Age-Related Differences in Face Recognition: Neural Correlates of Repetition and Semantic Priming in Young and Older Adults

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Difficulties in person recognition are among the common complaints associated with cognitive ageing. The present series of experiments therefore investigated face and person recognition in young and older adults. The authors examined how within-domain and cross-domain repetition as well as semantic priming affect familiar face recognition and analyzed both behavioral and event-related brain potential (ERP) measures to identify specific processing stages of age-related deficits. During repetition priming (Experiments 1 and 2), the authors observed evidence of an age-related deficit in behavioral priming and clear reductions of both the N250r and the N400 ERP priming effects in older participants. At the same time, both semantic priming (Experiment 3) and the associated N400 ERP effect of semantic priming were largely intact in older adults. The authors suggest that ageing selectively affects the access to domain-general representations of familiar people via bottom-up perceptual processing units. At the same time, accessing domain-general representations via top-down semantic units seems to be relatively preserved in older adults.

Keywords: face recognition, cognitive ageing, repetition priming, semantic priming, event-related potentials

The recognition of familiar faces is of outstanding relevance for social interactions in everyday life. Whereas difficulties in person recognition are frequently reported even in younger people (Young, Hay, & Ellis, 1985) and perceived as particularly disturbing by older adults (Leirer, Morrow, Sheikh, & Pariante, 1990), empirical research on face recognition in older adults is still relatively sparse. Although neuroscientific evidence suggests a reduced specialization of the ventral visual cortex for face processing (Park et al., 2004), a number of recent behavioral studies concluded that basic processes of face perception are relatively spared in older age (Boutet & Faubert, 2006; Konar, Bennett, &

This article was published Online First February 27, 2017.

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This work was funded by a grant of the German Research Council (Deutsche Forschungsgemeinschaft) to Holger Wiese (FOR 1097/2, WI 3219/4-2). The authors gratefully acknowledge help during EEG recordings by Kathrin Rauscher.

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Sekuler, 2013; Meinhardt-Injac, Persike, & Meinhardt, 2014b). At some variance with these studies using unfamiliar faces, learning new facial identities has been observed to be less efficient in older adults (Germine, Duchaine, & Nakayama, 2011). Moreover, only few studies have examined older adults' performance in recognizing familiar faces, which represents a fundamentally different process than the perception and recognition of preexperimentally unfamiliar faces (Bruce et al., 1999; Burton, 2013).

The extent to which familiar face processing is affected by ageing is not only relevant for research on face recognition but is also of broader theoretical interest. First, ageing seems to affect different cognitive abilities to varying extents (Baltes, 1987; Cattell, 1971; see also Craik & Bialystok, 2006): Whereas fluid abilities (or cognitive mechanics; e.g., working memory, problem solving) that represent the information processing aspect of intelligence, are typically seen to decline over the adult life span, crystallized abilities (or cognitive pragmatics; e.g., language or social intelligence) reflect cultural knowledge and are commonly assumed to remain stable or even increase in older age. As representations of highly familiar faces are typically formed over numerous learning episodes and reflect crystallized knowledge once they are firmly established, familiar face recognition should be preserved in older age. Second, and at some variance with the above suggestion, it is well documented that older adults have substantial difficulties in accessing familiar names (e.g., James, 2004, 2006). In cognitive models on person recognition, accessing name information is typically seen as the last step in a series of successive processing stages (Bruce & Young, 1986; Hanley, 2011). Importantly, these serial stage models imply that any deficit prior to the naming stage will propagate to subsequent stages and lead to difficulties in accessing name information (for a review of relevant neuropsychological case studies, see Bruce & Young, 2012). Less efficient processing of familiar faces may therefore contribute to the well-documented problems of older adults with name retrieval.

The aim of the present series of experiments was to examine whether familiar face recognition is affected by age-related differences, and to test at which processing stage potential deficits would manifest. To identify specific stages during face and person recognition, we analyzed event-related brain potentials (ERPs) in various priming paradigms.

Cognitive Processes and Neural Correlates of Face Recognition

Although various extensions and refinements have been suggested (e.g., Burton, Bruce, & Hancock, 1999; Schweinberger & Burton, 2003), the general structure of face and person recognition models is still remarkably similar to the proposal by Bruce and Young (1986). Here, we will mainly refer to the extension by Burton and colleagues (Burton, Bruce, & Johnston, 1990), which uses an interactive activation and competition (IAC) structure (McClelland & Rumelhart, 1981).

In the IAC architecture (see Figure 1), individual units are organized in pools. Units in different pools that belong to an individual person are linked via excitatory connections, and all units within a pool are linked via inhibitory connections (not shown). Once triggered by external stimulation, activity propa-

gates through the network as long as the corresponding units are activated above a given threshold. Once activation by lower-level units or external stimulation has ceased, activation levels decay and return to baseline.

For the present study, three types of representations need to be discriminated. First, pictorial representations reflect a direct internal copy of the stimulus. In the case of a familiar face or written name, pictorial representations activate corresponding perceptual representations, so-called face recognition units (FRU) or name recognition units (NRU). These units are image-independent, or robust (Burton, Jenkins, Hancock, & White, 2005), meaning that they become activated by any recognizable input representing the specific person. Moreover, these representations are domain-specific, meaning that only a specific stimulus category (e.g., faces, but not written names in the case of FRUs) can activate them. Once activated above threshold, FRUs/NRUs transmit activity to a so-called person identity node (PIN) of the specific person. PINs are domain-general, that is, input from any domain-specific representation of the particular person activates them. Importantly, a person is recognized as being familiar once a specific PIN is activated above threshold. Finally, PINs activate person-related semantic information (a person's occupation, nationality, etc.), which is stored in so-called semantic information units (SIUs). Specific SIUs can be thought of as semantic features (see, e.g., McRae, deSa, & Seidenberg, 1997), and the PINs of those who share a semantic feature are connected via bidirectional links between the PIN and SIU levels.

The aim of the present study was to examine effects of cognitive ageing on face and person recognition, and to identify the locus of

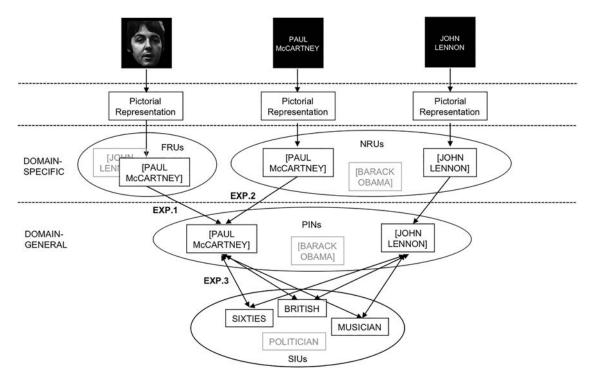


Figure 1. Modified illustration of the interactive activation and competition (IAC) model of person recognition (Burton et al., 1990). The putative cognitive loci for activating domain-general person representations, as investigated in Experiments 1–3, are also denoted.

potential age-related deficits. For instance, we were interested in whether ageing affected domain-specific, domain-general, or both types of representations. The analysis of ERPs is particularly well suited for this endeavor. ERPs are derived from the electroencephalogram (EEG) reflecting electrical activity at the postsynaptic membrane and therefore neural activity of the brain (Jackson & Bolger, 2014). They consist of voltage changes time-locked to a specific event and are depicted as a series of positive and negative deflections, so-called components.

Previous research has linked the various stages of person recognition with specific ERP components. First, accessing domainspecific representations of known faces has been associated with the so-called early repetition effect (ERE) or N250r (Schweinberger, Pfütze, & Sommer, 1995). The N250r (r for repetition) is measured when target faces are preceded by the same (related prime) relative to a different face (unrelated prime). A repetition of a familiar face results in more negative amplitudes at inferior occipito-temporal sites, particularly pronounced over the right hemisphere, starting approximately 180 ms and peaking approximately 250 ms after target onset. This effect is face-selective (Neumann, Mohamed, & Schweinberger, 2011; Schweinberger, Huddy, & Burton, 2004), although the repetition of familiar names shows a similar effect with a left-hemispheric distribution (Pickering & Schweinberger, 2003). N250r is reduced but still clearly observed when different images of the same persons are used as primes (Schweinberger, Pickering, Jentzsch, Burton, & Kaufmann, 2002; Zimmermann & Eimer, 2013), and thus does not exclusively reflect pictorial processing. Consequently, N250r, and particularly its image-independent part, appears to reflect the activation of domain-specific representations of known faces (see Schweinberger, 2011; Schweinberger & Burton, 2003).

In the IAC architecture, immediate repetition priming can be explained by enhanced activation levels of target FRU and PIN units after the presentation of a related prime, as both units' thresholds will be reached faster after target onset. Hence, immediate within-domain repetition priming is mediated via both a domain-specific and a domain-general locus of effect (see Calder & Young, 1996). Accordingly, ERP studies observed a second priming effect in the N400 (Schweinberger et al., 1995; Schweinberger et al., 2002). This component has been originally described in language research and is more negative for words incongruent to the semantic context of a sentence relative to congruent words from approximately 300 to 600 ms at central and parietal electrodes (Kutas & Federmeier, 2011; Kutas & Hillyard, 1980). Similarly, less negative N400 amplitudes for repeated relative to nonrepeated faces have been interpreted as reflecting facilitated access to domain-general representations (i.e., PINs).

However, repetition priming can also be examined exclusively at the domain-general level. More specifically, the presentation of a prime name results in faster recognition of a target face depicting the same relative to a different person. This cross-domain priming effect is weaker than within-domain priming (Calder & Young, 1996; see also Calder, Young, Benson, & Perrett, 1996), and it elicits an N400 effect but no N250r (Pickering & Schweinberger, 2003), which is both in line with a single, domain-general locus of priming.

Finally, PINs do not only receive input from FRUs/NRUs, but also from higher-level semantic units (SIUs). As different people can share SIUs, activity can propagate from one PIN via the SIU

level to another PIN. Accordingly, familiar primes facilitate the processing of a semantically related target (Bruce, 1983; for a review, see Wiese, 2011), a phenomenon known as semantic priming. Semantic priming was first observed in language research (McNamara, 2005; Meyer & Schvaneveldt, 1971) and is known to elicit less negative N400 amplitudes for targets preceded by related (chair \rightarrow table) relative to unrelated primes (river \rightarrow table; e.g., Bentin, McCarthy, & Wood, 1985; Kiefer, 2002). In person recognition, both the behavioral (Bruce & Valentine, 1986; Young, Flude, Hellawell, & Ellis, 1994) and the N400 semantic priming effect (Schweinberger, 1996; Wiese & Schweinberger, 2008, 2011) are known to cross stimulus-domains, as face or name targets are similarly primed by face or name primes. These findings suggest a domain-general locus of semantic priming, which occurs at the PIN level, but is mediated via higher-order semantic representations. Taken together, the combination of these various priming techniques with ERPs allows the examination of specific processing stages during person recognition. This was exploited here to systematically examine effects of cognitive ageing on familiar face processing.

Effects of Cognitive Ageing in Face and Person Recognition

Although a growing interest in age-related differences in person perception and person recognition can be determined in recent years, relatively little research has been undertaken in this area. It is known that recognition memory for faces decreases with higher age (e.g., Bartlett & Leslie, 1986; Hildebrandt, Sommer, Herzmann, & Wilhelm, 2010; Wiese, Schweinberger, & Hansen, 2008; Wolff, Wiese, & Schweinberger, 2012), whereas more basic abilities of face perception (such as holistic or configural processing of faces) appear to remain largely intact (Boutet & Faubert, 2006; Konar et al., 2013; Meinhardt-Injac et al., 2014b; but see Wiese, Kachel, & Schweinberger, 2013). Using structural equation modeling to examine individual differences in face processing, Hildebrandt and colleagues (2010) reported decreases in face memory to start in the fifth decade and decreases in face perception to start in the seventh decade of life. These effects seem to be specific to face processing to some degree, as they remain observable even after considering differences in general cognitive functioning (Hildebrandt, Wilhelm, Schmiedek, Herzmann, & Sommer, 2011). One study testing the learning of new facial identities over the life span (Germine et al., 2011) reported a peak in face learning in the early 30s and a slow subsequent decline in performance, with performance at 65 being comparable to that at 16

A number of studies also examined age-related differences in face processing using ERPs. The first ERP component clearly related to face processing is the so-called N170, a negative peak at approximately 170 ms after stimulus onset, which is maximal at occipito-temporal electrodes (Bentin, Allison, Puce, Perez, & McCarthy, 1996). The N170 is believed to reflect early stages of face perception, such as the structural encoding of faces (Eimer, 2011). Although some report a delayed N170 in older adults (Gazzaley et al., 2008; Wiese et al., 2008; Wolff et al., 2012), which might reflect slowing at perceptual stages of face processing, the observed effects are relatively small and not always found (Gao et al., 2009; Pfütze, Sommer, & Schweinberger, 2002; Wiese, Komes, &

Schweinberger, 2012). Similarly, some studies observed an enhanced N170 amplitude in older adults (Daniel & Bentin, 2012; Gao et al., 2009; Rousselet et al., 2009), whereas others did not (Wiese et al., 2008). N170 amplitude differences have been suggested to reflect more effortful processing during early stages of face perception in older adults, which is also in line with the finding of smaller N170 inversion effects in this age group (e.g., Gao et al., 2009; Komes, Schweinberger, & Wiese, 2015). More recent work suggests that the presence or absence of these agerelated effects may depend on both performance levels (Komes, Schweinberger, & Wiese, 2014b) and the exact age of the older participants (Komes et al., 2015).

Of particular importance for the present study, Pfütze et al. (2002) examined both the N250r and N400 repetition priming effects for famous and unfamiliar names and faces in young, middle-aged, and older adults. The authors observed a delay in the N250r with increasing age (starting at 220 ms in young, at 260 ms in middle-aged, and at 320 ms in older adults), which was independent of stimulus domain. The N400 priming effect was also delayed, but the magnitude of this delay was similar to the one observed for the N250r, which was interpreted as slowing with increasing age at the domain-specific, but no additional slowing at the domain-general processing stage. Of note, name and face stimuli were repeated with two, three, or four intervening items in this study. To the best of our knowledge, no previous ERP studies tested effects of cognitive ageing on face recognition in immediate within-domain or cross-domain repetition priming.

Similarly, effects of ageing on semantic priming in face recognition have not been tested before. At the same time, a number of previous studies have examined such effects with word material and have found larger priming in older adults (e.g., Laver & Burke, 1993). This increased effect has been related to overall slower response times (Myerson, Hale, Chen, & Lawrence, 1997) and may therefore not reflect stronger preactivations of the target representation. Instead, it may be seen as greater relative savings in the primed conditions in a probably more extended semantic network (see Laver & Burke, 1993, for a similar suggestion). Interestingly, previous studies examining the N400 with word material in older adults found reduced effects relative to young participants (e.g., Federmeier & Kutas, 2005; Federmeier, Kutas, & Schul, 2010; Gunter, Jackson, & Mulder, 1992, 1995; Kutas & Iragui, 1998). In the present study, we were interested whether a similar pattern would emerge for semantic priming in person recognition.

The Present Experiments

We conducted three ERP priming experiments to investigate ageing effects on different levels of face and person representation. In Experiment 1, we tested whether within-domain immediate repetition priming is affected by ageing. Enhanced levels of activation at target onset, both at the FRU and PIN level, drive this form of priming, and the respective ERP correlates are observed in the N250r and the N400. Age-related differences at both the domain-specific and domain-general level of representation can therefore be tested, although it needs to be kept in mind that potential deficits at an earlier processing stage may propagate to a later stage. However, in cross-domain repetition priming (Experiment 2) priming results exclusively from a pre-activation at the

domain-general PIN level. A neural correlate of this effect is only observed in the N400. Accordingly, if activation of domain-general person representations would be affected by cognitive ageing, behavioral and neural correlates of cross-domain repetition priming would be reduced in older adults.

Finally, domain-general representations, that is, PINs, are not only accessible via bottom-up domain-specific units (FRUs, NRUs), but also top-down via SIUs. This form of activating domain-general representations can be tested with semantic priming. Although the neural correlate is again an N400 priming modulation, semantic priming is mediated via preactivation at the PIN and SIU levels. In Experiment 3, we tested whether ageing affected the access to domain-general person representations via semantic information units.

Experiment 1: Within-Domain Repetition Priming

In Experiment 1, we tested whether within-domain immediate repetition priming and its neural correlates, the N250r and N400 priming effects, would be affected by ageing. Previous research found the N250r to be delayed in older participants (Pfütze et al., 2002). Importantly, this study did not test immediate repetition priming, but used two to four intervening items. This may have substantially reduced FRU and PIN preactivations due to within-pool inhibition (see Burton et al., 1990), presumably resulting in reduced priming effects. At the same time, as older adults are more prone to distraction from task-irrelevant stimuli (e.g., Hasher, Zacks, & May, 1999), intervening items between prime and target might have had a stronger influence on older relative to young adults. The present experiment avoided these potential confounds by using immediate repetitions of familiar faces.

Furthermore, the present study used a considerably shorter prime/target stimulus onset asynchrony (SOA) compared to previous studies (e.g., Schweinberger et al., 1995; Schweinberger et al., 2002) to avoid expectancy-related effects (e.g., Neely, 1991; Neely, Keefe, & Ross, 1989). During the experiment, participants will quickly notice that the same stimulus is repeated in a substantial number of trials. They may therefore develop a strategy of predicting a specific target when the prime is presented. The resulting priming effects cannot unequivocally be interpreted as reflecting propagation of activity within a network of representations, but is contaminated by expectancy. Critically, participants need time to actively predict an upcoming target after prime presentation, and expectancy effects are not observed with prime/ target SOAs faster than approximately 400 ms (see Neely, 1977). A short SOA therefore effectively disrupts this form of strategic processing. Importantly, studies on language processing have found that predictability affects young and older adults' ERPs to a different extent (Federmeier & Kutas, 2005; Federmeier et al., 2010). In the present study, a short prime/target SOA substantially reduced the possibility for using expectancy-based processes (Mc-Namara, 2005).

If ageing affected the efficiency of accessing domain-specific face representations, we would expect a reduced or even absent N250r in older adults. This finding should be further paralleled by a reduced or absent priming effect in performance. If, by contrast, deficits in person recognition occurred at a later processing stage, a similar N250r should be observed in older and younger adults,

whereas the subsequent N400 priming effect should be compromised by age-related differences.

Methods

Participants. Twenty younger adults (18–29 years, M = 23.2years +/-3.2 SD; 12 female) were recruited from the undergraduate and postgraduate student population at Jena University. Twenty older adults (60–79 years, M = 68.8 years +/-4.5 SD; 10 female) were recruited via newspaper ads and from senior citizen groups at a local community center. Modal level of formal education in the older group was a university degree (n = 14), while all remaining older participants had secondary school education, corresponding to German "Realschule" (n = 5) or "Hauptschule" (n = 1). Older adults were reimbursed with 7.50 Euro/h, younger adults either received course credits or monetary reimbursement. All participants were right-handed according to a modified version of the Edinburgh Handedness Inventory (Oldfield, 1971) and resided in independent living conditions. None reported neurological or psychiatric disorders or received central acting medication, and visual acuity and contrast sensitivity was formally tested (see below). All participants gave written informed consent, and the study was approved by the local ethics committee.

Stimuli. Stimulus selection for the present series of experiments was based on a pilot study (for a similar approach, see Komes, Schweinberger, & Wiese, 2014a; Wiese & Schweinberger, 2008), which was designed to generate a set suitable for all three experiments reported here, and in particular also for the semantic priming study (Experiment 3). Twenty-three older (M = 70.8years ± -4.1 SD; 13 female) and 18 younger adults (M = 22.2years ± -3.0 SD; 13 female), who did not participate in any of the experiments described below, were handed a list of 62 celebrity names (e.g., Brad Pitt, John Lennon etc.). For each of these names, participants were asked to write down up to three other famous people that came spontaneously to their mind when reading the name (e.g., Angelina Jolie, Paul McCartney etc.), or to indicate that the name was unfamiliar. Those 30 celebrities that generated the highest overlap in associated famous people were chosen as prime and target stimuli for Experiments 1 and 2, and as targets in Experiment 3. None of these celebrities was rated as unfamiliar by any of the young or older participants. The majority of these celebrities were male (24 male, six female), and the set included famous actors, musicians, politicians, athletes, British Royals, models and other TV personalities. Decades in which these celebrities became famous in Germany varied (1950s: two; 1960s: two; 1970s: four; 1980s: nine; 1990s: six; 2000s: seven). Moreover, those celebrities most commonly associated with these 30 names were used as prime stimuli in Experiment 3. These associated persons were spontaneously produced by 51% (\pm /- 13.6 SD) of the younger participants and by 54% (+/- 14.3 SD) of the older participants. Sixteen of the associated persons were female, and the set included famous actors, musicians, politicians, athletes, British Royals, models and other TV personalities. Again, decades in which these celebrities became famous varied (1950s: one; 1960s: three; 1970s: three; 1980s: two; 1990s: nine; 2000s: 11; 2010s: one).

For Experiment 1, images of 30 celebrities (see above) and 30 unfamiliar faces of similar age and sex were chosen. All pictures were edited using Adobe Photoshop to remove all information

apart from the face (e.g., clothing, background), and images were converted to gray-scale and placed in front of a black background. For each face, two images were created, which differed in size by 20%. More specifically, prime stimuli were framed within an area of 205 \times 260 pixels, corresponding to a visual angle of 6.9° \times 10.3° at a viewing distance of 90 cm. Target stimuli were resized to a 170 \times 216 pixel frame (5.7° \times 8.6° visual angle).

Target faces were either preceded by the prime stimulus of the same face (related condition), or by a different famous face (unrelated condition). Unfamiliar target stimuli were always preceded by famous prime stimuli. Each target was presented four times (once per block, see below). Famous targets were presented two times in the related and two times in the unrelated condition, resulting in 60 trials per condition. Prime stimuli were presented eight times (two times per block), four times preceding a famous target and four times preceding an unfamiliar target.

Procedure. Before the priming experiment, visual acuity and contrast sensitivity of all participants was tested using the Freiburg Visual Acuity Test (Version 3.5.5; Bach, 1996). Participants were asked to indicate the positions of Landolt's C gaps presented in different sizes (for visual acuity) or grayscales (for contrast sensitivity). Visual acuity was determined by the logarithm of the minimum angle of resolution. Contrast sensitivity was measured by Michelson Contrast scores, which refer to the difference between the highest and lowest luminance values divided by their sum. In addition, perceptual speed (digit-symbol substitution test; Wechsler, 1981) and verbal knowledge (spot-a-word test; Lehrl, 1977) were tested as markers of fluid mechanics and crystallized pragmatics of intelligence, respectively. Potential presence of depressive symptoms in older adults was examined using the 30-item version of the Geriatric Depression Scale (Yesavage et al., 1982).

For the EEG part of the experiment, participants were seated in a dimly lit, electrically shielded, and sound-attenuated chamber (400A-CT Special, Industrial Acoustics, Niederkruechten, Germany) with their heads in a chin rest. Approximate distance between the eyes and the computer monitor was 90 cm. The experiment began with a series of practice trials on stimuli not used in the main experiment, which were excluded from data analysis. In each trial, a prime face was presented for 100 ms, followed by a fixation cross for 100 ms. Next, the target face appeared on the screen for 2,000 ms. The trials ended with a fixation cross presented for 1,800 ms.

The 240 trials were presented in four blocks of 60 trials each. Within each block, 30 famous and 30 unfamiliar targets were presented. Furthermore, half of the famous targets per block were preceded by the same identity prime (related condition) and the other half was preceded by a different, semantically unrelated prime (unrelated condition), resulting in 60 trials for both related and unrelated conditions across the four blocks. Each target face was presented once per block, and equally often in the related and unrelated conditions across blocks. Trials of different conditions within each block were shown randomly intermixed. The task was to decide as fast and accurately as possible, via left or right index finger button presses, whether the target was a famous or unfamiliar face. Key assignment as well as block order (i.e., whether a specific target appeared in the related or unrelated condition first) was counterbalanced across participants. Trials with unfamiliar targets were used only to create the task demand for the familiarity

decision and were not further analyzed. For familiar targets, accuracy and mean correct response times (reaction time [RT], excluding outlier trials 2.5 SD above or below the condition mean) were analyzed.

EEG recording and analysis. During the main experiment, 32-channel EEG was recorded using a BioSemi Active II system (BioSemi, Amsterdam, The 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 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 5.3 (Berg & Scherg, 1994; MEGIS Software GmbH, Graefelding, Germany). EEG was segmented from -400 to 1,000 ms relative to target onset, with the first 200 ms (-400 to -200 ms) as baseline. Artifact rejection was carried out using the BESA 5.3 tool, with an amplitude threshold of 100 μ V and a gradient criterion of 75 μ V. Trials were then recalculated to average reference, digitally low-pass filtered at 40 Hz (12 db/oct, zero phase shift), and averaged according to experimental conditions. After EEG artifact rejection, the mean (and minimum) number of trials for the related and unrelated conditions were 47 (+/-8 SD; min = 31) and 46 (+/-8 SD; min = 26) in young adults, and 49 (+/-10 SD; min = 21) and 49 (+/-10 SD; min = 21) in older adults, respectively.

In the resulting waveforms, mean amplitudes of the N250r were determined between 100 and 300 ms at occipito-temporal channels (PO9/10, P9/10, TP9/10). This relatively early time window was chosen on the basis of previous studies examining the N250r with a short prime/target SOA (Trenner, Schweinberger, Jentzsch, & Sommer, 2004). N400 was analyzed between 300 and 600 ms at left, midline, and right frontal, central, and parietal electrodes (F3, Fz, F4, C3, Cz, C4, P3, Pz, P4). Statistical analyses were performed using mixed-model analyses of variance (ANOVA), with degrees of freedom corrected according to the Greenhouse-Geisser procedure where appropriate.

Results

Psychometric test results. Descriptive statistics are reported in Table 1. A one-way ANOVA on visual acuity revealed significantly better scores in young adults, F(1, 38) = 16.198, p < .001, $\eta_p^2 = .299$. Similarly, contrast vision was better in young relative to older adults, F(1, 38) = 17.358, p < .001, $\eta_p^2 = .314$. Whereas significantly higher scores for young than older adults were observed in the digit-symbol substitution test, F(1, 38) = 49.936, p <.001, $\eta_p^2 = .568$, older adults outperformed younger participants in the spot-a-word test of verbal knowledge, F(1, 38) = 16.174, p <.001, $\eta_p^2 = .299$. These findings are well in line with life span theories of cognition suggesting a decrease in fluid mechanics but intact (or even increased) crystallized pragmatics of cognition with increasing age (Baltes, 1987; Cattell, 1971). Finally, none of the older participants suffered from symptoms of depression (maximum GDS score of 4, which is substantially below the cut-off of 10; Kørner et al. (2006)).

Performance. A mixed-model ANOVA on mean correct RTs (see Table 2) with the within-subjects factors block (1, 2, 3, 4) and relatedness (related, unrelated), as well as a between-subjects factor group (young adults, older adults) resulted in significant main effects of block, F(3, 114) = 150.437, p < .001, $\eta_p^2 = .798$, and relatedness, F(1, 38) = 522.705, p < .001, $\eta_p^2 = .932$ (see also Figure 2). Moreover, an interaction of Block \times Relatedness was detected, F(3, 114) = 3.048, p = .040, $\eta_p^2 = .074$, which reflected somewhat larger relatedness effects in the third block as indicated by a quadratic trend for magnitude of priming over blocks, F(1, 39) = 4.275, p = .045, $\eta_p^2 = .099$. Neither the main effect of group nor any interaction involving the group factor was significant, all F < 2.760, all p > .104.

A corresponding ANOVA on mean accuracies (see Table 3) revealed significant main effects of block, F(3, 114) = 23.034, p < .001, $\eta_p^2 = .377$, and relatedness, F(1, 38) = 4.137, p = .049, $\eta_p^2 = .098$, which was further qualified by an interaction of Relatedness × Group, F(1, 38) = 4.218, p = .047, $\eta_p^2 = .100$. Post hoc tests yielded significantly more accurate responses in the related relative to the unrelated condition in young, F(1, 19) = 12.338, p = .002, $\eta_p^2 = .394$, but not older adults, F < 1 (see

Table 1
Demographic Data and Performance in Perceptual and Psychometric Tests of Participants in Experiments 1–3

	Exp. 1: Within-domain repetition priming				Exp. 2: Cross-domain repetition priming				Exp. 3: Semantic priming			
	Young participants		Older participants		Young participants		Older participants		Young participants		Older participants	
Variable	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD
Age Gender (female/male)	23.2 12/8	3.2	68.8 10/10	4.5	22.9 12/8	4.1	68.2 11/9	4.5	23.1 12/8	3.3	68.4 10/10	3.3
logMAR Michelson	.06 .80	.02 .20	.16 1.70	.11 .95	.08 .90	.05 .24	.20 2.10	.14 1.38	.06 .88	.05 .29	.19 2.02	.16 1.34
Digit-Symbol Spot-a-Word	66.0 29.6	9.1 1.6	46.0 32.0	8.8 2.1	68.4 30.7	12.8 2.4	46.6 32.6	7.3 2.3	70.1 31.3	9.3 2.2	41.3 33.3	10.1

Note. logMAR = logarithm of minimum angle of resolution, visual acuity as measured with FrACT (Bach, 1996); Michelson = Michelson contrast as measured with FrACT (Bach, 1996); Digit-Symbol = sum of correct items in the Digit-Symbol subtest; Wechsler Adult Intelligence Scale—Revised (Wechsler, 1981); Spot-a-Word = sum of correct items in the Spot-a-Word test (Lehrl, 1977).

Table 2
Response Time Data for Younger and Older Adults in Experiments 1–3

Experiment	Ble	ock 1	Block 2		Bl	ock 3	Block 4	
	Related	Unrelated	Related	Unrelated	Related	Unrelated	Related	Unrelated
Experiment 1								
Young adults								
M	848.00	981.52	662.30	851.65	601.46	735.50	593.07	738.56
SD	153.17	155.77	119.19	160.24	125.40	108.18	122.53	119.47
Older adults								
M	862.41	1028.14	742.49	877.71	646.21	884.55	696.88	789.10
SD	136.38	195.80	161.92	171.55	160.39	139.10	148.29	131.06
Experiment 2								
Young adults								
M	763.57	859.39	664.67	733.01	608.25	700.41	594.74	670.93
SD	114.15	105.10	96.32	78.89	80.11	78.23	72.16	69.81
Older adults								
M	933.06	1124.12	786.83	952.81	738.94	892.72	727.57	857.31
SD	176.53	188.79	164.30	170.84	177.20	156.92	164.52	140.10
Experiment 3								
Young adults								
M	745.68	784.61	659.16	684.17	610.05	643.07	600.91	623.88
SD	109.19	119.78	96.14	100.87	86.70	87.31	91.45	78.74
Older adults								
M	1108.33	1155.66	917.56	966.44	842.18	912.14	803.14	851.01
SD	157.48	127.48	145.33	147.15	113.51	123.61	95.84	108.63

Figure 2). No other significant effects were observed, all F < 2.443, all p > .107.

ERPs. Please note that since age-related differences in the overall topography of ERP components are well-known, and have been described in detail elsewhere (see, e.g., Friedman, 2011), the following description of ERP results does not include purely topographical effects or interactions of ERP topography with group, unless the relatedness factor is involved. Moreover, data was collapsed across the four blocks due to insufficient trial numbers for tests that include an additional block factor. Please note that priming was observed in RTs in each of the four blocks (see Table 2).

To capture the N250r (see Figure 3), a mixed-model ANOVA on mean amplitudes between 100 and 300 ms after target onset with the within-subjects factors hemisphere (left, right), site (PO, P, TP), and relatedness, as well as a between-subjects factor group was calculated. This analysis revealed a significant main effect of relatedness, F(1, 38) = 25.775, p < .001, $\eta_p^2 = .404$, which was further qualified by significant interactions of Relatedness × Site, F(2, 76) = 14.831, p < .001, $\eta_p^2 = .281$, with larger relatedness effects at P9/P10 and PO9/PO10 relative to more anterior sites, and Relatedness × Group, F(1, 38) = 5.307, p < .027, $\eta_p^2 = .123$. Post hoc tests yielded significant relatedness effects for both younger adults, F(1, 19) = 17.389, p = .001, $\eta_p^2 = .478$, and older adults, F(1, 19) = 8.868, p = .008, $\eta_p^2 = .318$, with larger effect sizes for younger adults.

N400 (see Figure 4) was analyzed in a time window from 300 to 600 ms by calculating a mixed-model ANOVA with the within-subjects factors laterality (left, midline, right), site (frontal, central, parietal), and relatedness, as well as the between-subjects factor group. This analysis revealed a significant main effect of relatedness, F(1, 38) = 14.237, p = .001, $\eta_p^2 = .273$, which was further qualified by interactions of Relatedness × Group, F(1, 38) = 6.003, p = .019, $\eta_p^2 = .136$, and Related-

ness × Site × Group, F(1, 38) = 6.146, p = .005, $\eta_p^2 = .139$. Post hoc tests in young adults indicated significant relatedness effects at frontal, F(1, 19) = 9.930, p = .005, $\eta_p^2 = .343$, and central, F(1, 19) = 39.397, p < .001, $\eta_p^2 = .675$, but not at parietal sites F(1, 19) = 1.087, p = .310, $\eta_p^2 = .054$. In older adults, no significant relatedness effects were observed, all F < 2.886, all p > .105.

Further inspection of the ERP waveforms resulted in the impression that this initial analysis may have not captured potential N400 effects in older adults, which appeared to be more restricted in time. We therefore calculated additional analyses in 100 ms steps from 300 to 600 ms. In the first time window (300-400 ms), we observed a significant relatedness effect, $F(1, 38) = 29.555, p < .001, \eta_p^2 = 437$, which was qualified by significant interactions of Relatedness \times Group, F(1, 38) =18.684, p < .001, $\eta_p^2 = .330$, Relatedness × Site, F(2, 76) =5.105, p = .013, $\eta_p^2 = .118$, and Relatedness \times Laterality \times Group, F(2, 76) = 4.814, p = .013, $\eta_p^2 = .112$. Post hoc tests yielded significant relatedness effects in young participants at left, F(1, 19) = 24.497, p < .001, $\eta_p^2 = .563$, midline, F(1, 19)19) = 44.916, p < .001, $\eta_p^2 = .703$, and right electrodes, $F(1, \frac{1}{2})$ 19) = 25.351, p < .001, $\eta_p^2 = .572$, with largest effects at midline sites. In older adults, no significant relatedness effects were detected, all F < 1.160, all p > .294.

In the subsequent 400–500 ms time window, a significant relatedness effect, F(1, 38) = 34.954, p < .001, $\eta_p^2 = 479$, was detected, which was qualified by significant interactions of Relatedness × Group, F(1, 38) = 9.117, p = .005, $\eta_p^2 = .194$,

 $^{^{1}}$ Although no significant three-way interaction was observed, we tested whether accuracy in the unrelated condition was reduced in younger relative to older adults in each block separately. These additional analyses did not result in significant effects (all t < 1.725, all p > .093).

Experiment 1 - Within-domain Reptition Priming

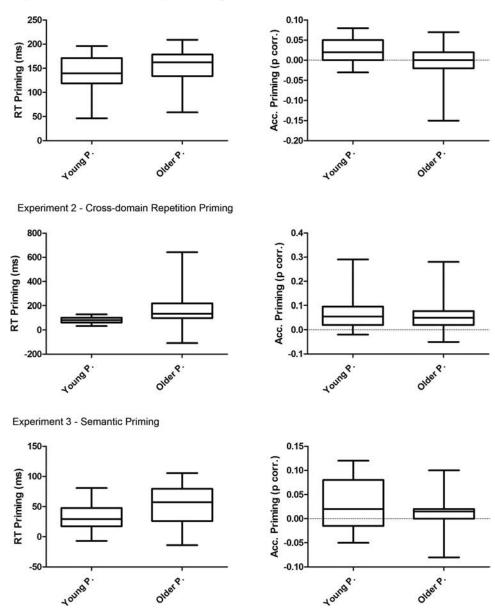


Figure 2. Magnitude of priming effects in response times (RT; unrelated minus related conditions) and accuracy (related minus unrelated conditions) for Experiments 1–3. Whiskers show maximum and minimum, bottom and top of the boxes show the first and third quartile, and bands inside the boxes show the mean.

Relatedness × Site, F(2, 76) = 4.499, p = .024, $\eta_p^2 = .106$, and Relatedness × Site × Group, F(2, 76) = 5.143, p = .015, $\eta_p^2 = .119$. Post hoc analyses in young adults detected significant relatedness effects at frontal, F(1, 19) = 15.479, p = .001, $\eta_p^2 = .449$, central, F(1, 19) = 64.344, p < .001, $\eta_p^2 = .772$, and parietal sites, F(1, 19) = 8.939, p = .008, $\eta_p^2 = .320$. For older participants, significant relatedness effects were detected at parietal, F(1, 19) = 9.585, p = .006, $\eta_p^2 = .335$, but neither at central, F(1, 19) = 3.255, p = .087, $\eta_p^2 = .146$, nor at frontal sites, F < 1.

Finally, in the subsequent 500-600 ms time window, a significant main effect of relatedness, F(1, 38) = 4.498, p = .041, $\eta_p^2 = .106$, as well as a significant interaction of Relatedness \times Site \times Group, F(2, 76) = 12.184, p < .001, $\eta_p^2 = .243$, was found. In younger adults, post hoc tests revealed significant relatedness effects, with more positive amplitudes for the unrelated relative to the related condition, at parietal, F(1, 19) = 10.935, p = .004, $\eta_p^2 = .365$, but neither at central, nor frontal sites, both F < 1. In older adults, a corresponding relatedness effect was observed at frontal, F(1, 19) = 7.424,

Table 3
Accuracy Data for Young and Older Participants in Experiments 1–3

Experiment	Ble	ock 1	Ble	ock 2	Bl	ock 3	Block 4	
	Related	Unrelated	Related	Unrelated	Related	Unrelated	Related	Unrelated
Experiment 1								
Young adults								
M	.73	.70	.79	.81	.83	.77	.79	.80
SD	.17	.18	.17	.15	.18	.20	.18	.19
Older adults								
M	.79	.62	.72	.82	.84	.75	.78	.85
SD	.16	.24	.26	.19	.14	.25	.22	.16
Experiment 2								
Young adults								
M	.88	.72	.90	.88	.95	.85	.90	.90
SD	.13	.23	.10	.08	.05	.15	.09	.08
Older adults								
M	.83	.70	.90	.85	.92	.89	.92	.91
SD	.22	.23	.15	.17	.14	.11	.11	.14
Experiment 3								
Young adults								
M	.78	.71	.80	.83	.85	.79	.80	.81
SD	.14	.13	.11	.13	.16	.14	.14	.18
Older adults								
M	.80	.80	.84	.85	.87	.85	.87	.88
SD	.22	.19	.18	.16	.12	.18	.15	.12

p = .013, $\eta_p^2 = .281$, but neither at central, F < 1, nor parietal sites, F(1, 19) = 1.993, p = .174, $\eta_p^2 = .095$.

Discussion

Complementing previous ERP studies (Pfütze et al., 2002), Experiment 1 tested immediate repetition priming, with no intervening items and a short prime/target SOA to avoid expectancy effects (Neely et al., 1989). We observed clear RT priming in both young and older adults, which was not significantly different (see also Pfütze et al., 2002). At the same time, repetition priming in accuracies was only observed in the young group, which is generally in line with the suggestion that repetition priming is affected by ageing (La Voie & Light, 1994). The N250r (Schweinberger et al., 1995) was observed in both groups, although it was reduced in older adults. Similarly, an N400 priming effect was evident in both group but was less widespread, and both delayed and temporally constricted in older adults.

The finding of a substantially smaller N250r in older participants suggests that reduced efficiency during face recognition in higher age begins at a domain-specific processing stage, which is generally in line with previous research (Pfütze et al., 2002). Of note, the N250r was observed earlier than in previous studies (e.g., at approximately 180 ms in Schweinberger et al., 1995), which is likely related to the short SOA in the present experiment (see Trenner et al., 2004). Moreover, the N250r is known to consist of an image-dependent and an image-independent part (Schweinberger et al., 2002). Although prime and target image were different in size in the present experiment, this early onset may indicate a larger portion of pictorial priming than in previous studies.

Interestingly, the timing of the N250r did not appear to differ between age groups, whereas earlier studies observed a delayed effect in older adults (Pfütze et al., 2002). This discrepancy may be related to a stronger effect of intervening items on older relative to young adults, resulting in a delayed effect in the previous, but not in the present study. Alternatively, age-related effects on the image-independent part of N250r were presumably more clearly observed in the previous study. This would indicate that the image-independent part is delayed with increasing age, but the image-dependent part is not. Future studies, using different images of the same person in the related condition, may help to decide between these alternative explanations. In the present study, we chose to test same-image priming, because the N250r is known to be substantially smaller when different images are used for prime and target (see Schweinberger et al., 2002). Accordingly, as the present experiment is the first immediate repetition priming study examining ERPs in older adults, we aimed for the maximum possible effect, as we assumed that age-related differences would then be easier to detect. We acknowledge that this decision left the question unanswered whether the image-dependent, the imageindependent or both aspects of N250r are different between groups. Importantly, however, the present experiment is in line with previous findings by showing age-related differences at the domain-specific processing stage.

Regarding the N400 results, one might suggest that not only domain-specific, but also domain-general stages of person recognition are affected by cognitive ageing. Alternatively, it is possible that the deficit at the earlier domain-specific processing stage hampered the activation of an intact later stage. In other words, the smaller N250r in older adults suggests a reduced FRU preactivation when the target stimulus was presented in the related condition. Accordingly, even if the domain-general PIN level were

 $^{^2}$ Please note that an analysis of the prime-elicited N170 (mean amplitude from 130 to 180 ms relative to prime onset) revealed significantly increased amplitudes in older adults, F(1, 38) = 21.445, p < .001, $\eta_p^2 = .361$, which is in line with previous studies (see the introduction).

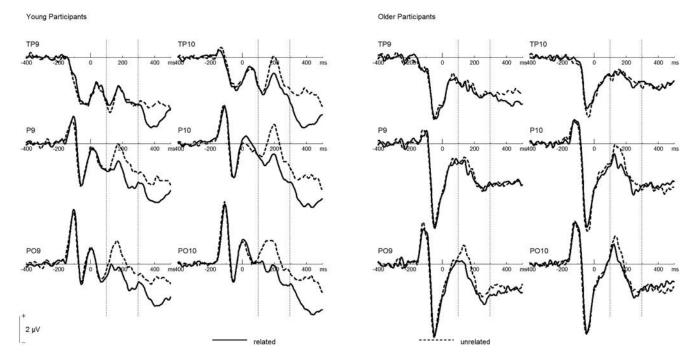


Figure 3. Grand average event-related potentials (ERPs) at occipito-temporal electrodes for within-domain repetition priming in Experiment 1. Zero reflects the time of target onset, dashed lines indicate the N250r time range. Please note that ERP components between -200 and 0 ms reflect processing of the prime stimulus.

unaffected by ageing, it would receive less input from the FRU level in older adults, which would result in a smaller and/or delayed N400 effect. Although this idea is supported to some extent by a trend toward a significant correlation of the N250r and the N400 priming effects in the older participants, r(18) = .428, p = .060, there is no clear evidence from Experiment 1 to decide about this alternative interpretation. Thus, Experiment 2 was designed to more unequivocally test whether cognitive ageing affects domain-general representations of familiar persons.

Experiment 2: Cross-Domain Repetition Priming

By using cross-domain priming, we probed whether the bottom-up activation of domain-general representations (PINs) is affected by ageing (see Figure 1). If, for instance, a target face is primed by its written name, the effect cannot be mediated by links between an FRU and a PIN. Thus, it has to occur at a stage at which information from several domains converge, that is, at the PIN level, which is in line with ERP studies that found a clear N400, but no N250r priming effect (Pickering & Schweinberger, 2003).

We therefore examined cross-domain repetition priming, with written names as primes and faces as targets. As in Experiment 1, prime and target could either depict the same (related condition) or a different person (unrelated condition). In line with previous studies, we predicted faster RTs and a less negative N400 in the related relative to the unrelated condition. As priming in this paradigm cannot be mediated by domain-specific representations, a reduced N400 effect in older adults could be interpreted as reflecting a deficit at a domain-general processing level.

Methods

Participants. Twenty young (18-35 years, M = 22.9 years +/- 4.1 SD; 12 female) and 20 older adults (60-74 years, M = 68.2 years +/- 4.5 SD; 11 female) were tested. Recruitment, inclusion and exclusion criteria, as well as compensation were analogous to Experiment 1. Young participants were under- and postgraduate students at Jena University. Modal level of formal education in the older group was a university degree (n = 10), while all remaining older participants had secondary school education, corresponding to German "Abitur" (n = 1), "Realschule" (n = 6), or "Hauptschule" (n = 3). All participants gave written informed consent, and the study was approved by the local ethics committee.

Stimuli. Target faces were identical to those used in Experiment 1, and written names were used as primes. Targets were either preceded by the name of the same person (related condition), or by the name of a different famous person from the set (unrelated condition). Unfamiliar target stimuli were always preceded by famous names. Names were presented in Arial font with a font size of 18. Surnames were presented under the corresponding forenames, resulting in a vertical viewing angle of 1.9° and a maximum horizontal viewing angle of 5.4°. As in Experiment 1, each target was presented four times (once per block), two times in the related and two times in the unrelated condition. Prime stimuli were presented eight times (two times per block), four times preceding a famous target and four times preceding an unfamiliar target face.

Procedure. The procedure was identical to Experiment 1, except for the following changes. In each trial, a prime name was

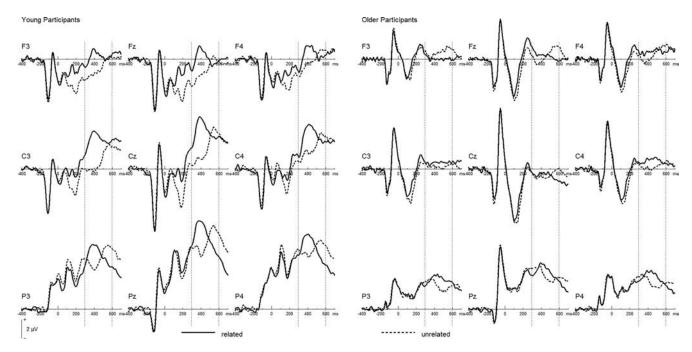


Figure 4. Grand average event-related potentials (ERPs) at frontal, central, and parietal electrodes for within-domain repetition priming in Experiment 1. Zero reflects the time of target onset, dashed lines indicate the N400 time range. Please note that ERP components between -200 and 0 ms reflect processing of the prime stimulus.

presented for 200 ms, and was immediately followed by the target face, which stayed on the screen for 2,000 ms. Please note that we decided to use longer presentation times of prime names (compared to prime faces in Experiment 1), to enable our older participants in particular to appropriately read written names. Note also that prime-target SOA was 200 ms, as in Experiment 1. The trials ended with a fixation cross, presented for 1,800 ms. Again, 240 trials were presented in four blocks of 60 trials each.

EEG Recording and Analysis. EEG procedures corresponded to those described for Experiment 1. The mean (and minimum) number of trials for the related and unrelated conditions respectively were 53 (+/-5 SD; min = 44) and 50 (+/-7 SD; min = 32) in young adults, and 50 (+/-9 SD; min = 23) and 47 (+/-8 SD; min = 24) in older adults.

Results

Test results. Descriptive statistics are reported in Table 1. Similar to Experiment 1, young adults demonstrated significantly better scores for visual acuity, F(1, 38) = 11.287, p < .001, $\eta_p^2 = .229$, and contrast sensitivity, F(1, 38) = 14.794, p < .001, $\eta_p^2 = .280$. Young participants also yielded higher scores in the digit-symbol-substitution test, F(1, 38) = 43.479, p < .001, $\eta_p^2 = .534$, whereas older adults outperformed the young group in the spot-aword test, F(1, 38) = 6.564, p = .014, $\eta_p^2 = .147$. Results of the Geriatric Depression Scale again indicated that none of the older participants suffered from symptoms of depression (M = 1.00 + /-2 SD; maximum score = 7).

Performance. A mixed-model ANOVA on mean correct response times (see Table 2) with the within-subjects factors block

and relatedness, as well as a between-subjects factor group yielded significant main effects of block, F(3, 114) = 108.373, p < .001, $\eta_p^2 = .740$, reflecting decreasing RT over blocks, relatedness, F(1, 38) = 57.792, p < .001, $\eta_p^2 = .603$, with faster RTs in the related condition, and group, F(1, 38) = 26.361, p < .001, $\eta_p^2 = .410$, reflecting faster RTs in young adults. A significant interaction of Relatedness \times Group, F(1, 38) = 5.791, p = .021, $\eta_p^2 = .132$, indicated numerically larger priming in older (160.14 ms) relative to young adults (83.13 ms), although the effect size was substantially larger in the young group, F(1, 19) = 210.334, p < .001, $\eta_p^2 = .917$, relative to older adults, F(1, 19) = 25.873, p < .001, $\eta_p^2 = .577$. As evident from Figure 2, this larger effect size in young adults resulted from substantially higher variability in the magnitude of priming in the older group. No further significant effects were detected.

A corresponding mixed-model ANOVA for accuracies (see Table 3) revealed significant main effects of block, F(3, 114) = 28.885, p < .001, $\eta_p^2 = .432$, reflecting increasing accuracies over blocks, and relatedness, F(1, 38) = 31.748, p < .001, $\eta_p^2 = .455$, with more accurate responses in the related condition. Moreover, a significant interaction of Block \times Relatedness was observed, F(3, 114) = 7.635, p = .002, $\eta_p^2 = .167$, reflecting larger priming in the

³ Please note that a trend toward larger priming effects in older adults was also detected when overall slower response times were taken into account by dividing the difference between the related and unrelated conditions by the mean response time for each participant, t(38) = 1.994, p = .053, d = 0.647.

first block. Neither the main effect of group, nor any interaction involving the group factor reached significance, all F < 1.

Event-related potentials. A mixed-model ANOVA on mean amplitudes in the N250r time window (100–300 ms) at occipito-temporal channels revealed neither a significant relatedness effect nor any significant interaction involving this factor, all F < 2.492, all p > .089.

A mixed-model ANOVA on mean amplitudes in the N400 time window (300–600 ms, see Figure 5) resulted in a significant main effect of relatedness, F(1, 38) = 10.863, p = .002, $\eta_p^2 = .222$, as well as a significant interaction of Relatedness × Group, F(1, 38) = 4.888, p = .033, $\eta_p^2 = .114$. Follow-up analyses revealed a significant relatedness effect in younger adults, F(1, 19) = 11.237, p = .003, $\eta_p^2 = .372$, with relatively more negative amplitudes in the unrelated condition. No significant relatedness effect was observed in older participants, F < 1.

Following the analysis strategy from Experiment 1, additional tests were carried out from 300 to 600 ms in 100 ms steps. A mixed-model ANOVA on mean amplitudes in the 300–400 ms time window yielded both significant main effects of relatedness, F(1, 38) = 4.170, p = .048, $\eta_p^2 = .099$, and an interaction of Relatedness × Group, F(1, 38) = 40.071, p = .002, $\eta_p^2 = .235$. Follow-up tests in younger adults revealed a significant relatedness effect, F(1, 19) = 10.237, p = .005, $\eta_p^2 = .350$, which was absent in the older group, F(1, 19) = 1.749, p = .202, $\eta_p^2 = .084$. A corresponding analysis of the 400–500 ms time segment again yielded a significant main effect of relatedness, F(1, 38) = 14.621, p < .001, $\eta_p^2 = .278$, and a significant interaction of Relatedness × Group, F(1, 38) = 18.432, p < .001, $\eta_p^2 = .327$. This interaction again was driven by a significant relatedness effect in younger

adults, F(1, 19) = 25.995, p < .001, $\eta_p^2 = .578$, but not in older adults, F < 1. Finally, the ANOVA in the 500–600 ms time segment resulted in a significant main effect of relatedness, F(1, 38) = 7.994, p = .007, $\eta_p^2 = .174$, whereas no significant interaction of Relatedness \times Group was observed, F < 1, which suggested similar relatedness effects in younger and older adults.

Discussion

Using cross-domain repetition priming, we found significant RT priming effects in both young and older adults, with substantially larger effect sizes in young adults. Interestingly, mean RT priming effects (i.e., the difference between the unrelated and the related condition) were larger in older adults. In combination, these finding suggest that priming was more consistent in young adults as a group, and that older adults varied more strongly, with some participants showing very large and some no priming effects (see Figure 2). Interindividual variability is known to be more pronounced in older adults (Salthouse, 2013), and may be related to an interaction of two opposing forces in the present experiment. On the one hand, consolidation of person representations over the life span may result in particularly strong priming in some participants. On the other hand, in other participants effects of cognitive ageing may weaken access to long-established representations, which would accordingly result in small or no priming effects. Athough this interpretation is clearly speculative at present, future studies may systematically examine individual differences in cognitive ageing and person recognition at the domain-general level.

It should be noted, however, that a similar finding, with larger interindividual variability in older adults was not observed in

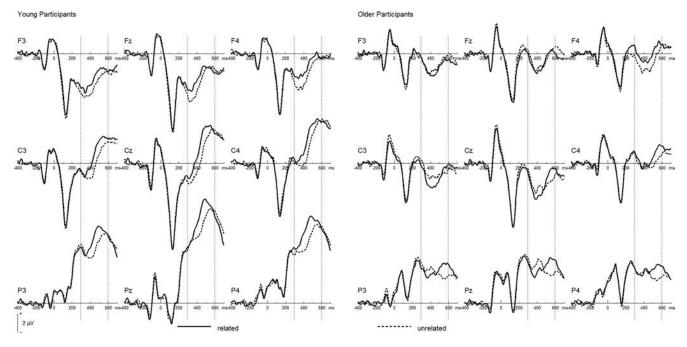


Figure 5. Grand average event-related potentials (ERPs) at frontal, central, and parietal electrodes for cross-domain repetition priming in Experiment 2. Zero reflects the time of target onset, dashed lines indicate the N400 time range. Please note that ERP components between -200 and 0 ms reflect processing of the prime stimulus.

Experiment 1. As indicated by Table 1, this difference cannot be explained by obvious differences between the two older participant groups, which were highly similar with respect to demographic factors and psychometric test results. As discussed above, it might be the case that in Experiment 1 effects at the PIN level were masked to some extent by deficits at the FRU level. As age-related differences at the neural level were evident prior to the domain-general processing stage, less efficient processing at the domain-specific stage may have substantially reduced activations at subsequent processing stages, and may have therefore masked interindividual variability at the domain-general PIN level.

Similar to Experiment 1, the N400 priming effect was substantially delayed and reduced in older participants, as the effect was only significant in the last 100 ms time window. This age-related effect cannot be explained by the propagation of a deficit located at a lower-level processing stage. Together with the smaller effect size for RT priming, this finding may therefore suggest that accessing domain-general representations via lower-level units is less efficient in older participants. It might however still be the case that the observed deficit is not related to the domain-general processing stage. Alternatively, preactivation at the PIN level may have been reduced, because less activation propagated from the name prime to the PIN. This possibility was further examined in Experiment 3.

ERP results from both experiments so far suggest an age-related deficit in the activation of domain-general person representations when accessed via domain-specific units. At the same time, semantic information (such as person-specific knowledge) is often considered as crystallized and therefore preserved in older adults. It is therefore possible that accessing domain-general representations via higher-order semantic units might be less affected or even spared—a possibility that can be empirically tested via semantic priming.

Experiment 3: Semantic Priming

Experiment 3 investigated whether the top-down activation of domain-general person representations would be affected by cognitive ageing. We conducted a semantic priming experiment in which prime names were immediately followed by either semantically related or unrelated target faces. Given that the personspecific semantic network reflects crystallized knowledge, which should be preserved in older adults (e.g., Baltes, 1987; Cattell, 1971), we expected no reduction in behavioral priming effects in older adults. As discussed in the introduction, previous studies from the language domain have reported even larger semantic priming effects in older adults (e.g., Laver & Burke, 1993). Moreover, reduced N400 effects have been demonstrated in older adults in previous research on accessing word knowledge (e.g., Gunter et al., 1992). However, no previous study has tested potential agerelated differences of semantic priming effects in person recognition.

Methods

Participants. We tested 20 young (18–31 years, M = 23.1 years +/-3.3 SD; 12 female) and 20 older adults (63–74 years, M = 68.4 years +/-3.3 SD; 10 female). Young participants were under- and postgraduate students at Jena University. Modal level

of formal education in the older group was a university degree (n=13), while all remaining older participants had secondary school education, corresponding to German "Realschule" (n=5) or "Hauptschule" (n=2). Recruitment, inclusion criteria, and compensation were analogous to Experiment 1. All participants gave written informed consent, and the study was approved by the local ethics committee.

Stimuli. Face stimuli were identical to those used in the previous studies. Name stimuli were those identified as highly associated to the face identities in the pilot study. Presentation parameters were identical to those reported for Experiment 2. Target faces were either preceded by the written name of a highly associated person as indicated by the pilot study described in the methods section of Experiment 1 (related condition), or by the written name of an unrelated famous person (unrelated condition). Unfamiliar target stimuli were always preceded by famous names. As in the previous experiments, each target was presented four times (once in each of four blocks), two times in the related and two times in the unrelated condition. Prime stimuli were presented eight times (two times per block), four times preceding a famous target and four times preceding an unfamiliar target face.

Procedure. The procedure was identical to Experiment 2. **EEG recording and analysis.** EEG procedures corresponded to those described for Experiment 2. The mean (and minimum) number of trials for the related and unrelated conditions respectively were $52 (+/-5SD; \min = 38)$ and $50 (+/-6SD; \min = 40)$ in young adults, and $51 (+/-6SD; \min = 37)$ and $51 (+/-7SD; \min = 36)$ in older adults.

Results

Test results. Descriptive statistics are reported in Table 1. Young adults obtained higher visual acuity, F(1, 38) = 11.867, p = .001, $\eta_p^2 = .238$, and contrast sensitivity, F(1, 38) = 14.094, p = .001, $\eta_p^2 = .271$. Young adults were better in the digit-symbol-substitution test, F(1, 38) = 87.806, p < .001, $\eta_p^2 = .698$, whereas older adults outperformed the younger group in the spot-a-word test, F(1, 38) = 9.530, p = .004, $\eta_p^2 = .201$. None of the older participants suffered from symptoms of depression according to the Geriatric Depression Scale (M = 0.8 + / -1.2 SD; maximum score = 5).

Performance. An ANOVA on RTs (see Table 2) yielded significant main effects of block, F(3, 114) = 209.539, p < .001, $\eta_p^2 = .846$, reflecting decreasing RT over blocks, relatedness, F(1, 38) = 86.108, p < .001, $\eta_p^2 = .694$, with faster RTs in the related condition, and group, F(1, 38) = 73.017, p < .001, $\eta_p^2 = .658$, with faster RTs in young adults. In addition, significant interactions of

⁴ Please note that names occur at two different levels in the IAC model, as a perceptual input (i.e., "written names") and as representations of knowledge about a particular person (as "name SIUs"). Wheras name SIUs presumably get activated after presentation of the corresponding written name, name SIUs do not mediate priming because they are not shared between different people. Please also note that priming via SIUs shared by different people tests how strongly these people are interconnected. Alternatively, it is plausible that priming a famous face with a related or unrelated occupational label would inform us about how strongly a particular person is associated with specific semantic information. Whereas age-related differences in such an experiment would be clearly interesting, this was not the focus of the present study and was therefore not examined here.

Block × Group, F(3, 114) = 21.655, p < .001, $\eta_p^2 = .363$, and Relatedness × Group, F(1, 38) = 6.837, p = .013, $\eta_p^2 = .152$, were observed. Post hoc analyses yielded significant priming effects in both groups, but somewhat larger effect sizes in older, F(1, 19) = 53.256, p < .001, $\eta_p^2 = .737$, than younger adults, F(1, 19) = 33.060, p < .001, $\eta_p^2 = .635$, see Figure 2. An additional analysis taking the overall longer RTs in older participants into account by dividing the difference between the related and the unrelated condition by the average response time across conditions revealed clear priming effects in both young, t(19) = 6.009, p < .001, t = 0.009, and older adults, t(19) = 0.009, t = 0.001, t = 0.001,

A corresponding analysis on accuracies (see Table 3) revealed significant main effects of block, F(3, 114) = 38.300, p < .001, $\eta_p^2 = .502$, with increasing accuracies over blocks, and relatedness, F(1, 38) = 9.006, p = .005, $\eta_p^2 = .192$, reflecting more accurate responses in the related condition. Moreover, a significant interaction of Block \times Relatedness was detected, F(3, 114) = 4.381, p < .016, $\eta_p^2 = .103$, reflecting larger priming in the first as compared to the following blocks. Neither the main effect of group nor any interaction involving the group factor reached significance, all F < 1, except for the interaction of Group \times Relatedness, F(1, 38) = 1.012, p = .321, $\eta_p^2 = .026$.

Event-related potentials. A mixed-model ANOVA on mean amplitudes in the N250r time window (100–300 ms) at occipito-temporal channels revealed neither a significant relatedness effect nor any significant interaction involving this factor, all F < 1.690, all p > .190.

An ANOVA on mean amplitudes in the N400 time window (300–600 ms, see Figure 6) revealed a significant interaction of Site \times Relatedness, F(2, 76) = 9.098, p = .001, $\eta_p^2 = .193$. Follow-up tests yielded significant relatedness effects at parietal, F(1, 39) = 13.157, p = .001, $\eta_p^2 = .252$, but neither at central, F(1, 39) = 2.357, p = .133, $\eta_p^2 = .057$, nor frontal sites, F < 1. Importantly, no interaction involving the group factor was observed, all F < 1.573, all p > .185.

Following the same strategy used in the previous experiments, additional analyses were calculated for 100 ms time windows from 300 to 600 ms. A mixed-model ANOVA in the 300-400 ms time window revealed no effects involving the relatedness factor, all F < 2.630, all p > .092. A corresponding ANOVA in the 400–500 ms time segment yielded a significant main effect of relatedness, $F(1, 38) = 11.122, p = .002, \eta_p^2 = .226$, which was qualified by an interaction of Site \times Relatedness \times Group, F(2, 76) = 3.992, p = .030, $\eta_p^2 = .095$. Follow-up tests in young participants revealed significant relatedness effects at central, F(1, 19) = 6.835, p = .017, $\eta_p^2 = .265$, and parietal, F(1, 19) = 22.034, p < .001, $\eta_p^2 = .537$, but not at frontal sites, F < 1. In older adults, a trend for a relatedness effect was observed at parietal sites, F(1,19) = 3.669, p = .071, $\eta_p^2 = .162$, but no corresponding effect was detected at central, F(1, 19) = 1.841, p < .191, $\eta_p^2 = .088$, or frontal sites, F < 1. Finally, the ANOVA in the 500–600 ms time window revealed a significant interaction of Site × Relatedness, F(2, 76) = 10.171, p < .001, $\eta_p^2 = .211$, which was not further qualified by the group factor, all F < 2.141, all p > 1.078. Follow-up analyses revealed relatedness effects at parietal, F(1, 39) = 10.437, p = .003, $\eta_p^2 = .211$, but neither at central, F(1, 39) = 2.199, p = .146, $\eta_p^2 = .053$, nor frontal sites, F < 1

Discussion

In Experiment 3, we did not find consistent evidence for agerelated deficits in the ERP correlates of semantic priming. Moreover, even larger RT priming effects were observed in older adults. This latter finding, however, was accompanied by overall slower responses (Myerson et al., 1997; but see Laver, 2000). Semantic priming effects were substantial and equivalent for young and older adults when corrected for overall RTs, arguing for intact semantic processing as indicated by behavioral measures.

The finding of intact RT priming in older adults in Experiment 3 sheds additional light on Experiment 2. As written names were used as primes in both experiments, a deficit at a domain-specific NRU stage is unlikely to explain the smaller effect sizes found in Experiment 2. Similarly, reduced activation of target FRUs and the resulting reduction in propagation of activity to target PINs is unlikely to explain reduced priming effects in Experiment 2, but no reduction in Experiment 3. Consequently, we suggest that accessing domain-general representations via lower-level processing units (FRUs, NRUs) is impaired, whereas accessing such representations via higher-order semantic units is less affected in older adults.

This interpretation is strengthened by the present ERP correlates of semantic priming, which initially indicated no significant interaction between group and relatedness in the N400 time window (300-600 ms)—a finding which is in clear contrast to our findings for within-domain (Experiment 1) and cross-domain repetition priming (Experiment 2). Moreover, the more fine-grained analyses found at best moderate evidence for age-related differences in the N400 priming effect. More specifically, the N400 effect in older adults appeared to be topographically more restricted between 400-500 ms, and slightly delayed compared to younger adults (see Figure 6). This finding is in line with a recent study on semantic word priming (Grieder et al., 2012) that, similar to the present experiment, used a short prime/target SOA and found only slight differences between age groups for the N400 priming effect. One might therefore argue that the previously observed more substantial ageing effects may have resulted from age differences in expectancy-based processes, or prediction (Federmeier & Kutas, 2005; Federmeier et al., 2010), rather than the automatic propagation of activity through the semantic network.

General Discussion

The present series of experiments examined the influence of cognitive ageing on face and person recognition. We analyzed both behavioral and ERP correlates of repetition and semantic priming to identify the specific processing stages potentially affected by ageing. In Experiment 1, we observed clear within-domain repetition priming in RTs in both groups, but significant priming in accuracies only in young adults. This finding was paralleled by reduced N250r and N400 priming effects. In Experiment 2, cross-domain repetition priming was used to more directly test whether ageing affects domain-general person representations. Both RT and N400 priming effects were less pronounced in older adults. Finally, Experiment 3 examined the activation of domain-general

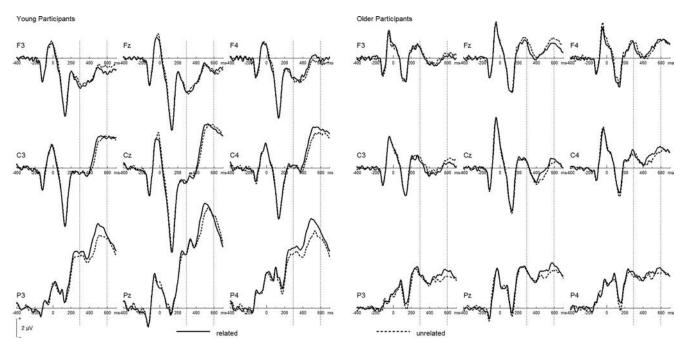


Figure 6. Grand average event-related potentials (ERPs) at frontal, central, and parietal electrodes for semantic priming in Experiment 3. Zero reflects the time of target onset, dashed lines indicate the N400 time range. Please note that ERP components between -200 and 0 ms reflect processing of the prime stimulus.

person representations via higher-order semantic units using semantic priming. Here, effects of ageing were less pronounced, as behavioral priming was not reduced and only a moderate reduction of the N400 effect was detected. These results, and their implications for theories of cognitive ageing and person recognition, are discussed in more detail below.

Immediate Repetition Priming

Behavioral and ERP priming effects in Experiments 1 and 2 suggest that the bottom-up route to domain-general representations of familiar persons is generally preserved, as most effects were evident in both groups. However, the observed age-related reductions suggest that this route is less efficient in older adults. This interpretation is in line with theoretical ideas that suggest crystallized mechanics of cognition, for example, representations, to be generally intact, but that accessing these representations is affected by ageing (Craik & Bialystok, 2006). It is further in accordance with the suggestion that perceptual representations are less dominant in older adults, and that processing shifts toward increased use of semantic representations in higher age (Ofen & Shing, 2013).

As a possible mechanism explaining this age effect, we suggest that domain-general representations were activated by the prime stimuli in both young and older adults, but that activity decayed faster after prime offset in older adults. Accordingly, preactivation of the target PIN was smaller in older adults by the time the target was presented, resulting in reduced priming effects. This interpretation is in line with the finding of delayed N400 effects in older adults, as more time would be needed for the PIN to reach its threshold after target presentation if its preactivation from the prime is reduced. Alternatively, the relatively short prime/target

SOA, and the relatively short presentation of the prime may have resulted in smaller activations in older adults. However, this interpretation appears unlikely, given that reduced bottom-up input to domain-general representations should have also led to smaller semantic priming in older adults, which was not observed (see below).

For now, we tentatively conclude that activation at domainspecific and domain-general person representations decays faster in older adults, resulting in smaller priming effects both at the behavioral and the neural level. However, as discussed in the following paragraphs, it appears to be important whether this activation has propagated from lower- or higher-level units.

Semantic Priming

In contrast to the above-described findings of reduced repetition priming, we observed similar semantic priming effects in young and older adults. According to the IAC model (Burton et al., 1990), cross-domain repetition priming is exclusively mediated by preactivations at the PIN level. Accordingly, to explain a reduced effect in older adults, parameters at the PIN level have to be different. At the same time, PINs are the input level to SIUs, and both units mediate semantic priming. Accordingly, if PINs were generally more difficult to activate or if their activation thresholds were higher in older adults, this age difference should also affect semantic priming, as activation would less likely propagate to the SIU level. By contrast, above-threshold but fast-decaying activation at the prime PIN, but similar time decay characteristics at the SIU level, would presumably more strongly affect repetition than semantic priming. In repetition priming, prime and target PIN are identical, and after prime offset, preactivation would quickly drop. In semantic priming, however, prime and target PIN are not identical, and target PINs receive input not only from bottom-up FRU/NRU levels, but also via the SIU level. If one assumes that prime PIN activation quickly decays, but SIU activation does not, the target PIN may well be preactivated via the SIU level when bottom-up activity from the target stimulus arrives, resulting in relatively intact semantic priming. In conclusion, although the present study does not directly support the idea of faster decay at the PIN level, this mechanism appears to be the best explanation of the present pattern of results within the IAC architecture.

At the same time, we observed slightly reduced ERP effects in older adults when analyzing temporally fine-grained time windows. It is possible that ERPs are a more sensitive measure of age-related differences, and that they already show reductions that may manifest in performance only at a higher age. Of note, age-related reductions in semantic memory have been described between 60 and 85 years (Rönnlund, Nyberg, Backman, & Nilsson, 2005), and future studies may examine whether reduced behavioral priming effects are observed in participants older than those examined in the present paper (see Komes et al., 2015, for a similar approach). Alternatively, there may be higher intraindividual variability in the onset of the N400 effect in older adults, which appears plausible, as higher intraindividual variability with older age is a typical finding (Hultsch, Strauss, Hunter, & Mac-Donald, 2008). The reduced effect in older adults' averaged ERP data might therefore not exclusively reflect reduced neural processing, but enhanced intraindividual variability of the onset and peak latency of a particular neural process that might still reach "normal" amplitudes in the single trials. Although intraindividual variability may also contribute to the reduced N400 effects in Experiments 1 and 2, it appears to be a more plausible explanation here, because it allows for the neural processes in individual trials to be similar in magnitude, while at the same time a stronger jitter in older adults will result in a slight reduction of the averaged response. In repetition priming, behavioral priming showed agerelated differences, and it therefore appears more plausible to assume that the underlying neural response is different as well.

We also note that the relatively intact N400 priming effect in the present semantic priming experiment is at some variance with previous results from the language domain (e.g., Gunter et al., 1992; Kutas & Iragui, 1998). One might therefore speculate that person-related semantic representations are less affected by cognitive ageing than general semantic knowledge. This appears possible in light of neuropsychological studies that have demonstrated double dissociations between the loss of person-related versus general semantic information (Thompson et al., 2004). Future studies, directly comparing priming effects from the two domains are necessary to substantiate this suggestion.

In any case, the present findings of only moderate age-related differences in semantic priming suggest that person-related semantics are largely intact in older adults. In fact, the overall larger RTs found in older adults may even indicate a larger person-related network (see also below) that has accumulated over the life span in older people. These ideas are generally in line with recent suggestions of a shift in relative importance from perceptual and episodic toward semantic representations with increasing age (Ofen & Shing, 2013), which is supported by brain imaging studies showing reduced differentiation of activity in face-sensitive regions of the fusiform gyrus (Grady et al., 1994; Park et al., 2004). Of

particular interest, more recent fMRI adaptation studies have not only found further evidence of reduced neural selectivity in these perceptual areas, but have also shown compensatory activity in higher-order frontal cortex regions (Burianová, Lee, Grady, & Moscovitch, 2013; Goh, Suzuki, & Park, 2010; Lee, Grady, Habak, Wilson, & Moscovitch, 2011). Although person-specific semantics are generally believed to be represented in anterior temporal brain regions (Haxby, Hoffman, & Gobbini, 2000; Thompson et al., 2004), these studies support the general idea of a shift from perceptual to higher-order (e.g., semantic) representations.

Potential Effects of Differential Familiarity and Age of Acquisition

Although name and face stimuli used in the present series of experiments were clearly familiar to both young and older adults, subtle differences in familiarity might have affected our results. Some of the celebrities became famous in the 1950s to 1970s, decades before the young adults in the present experiments were born. Accordingly, older participants may have encountered these celebrities more often over their life span, and may have accumulated higher levels of familiarity with them. This might have affected the magnitude of priming, as previous work has demonstrated smaller long-lag repetition priming for highly relative to less familiar faces (Stevenage & Spreadbury, 2006). Similarly, naming famous faces depends on the age of acquisition (AoA; Moore & Valentine, 1998), with faster naming of faces acquired early relative to later in life, and similar results have been obtained with the familiarity decision task used in the present experiments (e.g., Smith-Spark, Moore, & Valentine, 2012). Interestingly, Lewis, Chadwick, and Ellis (2002) found that the magnitude of long-lag repetition priming was predicted by the total number of times a person has been seen before, and not by the length of time a person is known.

Accordingly, both AoA effects and fine-grained differences in familiarity in principle may have influenced our findings. At the same time, the direction of this potential influence is hard to determine, as several factors need to be considered here. First, if AoA effects result from the number of times we have seen a person (Lewis, 1999), they should be stronger in older adults because they had more opportunities to see some of the celebrities. Second, if the age of the participants when they first encountered the celebrity is important, then younger adults should have a processing advantage, as their memory system was more plastic when they learnt some of the celebrities (e.g., who Bill Clinton is and what he looks like). Finally, if the order of acquisition is a critical factor, with earlier integrated items having an advantage over later items, than again young adults might have had a processing advantage in the present experiments, as celebrities from the 50s, 60s, 70s, and 80s were probably all learnt concurrently at an early time point, whereas learning in older adults presumably occurred more widespread over their life span (for a discussion of these factors, see, e.g., Smith-Spark et al., 2012).

It is possible that some or even all of these effects exist and interact with each other, but on the basis of the present data it is presumably impossible to disentangle them. At the same time, we note that AoA or fine-grained familiarity effects on immediate repetition or semantic priming in person recognition, to the best of

our knowledge, have not been demonstrated as yet, and long-lag and immediate priming are explained by different mechanisms within IAC. Importantly, in the present experiments, no consistent pattern of clearly smaller or larger RT priming in older or younger adults was observed, and it is unclear why fine-grained familiarity or AoA effects should affect the different forms of priming examined here in different ways. Nonetheless, future studies should collect familiarity and AoA ratings for the celebrities they use to address these issues.

Cognitive Ageing in Face and Person Recognition

The present series of experiments adds new findings to the steadily growing literature on the effects of cognitive ageing on face processing. Previous studies examined either more basic processes of face perception (Boutet & Faubert, 2006; Komes et al., 2014b, 2015; Konar et al., 2013; Meinhardt-Injac, Persike, & Meinhardt, 2014a; Wiese et al., 2013) or name generation (James, 2004, 2006; James, Fogler, & Tauber, 2008) in older adults, two processes that are often assumed as reflecting opposite end points in the sequence of processing steps in person recognition (Bruce & Young, 1986, 2012; Hanley, 2011). The present study examined the steps in-between these end points.

At first glance, our finding that both domain-specific and domain-general person representations are somewhat affected by ageing may seem at variance with the idea that crystallized knowledge is largely intact in older adults (Baltes, 1987; Cattell, 1971), and with other reports that priming effects are less affected than episodic memory in older adults (e.g., Balota, Dolan, & Duchek, 2000). It should be emphasized, however, that the present results do not indicate that long-established representations decay during normal ageing, as older participants recognized the famous faces with high accuracy. These results indicate that crystallized knowledge was clearly preserved. Reduced priming may at the same time suggest that the efficiency of accessing this knowledge is reduced (see also Craik & Bialystok, 2006).

Interestingly, the observed lack of efficiency in accessing person representations does not seem to be related to global factors, such as generally slower processing (Salthouse, 1996) or generally reduced resources (Craik, 1983; Craik & Rose, 2012), as no reduction in semantic priming was observed. Although an increased overall response time was found in this task, this finding may well reflect enhanced processing time due to an extended semantic network of person-related information rather than cognitive ageing. It is plausible that older adults have met more people in the course of their lifetime, establishing a larger and more interconnected network of person-related semantic representations. If so, the same level of incoming activation would spread more widely. This, in turn would increase the time until activation at a specific target PIN reaches the threshold, promoting longer response times in older adults.

Conclusions

In conclusion, the present series of experiments provide both behavioral and ERP evidence for age-related differences in face and person recognition. More specifically, the results show that both domain-specific (i.e., FRUs) and domain-general representations of familiar persons (PINs) work less efficiently in older age, whereas semantic representations are largely intact. It thus seems that both perceptual and post-perceptual representations of individual persons are more vulnerable to age-related loss of efficiency than more densely interconnected semantic information. These findings are well in line with recent theoretical developments in the cognitive ageing literature and extend models of face recognition by suggesting specific modifications in older age.

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Received April 4, 2016
Revision received October 3, 2016
Accepted November 17, 2016