features of humankind, which can be found whereever humans exist."

Johann Nicolaus Tetens (1736 – 1807)

13. Summary

Across our entire life span, we are not only subject to biological or environmental changes, we are often apt and able to actively create our personal trajectory, our development (Brandtstaedter & Rothermund 2002, Brandtstaedter, 2009). However, while younger adults perceive their future as manifold in options and designs, older adults see their lives as less open and controllable, but more confined by impairments or functional losses (see Brandtstaedter 2009), such as cognitive decline. Demographic changes, with an increasing percentage of older adults, underscore the need for research on aging and the effects that come with it (Grady, 2012). Although development is plastic and the consequences of aging can be diverse (Cabeza, 2002, Salthouse, 2013), a very common and serious age-related concern is cognitive frailty (see Bishop, 2010). Such concern is legitimate, as cognitive decline affects our quality of life, our (perceived) well-being and even whether we are able to live independently or not (Salthouse, 2004).

Cognitive decline in general, and memory decline in particular, is a highly relevant topic to examine both in the context of aging pathologies such as dementia (Pires, et al. 2012), but also because memory complaints are very common in healthy older adults (Ossher, Flegal & Lustig, 2013). Interestingly, it seems that deficits in the domain of person recognition are among the greatest hassles in older adults' every-day life. For example, older adults report difficulties both in learning new names and recognizing people they recently encountered for the first time (Naveh-Benjamin, Guez, Kilb & Reedy, 2004, Rendell, Castel and Craik, 2005, Ossher et al., 2013), as well as in naming friends and family members (Cohen & Faulkner 1986) – an issue perceived as particularly alarming, prompting older adults to seek for clinical support (Pires et al., 2012). Moreover, memory for names is of particular social relevance, as socializing makes up a great part of many older adults' everyday life, and social integration has been shown to predict changes in depressive symptoms (but not the other way around) in middle-aged and older adults (Cacioppo, Hawkley & Thisted, 2010). When participants were asked to indicate which specific memory skill they would like to improve, memory for people's names (as opposed to e.g. memory for dates and facts) was designated as a top priority by the majority of older respondents (see also Leirer, Morrow, Sheik & Pariante, 1990), underscoring the relevance of person recognition in older age.

This thesis focuses on two aspects of person recognition, namely face processing and the recognition of unfamiliar faces, as well as source memory for familiar names, as a form of associative memory. Both appear to be compromised in older age and can thus cause difficulties person recognition (see also James, Fogler & Tauber,. 2008).

The first experiment focused on the own-race bias (ORB; i.e. the memory advantage for own- relative to other-race faces) as a measure of experience-based specialization of the face processing system. This study examined a memory bias for own-race faces in both high- and low performing older adults using event-related brain potentials (ERPs). More specifically, the aim was to investigate whether poor face memory in older age is accompanied by reduced expertise-based specialization of early perceptual mechanisms in face processing. Importantly, a lack of an ORB in older adults could be interpreted as indicating less differentiated processing mechanisms in older adults. There is some evidence that face processing inefficiency might be the cause of reduced face memory in older adults (Chaby, Narme & George, 2011), and N170 is often larger in older as compared to younger adults (Wiese, Schweinberger & Hansen, 2008; Gao et al, 2009). However, no study has systematically tested the link between face memory and early face processing in older adults. Moreover, although two studies have speculated that the finding that N170 is sometimes less lateralized in older adults could signify a compensatory mechanism (Gao et al. 2009; Daniel & Bentin 2012), again there is no study that has directly tested this assumption.

In Experiment 1, both older groups demonstrated an equivalent pattern of a behavioral ORB, and a parallel increase in N170 for other-race faces. Group differences only emerged independent of face ethnicity: whereas low-performers exhibited a right-lateralized N170, high-performers showed a more bilateral response, suggestive of a neural mechanism compensating for age-related decline by recruiting additional resources. Overall, the results from Experiment 1 demonstrate that even a less efficient face processing system in older adults can exhibit preserved expertise-related specialization towards own-race faces, at least with respect to early perceptual mechanisms.

Experiment 2 followed up on this finding and examined the own-age bias (OAB; i.e., the memory advantage for own- relative to other-age faces). As the OAB appears to depend primarily on the fine-tuning of the face representational system, it can be exploited to determine whether this system becomes less flexible with increasing age or whether it can adapt to environmental demands due to more recent contact to older (own-age) persons. Effects of recent contact on the OAB in elderly participants would be in line with the idea of a more flexible face representation system even in older age. Evidence for this idea so far comes only from studies on young or young middle-aged experts who display reduced own-age biases (Harrison & Hole, 2009; Wiese, Wolff, Steffens & Schweinberger, 2013). No study has taken age-related differences in face recognition into account, despite the fact that these could hamper a potential plasticity of the face space. Furthermore, it is unclear which neural mechanisms would underlie a behavioral OAB in older adults, or how cognitive and brain aging would interact with potential differences in neural representations of own- versus other-age faces. Hence, Experiment 2 set out to close this gap. It compared behavioral and ERP effects in two groups of older adults who differed in their amount of contact towards own-age persons. In addition, young controls were tested to allow for comparisons between age groups.

The results revealed that the face representational system flexibly adapts to environmental demands in older age. This was reflected by the fact that for older adults with relatively high levels of contact to older (own-age) relative to younger (other-age) people, an OAB was found both behaviorally and in neural correlates related to representation (N250 time-window) and memory (later old/new effect time range). Strikingly, no such effects were apparent in a group with relatively little contact to same-age persons. In addition, age-related changes in neural activity were apparent between older adults and the younger controls, who, similar to old/high contact participants, exhibited an OAB and a neural correlate of this effect in the later old/new effect time window. Whereas a more pronounced old/new effect (i.e. more positive amplitudes for hits than correct rejections) for own- relative to other-age faces was found in young controls, the corresponding effect was more widespread and polarity-reversed (less positive amplitudes for hits than correct rejections) in old/high contact participants. This finding most probably relates to compensatory mechanisms aiming at the retrieval of study phase detail (see also Duarte, Ranganath, Trujillo & Knight, 2006; Friedman 2013).

Experiments 3, 4 and 5 focused on memory for item-context associations, and more particularly on source memory for familiar names – a class of stimuli which has been largely neglected in this area of research although, as stated above, personal names are of great relevance for older adults' daily lives (for similar arguments, see Dywan, Segalowitz, & Arsenault, 2002; Yovel & Paller, 2004). Source memory, as a form of associative memory, is often particularly impaired in older adults (see Old & Naveh-Benjamin, 2008; Spencer & Raz, 1995), whereas fluency-based processes, such as priming, are usually spared (Balota, Dolan, & Duchek, 2000). Importantly, for current purposes, fluency-based processes have recently been shown to contribute to source memory unless the exact mechanism as yet remains largely unclear (Bastin et al., 2013; Diana, Yonelinas, & Ranganath, 2008; Mollison & Curran, 2012). With Experiments 3, 4 and 5, I aimed at testing whether fluency-based processes catalyzed through within-modality long- term repetition priming could assist source decisions for familiar names to a similar extent in younger and older adults. Importantly, for present purposes, such pattern of results would imply that age-related differences in source memory might be less severe if deficient processes (i.e. recollection and monitoring) can be outweighed by spared fluency-based mechanisms. Furthermore, it was hypothesized that fluency-based processes would manifest in an FN400 or N400-like priming effect associated with correct source retrieval in younger and older adults. Finally, I was also interested to see whether cognitive and brain aging can lead to differences in the neural correlates associated with source retrieval, e.g. in an absent or reduced later, recollection-based old/new effect or in an intact FN400 priming effect.

Across the series of EEG experiments, an N400 priming effect differentiated between the two possible sources of a previously presented familiar name in both younger (Experiment 3 and 4) and older adults (Experiment 5), reflecting whether the name had been learned auditorily or visually. This effect occurred for correct source judgments only, which strongly suggests a beneficial influence of fluency-based processes on source memory. However, young adults additionally exhibited a later, most probably recollection-based ERP effect; no such effect was found in older adults. This absence of recollection-related ERP modulations in older adults may have contributed to source memory performance differences between age groups. In addition, the N400 priming effect was slightly reduced and polarity-reversed in older adults, Thus, fluency signals can also show age-related alterations, possibly to compensate for a lack of recollection-based retrieval.

A general conclusion from the experiments conducted in this thesis is that lower levels of person perception, such as early perceptual stages of face processing, are relatively spared in older adults (Experiment 1). In contrast, perceptual representations (Experiment 2) and associative memory processes (Experiment 3, 4, and 5) are more strongly affected by aging. Of note, these more age-vulnerable higher levels of processing involve not only controlled, effortful processes, such as recollection, but fluency mechanisms as well, which are generally thought to be largely preserved in older age. Interestingly, the present studies relatively consistently reveal that, in fact, these mechanisms are at least to some degree affected by participant age, evident in attenuations or polarity-reversals in ERPs in the N250 (see Experiment 2) and N400 time range (300-600 ms; see Experiment 4 and 5).

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14. Zusammenfassung

Über die gesamte Lebensspanne sind wir nicht nur genetischen oder umweltbedingten Einflüssen ausgesetzt, sondern gestalten unsere Entwicklung ganz aktiv selbst mit (Brandtstaedter & Rothermund 2002, Brandtstaedter 2009). Während jüngere Leute ihre Zukunft als vielfältig an Möglichkeiten und Entwürfen sehen, empfinden ältere Menschen ihr Leben als weniger offen und kontrollierbar, oft auf Grund von Einschränkungen in bestimmten Funktionsbereichen, wie zum Beispiel kognitiven Fähigkeiten. Demographische Veränderungen durch einen stark wachsenden Anteil älterer Menschen machen deutlich, wie wichtig Forschung ist, die sich mit Alterseffekten auseinandersetzt (Grady, 2012). Obwohl die menschliche Entwicklung plastisch ist und die Folgen von Alterungsprozessen sehr verschieden sein können (Cabeza, 2002; Salthouse, 2013), ist kognitive Fragilität ein sehr häufiges, altersbedingtes Besorgnis (Bishop et al., 2010). Diese Sorge erscheint sehr berechtigt, denn schließlich beeinflusst kognitive Funktionstüchtigkeit unsere Lebensqualität, unser Wohlbefinden, und das Ausmaß an Selbständigkeit im Alltag (Salthouse, 2004).

Das Nachlassen kognitiver Funktionen im Allgemeinen, und speziell die Abnahme gedächtnisrelatierer Funktionen, ist ein sehr wichtiges Thema, nicht nur im Kontext pathologischer Alterungsprozesse, wie beispielsweise Demenzerkankungen (Pires et al., 2012), sondern auch weil Beschwerden die Gedächtnisleistung betreffend sehr häufig von gesunden älteren Menschen berichtet werden (Ossher, Flegal & Lustig, 2013). Interessanterweise scheinen Defizite im Bezug auf das Gedächtnis für Personen und die Wiedererkennung von Personen eine der größten Schwierigkeiten im Alltag älterer Menschen darzustellen. So berichten ältere Leute von Problemen, sowohl wenn sie sich neue Namen von Personen, die sie kürzlich kennengelernt haben, merken sollen (Naveh-Benjamin, Guez, Kilb & Reedy, 2004, Rendell, Castel and Craik, 2005, Ossher et al., 2013), als auch dabei, Namen von Freunden und Verwandten abzurufen (Cohen & Faulkner, 1986). Vor allem dieser letzte Aspekt wird als besonders alarmierend wahrgenommen und veranlasst ältere Menschen klinische Beratung aufzusuchen (Pires, 2012).

Das Gedächtnis für Namen ist außerdem von besonderer Relevanz bis ins hohe Alter, da soziale Kontakte für den Alltag älterer Menschen wichtig sind (siehe auch Leirer, Morrow, Sheik & Pariante, 1990). Als Leirer und Kollegen (1990) ältere Menschen befragt haben, welche Gedächtnisfertigkeit sie am liebsten verbessern möchten, dann gab die Mehrheit die Erinnerung an Personennamen als Toppriorität (gegenüber bspw. der Erinnerung an Daten, Fakten) an. Auch dieses Ergebnis unterstreicht die Wichtigkeit des Personengedächtnisses im höheren Alter.

Die vorliegende Arbeit beschäftigt sich mit zwei Aspeketen des Personengedächtnisses, nämlich mit der Verarbeitung und dem Wiedererkennen unbekannter Gesichter einserseits, und mit dem Quellgedächtnis (als eine Form des Assoziativgedächtnisses) für bekannte Namen andererseits. Beide Aspekte scheinen im Alter deutlich beeinträchtigt zu sein und somit Schwierigkeiten im Personengedächtnis zu verursachen (siehe auch James, Fogler & Tauber, 2008).

Die erste Studie der vorliegenden Arbeit untersucht den own-race bias (ORB, dies ist die Bezeichnung für den Befund, dass Gesichter der eigenen Ethnizität besser erinnert werden, als Gesichter anderer Ethnizitäten) mittels Ereignis-korrelierter Hirnpotentiale (EKPs) bei älteren Probanden, die sich hinsichtlich der Gedächtnisleistung unterscheiden (high versus low performers). Der ORB gilt als ein Instrument zur Messung expertisebasierter Spezialisierung des Gesichterverarbeitungssytems auf Gesichter der eigenen Ethnizität. Ziel der Studie war es zu untersuchen, ob schlechte Gesichtergedächtnisleistung mit einer reduzierten Spezialisierung früher perzeptueller Verarbeitungsprozesse assoziert ist. Von besonderer Bedeutung ist dabei, dass das Ausbleiben eines ORB bei älteren Probanden auf weniger differenzierte frühe Verarbeitungsmechanisen hindeuten könnte. Es exisistieren bereits Befunde, die darauf hinweisen, dass Ineffizienz in frühen Stufen der Gesichterverarbeitung bei älteren Personen reduzierte Gedächtnisleistungen für Gesichter hervorrufen könnte (Chaby, Narme & George, 2011). Im Zusammenhang damit ist die N170, ein Korrelat früher konfiguraler Verabeitung, bei älterern Probanden häufig negativer als bei jüngeren Probanden (Wiese, Schweinberger & Hansen, 2008; Gao et al, 2009). Jedoch exisistiert meines Wissens nach bisher noch keine Untersuchung, die die potentielle Assoziation zwischen Gedächtnisleistung für Gesichter und früher perzeptueller Verarbeitung bei älteren Probanden explizit untersucht hat. Des Weiteren existieren bisher nur Spekulationen hinsichtlich der weniger ausgeprägten Rechtslateralisierung der N170 bei älteren Probanden im Zusammenhang mit Kompensationsmechanismen (Gao et al. 2009; Daniel & Bentin 2012). Es existiert bisher noch keine Studie, die diesen Zusammenhang explizit geprüft hat.

Die Ergebnisse von Experiment 1 in der vorliegenden Arbeit zeigen interessanterweise, dass beide älteren Gruppen sowohl einen ORB, als auch eine stärkere Negativierung der N170 für Gesichter der anderen Ethnizität aufweisen. Gruppenunterschiede traten nur auch im Bezug auf die Lateralisierung der N170 auf. Probanden mit eher durchschnittlichen bis schlechten Gesichtergedächtnisleistung (low performers) zeigten eine klar rechtslateralisierte N170, während Probanden mit sehr guter Gedächtnisleistung (high-performers) ein bilaterales Muster der N170 aufwiesen. Letzteres deutet auf einen neuronalen Mechanismus hin, der auf die Kompensation altersbedingter Einschränkungen abzielt, indem zusätzliche Ressourcen rekrutiert werden. Zusammenfassend kann festgehalten werden, dass auch bei einem weniger effizientem Gesichterverarbeitungssystem im höheren Alter, expertisebedingte Spezialisierung für Gesichter der eigenen Ethnizität, zumindest was frühe perzeptuelle Verarbeitungsstufen angeht, weitgehend erhalten bleibt.

Experiment 2 baut auf diesen Ergebnissen auf und untersucht den own-age bias (OAB; dies ist die Bezeichnung für den Befund, dass Gesichter der eigenen Altersgruppe besser erinnert werden als Gesichter anderer Altersgruppen). Da der OAB vor allem vom Feintuning des Gesichterrepräsentationssystem abzuhängen scheint, kann dieser genutzt werden um zu testen, ob sich dieses System Umweltgegebenheiten, wie erhöhtem Kontakt zu Personen der eigenen Altersgruppe, anpassen kann. Effekte auf den OAB bei älteren Probanden, die mit momentanem, alltäglichen Kontakt zu tun haben, würden für die Idee eines flexiblen Gesichterrepräsentationssystem auch im höheren Alter sprechen. Hinweise für die Gültigkeit dieser Idee stammen bisher aus Untersuchungen mit Probanden jüngeren oder mittleren Erwachsenenalters, die aufgrund von erhöhtem Kontakt zu anderen Altersgruppen keinen OAB aufwiesen (Harrison & Hole, 2009; Wiese, Wolff, Steffens & Schweinberger, 2013). Es existiert jedoch noch keine Studie, die altersbedingte Unterschiede in Wiedererkennungsfähigkeiten in Betracht zieht, obwohl diese die potentielle Plastizität des Gesichterrepräsentationssystem stark einschränken könnten. Des Weiteren ist bisher unklar, welche neuronalen Mechanismen einem behavioralen OAB in älteren Probanden bedingen können, oder wie kognitive und neuronale Alterungsprozesse mit Unterschieden zwischen neuronalen Repräsentationen für Gesichter der eigenen im Vergleich zu anderen Altersgruppen interagieren würden. Experiment 2 versucht die oben genannten Forschungslücken zu füllen und vergleicht behaviorale und EKP Effekte in zwei Gruppen von älteren Probanden, die sich hinsichtlich des Kontakts zur eigenen Altersgruppe unterschieden. Um Altersvergleiche zu ermöglichen, wurde in Experiment 2 außerdem noch eine jüngere Kontrollgruppe getestet.

Die Ergebnisse zeigen, dass es dem Gesichterrepräsentationssystem auch mit höherem Alter möglich ist, sich an Umweltgegebenheiten anzupassen. Dies wurde deutlich durch das gemeinsame Auftreten eines OAB sowie repräsentationaler und gedächtnisrelatierter neuronaler Korrelate (im N250 und späterem Alt/Neu Effekt Zeitfenster) für Gesichter der eigenen im Vergleich zur jüngeren Altersgruppe in jenen älteren Probanden, die auch relativ viel Kontakt zur eigenen (älteren) versus jüngeren Altersgruppe berichteten (old/high contact Gruppe). Interessanterweise blieben vergleichbare Befunde in der Gruppe von älteren Probanden, die relativ wenig Kontakt zur eigenen Altersgruppe berichteten (old/low contact Gruppe), aus. Altersbedingte Veränderungen in neuronalen Aktivierungen wurden ebenfalls deutlich. Junge Probanden, ähnliche wie die old/high contact Gruppe, wiesen einen OAB auf sowie ein neuronales Korrelat dieses Effektes im späteren Alt/Neu Effekt Zeitfenster. Jedoch wurde bei jungen Probanden ein stärkerer Alt/Neu Effekt (mit positiveren Amplituden für hits versus correct rejections) für Gesichter der eigenen versus der älteren Altersgruppe gefunden, während der entsprechende Effekt bei old/high contact Probanden ausgedehnter und polaritätsvertauscht war (weniger positive Amplituden für Hits versus correct rejections). Letzteres steht vermutlich im Zusammenhang mit einem Kompensationsmechanismus, der darauf abzielt, Details aus der Lernphase abzurufen (siehe auch Duarte, Ranganath, Trujillo & Knight, 2006; Friedman, 2013).

Experimente 3, 4 und 5 untersuchen das Gedächtnis für Item-Kontext Assoziationen bzw. das Quellgedächtnis für bekannte Namen im Speziellen. (Bekannte) Namen wurden als Stimulusklasse in diesem Forschungsbereich eher vernachlässigt (siehe auch Dywan, Segalowitz, & Arsenault, 2002; Yovel & Paller, 2004 für ähnliches Argument), obwohl sie, wie oben angesprochen, von besonderer Relevanz im Alltag älterer Menschen sind.

Das Quellgedächtnis, als eine Form des Assoziativgedächtnisses, ist häufig besonders betroffen von Alterungsprozessen (Old & Naveh-Benjamin, 2008; Spencer & Raz, 1995). Im Gegensatz dazu, sind fluency-basierte Prozesse, wie bspw. Priming, oft altersinvariant (Balota, Dolan, & Duchek, 2000). Besonders relevant für die vorliegende Arbeit ist der Umstand, dass diese fluency-basierten Prozesse offenbar zum Quellgedächtnis beitragen können, wobei der exakte Mechanismus dahinter bisher weitgehend unklar ist (Bastin et al., 2013; Diana, Yonelinas, & Ranganath, 2008; Mollison & Curran, 2012). Experimente 3, 4 und 5 zielten darauf ab, zu untersuchen, ob fluency-basierte Prozesse, die durch perzeptuelles Langzeit-Priming (within-modality long-term repetition priming) hervorgerufen wurden, Quellgedächtnisentscheidungen über bekannte Namen bei älteren und jüngeren Probanden günstig beeinflussen können. Altersbedingte Unterschiede im Quellgedächntis könnten in diesem Falle weniger bedeutsam sein, da defizitäre Prozesse (wie bewusste Erinnerung, im Folgenden recollection, oder Abrufkontrollprozesse wie monitoring) durch intakte fluency-basierte Mechanismen ausgeglichen werden können. Desweiteren wurde die Hypothese aufgestellt, dass fluency-basierte Prozesse in FN400 oder N400-ähnlichen EKP Effekten zu

Tage treten würden. Diese EKP Effekte sollten dann mit korrekten Quellgedächtnisentscheidungen assoziiert sein. Als letzten Punkt war ich daran interessiert herauszufinden, ob kognitive oder neuronale Alterungsprozesse Unterschiede in neuronalen Korrelaten von Quellgedächtnis hervorrufen könnten. Genauer gesagt, ob diese sich also in einem reduzierten oder fehlenden späteren, recollection-basiertem Alt/Neu Effekt und einem intakten FN400 oder Priming Effekt äußern würden.

Über eine Serie von EEG Experimenten hinweg wurde sowohl in jungen (Experiment 3 und 4), als auch in älteren Probanden (Experiment 5), ein N400-ähnlicher Priming Effekt gefunden, der zwischen zwei möglichen Quellen (visuell oder auditorisches Lernformat) eines präsentierten Namen differenzierte. Da dieser Effekt nur bei korrekten und nicht bei inkorrekten Quellgedächtnisentscheidungen auftrat, ist anzunehmen, dass er einen begünstigenden Einfluss von fluency-basierten Prozessen auf Quellgedächtnisvorgänge widerspiegelt. Jüngere Probanden zeigten zudem auch einen späteren, höchstwahrscheinlich recollection-basierten EKP Effekt. Dieser Effekt zeigte sich nicht in den älteren Teilnehmern, was eine mögliche Ursache für Performanzunterschiede zwischen den Gruppen sein könnte. Bei den älteren Probanden war außerdem auch der N400 Priming Effekt etwas weniger ausgeprägt und polaritätsvertauscht. Dieser Befund zeigt, dass auch Fluency-Signale altersbedingte Veränderungen aufweisen und/oder möglicherweise mit Kompensationsmechanismen für defizitäre recollection-basierte Abrufprozesse in Verbindung stehen können.

Aufgrund der Ergebnisse dieser Studien kann geschlussfolgert werden, dass relativ basale Prozesse der Personenwahrnehmung, wie frühe perzeptuelle Gesichterverarbeitung, von Alterungssprozessen eher verschont bleiben (Experiment 1). Im Gegensatz dazu sind spätere, höher geordnete Prozesse, wie perzeptuelle Repräsentationen (Experiment 2) oder das Assoziativgedächtnis (Experiment 3, 4, and 5), stärker von Alterungsprozessen betroffen.

Zu bemerken ist dabei, dass diese eher altersfragilen, höher geordneten Verarbeitungsstufen nicht nur kontrollierte, mühevolle Prozesse, wie recollection beinhalten, sondern auch Fluency-Mechanismen, die eigentlich als eher altersinvariant gelten. Interessanterweise zeigen die vorliegenden Studien, dass auch diese Mechanismen, zumindest zu einem bestimmten Grad, von Alterungsprozessen beeinträchtigt sind. Sichtbar wurde dies in abgeschwächten und polaritätsvertauschten EKP Effekten in den Zeitfenstern der N250 (Experiment 2) und der N400 (Experiment 4 und 5).

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List of Abbreviations

ANOVA	analysis of variance
BOLD	blood oxygenation level dependent
C	response bias according to signal detection theory
CR	correct rejection
d’	sensitivity according to signal detection theory
EEG	electroencephalography
ERP	event-related potential
FFA	fusiform face area
FG	fusiform gyrus
fMRI	functional magnetic resonance imaging
FRU	face recognition unit
IOG	inferior occipital gyrus
LFE	late frontal effect
LPC	late positive component
M	mean
MDFS	multidimensional face space
MTL	medial temporal lobe
NRU	name recognition unit
OAB	own-age bias
OFA	occipital face area
ORB	own-race bias
PCA	prinicipal component analysis

PFC	prefrontal cortex
PRC	perirhinal cortex
PIN	person identity note
RT	reaction time
SD	standard deviation
SEM	standard error of the mean
STS	superior temporal sulcus
TAP	transfer-appropriate processing
TOT	tip-of-the-tongue
VPP	vertex positiv potential

Eigenständigkeits – und Ehrenwörtliche Erklärung

Ich erkläre, dass mir die geltende Promotionsordnung der Fakultät für Sozial- und Verhaltenswissenschaften der Friedrich-Schiller-Universität Jena bekannt ist.

Ferner erkläre ich, dass ich die vorliegende Dissertation selbstständig ohne die Hilfe Dritter angefertigt habe, keine Textabschnitte eines Dritten oder eigener Prüfungsarbeiten ohne Kennzeichnung übernommen habe, sowie alle benutzten Quellen und Hilfsmittel in der Arbeit angegeben habe. Insbesondere habe ich keine Hilfe eines Promotionsberaters in Anspruch genommen.

Bei der Auswahl und Auswertung des Materials sowie der Herstellung des Manuskripts haben mich Prof. Schweinberger und PD Dr. Holger Wiese unentgeltlich unterstützt. Darüber hinaus hat kein Dritter unmittelbar oder mittelbar geldwerte Leistungen von mir für Arbeiten erhalten, die im Zusammenhang mit dem Inhalt der vorgelegten Dissertation stehen.

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Jena, den 25.10.2013

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