The influence of facial attractiveness on recognition memory: Behavioural findings and electrophysiological evidence

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LIST OF ABBREVIATIONS

ACC	Anterior cingulate cortex
ANCOVA	Analysis of covariances
ANOVA	Analysis of variances
CMS	Common mode sense
CR	Correct rejection
Df	Degrees of freedom
Dm	Differential neural activity based on memory
DRL	Drive right leg
EEG	Electroencephalogram
EPN	Early posterior negativity
ERP	Event-related potential
F1	First filial generation
F2	Second filial generation
FA	False alarm
FITC	Face-in-the-crowd distinctiveness
fMRI	Functional magnetic resonance imaging
FRU	Face recognition unit
HFC	Heterozygosity-fitness correlations
LPC	Late positive component
MDFS	Multidimensional face space
MHC	Major histocompatibility complex
mPFC	Medial prefrontal cortex
MSES	Multiple source eye correction
NAcc	Nucleus accumbens
OFC	Orbitofrontal cortex
OGB	Own-gender bias
ORB	Own-race bias
PCA	Principal component analysis
RGB	Red-green-blue colour space
RT	Reaction time
SAM	Self-assessment mannequin
SD	Standard deviation
VS	Ventral striatum
VTA	Ventral tegmental area

VORWORT - ZUSAMMENFASSUNG

Die Fähigkeit, Gesichter richtig zu lernen und wiederzuerkennen, ist für unser tägliches Leben und unsere sozialen Interaktionen von hoher Relevanz. Während Leute im Allgemeinen sehr leistungsfähig sind, wenn sie sich an Gesichter erinnern, ist diese Fähigkeit jedoch auch überraschend anfällig für robuste Verzerrungen zugunsten bestimmter Gesichtergruppen. So wurde vielfach gezeigt, dass Betrachter Gesichter ihrer eigenen Ethnie besser in Erinnerung behalten als Gesichter anderer Ethnien, ein Phänomen bekannt als Own-Race-Bias (z. B. Wiese, Kaufmann, & Schweinberger, 2014). In der Literatur herrscht weiterhin eine Debatte über die Mechanismen, die hinter diesen Verzerrungen stehen, wobei die Mehrzahl der theoretischen Annahmen je einem der beiden prominentesten Ansätze zugeordnet werden kann: Auf der einen Seite argumentieren Theorien der sozialen Kognition, dass Menschen motivierter sind, Gesichter ihrer eigenen sozialen Gruppe aufgrund ihres Gruppenstatus zu individualisieren, was zu einer effizienteren Verarbeitung und damit besseren Gedächtnisleistung von Eigengruppengesichtern führe. Auf der anderen Seite gehen Theorien der Wahrnehmungsexpertise davon aus, dass ein besseres Gedächtnis für bestimmte Gesichtergruppen durch die regelmäßige Exposition mit vielen verschiedenen Gesichtern dieser Kategorie entsteht. Eine Möglichkeit, die Universalität dieser Vorhersagen über den Rahmen des Own-Race-Bias hinaus gegeneinander zu testen, besteht darin, das Gedächtnis für zwei Gesichtsgruppen zu messen, die uns einerseits beide im Alltag nur selten begegnen, die sich aber andererseits in ihrem Motivationsgehalt stark unterscheiden. In einer früheren Studie verglich ich deshalb das Gedächtnis für attraktive Gesichter mit dem für unattraktive Gesichter. Dabei wurde in Erweiterung vorheriger Studien der Einfluss wahrgenommenen Distinktheit, einer starken Determinante des Gesichtergedächtnisses, in der Stimulusauswahl kontrolliert.

Die vorliegende Arbeit beschreibt eine Reihe von Studien, deren Ziel es war, zum besseren Verständnis des Einflusses von Attraktivität auf das Gesichtergedächtnis beizutragen. Zunächst habe ich einen großen Stimuluspool von 1100 Gesichtern erstellt und Ratings für eine Reihe relevanter Dimensionen erhoben (siehe Abschnitte 2.1 und 3). In der ersten Studie untersuchte ich, ob die Erinnerung an Gesichter linear mit zunehmender Attraktivität zunimmt oder ob diese Beziehung komplexer ist (siehe Abschnitt 3). In der zweiten Studie untersuchte ich den kombinierten Einfluss von Attraktivität und Geschlecht auf das Gesichtergedächtnis, um

Vorhersagen von Wahrnehmungsexpertise, sozialer Kognition und anderen alternativen Theorien kompetitiv zu testen (siehe Abschnitt 4). Während sich die ersten beiden Experimente auf Gedächtniseffekte beim Abruf konzentrierten, untersuchte ich in einer dritten Studie enkodierungsrelatierte neuronale Korrelate des Attraktivitätseffekts für Gesichtergedächtnis (siehe Abschnitt 5).

Zusammenfassend fand sich durchweg ein besseres Gedächtnis für unattraktive Gesichter gegenüber sowohl attraktiven als auch mittelattraktiven Gesichtern. Darüber hinaus wurden mittelattraktive Gesichter in den Studien 1 und 2, und numerisch in Studie 3, deutlich schlechter erinnert als attraktive Gesichter. Dieser Unterschied verschwand jedoch wenn emotionale Relevanz, d. h. Valenz und Erregung, mitberücksichtigt wurden. In den ereigniskorrelierten Potentialen im Enzephalogramm zeigten sich erhöhte P2-Amplituden für mittelattraktive Gesichter beim Gedächtnisabruf (Studien 1 und 2), und ein ausgeprägter Dm-Effekt in dieser Komponente (Studie 3). Der Attraktivitätseffekt auf das Gesichtserkennungsgedächtnis zeigt sich somit bereits in Prozessen der fortgeschrittenen Wahrnehmungsverarbeitung von Gesichtern, die in der P2 reflektiert werden. Diese Befunde sprechen übergreifend eher für Annahmen der Wahrnehmungsexpertise, im speziellen basierend auf der Dichte von Repräsentationsclustern (siehe Abschnitte 1.4.1 und 6.2.4), da sowohl attraktive als auch mittelattraktive Gesichter dichter mental verortet werden. Die aktuellen Daten deuten darüber hinaus auf eine Beteiligung emotionaler Verarbeitung hin. Da kein signifikanter Einfluss des Gesichts- oder Teilnehmergeschlechts beobachtet wurde, gab es keine zwingenden Anhaltspunkte für die Theorien sozialer Kognition.

PREFACE - SUMMARY

The ability to correctly memorize faces is of high relevance to our daily lives and social interactions. While people are generally very efficient in remembering faces, this skill is also surprisingly prone to robust biases for certain groups of faces. In that vein, it has been shown consistently that observers remember faces of their own race better than other-race faces, an effect coined as the own-race bias (ORB; e.g. Wiese, Kaufmann, & Schweinberger, 2014). There has been considerable debate on the functional nature, i.e. the mechanisms behind such biases, with the majority of accounts falling roughly into one of two prominent frameworks: on the one hand, theories of social cognition argue that people are more motivated to individuate faces based on their social group membership and this would lead to a more proficient processing and concurringly better memory for in-group faces. On the other hand, theories of perceptual expertise assume that better memory for in-group faces results from regular exposure to many different facial exemplars. One way to competitively test the universality of these predictions beyond the context of the own-race bias is to assess memory for two facial groups that we rarely encounter in everyday life, but that differ highly in their motivational value. Thus, in an earlier study, I compared memory for attractive faces with unattractive faces. Extending previous studies, perceived distinctiveness, a strong determinant of face recognition memory, was kept equal between these groups.

This thesis is based on a series of experiments that aimed to better understand the influence attractiveness has on memory while always controlling for perceived distinctiveness. First, I created a large stimulus pool of 1100 faces and obtained ratings on a number of relevant dimensions (see sections 2.1 and 3). In the first study, I investigated if memory for faces increased linearly with increasing attractiveness or whether this relationship was more complex (see section 3). In the second study, I investigated the combined influence of attractiveness and gender on recognition memory to competitively test predictions of perceptual expertise, social cognition, and alternative accounts (see section 4). In the third study, l, I investigated encoding-related neural correlates of the attractiveness effect on memory at retrieval (see section 5) whereas the first two experiments focused on ERP memory effects during retrieval.

Taken together, I found consistently higher memory for unattractive over both attractive and medium-attractive faces. Further, medium-attractive faces were significantly less well remembered than attractive faces in studies 1 and 2, and numerically in study 3. This difference disappeared when emotional relevance, i.e. valence and arousal, was taken into account. Inspection of ERPs showed increased P2 amplitudes for medium-attractive faces at retrieval in studies 1 and 2, and a pronounced Dm effect in this component in study 3. Thus, the attractiveness effect on face recognition memory seems already rooted in evolved, i.e. more refined and higher-level, perceptual processing of faces reflected in the P2. Overarchingly, these findings argue in favour of perceptual accounts, i.e. representational clustering (see sections 1.6.1 and 6.2.4), as both attractive and medium-attractive faces are supposedly more densely clustered in participants' mental storage. The current data further indicate some contribution of emotional relevance. As no significant influence of face or participant gender was observed, there was also no compelling evidence for accounts of social cognition.

1 GENERAL INTRODUCTION

1.1 The beauty premium - attractiveness and memory biases

Attractiveness is an inherently advantageous attribute to have. Attractive people not only receive more attention (Sui & Liu, 2009), but are also are favoured with a wide range of desirable social outcomes: they benefit with regard to mate choice and romantic relationships (A. Feingold, 1990; Simpson, Lerma, & Gangestad, 1990), good grades (Lerner & Lerner, 1977), hiring decisions (Hosoda, Stone-Romero, & Coats, 2003), and even democratic votes (Efran & Patterson, 1974). There is evidence that attractive people also receive the benefit of the doubt where unattractive people are judged more harshly in court sentencing (Castellow, Wuensch, & Moore, 1990; DeSantis & Kayson, 1997; Downs & Lyons, 1991). These outcomes, however, are not necessarily based on merit, but rather stem from heuristical ascriptions captured in the so called ‘what-is-beautiful-is-good’ stereotype (Dion, Walster, & Berscheid, 1972). This ‘beauty premium’, favouring attractiveness in social decisions, evolved as a behavioural shortcut to more effortful alternatives used to evaluate an individual’s social merit and abilities (see Maestripieri, Henry, & Nickels, 2017 for a recent and detailed review).

As memory for faces is crucial for daily social interactions, any reduction based on specific facial characteristics will likely result in pervasive constraints or even considerable biases with potentially far-reaching consequences. The objective of this thesis is to identify mechanisms behind face memory biases in relation to attractiveness. In the context of face recognition memory, this becomes highly relevant when correct identification of people is essential, e.g. in culprit identification via eye-witness testimony. Indeed, people are notoriously inefficient in telling unfamiliar people apart (Bruce et al., 1999; Jenkins, White, Van Montfort, & Burton, 2011), and tend to rely more on heuristical information under conditions of uncertainty (Tversky & Kahneman, 1974), e.g when they are challenged to identify a person after just a limited amount of exposure.

1.2 Models of face perception and memory

The ability to correctly recognize individuals is immensely important for social interaction. Yet, even though humans are often considered to be face experts, their aptitude in face recognition is surprisingly susceptible to a multitude of biases, the most prominent example being the own-race bias (G. A. Feingold, 1914). As memory biases for certain face groups may well stem from differences in perception, i.e. visual encryption of faces, it is of particular interest to understand the underlying principles of face perception and mental storage.

An early and very prominent model by Bruce and Young (1986) describes sequential stages of processing and recognizing familiar faces. This model assumes that identity processing is functionally independent from the processing of other socially relevant information contained in the face, i.e. age, gender, or expression. These attributes—so-called visually-derivable semantics—can be inferred from both familiar and unfamiliar faces by means of an initial perceptual analysis employed during structural encoding. *Familiar* face recognition further relies on the successful matching of the derived information to a robust mental representation, termed Face Recognition Unit (FRU)—one of which is stored in long-term memory for every known identity.

This model, however, remains vague on how representations of identity are formed and stored for newly encountered faces. Abstracting and organising this information is a complex demand on the human mental system, as faces differ in many aspects from one another—such as shape or spacing of their features (e.g., distance between the eyes, length of the nose), or properties of their texture (e.g., skin colour, blemishes, or wrinkles). Consequently, efficient usage of multiple dimensions is required to encode relevant idiosyncrasies of individual faces for later recognition. The Multidimensional Face Space model (MDFS; Valentine, 1991; Valentine & Endo, 1992; Valentine, Lewis, & Hills, 2015) hence describes storage of internal cognitive representations of seen faces as multidimensional engrams. These denote physiognomic characteristics encoded as parametric values on an unspecified number of dimensions. Presumably, these dimensions are formed by perceptual learning over the life-span. Their central tendency denotes the origin of the multidimensional (Euclidian) space, assuming that the manifestations of features in the encountered face population are normally distributed around the mean dimension value—although this assumption is not without challenge (Burton & Vokey, 1998). Putatively, a face that is average on all possible dimensions would be represented right in the centre of this MDFS.

Less central to this thesis, Valentine proposed two versions of this model. A norm-based coding model assumes that faces are coded with reference to such a dimensionally average face located at the origin, i.e. a prototype or norm face. A specific face is hence encoded as a vector denoting the location at which the origin converges with n-dimensional values for that face. Alternatively, an exemplar-based view of the MDFS rather assumes that every face is represented as a dot in the MDFS, i.e. as a collection of absolute dimensional values, with no relation to the norm face.

In either version, face recognition success depends on how well the cognitive system can match the incoming percept to the correct pre-existing representation while simultaneously rejecting other competing identities stored in close proximity. This process may be complicated when a) faces bear close similarity, and many exemplars are stored within a certain region of the MDFS, and/or b) there is a considerable encoding error, for instance resulting from adverse viewing conditions (e.g. insufficient lighting). Recognition is facilitated, however, if a given face attains a very high value on one dimension (e.g., very wide-set eyes), as it then appears atypical due to its unusual perceptual configuration. Those faces are perceived as distinctive in relation to other faces. One of the most consistent findings in experiments of face recognition memory is that distinctive faces are correctly recognized more frequently than typical faces, as reflected by higher hit rates and lower false alarm rates. This ‘distinctiveness effect’ is robust and has been widely reported in the literature (Byatt & Rhodes, 2004; Dewhurst, Hay, & Wickham, 2005; Morris & Wickham, 2001). In the original MDFS model, memory accuracy hence for a given face depends on cluster density, and thus largely on its distance to the origin.

1.3 Memory for faces and attractiveness

1.3.1 Attractiveness and distinctiveness

According to an averageness account of attractiveness, adults’ perception of attractiveness results from norm-based coding. In other words, facial attractiveness is thought to be inversely related to the distance from the mean (Langlois & Roggman, 1990; Light, Hollander, & Kayra-Stuart, 1981; Morris & Wickham, 2001; Rhodes, 2006; Rhodes & Tremewan, 1996). In other words, perceived facial attractiveness changes as a function of proximity to an average. Thus, attractiveness decreases the farther a face is from the norm, but increases when dimensional averageness is enhanced, e.g. by digital morphing manipulations (Langlois & Roggman, 1990; Langlois, Roggman, & Musselman, 1994).

Different mechanisms have been proposed as the functional basis of this relationship. A perceptual processing framework assumes that the perception of attractiveness results from perceptual fluency (e.g. Winkielman, Halberstadt, Fazendeiro, & Catty, 2006). According to this view, the human neurocognitive system is particularly adept at processing certain stimuli more efficiently than others. This more ‘fluent’ processing is thought to result in positive affect that is then attributed to the stimulus itself. Hence, these stimuli gain positive valence. It has been argued that attractive faces are more fluently processed because they are more prototypical, and thus better representations of their stimulus class, i.e. nearer to the norm face (Winkielman et al., 2006).

From an evolutionary point of view, average attributes of attractive faces, like high facial symmetry or blemish-free skin (Langlois et al., 1994), are thought to indicate unimpeded development of the individual and thus evolutionary competency: they signal adaptive fitness to meet environmental challenges like diseases, parasites, or competition for resources (Fink, Grammer, & Thornhill, 2001; Fink, Neave, Manning, & Grammer, 2006). It has been proposed that these adaptive benefits result at least to some degree from genetic heterozygosity, assuming that an average facial phenotype results from expressing mixed allele genotypes (Grammer & Thornhill, 1994). Positive correlations between heterozygosity and fitness-related traits have been found across many different organisms (Chapman, Nakagawa, Coltman, Slate, & Sheldon, 2009; but see David, 1998; Szulkin, Bierne, & David, 2010 for critical discussions). In genetics, such heterozygote advantages are seen as major underlying mechanism for heterosis, also termed ‘hybrid vigor’ or outbreeding enhancement, which is the improved function of biological qualities in hybrid offsprings (Shull, 1948)[1]. This is often discussed in direct opposition to inbreeding depression that results largely from homozygosity.

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[1] Of note, the terminology presented in many face research publications is often not very precise. For instance, the idea of a heterozygous genotype driving a fitter and therefore more attractive phenotype is a grave oversimplification of genetic principles. For one, heterozygosity can be advantageous for natural selection in some cases, but can also have a detrimental effect in others (often discussed as overdominance vs. underdominance; Gillespie, 2010). Second, this reasoning largely overlooks the influences of allelic dominance that may well not result in an average phenotype in a heterozygote F1 on an individual level (see also dominance vs. incomplete dominance; King, Stansfield, & Mulligan, 2006). Third, evolutionary accounts of attractiveness rarely disentangle effects of genetic differences from effects of assortative mating. To the author’s knowledge, there is no study to date that showed a direct link between a heterozygote genotype in loci directly involved in face shape and rated attractiveness of the resulting phenotype (but see Lie, Simmons, & Rhodes, 2010, for an indirect link). Even the finding of mixed-race faces being rated as more attractive may well be a result from assortative mating, i.e. very attractive, resourceful individuals being more likely to produce mixed-race offspring from traveling and living in greater distance from their place of origin, rather than a direct effect of genetic heterozygosity. Furthermore, heterosis is usually described in settings of selective breeding, for example of F1 hybrids with desirable attributes for agriculture, rather than for natural selection settings. Please note, however, that these advantages from heterosis only apply to the first filial generation F1, and can reliably be predicted only when the paternal genotype is homozygous. These beneficial attributes do not per principle persist in the F2 generation on a population level by means of Mendelian recombination. Thus, pairing with heterozygous F1 members may not necessarily result in competitive offspring in F2: While some F1 hybrid qualities like higher crop yield may make individuals preferable for human use, others like infertility issues, e.g. in mules, imply that these traits would probably become extinct if not for human intervention through agricultural husbandry. Thus, while some heterozygote attributes in F1 may be desirable for short-term breeding, they may also be disadvantageous in the context of natural selection and long-term evolution. This is not to say that proposing such mechanisms for evolutionary development of attractive traits is per se inadequate. It is more a cautionary warning that many common depictions of genetic principles in publications in the face literature potentially suffer from oversimplifications, overgeneralizations, and/or partial misconceptions.

It has been proposed that the preference for average traits in faces evolved due to such heterozygosity-fitness correlations (HFC). For instance, men showing heterozygosity at three key loci in the major histocompatibility complex (MHC; genes coding for proteins involved in immune responses) are judged more attractive and more healthy by women than faces of men who are homozygous at one or more of these loci (Roberts et al., 2005; see also Lie, Simmons, & Rhodes, 2010 for similar results). Further, the finding that mixed-race faces are rated as more attractive than single-race faces has been discussed as a perceptual demonstration of heterosis in humans (Lewis, 2010). Taken together, average traits are commonly seen as phenotypical markers of high reproductive fitness in potential mates and rivals.

While factors described in the previous paragraphs render attractive faces highly prototypical, other attributes of particularly attractive faces, i.e. increased secondary sexual characteristics, move them perceptually away from the population mean (Alley & Cunningham, 1991; DeBruine, Jones, Unger, Little, & Feinberg, 2007). Our faces are sexual dimorphic, i.e. having an own set of visual codes specific to either biological sex. For women, these include fuller lips, softer features from increased fat storage, higher local contrast of facial features (Russell, 2003), larger eyes, and larger distance between upper eyelids and the eyebrow (R. Campbell, Benson, Wallace, Doesbergh, & Coleman, 1999). Men's faces are characterized by, for example, more prominent brow bones and facial hair growth (Bruce et al., 1993), and are preferred when testosterone-facilitated features (e.g. jaw width) are particularly pronounced (Grammer & Thornhill, 1994). As these cues to femininity and masculinity develop under the differential influence of reproductive hormones, they are seen as intimately interlinked with mate quality and selection (but see Foo, Simmons, & Rhodes, 2017, for a recent empirical evaluation). A recent study found that participants generally prioritized sexual dimorphism over symmetry and colour cues to health in attractiveness ratings (Mogilski & Welling, 2017). In this study, sexual dimorphism seemed relatively more important for the evaluation of male faces, whereas symmetry and colour cues to health are relatively prioritized for judging female faces.

These findings suggest that highly attractive faces can be average in terms of some perceptual dimensions, but also are perceived as distinctive on others. To further inspect this, Said and Todorov (2011) used a statistical modelling approach to define attractiveness as a function of a face's location in an MDFS based on shape and texture information of digitally created faces. The authors report that for many dimensions averageness yields the most attractive faces (especially shape dimensions), yet this does not hold for a considerable number of other characteristics (especially textural features). In other words, averageness is indeed attractive in some dimensions, but not in others. Furthermore, the effect of averageness has been more consistently found for female relative to male faces (Grammer & Thornhill, 1994; Perrett et al., 1998). Thus, while distinctiveness explains variance in attractiveness ratings, this relationship seems far from simple, yet may well affect memory for differently attractive faces. These links are further complicated by influences of face and participant gender.

1.3.2 Attractiveness effects in face memory - previous findings

As distinctiveness has a major impact on recognition memory (see above), but an attractive appearance seems characterized by an optimal combination of both average and distinctive features, predicting the relation of recognition memory and attractiveness per se is difficult. Several attempts have been made to link memory performance for faces to facial attractiveness, yet the overall results remain inconclusive. Some studies report a facilitation of recognition and memory judgments for attractive faces (Carroo & Mozingo, 1989; John F. Cross, Cross, & Daly, 1971; Fleishman, Buckley, Klosinsky, Smith, & Tuck, 1976; Marzi & Viggiano, 2010; Zhang et al., 2011), whereas others find poorer performance (Light et al., 1981; Sarno & Alley, 1997). There is also a considerable number of studies reporting complex interactions of facial attractiveness and other factors such as participants' and stimulus' gender (Mallet & Lallemand, 2003; Maner et al., 2003; Watkins et al., 2017), or non-linear influences of attractiveness on memory performance (Deblieck & Zaidel, 2003; Shepherd & Ellis, 1973). Finally, some studies report no effect of attractiveness on memory accuracy (Brigham, 1990; Wickham & Morris, 2003).

In addition to various methodological shortcomings, e.g. truncated range of attractiveness (John F. Cross et al., 1971; Sarno & Alley, 1997), inadequate assessment of memory performance (Deblieck & Zaidel, 2003; Marzi & Viggiano, 2010; Wickham & Morris, 2003), or sampling biases (Carroo & Mozingo, 1989; John F. Cross et al., 1971), most of these studies largely ignore the impact of distinctiveness on face memory. Extending previous reports, Wiese, Altmann, and Schweinberger (2014) examined effects of attractiveness on behavioural and event-related potentials (ERPs, discussed below) of face memory while controlling for perceived distinctiveness. In this study, attractive and unattractive faces were selected on the basis of attractiveness ratings, and matched for a measure of perceived distinctiveness. In a subsequent recognition memory experiment, memory was more accurate for unattractive relative to attractive faces. This result indicated that facial attractiveness biases recognition memory over and above perceived distinctiveness. This thesis presents a series of experiments designed to competitively test assumptions from several frameworks explaining face memory differences. The following section introduces these frameworks.

1.4 Theoretical accounts

1.4.1 Perceptual account: Representational clustering

The original proposition of an MDFS predicts better memory for faces located in the periphery. The reason behind this, however, may not be the distance between the face and the space's origin per se, but hinges on the assumption that the origin is the most densely clustered region within the MDFS. Crucially however, and at variance with this original proposition, the majority of faces are usually rated as being of medium typicality/distinctiveness (see Burton & Vokey, 1998, for a detailed discussion). Hence, 'local' cluster density may still differ between attractive and unattractive faces even when these groups are matched for 'global' perceived distinctiveness. That is, it is still possible that individual faces within groups cluster closely together on a local level, even when the overall group means are matched on a global scale. In terms of the MDFS, while the mean distance between attractive and unattractive faces from the perceivers' point of reference has been matched in value, it is still possible that they systematically differ in direction (one possibility illustrated in Figure 1).

As detailed in section 1.2, close proximity between facial representations in an MDFS may adversely affect memory efficiency due to inter-item confusion (Valentine & Endo, 1992). Such local clustering can result from perceived similarity, i.e. when rarely encountered faces like other-race faces are insufficiently individuated to create distinct engrams. Studies using multi-dimensional scaling approaches on similarity ratings provide evidence that less-well remembered other-race faces are indeed perceptually more densely clustered relative to own-race faces (Byatt & Rhodes, 2004; Papesh & Goldinger, 2010). This tighter clustering has likewise been reported for attractive compared to unattractive faces (Potter, Corneille, Ruys, & Rhodes, 2007), thus also predicting worse memory for attractive faces as found by Wiese, Altmann, et al. (2014).

Local clustering can also result when a large number of faces of a given group are regularly seen and encoded into an MDFS. Assuming that attractiveness is roughly normally distributed, by far the most commonly encountered faces in everyday life are medium-attractive (see Figure 1 for a simplified 2D-illustration). Thus, forming sufficiently discrete engrams for these faces requires more effort and/or more detailed information storage, and may yet still result in worse memory. Taken together, this framework predicts better memory for unattractive faces over other face groups as they are less densely clustered.

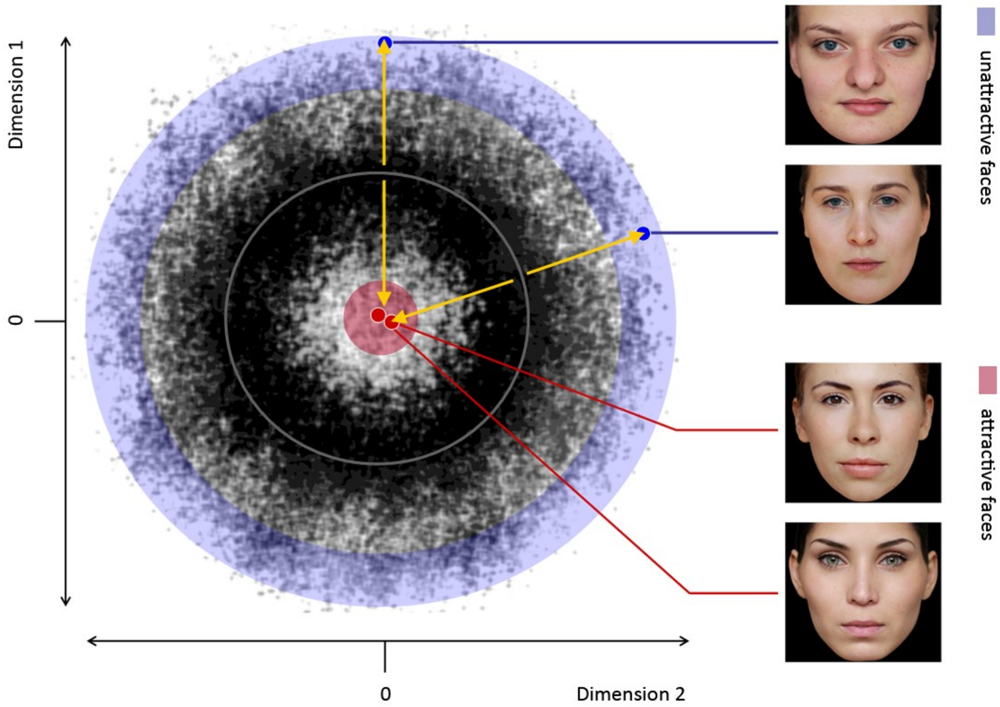


Figure 1. A modified version of the MDFS model based on the data obtained in Wiese, Altmann, et al. (2014). The grey dots indicate the distribution of faces along two arbitrary theoretical dimensions. Darker shades indicate tighter clustering. Yellow arrows illustrate the distances between the most common faces, which are clustered as a ring in the 2D illustration (marked by the grey circle at the points of highest density in the distribution) and face groups of varying attractiveness.

1.4.2 Social cognition account: Social group membership

Socio-cognitive models assume that enhanced motivation to process faces of the perceiver's social in-group compared to their out-group results in better memory. The Categorization-Individuation Model (Hugenberg, Young, Bernstein, & Sacco, 2010), for instance, postulates that memory biases arise due to the tendency to categorize out-group members but individuate in-group members. These frameworks assume differential processing strategies (i.e. configural/holistic versus more feature-based processing) following an initial stage of social categorisation into in- and out-group (Sporer, 2001).

Of particular interest to this line of work, social cognition accounts can be used to explain the own-gender-bias (OGB), i.e. better memory for faces of the perceiver's own gender (see Herlitz & Lovén, 2013, for a meta-analysis of the OGB; Lovén, Herlitz, & Rehnman, 2011; Wolff, Kemter, Schweinberger, & Wiese, 2014). Furthermore, attractive faces are more readily seen as belonging to the perceiver's in-group (e.g. as sharing the same political affiliation, Johnson, 1981). Socio-cognitive accounts would thus predict not only better memory for attractive faces, but potentially best memory for attractive own-gender faces (see section XYZ for a more detailed discussion).

1.4.3 Evolutionary account: Adaptive memory

The evolutionary framework of adaptive memory assumes that memory systems have evolved to help retain survival- and fitness-related information, i.e., information geared toward enhancing an organism's competitiveness for reproduction and resources (Nairne, Pandeirada, & Thompson, 2008; Nairne, Thompson, & Pandeirada, 2007). In the context of face recognition memory, it can be argued that the level of attractiveness is fitness-related information for both same-sex and opposite-sex faces. As detailed above, attractive appearance is widely seen as an emerging property of evolutionary adaptation that signals the optimum reproductive status of its bearer (Senior, 2003). It is thought to indicate not only good genetic quality, but also successful phenotypical translation during individual development (e.g. Grammer & Thornhill, 1994; Scheib, Gangestad, & Thornhill, 1999; Thornhill & Gangestad, 1999). Thus, high attractiveness signals overall fitness and competitiveness to both potential mates and rivals.

Even beyond mating contexts, the universal presence of the 'beauty premium', i.e. favouring attractiveness in social decisions, is suggested to promote evolutionary success. For example, affiliating with attractive, i.e. resourceful others—by choosing attractive friends or hiring attractive co-workers—may in turn increase the individual's own competitiveness. As recently reviewed, social decision biases for attractiveness probably evolved as a behavioural shortcut to more effortful evaluations of an individual's social merit and abilities (see Maestripieri et al., 2017, for an extensive review and multi-author discussion).

As an evolutionary account assumes that face memory evolved to attain evolutionary goals, this would predict particularly good memory for attractive relative to unattractive faces, especially of the opposite sex (in heterosexual participants). This pattern has indeed been reported for several non-human species (Brennan & Kendrick, 2006). In line with this idea, recent research suggested that increased memory for attractive relative to unattractive male faces in female participants arises due to their romantic goals in mate selection, while more accurate memory for attractive relative to less attractive same-sex female faces putatively serves to retain details about potential rivals (Watkins et al., 2017).

1.4.4 Emotional memory account: Affective relevance and saliency

This account assumes that affectively relevant material is more efficiently encoded, consolidated, and/or retrieved than neutral stimuli (Hamann, 2001; LaBar & Cabeza, 2006) (Kensinger, 2004). Memory for emotional stimuli, including word lists, scenes, and also faces, is described as more vivid and more accurate than for neutral material of the same categories (Hamann, Ely, Grafton, & Kilts, 1999; Kensinger, 2004; Kensinger & Schacter, 2005; LaBar & Cabeza, 2006). There is abundant evidence showing that emotionally *arousing* stimuli are generally better remembered than non-arousing material (e.g. Bradley, Greenwald, Petry, & Lang, 1992). Further, effects of emotional *valence* are also often discussed in terms of positivity/negativity biases in memory (Kensinger & Schacter, 2008; Ohira, Winton, & Oyama, 1998). Both valence and arousal effects are commonly attributed to increased saliency of emotional material.

Studies focussing on the influence of emotional expression on face recognition memory most consistently report that happy faces are remembered and identified more accurately than faces with other expressions, including surprise, anger, fear, and neutral expressions (Baudouin, Gilibert, Sansone, & Tiberghien, 2000; D'Argembeau & Van der Linden, 2007, 2011; D'Argembeau, Van der Linden, Comblain, & Etienne, 2003; Endo, Endo, Kirita, & Maruyama, 1992; Gallegos & Tranel, 2005; Hagemann, Straube, & Schulz, 2016; Kaufmann & Schweinberger, 2004; Patel, Girard, & Green, 2012; Shimamura, Ross, & Bennett, 2006). Despite these reports, the happy-face advantage is not clear-cut, as several other studies yielded mixed results: Whereas a previous experiment observed no differential memory for happy versus neutral faces (Johansson, Mecklinger, & Treese, 2004), several others even report memory benefits for faces with negative expressions (Righi et al., 2012; Sergerie, Armony, Menear, Sutton, & Lepage, 2010; Sergerie, Lepage, & Armony, 2005).

As attractiveness is an inherently valenced characteristic, it seems possible that its impact on memory results from its affective relevance. However, due to the inconsistency of results in previous studies, it is difficult to make specific predictions with respect to attractiveness.

Based on increased ERP markers of affective processing (reviewed in more detail below), Marzi and Viggiano (2010) proposed that a benefit in memory for attractive faces arises due to the affective nature of these stimuli. In direct opposition to this, Wiese, Altmann, et al. (2014) found a negative correlation between markers of affective processing during encoding and the memory differences between attractive and unattractive faces when distinctiveness was controlled. If anything, beneficial effects of positive affect should have been more pronounced after this matching, which would have resulted in a positive correlation. Thus, emotional content in attractive faces may even have hampered, rather than boosted, mnemonic processing. Of note, however, both interpretations hinge on ERPs as implicit measures of affective relevance. It is not clear to what extent attractive, medium-attractive and unattractive faces explicitly differed in perceived ratings of emotional content. Again, it appears crucial to measure the affective qualities of the used images. The work in this thesis hence further assesses influences of explicit ratings of emotional arousal and valence, obtained by using the Self-Assessment Mannequin scales (SAM scales; Bradley & Lang, 1994, see section 2.1 and Appendix 1 for details).

1.5 Neurophysiological correlates of facial attractiveness and memory

1.5.1 A short overview: Brain imaging studies and reward value

Extending on the functional assumptions of the Bruce and Young model, the Haxby model describes neurocognitive mechanisms underlying face perception (Haxby, Hoffman, & Gobbini, 2000; recently reviewed and revised by Duchaine & Yovel, 2015). This model was adapted by Senior (2003) to account for the ever-growing body of neuropsychological evidence highlighting networks involved in the processing of facial attractiveness. Recently, Hahn and Perrett (2014) reviewed these findings and combined distributed neural networks for face processing proposed Haxby et al. (2000) and Senior (2003, see Figure 2).

Perceiving attractive faces activates reward-related regions such as the nucleus accumbens (NAcc), ventral tegmental area (VTA), the ventral striatum (VS), and medial and dorsal parts of the orbitofrontal cortex (OFC, Cloutier, Heatherton, Whalen, & Kelley, 2008; Ishai, 2007; Kampe, Frith, Dolan, & Frith, 2001; Kranz & Ishai, 2006; O'Doherty et al., 2003; Senior, 2003; Winston, O'Doherty, Kilner, Perrett, & Dolan, 2007). This reward-related activation for attractive faces contributes to participants' willingness to work in order to view them (Aharon et al., 2001). It has also been discussed to increase verbal working memory when attractive faces are presented as a reward (Kajimura, Himichi, & Nomura, 2014).

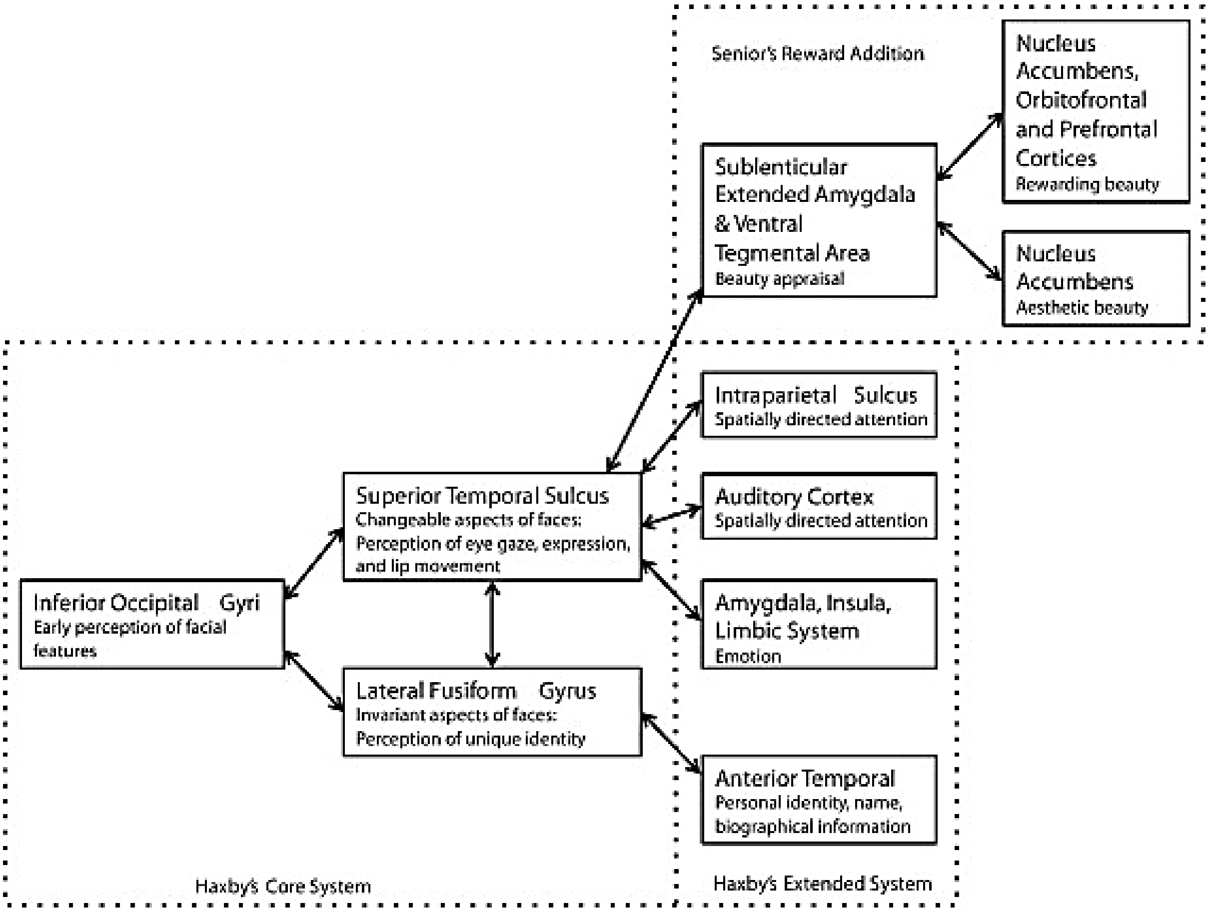


Figure 2: The distributed neural network for face processing as described by Haxby et al. (2000) and Senior (2003), as combined in Hahn and Perrett (2014).

1.5.2 Face-sensitive event-related potentials (ERPs) and facial attractiveness

Visual perception of faces is marked by a cascade of characteristic ERP components in the EEG thought to depict several stages of processing. ERPs measure neuronal activity, i.e. local voltage changes, with high temporal resolution in the range of milliseconds. Hence, they provide an on-line window to the dynamics of neural processes. Here, those ERPs important for the present purpose, their functional relevance, and their relation to facial attractiveness will be reviewed briefly.

Perceptual and face processing

P1. Initially, a positive potential over occipital electrodes is elicited by the perception of visual material, with maximum amplitudes between 90 and 120 ms after stimulus onset, often referred to as the P1 component. The amplitude of this early waveform is sensitive to basic physical stimulus characteristics, i.e., luminance or contrast (e.g. Luck, 2005). To prevent the carry-over effect of differences in low-level features captured in this component on later processing stages, picture size, head orientation, facial expression, as well as global luminance and contrast of the present stimuli have been controlled by means of Gradation Curve Adjustments of RGB value histograms in all studies presented here. Thus, no prominent P1 effects are expected.

N170. The N170 is typically seen for facial stimuli as opposed to pictures of objects, peaking after approximately 170 ms at occipito-parietal electrode sites (Eimer, 2011b), and has been proposed to reflect an early stage of perceptual analysis like structural encoding or the detection of a facial pattern by which the stimulus is classified as a face (Schweinberger & Burton, 2003). The fusiform gyrus (Allison et al., 1999; Ghuman et al., 2014) and the lateral occipito-temporal cortex (Schweinberger, Pickering, Jentzsch, Burton, & Kaufmann, 2002) have been identified as likely sources for N170 activity (see Itier & Batty, 2009, for a 2-generator model of the N170). There is some variance in results regarding the N170 sensitivity to facial distinctiveness, with some reporting increased negativity for digitally enhanced distinctiveness by means of caricaturing (Kaufmann & Schweinberger, 2008, 2012; Schulz, Kaufmann, Walther, & Schweinberger, 2012), and others not finding similar evidence for this modulation (e.g. Schulz, Kaufmann, Kurt, & Schweinberger, 2012).

Results for attractiveness effects in the N170 are likewise inconsistent: The majority of studies report insensitivity of the deflection to differences in attractiveness (e.g. Roye, Höfel, & Jacobsen, 2008; Schacht, Werheid, & Sommer, 2008). Marzi and Viggiano (2010) found that highly attractive faces yielded greater negativity than unattractive faces in a memory paradigm, which they discuss with reference to studies showing emotional modulation of the N170 amplitude. In some contrast, a more recent study found N170 amplitudes to be smaller in response to highly attractive and averaged faces versus low attractive faces in a face/non-face classification task, and interprets this finding as a marker of perceptual fluency for attractive faces (Trujillo, Jankowitsch, & Langlois, 2014).

P2. Faces elicit an occipito-temporal P2 (or P200) with a peak latency between 200 and 250 ms. Previous reports indicate a reduction in P2 amplitudes for faces that have been spatially distorted (Halit, de Haan, & Johnson, 2000) or exaggerated by means of digital caricaturing (Kaufmann & Schweinberger, 2012; Schulz, Kaufmann, Walther, et al., 2012). Accordingly, it has been suggested that modulations of the P2 are linked to the perceived typicality of facial stimuli (Wiese, Kaufmann, et al., 2014). A recent study further established that the P2 can serve as an indicator of ongoing renormalization of the visual system following face adaptation (Kloth, Rhodes, & Schweinberger, 2017). Specifically, it has been implicated in the encoding of a face's second-order spatial configurations relative to a prototype (Latinus & Taylor, 2006).

Larger P2 amplitudes for unattractive faces compared to attractive faces were observed in Wiese, Altmann, et al. (2014; see Figure 3), even though faces were matched for distinctiveness. As more faces were rated as being unattractive than attractive in a pilot study for this experiment, P2 responses were interpreted to indicate more commonly encountered (rather than prototypical) faces. In line with this, P2 amplitudes were also reported to be smaller for other-race compared to own-race faces, but only in people with no perceptual expertise for other-race faces (Stahl, Wiese, & Schweinberger, 2008). This effect was greatly diminished or even disappeared in 'experts', i.e. European participants with extensive personal contacts to Asians If P2 amplitudes indeed increase with exposure frequency, medium-attractive faces, which are the most commonly encountered in daily-life, should elicit even more positive P2 amplitudes than both attractive and unattractive faces. Differences have also been observed between male and female participants in lateralization of the P2 component to facial stimuli, however these sex differences were not linked to attractiveness of the facial stimuli (van Hooff, Crawford, & van Vugt, 2011). Hence, no major interaction between gender and attractiveness effects are expected.

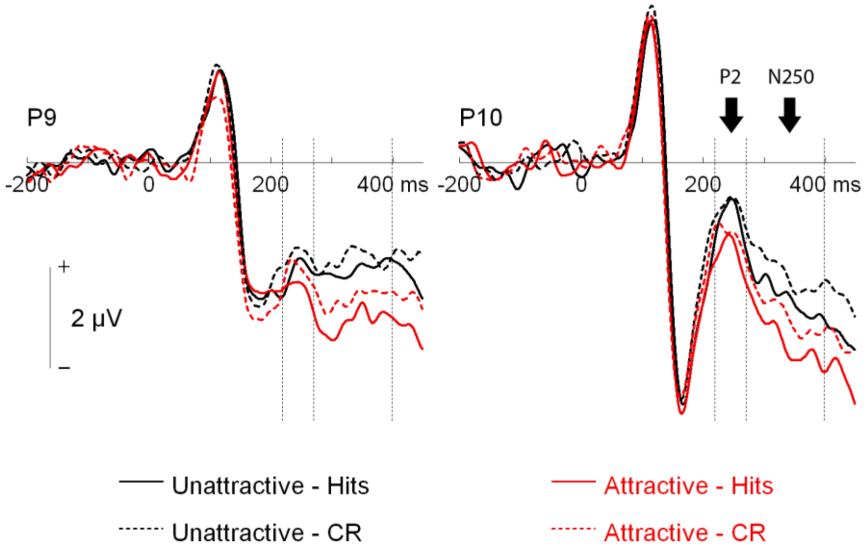


Figure 3. Attractiveness effects in the P2 and N250 time range during test at ventral temporal electrodes over the left and right hemisphere (selected from the data presented in Wiese, Altmann, et al., 2014).

N250. The N250 has a similar scalp distribution to the P2, is more prominent over the right than the left hemisphere, and has a peak latency between 230 and 330 ms (Schweinberger & Neumann, 2016). Reduced amplitudes in this component upon second presentations of formerly unfamiliar faces have been connected to processes of face identity learning (Kaufmann, Schweinberger, & Burton, 2009; Tanaka, Curran, Porterfield, & Collins, 2006). Kaufmann and Schweinberger (2012) report influences of facial distinctiveness—specifically caricatured shape information—that elicited prolonged enhancement of the N250 (and late positive component LPC, discussed in more detail below). They suggest that this may reflect the subsequent acquisition of a holistic face representation (e.g. Schulz, Kaufmann, Kurt, et al., 2012). More recently, it has been suggested that an enhanced N250 for hits over correct rejections reflects the transient activation of facial representations for recognition (e.g. Eimer, Gosling, & Duchaine, 2012; Schweinberger & Neumann, 2016). Attractive faces also yield larger amplitudes for the N250 and the LPC (Wiese, Altmann, et al., 2014; see Figures 3, 4, and 5). Other studies describe similar effects in terms of an Early Posterior Negativity (EPN) that overlaps with the N250 both with respect to its temporal characteristics and scalp distribution. This literature is briefly discussed below.

Affective processing

Early Posterior Negativity (*EPN)*. Spatially and temporarily overlapping with the N250, the EPN exhibits an occipito-temporal maximum and is observed in a time window between 150 and 350 ms post-stimulus (e.g. Junghöfer, Bradley, Elbert, & Lang, 2001; Schupp et al., 2004). Wiese, Kaufmann, et al. (2014) recently suggested that larger N250 amplitudes for specific categories of faces may mirror modulations of the EPN observed in studies varying the emotional content of pictures or facial expressions (Rellecke, Sommer, & Schacht, 2012; Schupp et al., 2004). It has been assumed to represent a 'tagging' of motivationally relevant material for later in-depth affective processing (Schupp et al., 2007)

Several studies observed increased EPN amplitudes for attractive faces (Schacht et al., 2008; Werheid, Schacht, & Sommer, 2007). Wiese, Altmann, et al. (2014) observed both more negative amplitudes for attractive versus unattractive faces reminiscent of this EPN effect and a difference between hits and correct rejections as reported for the N250. Importantly, these effects did not interact, possibly indicating independent determinants of both ERP components to be active simultaneously. Recently, Thiruchselvam, Harper, and Homer (2016) replicated this pattern. Larger EPN components have been observed to potentially interfere with recognition performance at test (Wiese, Altmann, et al., 2014). Similarly, the attractiveness effect in the EPN during learning correlated significantly with the magnitude of the memory advantage for unattractive faces at test in the study by Wiese, Altmann, et al. (2014).

Late Positive Component (LPC): The LPC is a positive shift that is widely distributed across the scalp, typically with a centroparietal maximum, and is likely generated by an extensive network of cortical and subcortical structures associated with visual and emotional processing (Liu, Huang, McGinnis-Deweese, Keil, & Ding, 2012). It starts as early as 200 ms after stimulus onset for pleasant pictures, is slightly delayed for unpleasant pictures, and may be sustained over a long period of stimulus presentation. This component is larger for both pleasant and unpleasant pictures compared to neutral pictures, as consistently reported in a variety of experimental setups, e.g. emotional oddball tasks, randomized passive viewing, or affective evaluation (Schupp et al., 2000). The effect is accentuated for valenced pictures of high emotional intensity or arousal, e.g., images with erotic or violent content (Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000). Thus, the LPC is thought to reflect in-depth affective processing following the initial 'tagging' reflected in the EPN (Schupp et al., 2000).

Specifically, it is thought to signify the perception of intrinsic motivational significance in affective material. The sustained positivity may result from engagement of appetitive and defensive motivational systems, and allocation of attentional resources to pleasant and unpleasant stimuli that are highly salient in natural environments (Cuthbert et al., 2000; Lang et al., 1998).

Elated LPC amplitudes for emotional facial expressions (Eimer & Holmes, 2007; Rellecke et al., 2012) have been interpreted as correlates of emotion-dependent motivated attention (Schupp et al., 2004). Higher LPC amplitudes for attractive faces have consistently been reported and interpreted in terms of enhanced affective processing in several studies. (Johnston & Oliver-Rodríguez, 1997; Marzi & Viggiano, 2010; Schacht et al., 2008; Thiruchselvam et al., 2016; Werheid et al., 2007). Interestingly, men showed larger LPC attractiveness effects for opposite-sex faces, whereas women exhibited similar attractiveness effects for male and female faces in another study (van Hooff et al., 2011). Wiese, Altmann, et al. (2014) suggested that such affective processing as reflected in a larger LPC during learning may hamper task performance at test in recognition paradigms (see Wiese, Kaufmann, et al., 2014, for a similar line of reasoning). If so, there should be a correspondence between high LPC amplitudes and reduced memory accuarcy. This may be further influenced by participant and face gender interactions.

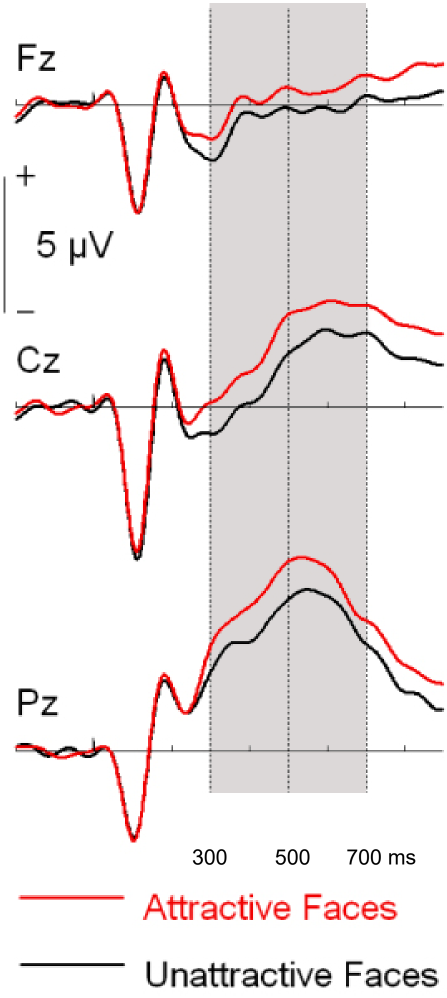
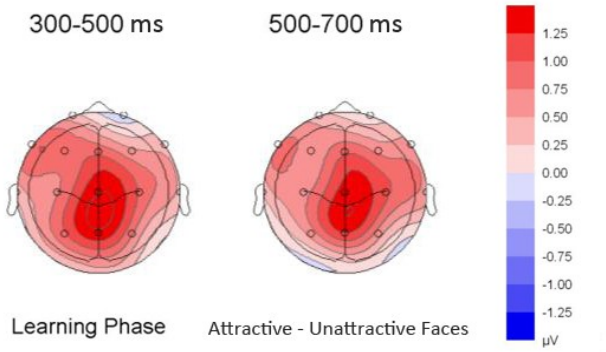


Figure 4 (left). Grand mean ERPs at frontal (Fz), central (Cz) and parietal (Pz) scalp sites, depicting enhanced LPC modulations for attractive versus unattractive faces during learning (selected from the data presented in Wiese, Altmann, et al., 2014).

Figure 5 (below). Scalp topographical voltage maps, depicting the distribution of the attractiveness effect (attractive faces minus unattractive faces) during learning. Red indicates more positive activation for attractive faces.



Mnemonic processing

Dm effects: To inspect encoding-related brain activity during learning, neural responses to those stimuli which are later remembered (subsequent hits) can be compared to those later forgotten (subsequent misses). These ERP differences, termed '*D*ifferential neural activity based on *m*emory', short 'Dm' (Paller, Kutas, & Mayes, 1987), are widely distributed in scalp topography and often extend over a considerable time period between 250 and 800 ms post-stimulus (Johnson Jr, 1995; Sommer, Schweinberger, & Matt, 1991). A large network of cooperating brain structures, including among others the bilateral medial temporal lobe and face-responsive regions in fusiform gyrus, has been identified as the neural origin of Dm effects (Paller & Wagner, 2002). Dm scalp topography for faces are more posterior than that observed for verbal material, and lateralized with a maximum over the right hemisphere, thus indexing some domain-specificity (Sommer, Komoss, & Schweinberger, 1997; Sommer et al., 1991). Its functional significance is still debated. Due to the wide-spread topography and sustained time course of the Dm effect, Friedman, Ritter, and Snodgrass (1996) suggested that it could either be `unitary ERP activity with a unique functional role that overlaps several ERP deflections, or it could reflect the contribution of several overlapping components, each reflecting a different function' (p.11).

Previous research into the functional nature of the Dm effect established that its relative size depends at least to some degree on the difficulty and effort required for a given memory task (e.g. Fabiani, Karis, & Donchin, 1990; Paller et al., 1987). Using these attributes, Study 3 inspects the relative size of Dm effects for faces of varying attractiveness in order to capture differences in processing demands across several stages implicated in face encoding. To the author’s knowledge, no previous study inspected encoding-related activity captured in the Dm effect for faces of varying attractiveness.

Old-new effects: Typically, ERPs elicited by correctly classified old (studied) items are more positive-going than those elicited by correctly classified new (unstudied) test items (Warren, 1980). These differences in ERP deflections for hits and correct rejections are referred to as old-new effects (see Rugg & Curran, 2007, for a review) and are thought to represent retrieval-related activity during recognition.

Recognition memory decisions entail at least two functionally independent sources of information about previous occurrences (see Yonelinas, 2002, for a review). On one the hand, recognition can be based on an undifferentiated memory signal referred to as familiarity. Familiarity-driven memory is regarded as non-episodic, since it entails no information specific to a given study episode. On the other hand, the retrieval of qualitative information about the study episode, e.g., contextual details, is regarded as the second factor of recognition memory and has been termed recollection or ‘episodic retrieval’ (Vilberg & Rugg, 2008). These two processes are thought to be reflected in two distinct, specific ERP signatures: Rugg et al. (1998) report an old-new effect in the timeframe between 300 and 500ms post-stimulus with a frontal scalp distribution that was unaffected by depth-of-study processing, and interpret this as an ERP correlate of familiarity-driven recognition. Recollection is reflected in a later ERP signature starting around 400–500 ms post-stimulus onset, termed as a ‘parietal’ old/new effect due to its left-hemispheric parietal maximum.

The size of old-new effects has been linked to behavioural memory biases for in-group faces like the own-race or own-age bias (e.g. Stahl, Wiese, & Schweinberger, 2010; Wiese, Schweinberger, & Hansen, 2008). Marzi and Viggiano (2010) tested recognition memory for faces varying in attractiveness and inspected early and late old-new effects. Attractive faces elicited enhanced frontal activity, resulting in a significant early old-new effect that was not found for faces of lesser attractiveness. Late old/new effects, however, showed no differential sensitivity to attractiveness. Hence, there was no conclusive evidence for an interaction of perceived attractiveness with recollection. The authors suggested that the enhanced recognition memory, i.e. increase in hit rate for attractive faces was linked to familiarity-based processes reflected in an early old-new effect.

As a complication, increased hit rates can be due to a more liberal response tendency rather than increased memory accuracy. What is more, facial distinctiveness was not accounted for in this study. When analysing d’ and controlling for distinctiveness, Wiese, Altmann, et al. (2014) found both early and late old-new effects that were not further influenced by attractiveness. Similar to the results by Marzi and Viggiano (2010), there was a general amplitude increase for attractive over unattractive faces, reminiscent of LPC effects previously described for attractiveness. This suggests that mnemonic and affective processing in this time frame are relatively independent.

2 THE PRESENT STUDIES

2.1 Rating study

Facial evaluations: theoretical considerations and interrater agreement

As discussed previously, mating with attractive individuals may promise maximum chances of producing and successfully raising fit offspring. Thus, the ability to perceive and the inclination to prefer those traits that signal evolutionary resilience and fertility should co-evolve, and thus also be an emerging property of general adaptation. If so, there should be a certain extent of intercultural agreement behind individual's judgments of facial attractiveness. Indeed, there is systematic agreement within our species in what we do and do not find attractive, both across cultures (Cunningham, Roberts, Wu, Barbee, & Druen, 1995; Langlois et al., 2000) and age groups (J. F. Cross & Cross, 1971). Moreover, Bronstad and Russell (2007) found that close relations (e.g. family members, friends, etc.) agree more on evaluations of attractiveness than strangers do. However, shared taste does on average only account for approximately half of the variance in attractiveness judgments. Private taste does also play a role, which may serve to reduce intraspecies competition (Germine et al., 2015; Hönekopp, 2006). However, the sources of individual differences in face preferences are not random, but result from systematic influences of for instance hormonal and fertility status, own attractiveness and personality, visual experience, social learning and shared environment (as extensively reviewed by Little, Jones, & DeBruine, 2011). Of relevance to this line of work, however, these shifts in preferences are relatively small and thus may affect preferences of one face over another if these are already relatively similar in perceived attractiveness.

Considering its pervasive social impact and the large body of research devoted to the topic of attractiveness, it is surprisingly hard to find scientific consensus on a common definition or even a method of measurement. A plethora of methods has been employed to assess attractiveness. For the scope of this thesis, facial attractiveness is understood as the entirety of characteristics in a given face that renders it appealing for a given perceiver. Such an open definition is in line with the instruction given to our participants (see Appendix for full instructions for all rated dimensions).

In order to identify a large number of faces regarded as attractive, medium- attractive or unattractive by most perceivers, an extensive rating study was conducted to assess attractiveness and other dimensions of relevance to this line of work. This was done to a) ensure optimal stimulus selection based on the experimental setting for all experiments presented in this thesis, and b) allow for statistical control of potential confounds. Following the recommendations by Bronstad and Russell (2007), the permeation coefficient r^2 was calculated as an index for inter-rater agreement for all rated dimensions. It reflects the proportion of explained (i.e. shared) variance (r^2) between individual raters and the average ratings of the sample. Relevant aspects and results of these ratings will be discussed throughout this thesis.

For the scope of this work, rated dimensions included attractiveness, distinctiveness, emotional valence and arousal, and gender typicality for reasons already discussed in the introduction. Furthermore, ratings of trustworthiness were included as this dimension is closely related to attractiveness (Todorov, Baron, & Oosterhof, 2008). Dominance was included as it had been identified as a second axis central to social judgments beside trustworthiness in data driven approaches (Oosterhof & Todorov, 2008; Todorov, Said, Engell, & Oosterhof, 2008). Further, perceived age was assessed as it both correlated negatively with attractiveness and is also known to influence face memory (Wiese et al., 2008; Wolff, Wiese, & Schweinberger, 2012).

2.2 Study 1

Memory for faces of high, medium and low attractiveness

This study was designed to inspect whether there is a linear relationship between attractiveness and recognition memory or a more complex pattern when distinctiveness is controlled. A potential limitation of the study described in Wiese, Altmann, et al. (2014) is the lack of a neutral point of comparison for memory performance to attractive and unattractive faces. Thus, this study did not allow to disentangle influences of affective processing from other processes (see below). To overcome this limitation, faces of intermediate attractiveness were included as a novel condition to the previous paradigm.

Medium-attractive faces are simultaneously a) affectively relatively neutral compared to affectively valenced attractive and unattractive faces, and b) by far the most commonly encountered class of faces in everyday life. These attributes thus allow to competitively test predictions from a representational density account compared to affective processing accounts. If memory performance is negatively related to MDFS density, a memory disadvantage would be predicted for medium-attractive faces. If alternatively face recognition is hampered by affective processing, as discussed in Wiese, Altmann, et al. (2014), best memory performance for affectively neutral, i.e. medium-attractive faces, is predicted.

In terms of ERPs, this experiment tested whether the relationship between attractiveness and recognition memory could be reflected in a single neural correlate or if several neurophysiological markers contribute to the behavioural outcome. To disentangle effects of perceptual face processing and affective processing, this study focuses on the inspection of P2 and the N250/EPN time range. If the P2 amplitude indeed mirrors MDFS density due to frequency of exposure with a stimulus class (and not typicality/distinctiveness), faces of medium-attractiveness should elicit more positive P2 amplitudes than other faces. If emotional memory accounts hold true, memory effects should be mirrored in the N250/EPN time range. Specifically, if affective processing indeed hampered memory processing, largest amplitudes in this time window should parallel lower memory accuracy. See section 3 of this thesis for a detailed report.

2.3 Study 2

Influences of face and participant gender

To investigate potential modulations by face and participants' gender on the attractiveness effect in face memory, Study 2 inspected memory in male and female participants for both male and female faces varying in attractiveness in a full factorial design. Most former studies only examined participants and/or stimuli of one gender (e.g. Brigham, 1990; Fleishman et al., 1976; Light et al., 1981; Shepherd & Ellis, 1973).

Similar to the procedure described for Study 1, memory for faces varying with respect to both gender (male, female) and attractiveness (low, medium, high) was tested in male and female participants. This design systematically tested assumptions of social cognition accounts, evolutionary accounts, as well as accounts of representational density. Social cognition would predict best memory for social in-groups, i.e. own-gender faces. This benefit may be even stronger in attractive faces, as these are a) high in sexual dimorphism, and thus easily identified as own-gender faces, and b) more readily accepted as in-group members. Evolutionary predictions would predict better memory for attractive opposite-gender faces, i.e. potential mates, and possibly also for attractive own-gender faces, i.e. potential rivals. In contrast to social cognition accounts, however, adaptive memory accounts would not predict a general benefit for own-gender faces. According to representational accounts, best memory is expected for unattractive faces. No differential effects for face and/or participants' gender are expected as exposure to male and female faces of all attractiveness levels should be relatively similar across men and women in a young adult, Western cohort.

If motivation is the driving factor, either in terms of social cognition or based on evolutionary goals, memory differences should be mirrored in markers of motivational processing, i.e. at the N250/EPN time frame or in the LPC. If representational density is a relevant factor, a differential response to attractiveness should be seen in earlier components, i.e. P2—with no further contributions from face or participants gender. See section 4 of this thesis for a detailed report.

2.4 Study 3

Encoding impairments for faces across the attractiveness spectrum

Former studies did not find convincing links between retrieval related activity in ERPs and attractiveness effects in recogntion memory. Indeed, the pattern observed in Wiese, Altmann, et al. (2014), and to some extent also in Thiruchselvam et al. (2016), suggests relative independence of attractiveness and processing of face memory, and in a wider sense also face repetitions (but see Marzi & Viggiano, 2010). Tsukiura and Cabeza (2011) investigated the neural mechanisms behind attractiveness effects in memory in an fMRI paradigm. They found that functional connectivity between orbitofrontal regions (involved in attractiveness processing) and hippocampal regions (involved in memory processing) was stronger during the encoding of attractive compared to neutral or unattractive faces. Wiese, Altmann, et al. (2014) also found increased affective processing, i.e. more negative EPN amplitudes, for attractive over unattractive faces during learning. This effect in the EPN during learning, however, correlated with the magnitude of the memory advantage for unattractive faces at test.

Taken together, the decrease in memory performance may not be due to deficiencies during retrieval, but may rather result from interferences during encoding. To test this more systematically, ERPs in the study phase were inspected with respect to *D*ifferences due to subsequent *m*emory (Dm) at test (described above). Different to Studies 1 and 2, participants were presented with more faces during each study phase. Crucially, the higher number of faces per learning phase resulted in increased miss rates, which allows for the analysis of ERPs for both subsequent hits and misses. As more extensively reviewed in section 5 of this thesis, Dm effects can serve as an index of processing effort: the relative size of Dm effects diminished for ‘easier’ tasks, and increases for harder and more elaborate tasks. Thus, inspecting them across the time course of several ERPs can highlight the nuanced contributions of perceptual, affective and mnemonic processing to attractiveness effects in recognition memory.

In addition to the analysis of ‘classic’ Dm effects in the LPC time range, the presented study also inspects subsequent memory effects in the P2 and in the N250/EPN time range. Representational density should increase processing effort for medium-attractive, and to a smaller extent also for attractive faces at perceptual stages reflected in the P2. In contrast, Dm effects for sparsely clustered, unattractive faces should only emerge at later processing stages. Other accounts, would predict a manifestation of Dm differences in later components that index either affective processing or motivational relevance, i.e. EPN and LPC. Specifically, social cognition accounts would predict differential processing for attractive own-gender faces in the EPN, whereas adaptive memory accounts would predict preferred processing in this time range for attractive other-gender faces. See section 5 of this thesis for a detailed report.

STUDY REPORTS

3 STUDY 1

Lost in the Middle: Recognition Memory and Neuronal Correlates for Faces Differing in Attractiveness

3.1 Abstract

Recent research showed that attractive faces are remembered less well than unattractive faces when distinctiveness, a powerful determinant of face memory, is controlled. It is unclear if this effect reflects a disadvantage for attractive faces, an advantage for unattractive faces, or both. To clarify, a recognition memory experiment was conducted using attractive, medium-attractive and unattractive faces, all matched for distinctiveness. Memory was best for unattractive faces, followed by attractive faces, with poorest performance for medium-attractive faces. Item analyses confirmed that the benefit for unattractive faces remained after accounting for emotional valence and arousal. Attractiveness effects in event-related brain potentials were found in the occipito-temporal P2, with larger amplitudes for medium-attractive compared to attractive and unattractive faces, mirroring the memory disadvantage for medium-attractive faces in behaviour. Furthermore, participants exhibited a more liberal response criterion (more hits and more false alarms) to attractive compared to medium- and unattractive faces; a corresponding neural correlate could be identified in the early posterior negativity (EPN). This study suggests an explanation based on a modified face-space model in which medium-attractive faces are more densely clustered, and hence less distinguishable, than attractive and unattractive faces.

Keywords: Event-related potentials, faces, attractiveness, distinctiveness, recognition, memory

Highlights:

- Attractiveness influences recognition memory over and above facial distinctiveness and emotional content.
- Memory for medium-attractive faces is worse than for attractive and unattractive faces.
- Participants responded less conservatively to attractive than to medium-attractive and unattractive faces.
- P2 ERP amplitudes are larger for frequently encountered, medium-attractive faces.
- EPN amplitudes correspond to shifts in response bias during recognition.

3.2 Introduction

Memory for faces, though important in most social situations, is also prone to systematic biases. Of relevance, attractiveness of someone's face biases judgments and decisions about that person, commonly disfavouring individuals perceived as less attractive while benefiting attractive people. For instance, people see attractive individuals in a more positive light regarding their likeability (Eagly, Makhijani, Ashmore, & Longo, 1991) and intelligence (Dion et al., 1972), which may lead to unmerited advantages in hiring decisions (Hosoda et al., 2003), jurisdiction (DeSantis & Kayson, 1997), and democratic votes (Efran & Patterson, 1974).

While some previous studies also reported a benefit in memory for attractive relative to unattractive faces (John F. Cross et al., 1971; Marzi & Viggiano, 2010; Zhang et al., 2011), others reported the opposite finding (Light et al., 1981; Sarno & Alley, 1997), or no difference (Brigham, 1990; Wickham & Morris, 2003). These discrepant findings may be largely due to differences in facial distinctiveness, as it is well-known that distinctive faces are remembered particularly well (e.g. Valentine, 1991). Previous research suggests that while attractive faces possess many average traits (Langlois & Roggman, 1990), they also exhibit systematic deviations perceived as distinctive—i.e. pronounced sexual dimorphisms like full lips in females or broad chins in males (DeBruine et al., 2007; Perrett et al., 1998; Said & Todorov, 2011).

A recent study found a robust benefit of memory for unattractive over attractive faces when distinctiveness was matched (Wiese, Altmann, et al., 2014), arguing against the idea that attractiveness effects on memory are exclusively driven by distinctiveness. As this study did not include a medium-attractive condition, performance for extreme poles of attractiveness could not be compared to performance for medium-attractive faces. It is unclear whether memory is particularly good for unattractive faces, particularly inaccurate for attractive faces, both, or even generally different relative to medium-attractive faces. This question is of considerable theoretical importance as it allows differentiating between competing alternative accounts detailed below.

First, it is possible that the reported memory difference between attractive and unattractive faces arises from differences in emotional relevance, i.e. perceived emotional valence and/or arousal. It may be that the memory difference constitutes an effect of emotional *valence*, and thus either a disruptive effect of positive affective processing on memory, or an advantage of negative content in terms of a negativity bias (e.g. Ohira et al., 1998). If so, performance for medium-attractive faces should be similar to either unattractive or attractive faces, respectively. It may further be that emotional *arousal* influences memory based on the assumption that both attractive and unattractive faces elicit more arousal than medium-attractive faces. Such an account would predict an approximately curvilinear relationship of attractiveness and memory. Specifically, if processing of affectively relevant—and thus arousing—content generally hampered performance (as discussed by Wiese, Altmann, et al., 2014), medium-attractive faces should be remembered better than the other groups.

Alternatively, perceptual expertise accounts of face recognition assume that memory accuracy relies on previous visual experiences. An influential framework is provided by the Multidimensional Face Space account (MDFS; Valentine, 1991), which assumes an n-dimensional coding of faces, reflecting for example variations in shape or texture (e.g. Calder, Burton, Miller, Young, & Akamatsu, 2001). While the original model remained vague on the nature of these dimensions, several attempts aimed at specifying relevant aspects for facial variations by means of principal component analyses (Calder et al., 2001), or more recently in combining single-cell recording data and neural network approaches (Chang & Tsao, 2017). Valentine (1991) originally assumed that most faces were represented near the origin of the MDFS, thought to reflect an average or prototypical face, with distinctive faces in the sparsely clustered periphery. Burton and Vokey (1998), however, argued that most faces are neither very distinct nor very typical, and would therefore be represented in an area of medium distance to the centre (see Figure 1 for a simplified two-dimensional visualization). Crucially, MDFS models assume that memory performance is inversely related to the density of face representations in a given area of the space (Valentine, 1991; Valentine et al., 2015). In other words, if the test face falls into a low-density region of MDFS, it will be easily determined whether a stored representation matches the incoming face. If, however, the test face falls into a high-density region of the space, an unequivocal match will be difficult due to neighbouring competitors. Accordingly, confusion errors and high false alarm rates should result.

As most faces are rated as neither very attractive nor unattractive, a large majority of commonly encountered, medium-attractive faces will occupy a densely clustered region of space between centre and periphery. Simultaneously, systematic perceptual similarities between faces could account for enhanced local density in face representations. Research into unifying characteristics of attractive faces suggests that they are more similar to one another and thus more tightly clustered compared to less attractive faces (Potter et al., 2007), possibly due to evolutionary selection for specific characteristics (e.g., averageness, sexual dimorphisms; Langlois et al., 1994; Perrett et al., 1998). In addition, when distinctiveness is equated for different levels of facial attractiveness, influences of sexual dimorphisms should be largely eliminated from the stimulus set. In this situation, the main difference between attractive and less attractive faces is presumably related to averageness, reflecting characteristics such as symmetry and smooth skin texture (Said & Todorov, 2011). Accordingly, attractive faces will be represented close to the centre of MDFS whereas less attractive faces will be projected into the periphery.

Overall, density is supposedly high for attractive faces (because they are visually similar to one another) and also for medium-attractive faces (because they are very frequently seen on an everyday basis). Unattractive faces are not necessarily clustered as densely, because a) they are relatively rare compared to medium-attractive faces and b) unfortunately, there are many ways of being unattractive whereas attractive faces fit a relatively narrow and selective scheme. Although the reasons for dense clustering may thus differ for medium- and attractive faces, the prediction is that memory should not only be more accurate for unattractive relative to attractive faces (as the former category is more spread out in face space), it also suggests that memory for medium-attractive faces should be even less accurate as there are more previously encoded facial representations in close proximity to reject.

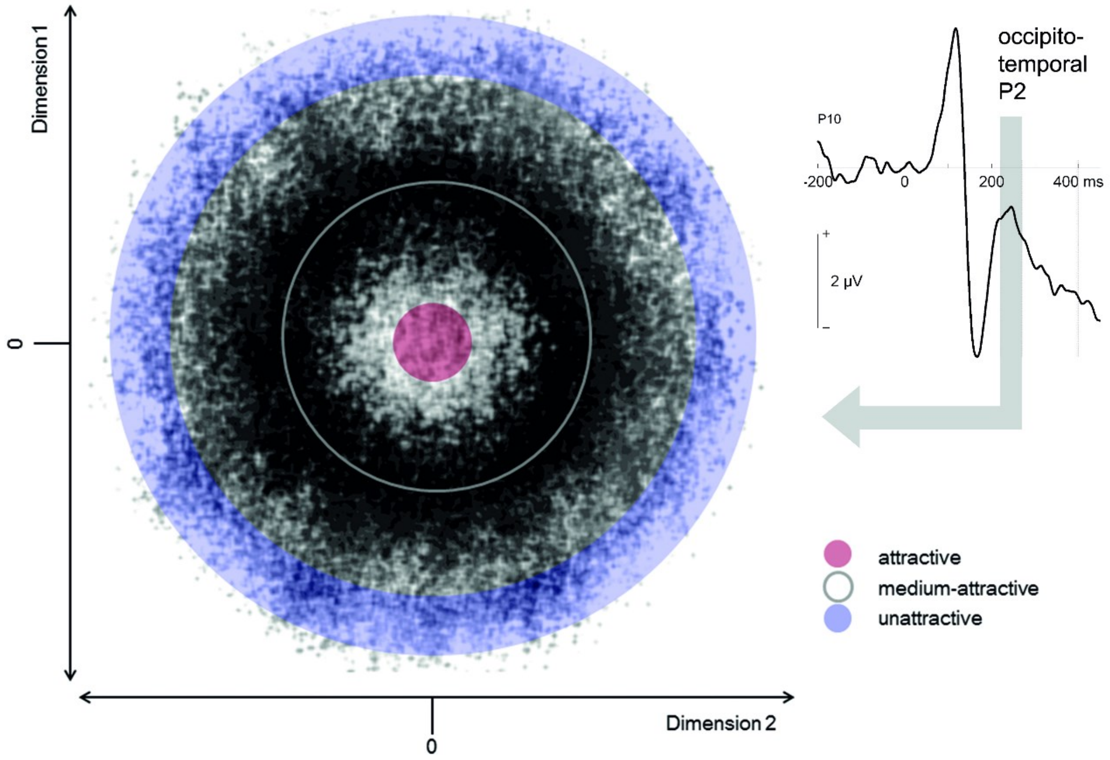


Figure 1. Simplified visualization of an MDFS. The grey dots indicate the distribution of faces along two arbitrary theoretical dimensions. Darker shades indicate tighter clustering. Please note that the majority of faces are clustered as a ring around the centre in the 2D illustration (marked by the grey circle at the points of highest density in the distribution). Red and blue areas and the grey circle indicate possible locations of varying degrees of attractiveness.

While behavioral measures reflect the outcome of cascading mental processes, event-related potentials (ERPs) provide detailed information about neural correlates of specific perceptual and affective processing stages. Importantly, the P2, a positive occipito-temporal component observed at ~200-250 ms, is assumed to reflect processing of metric distances between facial features (Latinus & Taylor, 2006) or perceived typicality of a face (e.g., Wiese, Kaufmann, et al., 2014), with larger P2 responses for typical relative to distinctive faces (Schulz, Kaufmann, Kurt, et al., 2012; Schulz, Kaufmann, Walther, et al., 2012). However, unattractive faces yielded larger P2 amplitudes compared to attractive faces matched for distinctiveness (Wiese, Altmann, et al., 2014). To the extent that more faces are usually rated as being unattractive than attractive, larger P2 responses to unattractive faces may correspond to more commonly encountered (rather than prototypical) faces. The P2 could be a neural marker for the relative frequency with which a certain category of faces is seen in daily life. If so, faces of intermediate attractiveness should elicit the largest P2 amplitudes.

A ventral temporal ERP subsequent to the P2, the N250 component, is larger for learned relative to novel facial identities (Kaufmann et al., 2009; Tanaka et al., 2006). Previous recognition memory studies observed stronger memory effects in the N250 time range for specific categories of faces, for instance for young relative to old faces in young participants (Wiese et al., 2008). Moreover, distinctive faces have been reported to elicit larger N250 amplitudes than typical faces (Schulz, Kaufmann, Kurt, et al., 2012; Schulz, Kaufmann, Walther, et al., 2012). Previous studies reported more negative amplitudes for attractive relative to unattractive faces in a similar time window and at similar electrodes, commonly interpreted as a so-called Early Posterior Negativity (EPN; Werheid et al., 2007; Wiese, Altmann, et al., 2014). The EPN reflects enhanced reflexive attention to and perceptual processing of affective stimuli, and is enlarged for emotional relative to neutral faces (Junghöfer et al., 2001; Rellecke et al., 2012; Schupp et al., 2004) and pictures (Schupp et al., 2007). Of note, timing as well as topography of N250 and EPN effects show substantial overlap. Their common time frame (henceforth referred to as N250/EPN) may therefore represent a processing stage at which emotional processing and face recognition interact. In fact, a recent study provided some evidence for a possible link between the EPN attractiveness effect and the memory costs for attractive relative to unattractive faces (Wiese, Altmann, et al., 2014). The present work considers that a more specific interpretation of those findings requires to assess interactive N250 and EPN responses for medium-attractive compared to high and low attractive faces. Previous findings predict more negative amplitudes for hits compared to correct rejections, as well as for emotionally more relevant, attractive faces. If mnemonic and affective processing indeed interact, some modulation of the N250 memory effect by attractiveness effects reflected in the EPN should emerge in accordance with behavioural performance shifts.

The present study consists of a rating experiment in which Face-In-The-Crowd (FITC) distinctiveness (Valentine & Bruce, 1986), deviation-based distinctiveness (Wickham & Morris, 2003), and attractiveness were assessed in a large set of face stimuli beside other characteristics. In a second step, recognition memory for subsets of attractive, medium-attractive, and unattractive faces matched for distinctiveness was assessed while simultaneously recording participants' EEG. Deviation-based distinctiveness was controlled because a) this is conceptually related more directly to the MDFS model (Faerber, Kaufmann, Leder, Martin, & Schweinberger, 2016), and because b) FITC-ratings may be biased by heuristics arising for attractive faces specifically (please see Wiese, Altmann, et al., 2014, for details). In that sense, deviation-based distinctiveness ratings may be a less biased measure of perceptual aspects of facial distinctiveness.

3.3 Rating study

3.3.1 Methods

Participants

Twenty participants (10 female, 19-30 years, mean age = 23.43 years ± 3.19 *SD*), all right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971), were recruited. All participants reported normal or corrected to normal vision, and none reported neurological or psychiatric disorders. All participants gave written informed consent prior to testing. Participants received either course credit or monetary reimbursement after testing.

Stimuli

1140 full-colour facial photographs (50 % female faces) were collected from various internet sources. Using Adobe Photoshop CS5$^{\text{TM}}$ all pictures were cropped to show only the face without clothing or hair, and placed before a standardized black background. Luminance and contrast of each individual face (without background) were equated to match the overall mean luminance of all faces by employing gradation curve adjustments (mean luminance: 145 RGB units, mean contrast: 50 RGB units). All stimuli were presented on a 17’ CRT computer monitor using *E*-Prime™ with a constant image size of 440 x 400 pixels, corresponding to a viewing angle of approximately 7.4° x 6.9° at a viewing distance of 90 cm.

Procedure and experimental design

Due to the high number of stimuli, the rating procedure was split into two sessions (max. 14 days apart), each consisting of a subset of 570 images from the entire stimulus set. In both sessions, participants were seated in a dimly lit room with their head in a chin rest.

Participants were asked to perform a series of rating tasks. Rated dimensions included attractiveness, deviation-based distinctiveness, FITC distinctiveness, emotional valence and arousal (using Self-Assessment Mannequins [SAM] scales, Bradley & Lang, 1994), perceived age, trustworthiness, dominance, and gender typicality, all rated on the scales described in Table

1. Attractiveness was assessed for every face on a six-point scale (1 = ‘very unattractive’ to 6 = ‘very attractive’). *Face-In-The-Crowd* (FITC) distinctiveness for each of the faces was obtained following Valentine and Bruce (1986): 1 = ‘very lowly distinctive’ to 6 = ‘very distinctive’ (see e.g. Wiese, Altmann, et al., 2014, for a methodological discussion). A second measure of distinctiveness was adapted from the deviation ratings used by Wickham and Morris (2003). Here, participants were asked to rate how average or atypical a face is. To rate averageness/typicality, participants were instructed to ask themselves to which extent facial characteristics deviate from other faces they know, on a scale between 1 and 6 (1 = ‘very typical’ to 6 = ‘very atypical’). Tasks were changed after each block, following self-paced breaks. Block order was randomized across participants. Images remained on the screen until a response was recorded, and participants were instructed to respond as spontaneously as possible.

3.3.2 Results

Data of one additional participant were excluded as the response times for the majority of trials on 4 scales lay below the 400ms threshold, suggesting lack of task adherence. On average, faces were rated as being slightly less attractive than the medium-point of the scale ($M = 3.33 \pm 0.81$ *SD*). Similarly, on average, face stimuli were rated as rather non-distinctive, both on the FITC ($M = 3.18 \pm 0.62$ *SD*) and the deviation scale ($M = 3.12 \pm 0.49$ *SD*). To analyse interrelations between these measures, Spearman’s Rho (ρ) was calculated for each combination of these variables, as well as the permeation coefficient r^2 (Bronstad & Russell, 2007) indicating good interrater agreement for attractiveness (see Table 2). At some variance with previous results (Wiese, Altmann, et al., 2014), this procedure revealed a significant positive correlation between rated attractiveness and the FITC measure ($\rho[1098] = .55$, $p < .001$), but no correlation between attractiveness and the deviation measure ($\rho[1098] = .01, p = .685$).

To further investigate the relationship between the three dimensions, partial rank correlations were calculated, adjusted for FITC, deviation, and attractiveness, respectively. Of note, attractiveness ratings *increased* with higher ratings of distinctiveness as assessed by the FITC measure ($\rho_P[1097] = .69; p < .001$), but *decreased* when faces were perceived as more distinct as assessed by the deviation measure (ρ_P 1097] = −.51; $p < .001$), following the pattern described by Wiese, Altmann, et al. (2014). Finally, a moderate positive correlation between the FITC and deviation measures was observed (ρ_p [1097] = .53; $p < .001$). Overall, this pattern of results again suggests that a non-shared portions of variance between the FITC and deviation measures relate to their reversed correlational pattern with attractiveness.

Table 1: Correlations between dimensions in the rating experiment.

Stimulus Group	**Attractiveness**	**Deviation**	**FITC**	**Valence**	**Arousal**	**Gender Typicality**	**Trust-worthiness**	**Dominance**	**Perceived Age**
	ρ; *p*	ρ; *p*	ρ; *p*	ρ; *p*	ρ; *p*	ρ; *p*	ρ; *p*	ρ; *p*	ρ; *p*
Attractiveness	-	0.1; .685	.58; <.001	.84; <.001	.68; <.001	.57; <.001	.65; <.001	.58; <.001	−.44; <.001
Deviation	-	-	.53; <.001	−.02; .441	.35; <.001	−.06; .059	−.23; <.001	.18; <.001	−.03; .327
FITC	-	-	-	.44; <.001	.73; <.001	.38; <.001	.18; <.001	.53; <.001	−.25; <.001
Valence	-	-	-	-	.60; <.001	.48; <.001	.78; <.001	.43; <.001	−.39; <.001
Arousal	-	-	-	-	-	.45; <.001	.37; <.001	.56; <.001	−.30; <.001
Gender Typicality	-	-	-	-	-	-	.33; <.001	.55; <.001	−.01; .940
Trustworthiness	-	-	-	-	-	-	-	.17; <.001	−.29; <.001
Dominance	-	-	-	-	-	-	-	-	−.04; .221
Perceived Age	-	-	-	-	-	-	-	-	-

*all *df* = 1099

3.4 Memory experiment

3.4.1 Methods

Participants

Twenty participants (18 – 35 years; *M* = 23.8 years ± 3.08 *SD*; 10 female; 18 heterosexual, 1 bisexual, 1 undisclosed sexual orientation) took part in the experiment after giving written informed consent, and contributed data that were fully analysed. Due to insufficient trial numbers (*N* < 15, 1 case), incorrect keys usage (1 case) and technical difficulties during data recording (2 cases), data of 4 additional participants were excluded. All participants reported normal/corrected-to-normal vision and were right-handed as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). None reported neurological or psychiatric disorders. Participants received course credit or monetary reimbursement after testing.

Stimuli

A set of 300 faces, of which 100 each were rated as unattractive (*M* = 2.49 ± 0.37 *SD*; range 1.30 – 2.99), medium-attractive (*M* = 3.48 ± 0.26 *SD;* range 3.05 – 3.95) or attractive (*M* = 4.45 ± 0.33 *SD*; range 4.00 – 5.25) was chosen (50% female, respectively) from the rated stimulus pool. Pictures were scaled to correspond to a viewing angle of ~ 4.6° x 4.4° at a viewing distance of 90 cm.

Table 2: Rating data for the stimulus set employed in the recognition experiment.

Stimulus Group	Attractiveness	Deviation	FITC	Valence	Arousal	Gender Typicality	Trust-worthiness	Dominance	Perceived Age
	M ± *SD*	*M* ± *SD*	*M* ± *SD*	*M* ± *SD*	*M* ± *SD*	*M* ± *SD*	*M* ± *SD*	*M* ± *SD*	*M* ± *SD*
attractive female	4.45 ± 0.36	3.19 ± 0.51	3.65 ± 0.63	5.88 ± 0.59	4.73 ± 0.72	2.06 ± 0.28	3.88 ± 0.30	3.54 ± 0.40	27.20 ± 2.06
attractive male	4.45 ± 0.30	3.19 ± 0.46	3.85 ± 0.44	5.64 ± 0.43	4.66 ± 0.56	2.10 ± 0.30	3.69 ± 0.45	4.22 ± 0.49	30.71 ± 2.88
attractive mean	4.45 ± 0.33	3.19 ± 0.49	3.75 ± 0.55	5.76 ± 0.53	4.69 ± 0.64	2.08 ± 0.29	3.79 ± 0.39	3.88 ± 0.56	28.96 ± 3.05
medium-attractive female	3.51 ± 0.26	3.15 ± 0.50	3.14 ± 0.53	5.19 ± 0.52	3.96 ± 0.56	1.56 ± 0.34	3.57 ± 0.34	3.27 ± 0.31	28.45 ± 2.33
medium-attractive male	3.46 ± 0.26	3.13 ± 0.43	3.12 ± 0.49	5.07 ± 0.52	3.92 ± 0.52	1.86 ± 0.27	3.36 ± 0.36	3.60 ± 0.41	28.63 ± 3.22
medium-attractive mean	3.48 ± 0.26	3.14 ± 0.47	3.13 ± 0.51	5.13 ± 0.53	3.94 ± 0.54	1.71 ± 0.34	3.47 ± 0.36	3.43 ± 0.40	28.54 ± 2.81
unattractive female	2.44 ± 0.39	3.25 ± 0.57	3.01 ± 0.54	4.05 ± 0.68	3.57 ± 0.63	1.15 ± 0.46	2.99 ± 0.46	2.87 ± 0.44	31.97 ± 4.61
unattractive male	2.54 ± 0.35	3.19 ± 0.64	3.05 ± 0.71	4.10 ± 0.56	3.57 ± 0.59	1.76 ± 0.36	2.97 ± 0.42	3.18 ± 0.56	30.76 ± 4.96
unattractive mean	2.49 ± 0.38	3.22 ± 0.61	3.03 ± 0.63	4.08 ± 0.63	3.57 ± 0.61	1.46 ± 0.51	2.98 ± 0.44	3.02 ± 0.53	31.36 ± 4.83
Overall mean	3.48 ± 0.84	3.19 ± 0.53	3.30 ± 0.65	4.99 ± 0.89	4.07 ± 0.76	1.75 ± 0.47	3.41 ± 0.52	3.44 ± 0.61	29.62 ± 3.88
Scale	*1 = very unattractive* *6 = very attractive*	*1 = very typical* *6 = very atypical*	*1 = very lowly distinctive* *6 = very distinctive*	*1 = very negative* *9 = very positive*	*1 = low arousal* *9 = high arousal*	*0 = very atypical* *3 = very typical*	*1 = very untrustworthy* *6 = very trustworthy*	*1 = very submissive* *6 = very dominant*	*years*
Permeation coefficient r^2 (Bronstad & Russell, 2007)	.44 ± .14 *SD*	.16 ± .08 *SD*	.23 ± .11 *SD*	29 ± .15 *SD*	.16 ± .10 *SD*	.79 ± .16 *SD*	.21 ± .11 *SD*	.25 ± .12 *SD*	.43 ± .11 *SD*

Table 3: Statistics for rating differences in the stimulus set in the recognition experiment as tested by Mann-Whitney-U tests*.

Stimulus Group	**Attractiveness**	**Deviation**	**FITC**	**Valence**	**Arousal**	**Gender Typicality**	**Trust-worthiness**	**Dominance**	**Perceived Age**
	U; *p*	*U*; *p*	*U*; *p*	*U*; *p*	*U*; *p*	*U*; *p*	*U*; *p*	*U*; *p*	*U*; *p*
attractive vs. medium	0.00; <.001	4734.00; .516	2025.50; <.001	2007.50; <.001	1763.00; <.001	2021.00; <.001	2742.00; <.001	2731.00; <.001	4674.50; .426
attractive vs. unattractive	0.00; <.001	4833.50; .684	1859.00; <.001	181.00; <.001	1058,00; <.001	1303,50; <.001	928.00; <.001	1306.50; <.001	3547.00; <.001
medium vs. unattractive	0.00; <.001	4889.50; .787	4080.50; .025	1002.00; <.001	2880.50; <.001	3409.00; <.001	2009.00; <.001	2518.50; <.001	3170.50; <.001

*all *df* = 198

Faces in the three attractiveness categories were matched for deviation-based distinctiveness (*M*unattractive = 3.22 ± 0.61 *SD*; *M*medium-attractive = 3.14 ± 0.47 *SD*; *M*attractive = 3.19 ± 0.49 *SD*), and did not statistically differ in that respect as indicated by a Kruskal-Wallis test (χ^2= 0.45; *df* = 2; *p* = .798; $\eta^2 < .01$). For the FITC ratings (*M*unattractive = 3.03 ± 0.63 *SD*; *M*medium-attractive = 3.13 ± 0.51 *SD*; *M*attractive = 3.75 ± 0.55 *SD*) a main effect of stimulus category was found (χ^2= 77.22; *df* = 2; *p* < .001; $\eta^2 = .26$), with higher scores for attractive relative to medium-attractive (*U* = 2025.50; *z* = -7.28; *df* = 198; *p* < .001; $r_b = .60$) and unattractive faces (*U* = 1859.00; *z* = -7.68; *df* = 198; *p* < .001; $r_b = .81$; see Figure 2). See Table 3 for additional statistics testing for differences between stimulus groups selected for the recognition experiment.

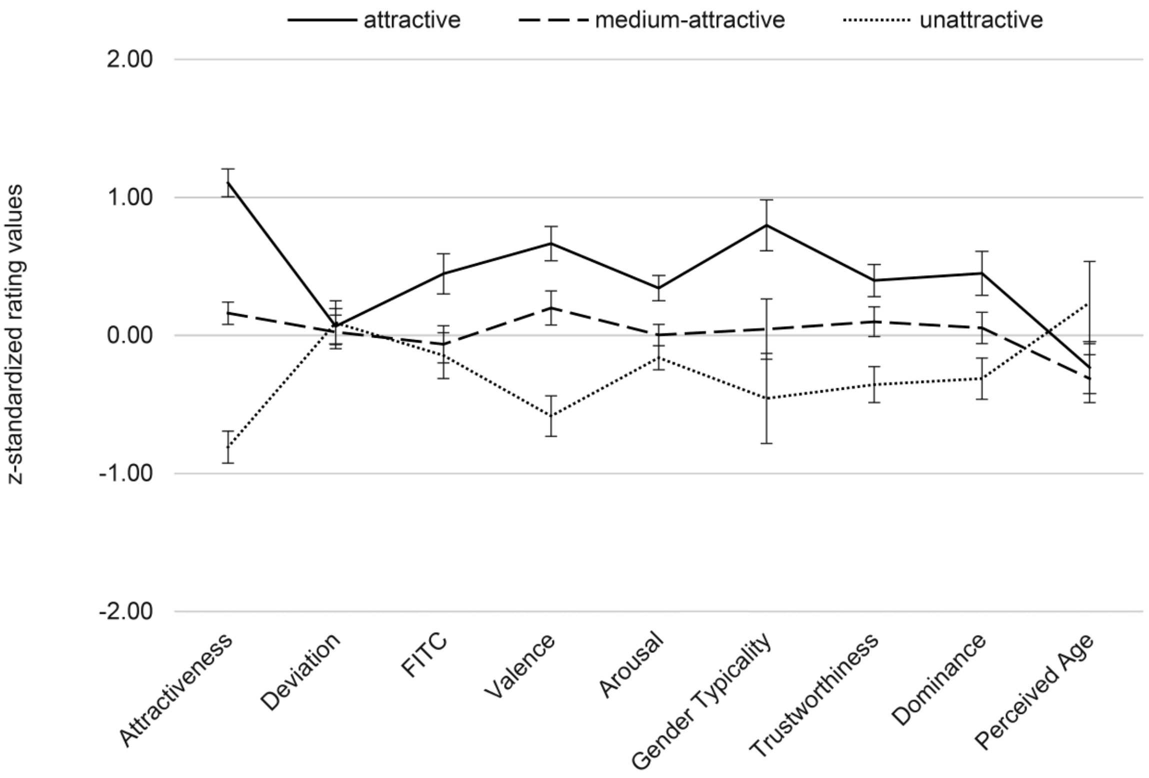


Figure 2. Mean z-standardized ratings for those face stimuli selected for the three attractiveness categories in the recognition experiment. Rated dimensions included attractiveness, deviation-based distinctiveness, FITC distinctiveness, emotional valence and arousal (using Self-Assessment Mannequins [SAM] scales, Bradley & Lang, 1994), gender typicality, trustworthiness, dominance, and perceived age. Error bars depict *SEM*.

Experimental design and procedure

Participants were seated in an electrically shielded and sound-attenuated cabin (400-A-CT-Special, Industrial Acoustics, Niederkrüchten, Germany), with their head in a chin rest approximately 90 cm away from the monitor. Stimuli were presented with an average luminance of 26.84 cd/m². Following a short practise block, the experiment consisted of 6 blocks, each divided into alternating study and test phases. During each study phase 25 faces (50% female, equal trial numbers of all attractiveness conditions across blocks) were presented in randomized order. Participants were instructed to memorize faces and categorize them according to gender via key presses. Each study trial consisted of a fixation cross (500 ms), a face (5000 ms) and a final blank screen (500 ms). Study and test phases were separated by fixed breaks of 30 s duration. In each test phase, the 25 faces from the immediately preceding study phase and 25 new faces (again 50% female, equal numbers of attractiveness conditions across blocks) were presented for 2000 ms in randomized order, again with a preceding fixation cross (500 ms) and subsequent blank screen (500 ms). Participants indicated via key presses whether the faces had been presented in the preceding study phase (‘old’) or not (‘new’). Key allocation and assignment of stimuli to studied or non-studied conditions was counterbalanced across participants.

For the study phases, mean correct reaction times (RT) and accuracies served as dependent variables. Behavioural test phase data was analysed according to signal detection theory (Green & Swets, 1966). Trials were sorted into hits, misses, correct rejections (CR), and false alarms (FA), separately for attractive, medium-attractive, and unattractive faces, to calculate sensitivity (d’) and response bias (C). Statistical analyses included paired samples t-tests, repeated-measures analyses of variance (ANOVAs), and simple contrasts with degrees of freedom corrected via the Greenhouse-Geisser procedure where assumptions of sphericity were violated as indexed by Mauchly’s test. Corrections for multiple tests were performed following the Bonferroni-Holm approach. Cohen’s d_{av} was calculated using the averaged standard deviation of the compared measurements (Lakens, 2013). This measure is interpreted following (Cohen, 1988), with $d \geq 0.2$ reflecting small, $d \geq 0.5$ reflecting medium, and $d \geq 0.8$ reflecting large effects.

EEG recording and analyses

EEG was recorded from 32 active sintered Ag/Ag-Cl electrodes using a Biosemi Active II system (BioSemi, Amsterdam, Netherlands). Active electrodes amplify the signal close to the measurement site, which substantially reduces the influence of electrical noise picked during its transmission via cables to the main amplifier. BioSemi systems work with a "zero-Ref" set-up with ground and reference electrodes replaced by a CMS/DRL circuit (CMS = Common Mode Sense; DRL = Drive Right Leg; cf. http://www.biosemi.com/faq/cms&drl.htm; for a detailed technical description, see T. Campbell, Kerlin, Bishop, & Miller, 2012; Sysoeva, Lange, Sorokin, & Campbell, 2015). EEG was recorded continuously and digitized with a sampling rate of 512-Hz (DC, with low-pass filters set to 155 Hz) 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, and I2.

Blinks were corrected using the multiple source eye correction (MSEC) method algorithm implemented in BESA 5.1.8 (Berg & Scherg, 1994). The EEG was segmented from −200 until 1000 ms relative to stimulus onset, with the first 200 ms as baseline. Artefact rejection was performed using an amplitude threshold of ±100 µV and a gradient criterion of 50 µV. Only trials with correct responses were analysed. Offline, trials were recalculated to average reference, averaged according to experimental condition and digitally low-pass filtered at 40 Hz (12 db/oct, zero phase shift). Three different waveforms (study phase, hits, CR) were calculated separately for attractive, medium-attractive, and unattractive faces. The minimum number of trials for an individual subject in any of these conditions was 15 and mean trial numbers for the learning phase were 46.37 ± 4.79 *SD* (attractive), 46.42 ± 3.01 *SD* (medium-attractive), and 44.95 ± 3.87 *SD* (unattractive), for hits 33.63 ± 6.24 *SD* (attractive), 27.52 ± 5.90 *SD* (medium-attractive) and 31.68 ± 7.46 *SD* (unattractive), and for CRs 34.84 ± 6.14 *SD* (attractive), 38.05 ± 6.35 *SD* (medium-attractive) and 40.73 ± 5.94 *SD* (unattractive), and 38.24 ± 5.52 *SD* averaged across all conditions. Mean amplitudes of the P2 (200 - 260 ms) were analysed at electrodes P9/P10. The more anteriorly distributed N250/EPN (270 - 400 ms) was measured at P9/P10 and TP9/TP10 (see e.g. Schweinberger et al., 2002). Please refer to the Appendix for further analyses of the P1, N170 and Late Positive Component (LPC).

3.4.2 Results

Behavioural results

During study, univariate ANOVAs revealed a main effect of Attractiveness for reaction times ($F[2,38] = 16.08$; $p < .001$; $\eta_p^2 = 0.46$) and accuracy ($F[2,38] = 38.78$; $p < .001$; $\eta_p^2 = 0.67$) of the gender categorization. Decisions were performed faster for attractive than medium-attractive and unattractive faces, which in turn did not differ (see Tables 4 and 5 for statistics). Further, unattractive faces were categorized less accurately than attractive and medium-attractive faces, which in turn did not differ.

Table 4: Behavioural data from the recognition experiment.

Face Groups	**attractive**	**medium-attractive**	**unattractive**
Study phase			
RT (ms)	851.1 ± 164.7 *SD*	902.8 ± 187.9 *SD*	924.8 ± 179.4 *SD*
ACC	.98 ± 0.02 *SD*	.97 ± 0.03 *SD*	.92 ± 0.04 *SD*
Test phase			
p (hits)	.67 ± 0.08 *SD*	.55 ± 0.12 *SD*	.68 ± 0.15 *SD*
p (misses)	.33 ± 0.08 *SD*	.45 ± 0.12 *SD*	.32 ± 0.15 *SD*
p (correct rejections)	.75 ± 0.13 *SD*	.79 ± 0.13 *SD*	.83 ± 0.12 *SD*
p (false alarms)	.25 ± 0.13 *SD*	.21 ± 0.13 *SD*	.17 ± 0.12 *SD*
d’	1.23 ± 0.66 *SD*	1.02 ± 0.59 *SD*	1.59 ± 0.79 *SD*
C	.17 ± 0.31 *SD*	.38 ± 0.28 *SD*	.30 ± 0.32 *SD*

Table 5: Statistics from the recognition experiment.

Behavioural data	**t-value (df)**	**p-value**	**Cohen's d_{av} [1]**	**Mean difference**	**95% Confidence Intervall**
Study phases					
Reaction time (ms)					
attractive vs. medium	$t(19) = 3.51$	$p = .002$	$d = 0.29$	$M_{diff} = 51.68$	CI[20.85, 82.51]
attractive vs. unattractive	$t(19) = 6.90$	$p < .001$	$d = 0.43$	$M_{diff} = 73.69$	CI[51.35, 96.03]
medium vs. unattractive	$t(19) = 1.54$	$p = .139$	$d = 0.12$	$M_{diff} = 22.01$	CI[-7.82, 51.85]
Accuracy (%)					
attractive vs. medium	$t(19) = 1.25$	$p = .225$	$d = 0.28$	$M_{diff} = .01$	CI[-0.01, 0.02]
attractive vs. unattractive	$t(19) = 8.72$	$p < .001$	$d = 1.09$	$M_{diff} = .05$	CI[0.05, 0.07]
medium vs. unattractive	$t(19) = 6.42$	$p < .001$	$d = 1.41$	$M_{diff} = .06$	CI[0.03, 0.07]
Test phases					
Miss rate (%)					
attractive vs. medium	$t(19) = 5.36$	$p < .001$	$d = 1.17$	$M_{diff} = 0.12$	CI[0.07, 0.16]
attractive vs. unattractive	$t(19) = 0.32$	$p = .755$	$d = 0.08$	$M_{diff} = 0.01$	CI[-0.05, 0.07]
medium vs. unattractive	$t(19) = 6.26$	$p < .001$	$d = 0.97$	$M_{diff} = 0.13$	CI[0.08, 0.17]
False alarm rate (%)					
attractive vs. medium	$t(19) = 2.59$	$p = .018$	$d = 0.31$	$M_{diff} = 0.04$	CI[0.01, 0.07]
attractive vs. unattractive	$t(19) = 4.65$	$p < .001$	$d = 0.65$	$M_{diff} = 0.08$	CI[0.05, 0.12]
medium vs. unattractive	$t(19) = 2.51$	$p = .021$	$d = 0.33$	$M_{diff} = 0.04$	CI[0.01, 0.08]
d-prime					
attractive vs. medium	$t(19) = 2.25$	$p = .037$	$d = 0.33$	$M_{diff} = 0.21$	CI[0.01, 0.40]
attractive vs. unattractive	$t(19) = 2.79$	$p = .012$	$d = 0.50$	$M_{diff} = 0.37$	CI[0.09, 0.64]
medium vs. unattractive	$t(19) = 5.67$	$p < .001$	$d = 0.82$	$M_{diff} = 0.57$	CI[0.36, 0.79]
Response bias					
attractive vs. medium	$t(19) = 4.02$	$p < .001$	$d = 0.72$	$M_{diff} = 0.21$	CI[0.10, 0.32]
attractive vs. unattractive	$t(19) = 2.22$	$p = .039$	$d = 0.41$	$M_{diff} = 0.13$	CI[0.01, 0.25]
medium vs. unattractive	$t(19) = 1.63$	$p = .119$	$d = 0.28$	$M_{diff} = 0.08$	CI[-0.02, 0.19]
ERP results					
Study phases					
N250/EPN amplitude					
attractive vs. medium	$t(19) = 1.68$	$p = .109$	$d = 0.15$	$M_{diff} = 0.25$	CI[-0.06, 0.55]
attractive vs. unattractive	$t(19) = 4.63$	$p < .001$	$d = 0.31$	$M_{diff} = 0.52$	CI[0.29, 0.76]
medium vs. unattractive	$t(19) = 2.03$	$p = .057$	$d = 0.17$	$M_{diff} = 0.28$	CI[-0.01, 0.56]

Test phases					
P2 amplitude					
attractive vs. medium	$t(19) = 2.82$	$p = .011$	$d = 0.18$	$M_{diff} = 0.40$	CI[0.10, 0.70]
attractive vs. unattractive	$t(19) = 1.69$	$p = .108$	$d = 0.11$	$M_{diff} = 0.23$	CI[-0.06, 0.52]
medium vs. unattractive	$t(19) = 1.66$	$p = .113$	$d = 0.08$	$M_{diff} = 0.17$	CI[-0.05, 0.39]
right hemisphere:					
attractive vs. medium	$t(19) = 3.13$	$p = .006$	$d = 0.21$	$M_{diff} = 0.57$	CI[0.19, 0.94]
attractive vs. unattractive	$t(19) = 1.47$	$p = .157$	$d = 0.10$	$M_{diff} = 0.27$	CI[-0.11, 0.65]
medium vs. unattractive	$t(19) = 2.45$	$p = .024$	$d = 0.11$	$M_{diff} = 0.30$	CI[0.04, 0.55]
N250/EPN amplitude					
attractive vs. medium	$t(19) = 2.93$	$p = .009$	$d = 0.24$	$M_{diff} = 0.40$	CI[0.11, 0.69]
attractive vs. unattractive	$t(19) = 4.56$	$p < .001$	$d = 0.36$	$M_{diff} = 0.58$	CI[0.31, 0.84]
medium vs. unattractive	$t(19) = 1.26$	$p = .225$	$d = 0.11$	$M_{diff} = 0.17$	CI[-0.12, 0.46]
Hits vs. CR - attractive	$t(19) = 0.90$	$p = .380$	$d = 0.10$	$M_{diff} = 0.15$	CI[-0.20, 0.51]
Hits vs. CR - medium	$t(19) = 1.97$	$p = .064$	$d = 0.23$	$M_{diff} = 0.26$	CI[-0.02, 0.54]
Hits vs. CR - unattractive	$t(19) = 2.60$	$p = .017$	$d = 0.30$	$M_{diff} = 0.43$	CI[0.08, 0.78]

[1] Interpretation: small effect: $d_{av} = 0.20$; medium effect: $d_{av} = 0.50$; large effect: $d_{av} = 0.80$ (Cohen, 1988)

At test, univariate ANOVAs revealed a main effect of Attractiveness for d' ($F[2,38] = 14.04$; $p < .001$; $\eta_p^2 = 0.43$) and C ($F[2,38] = 7.83$; $p = .001$; $\eta_p^2 = 0.29$). Paired samples t-test on d' revealed less accurate memory for attractive as compared to unattractive faces, and a further decline in memory performance from attractive to medium-attractive faces. Moreover, the response bias C was less conservative for attractive faces, relative to both medium-attractive, and unattractive faces, which did not differ.

Isolated inspection of misses also yielded a main effect of Attractiveness ($F[2,38] = 17.72$; $p < .001$; $\eta_p^2 = 0.48$) that indicated a higher proportion of misses for medium-attractive compared to attractive and unattractive faces, which did not differ. There was also a main effect of Attractiveness for the false alarm rates ($F[2,38] = 12.16$; $p < .001$; $\eta_p^2 = 0.39$): The proportion of false alarms was higher for attractive compared to medium and unattractive faces. Further, the false alarm rate was also slightly increased for medium- over unattractive faces.

To test for a potential influence of valence, arousal ratings and FITC distinctiveness on memory, an item analysis was conducted. A univariate ANCOVA with item d’ as cases, attractiveness as a single factor and valence, arousal, and FITC as covariates yielded a significant effect of valence ($F[1,294] = 5.54$; $p = .019$; $\eta_p^2 = 0.02$) and FITC ($F[1,294] = 21.86$; $p < .001$; $\eta_p^2 = 0.07$). Importantly, the main effect of Attractiveness was still significant in this analysis ($F[2,294] = 4.15$; $p = .017$; $\eta_p^2 = 0.03$), with more accurate memory for unattractive relative to medium-attractive (adj. mean d’-difference = .43; $p = .009$) and to attractive faces (adj. mean d’-difference = .59; $p = .007$); the d’ difference between attractive and medium-attractive faces, however, was not maintained (adj. mean d’-difference = .14; $p = .299$).

In view of the differences related to attractiveness in speed of gender categorization at study, differences in encoding due to the difficulty of the study task might relate to memory differences observed at test. To control for differences in response time during learning an additional item analysis of covariance (ANCOVA) with item d’ as cases, attractiveness as a factor and average response time during learning as a covariate was performed. In this analysis, the effect of Attractiveness was maintained ($F[1,296] = 8.00$; $p < .001$; $\eta_p^2 = 0.05$), with more accurate memory for unattractive relative to medium-attractive (adj. mean d’-difference = .55; $p < .001$) and to attractive faces (adj. mean d’-difference = .38; $p = .008$). Importantly, response time during learning did not significantly moderate the effect of attractiveness ($p = .157$).

Event-related potentials

ERP analyses for the study phases were conducted by calculating repeated-measures ANOVAs with the within-subject factors Attractiveness (attractive, medium-attractive, unattractive) and Hemisphere (left, right). For test phases, the additional factor Response Type (hits, CR) was included. The description of ERP results focuses on effects of facial attractiveness, memory, and their interactions. Thus, main effects and interactions with factors exclusively specifying electrode positions or non-significant results are omitted.

Learning phase ERPs.

P2. No significant main effects or interactions of interest were found in the P2 (all $F < 2.75$, all $p > .114$).

N250/EPN. In the N250/EPN time range, a main effect of Attractiveness was found ($F[2,38] = 7.77$; $p = .001$; $\eta_p^2 = 0.29$), with attractive faces eliciting more negative amplitudes than unattractive faces, but not compared to medium-attractive faces, which in turn did not differ (see Figure 3).

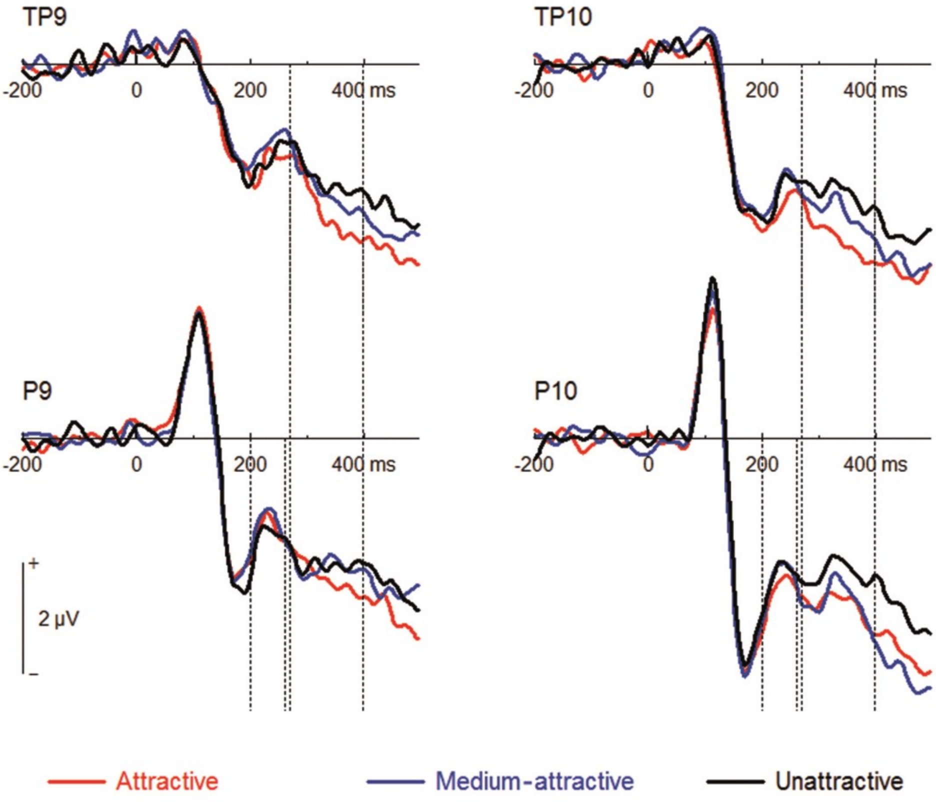


Figure 3. Grand mean ERPs from the learning phases of the recognition experiment at occipital and occipito-temporal electrodes. Dashed lines indicate P2 and N250/EPN time ranges.

Test phase ERPs.

P2. In the P2 time range, a main effect of Attractiveness was observed ($F[2,38] = 4.93$; $p = .013$; $\eta_p^2 = 0.21$), with medium-attractive faces eliciting larger P2 amplitudes compared to attractive faces. Medium-attractive faces also yielded significantly larger P2 amplitudes than unattractive faces over the face-dominant right hemisphere, yet this was only numerically seen independent of Hemisphere. There was no significant difference between attractive and unattractive faces (see Figure 4).

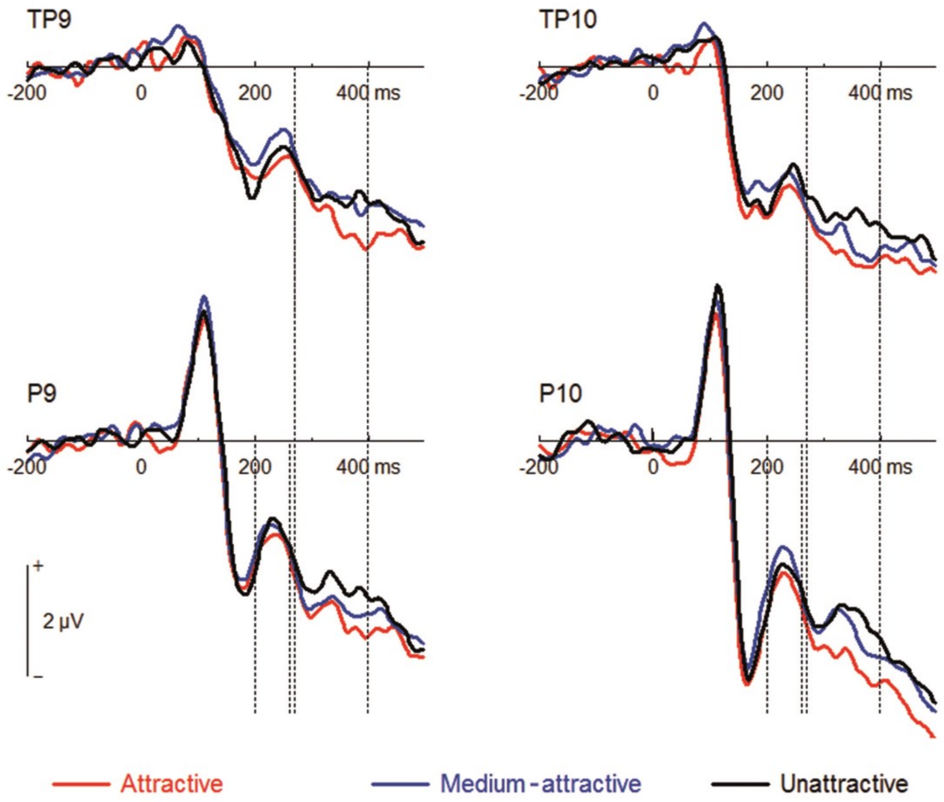


Figure 4. Grand mean ERPs from the test phases of the recognition experiment at occipital and occipito-temporal electrodes. Dashed lines indicate P2 and N250/EPN time ranges.

N250/EPN. Analyses yielded a main effect of Attractiveness ($F[2,38] = 9.67$; $p < .001$; $\eta_p^2 = 0.34$), with more negative amplitudes for attractive compared to medium-attractive faces as well as unattractive faces (Figure 5), which in turn did not differ. Additionally, an interaction of Response Type by Attractiveness was found ($F[2,38] = 3.48$; $p = .041$; $\eta_p^2 = 0.16$), reflecting a significant Response Type effect for unattractive faces only, with CRs eliciting more negative amplitudes than hits. No Response Type effects were found for attractive and medium-attractive faces (Figure 5).

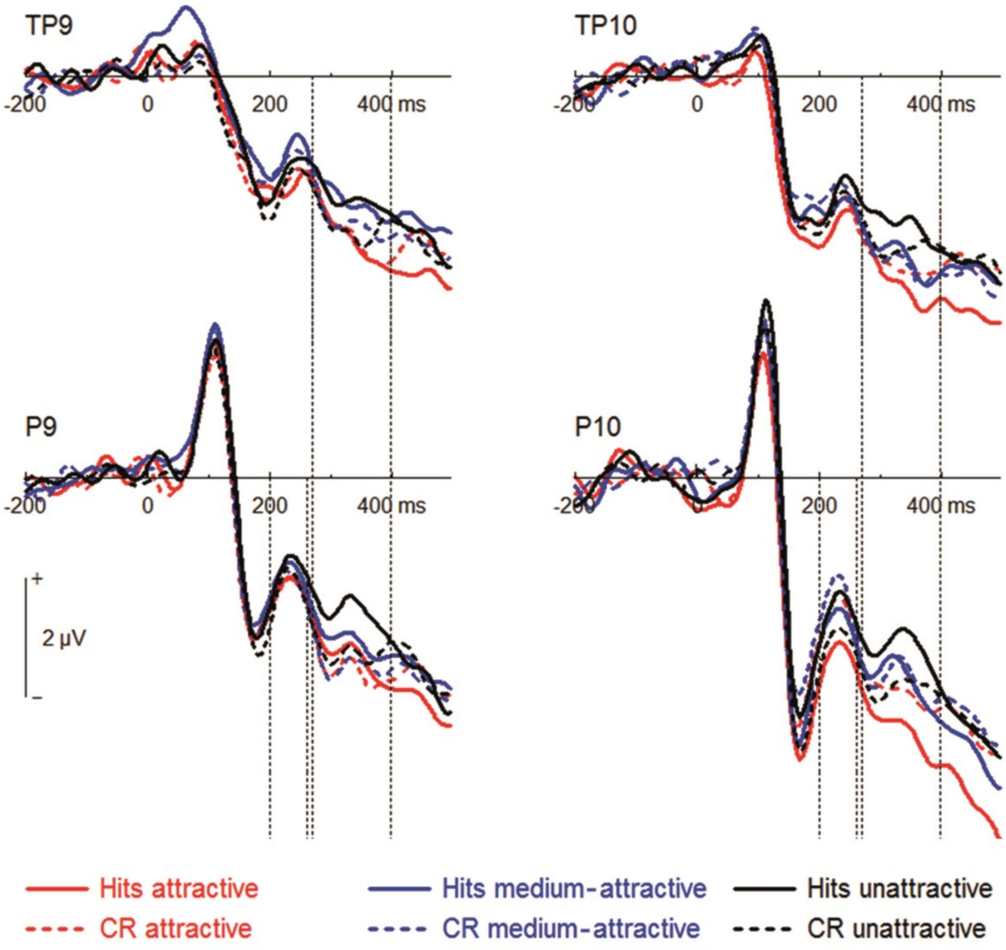


Figure 5. Grand mean ERPs from the test phases of the recognition experiment at occipito-temporal electrodes. Dashed lines indicate P2 and N250 time ranges. CR = Correct Rejections.

3.5 Discussion

Using face sets carefully matched for deviation-based distinctiveness, the present study investigates competing interpretations of the recognition memory advantage for unattractive over attractive faces by including a medium-attractive category. Replicating previous results in a different stimulus set (Wiese, Altmann, et al., 2014), attractive faces are less well remembered than unattractive faces. Importantly, poorest recognition memory is found for medium-attractive faces. ERPs reveal neural correlates of these attractiveness effects on recognition memory in the P2 and N250 components which have been implicated in the processing of facial typicality and identity, respectively (Schweinberger & Neumann, 2016).

The present results mirror recent findings of better memory for faces perceived as untrustworthy compared to trustworthy faces (Rule, Slepian, & Ambady, 2012), with a further drop in memory for medium-trustworthy faces (Mattarozzi, Todorov, & Codispoti, 2015). As it is assumed that individuals largely rely on facial attractiveness cues when they judge another person's trustworthiness (Xu et al., 2012), the underlying mechanisms of these memory effects may well be similar to the processes underlying the present results. Of note, neither these reports nor the present data are easily integrated with socio-cognitive accounts (Hugenberg et al., 2010) which imply more accurate recognition of attractive/trustworthy faces, resulting from a stronger motivation to view such stimuli (see e.g., Aharon et al., 2001).

The finding of faster response time and higher accuracy during gender categorization with increasing attractiveness may appear consistent with notions of more fluent processing of attractive compared to unattractive faces (Principe & Langlois, 2012; Trujillo et al., 2014; Winkielman et al., 2006). Notably, fluent processing is typically assumed to be error-free and indicates successful recognition of a stimulus. As proposed by Winkielman et al. (2006), fluency may be seen as a cue to familiarity, mirrored in faster reaction times. However, this cue may well serve as a faulty internal heuristic, giving rise to a 'false' sense of familiarity as indexed by high false alarm rates, and accordingly low d' and less conservative response bias as reported here for attractive faces. While attractive faces are quickly recognized as faces in object classification tasks, a fluency account may thus not hold true for elaborate mnemonic face recognition tasks as indexed by more error-prone memory performance for attractive faces. Possibly, precisely those attributes making attractive faces easy to classify for gender may simultaneously make them hard to differentiate from other identities.

The current data suggest instead that frequency of occurrence and face similarity, and the resulting increased exemplar density in face space are the crucial factors underlying the present memory findings. As detailed in the introduction, representations of unattractive faces are likely widespread and located in the periphery of the space. Medium-attractive faces may be particularly tightly clustered as these are most frequently encountered in everyday life. Attractive faces, even when more rarely encountered, may be clustered with intermediate density due to their proximity to the centre of face space. This assumption is well in line with findings that attractive relative to unattractive faces are perceived as more similar to each other—and therefore closer to each other in face space (Potter et al., 2007). This is also mirrored in increased false alarm rates for attractive and, to a lesser extent, medium-attractive faces, possibly suggesting that participants tend to mistake unseen faces for other previously presented ones. Overall, the observed pattern of less accurate memory for attractive relative to unattractive faces, and even worse memory for medium-attractive faces is in line with the idea that face memory is inversely related to representational density of faces in an MDFS, given that distinctive features of the face stimuli were controlled in the present study.

At the same time, the present results are at some variance with a previous interpretation that the disadvantage for attractive compared to unattractive faces mainly reflects an interference of enhanced affective processing with memory (Wiese, Altmann, et al., 2014). If so, performance for medium-attractive should have been improved over other faces—yet the exact opposite was the case. Thus, the current data do not support either a disruptive effect of positive content in attractive faces, or the assumption of a general hampering influence of emotional arousal.

Moreover, while at first sight the present behavioural data may suggest a negativity bias (Ohira et al., 1998) benefitting memory for unattractive faces, this interpretation is not supported by the rating data. Notably, while unattractive faces are indeed evaluated more negatively, they still elicit very low arousal, and thus may not be strongly affectively relevant. Further, it appears plausible that the mechanisms underlying attractiveness effects in face recognition memory are at least similar to other well-known face memory biases, such as the own-race or the own-age bias. In these cases, however, more negatively evaluated (i.e. out-group) faces are not better, but less accurately remembered compared to the more positive in-group faces (e.g. Wiese, Kaufmann, et al., 2014). It seems unlikely that negative affect benefitted one category and at the same time hampered memory for a different category of faces.

If anything, recent evidence suggests a positivity benefit in face memory not only in healthy controls, but even in social anxiety patients that exhibit attentional biases for displays of negative affect (Hagemann et al., 2016). In line with this finding, yet at some variance with a purely perceptual account of the reported data, the difference in memory performance between attractive and medium-attractive faces disappears when either FITC, emotional arousal, or both[21] are accounted for in an item analysis, while the increased performance to unattractive faces is maintained. Thus, the relatively small memory difference between medium-attractive and attractive faces is likely related to affective processes, while the larger benefit for

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[2] Please note that FITC and SAM arousal were strongly correlated ($\rho[1098] = .73$; $p < .001$) and thus shared a considerable amount of variance.

unattractive relative to both other categories results from less densely clustered representations in face space.

While behavioural data as well as subjective ratings via SAM scales represent the outcomes of a cascade of mental processes accompanying affective evaluations, ERP data allow for a more direct measurement of the underlying neural procedures, and can depict even non-conscious and automatic aspects. The present ERP findings further support an exemplar density account. First, P2 amplitude was larger for medium-attractive than attractive and unattractive faces. As both attractive and unattractive faces are relatively rarely seen in daily life compared with faces of medium attractiveness, this finding supports the interpretation of P2 amplitude as reflecting the frequency with which a certain category of faces is seen. This is in line with findings of smaller P2 amplitudes for other-race faces in control participants but not in experts with substantial contact to other-race people (Stahl et al., 2008).

Of note, faces that were better remembered yielded larger P2 responses in a recent study (Wiese, Altmann, et al., 2014). As in the current case the largest P2 is seen for those faces that were least well-remembered, the processes underlying P2 amplitude may not directly map onto memory performance (see also Itz, Schweinberger, Schulz, & Kaufmann, 2014). Instead, P2 potentially signifies the transcription of facial characteristics into an existing MDFS which may be influenced both by long-term exposure and by more transient adaptation to specific facial characteristics (Burkhardt et al., 2010). In other words, in any of the discussed cases, P2 is smaller for the less frequently encountered face categories (other- versus own-race, attractive versus unattractive, or both attractive and unattractive relative to medium attractive faces). Memory performance, however, may depend on various additional processes, with some of the likely candidates discussed below. Other evidence (cf. Schweinberger & Neumann, 2016, for a review) suggests that the P2 may be particularly sensitive to spatial aspects of face processing with reference to previous face exposure. Finally, the present finding that effects of facial attractiveness on P2 are more prominent during test than during learning corresponds well with previous results (Wiese, Altmann, et al., 2014), and could relate to task factors such as more efficient processing of attractiveness at test, when no prior categorization of the faces according to gender and/or initial encoding is necessary.

Interestingly, attractive faces are rated as more arousing relative to the other face categories, and also elicit the most prominent EPN, a neural marker of emotional tagging for successive preferential processing (Schupp et al., 2004). EPN attractiveness effects in this time range during learning have previously been found to correlate with later recognition performance (Wiese, Altmann, et al., 2014), with more negative amplitudes coinciding with worse memory for attractive faces. If there indeed was a direct link between memory and affective processing of attractiveness, there should be a direct correspondence between EPN amplitudes and the pattern in d'—which was not the case in the current data.

Although the connection between emotion and memory is multifaceted (Kensinger & Schacter, 2008), emotional processing can hamper rather than benefit memory for faces (see also Wiese, Altmann, et al., 2014), and this may have contributed to the reduced memory for attractive faces. Alternatively, other experiments on face memory show that positively valenced faces (i.e. with positive vs. neutral facial expressions) elicit a shift in criterion, in the sense that higher proportions of both hits and false alarms are observed for positive than neutral faces (Baudouin et al., 2000; Lander & Metcalfe, 2007). Johansson et al. (2004) suggested that emotion can affect recognition performance by inducing a more liberal criterion setting which matches reports of a 'warm-glow heuristic' for attractive faces (Monin, 2003). In line with this idea, the EPN effect in the current data corresponds to the difference in response criteria between attractive and unattractive faces which were at the same time the two categories rated as most and least arousing, respectively. Notably, a recent paper by Thiruchselvam et al. (2016) reported increases in attractiveness judgment from first to second presentation of attractive faces, but no similar exposure effects for repeated unattractive faces. Similar effects of increased liking upon repetition could also influence the criterion shift for attractive faces in the present study to at least some extent. Taken together, the present findings thus suggest that enhanced emotional processing relates to higher false alarm rates for attractive faces (as inferred from a less conservative response criterion and at the same time smaller sensitivity). Importantly, however, neither arousal, valence, FITC, nor any combination of these factors can fully explain superior memory for unattractive faces. Thus, attractiveness modulates recognition memory beyond distinctiveness and emotional content. Overall, the present memory effects of facial attractiveness appear to be best explained by the frequency with which a particular face category is observed and the resulting density of representations in face space, while affective mechanisms may further contribute to the reported differences in memory to varying extent across the attractiveness spectrum.

In summary, this study suggests a representational account for the present finding of reduced memory for medium-attractive relative to both attractive and unattractive faces. More specifically, given that distinctiveness is controlled for, medium-attractive faces presumably are most densely clustered in face space, resulting in least accurate memory. The occipito-temporal P2 likely reflects a neural correlate of face exemplar density: Larger P2 responses are elicited by medium-attractive relative to both attractive and unattractive faces, and poorer memory coincide with larger P2 amplitudes. An analysis of the subsequent N250/EPN time window and the results of an item analysis indicated an additional contribution of affective processing to face memory. However, this contribution appeared to be limited to attractive faces, and did not explain the findings for medium-attractive compared with unattractive faces. Overall, the present findings show that attractiveness modulates face memory over and above the effects of distinctiveness and affective processing, and affects neuronal processing at temporally distinct processing stages.

Acknowledgments

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3.6 Appendix

3.6.1 Additional ERP analyses

As is routinely done in our lab, we also analysed two earlier components (occipital P1 and occipito-temporal N170) and an early and late segment of the Late Positive Component (LPC), but since these results were not directly related to the main purpose of the present paper, we decided to report them in the form of an Appendix only. Although some researchers (e.g. Herrmann, Ehlis, Ellgring, & Fallgatter, 2005) suggested that the P1 is the first face-sensitive ERP component, the occipito-temporal N170 is more typically regarded as the earliest face-sensitive ERP. The N170 is a negative peak at ~170 ms, typically larger for faces relative to other objects (e.g. Eimer, 2011a). It is assumed to reflect early structural face encoding (Bentin, Allison, Puce, Perez, & McCarthy, 1996), or the detection of a face-like pattern (Amihai, Deouell, & Bentin, 2011; Schweinberger & Burton, 2003). Some previous studies reported larger N170 amplitudes for unattractive relative to attractive faces or no significant difference (Roye et al., 2008). Others, however, found larger amplitudes for attractive faces (Marzi & Viggiano, 2010), and interpreted these findings with respect to attractiveness as an affective, yet temporarily stable facial feature (and thus similar in processing demands to other features known to influence N170 amplitudes, i.e. identity and gender). Alternatively, the mixed results may reflect global low-level differences between stimulus categories in previous studies. If so, we do not expect pronounced amplitude differences as we controlled our stimuli for some characteristics, i.e. luminance and contrast.

Lastly, the LPC is a shorthand label for a family of sustained positivities which typically start around or after 300 ms after the presentation of task-relevant stimuli. Its amplitude has been linked to enhanced affective processing of motivationally relevant material (Schupp et al., 2000) and has been demonstrated to be larger for attractive than unattractive faces (Werheid et al., 2007; Wiese, Altmann, et al., 2014). In addition, hits (compared to correct rejections) generally elicit larger amplitudes in this component, often referred to as the old-new effect (see Rugg & Curran, 2007, for a review). Early and late portions of the old-new effect may reflect different aspect of memory, where an early part (300-500 ms) is thought to reflect familiarity-driven recognition or conceptual priming (Paller, Voss, & Boehm, 2007), whereas a late part (500-700 ms) is related to recollection. Of note, two previous studies did not find a modulation of late old-new effects by attractiveness (Marzi & Viggiano, 2010; Wiese, Altmann, et al., 2014). Hence, we expect to find main effects of Response Type and Attractiveness, but no interaction of these factors.

In the analyses below, mean amplitudes of P1 were measured at O1/O2 between 100 and 140 ms, mean amplitudes of N170 were measured at P9/P10 between 145 and 185 ms, and the early (300-500) and late (500-700) segment of the LPC over a grid of nine electrodes including F3, Fz, F4, C3, Cz, C4, P3, Pz, and P4, captured in the experimental factors Site (frontal vs. central vs. parietal) and Laterality (left hemisphere vs. midline vs. right hemisphere).

3.6.2 Results

Learning phase ERPs

P1 and N170. No effects of interest were found.

Early LPC (300-500 ms). A main effect of Attractiveness was found ($F[2,38] = 6.242$; $p = .005$; $\eta_p^2 = 0.247$), with larger amplitudes for attractive compared to unattractive faces ($t[19] = 3.351$; $p = .003$; $d = 0.749$). No other amplitude differences were detected (all $p > .074$; see Figure 6).

Late LPC (500-700 ms). No effects of interest were found.

Test phase ERPs

P1. A significant interaction of hemisphere and attractiveness ($F[2,38] = 5.916$; $p = .006$; $\eta_p^2 = 0.237$) indicated slightly larger P1 amplitudes over the left hemisphere for medium-attractive faces compared to both attractive ($t[19] = -2.334$; $p = .031$; $d = -0.107$) and unattractive faces ($t[19] = -2.276$; $p = .035$; $d = 0.152$; $M = 5.188 \pm 3.148$, 5.520 ± 3.053, and 5.068 ± 2.878 µV for attractive, medium-attractive, and unattractive faces, respectively), but not over the right hemisphere (all p's $> .05$). None of these comparisons survived Bonferroni correction.

N170. An ANOVA on mean amplitudes of the N170 revealed a main effect of attractiveness ($F[2,38] = 3.787$; $p = .032$; $\eta_p^2 = 0.166$), indicating more negative N170 amplitudes for attractive compared to both medium-attractive ($F[1,19] = 6.029$; $p = .024$; $\eta_p^2 = 0.241$) and unattractive faces ($F[1,19] = 4.734$; $p = .042$; $\eta_p^2 = 0.199$).

Early LPC (300-500 ms). A main effect of Attractiveness was found ($F[2,38] = 6.523$; $p = .004$; $\eta_p^2 = 0.256$) with larger amplitudes for attractive compared to unattractive faces ($t[19] = 3.341$; $p = .003$; $d = 0.747$), and also slightly larger amplitudes for medium-attractive over unattractive faces ($t[19] = 2.113$; $p = .048$; $d = 0.473$; see Figure 6). No other amplitude differences were detected (all $p > .132$).

Late LPC (500-700 ms). A main effect of Response Type was found ($F[1,19] = 14.627$; $p = .001$; $\eta_p^2 = 0.435$) with larger amplitudes for hits than correct rejections. Further, there was an interaction of Laterality by Response Type by Attractiveness ($F[4,76] = 3.245$; $p = .016$; $\eta_p^2 = 0.146$). Post-hoc tests indicated a slightly larger effect of Response Type (hits > CR) for attractive than medium-attractive faces over the left hemisphere ($t[19] = 2.209$; $p = .040$; $d = 0.494$), but this effect did not survive Bonferroni correction (critical alpha = .017; see Figure 6).

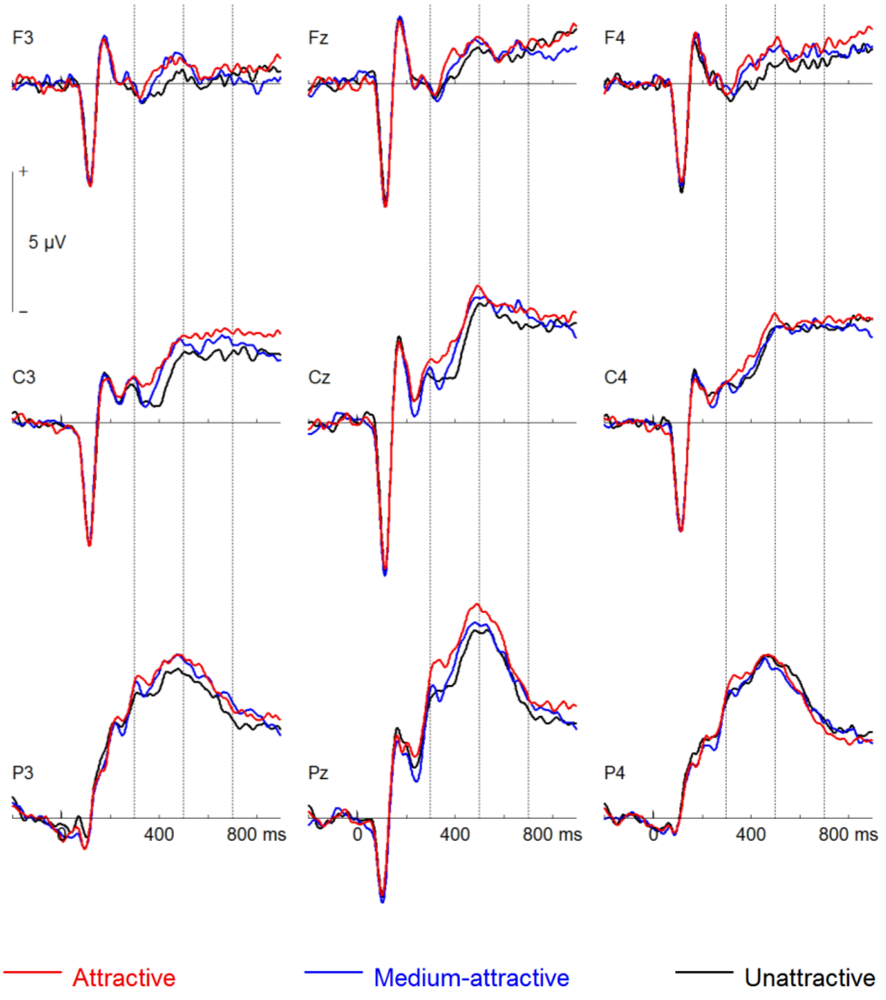

Figure 6: Grand mean ERPs from the test phases of the recognition memory experiment. Dashed lines indicate early and late LPC time ranges.

3.6.3 Discussion

P1. There was a significantly larger P1 at test for medium-attractive faces over the left hemisphere compared to the other face groups. The P1 shows stimulus category effects that are generally associated with low-level stimulus characteristics (Regan, 1989). Here, we controlled our stimulus material for global brightness and contrast. The difference in P1 amplitudes may thus be due to variations of local visual features between our stimulus groups that we did not control for as we aimed to employ the strongest possible manipulation of natural variations in attractiveness while at the same time hand controlling for deviation-based distinctiveness. Controlling high-level properties, such as skin texture or facial symmetry, would have significantly limited the range and validity of the very attribute we aimed to investigate. Further, as face recognition memory per definition relies on the ability to differentiate between individual faces, we wanted to make sure to leave individuating characteristics, such as skin texture, intact. Because P1 results did not survive Bonferroni correction, we believe it is appropriate to refrain from further interpretation in the absence of replication.

N170. It may be assumed that very basic perceptual differences underlie the attractiveness differences in recognition memory, in which case early ERP components should mirror effects in behaviour. The earliest effect of attractiveness was found in the N170 at test, with attractive faces eliciting more negative waveforms (also reported by e.g., Marzi & Viggiano, 2010). Notably, this pattern is qualitatively different from later processing reflected in the P2, with equal amplitudes for attractive and unattractive faces, suggesting at least partially different mechanisms underlying these ERP components.

This amplitude change could reflect systematic differences in low-level characteristics other than global luminance and contrast—such as increased local contrasts in attractive faces (Russell, 2003). As the effect was only moderate in size, it may not have reached significance during learning owing to the smaller trial number and thus the increased noise in the ERP averages. We did not observe any correspondence between N170 amplitudes and memory behaviour.

Early and late LPC. Earlier research found main effects of attractiveness and response type consistently for both the early and late LPC. Here, we selectively found sensitivity for attractiveness in the early segment, while inspection of the late time window only yielded a main effect of response type. Speculatively, this may indicate some sequential shift from affectively driven processing during the earlier stage towards (recollection-driven) mnemonic processing in the late LPC. Importantly, there was no stable interaction of both factors in either segment, following the pattern of earlier results from our lab (Wiese, Altmann, et al., 2014).

4 STUDY 2

No gender influences on memory for faces of varying attractiveness.

4.1 Abstract

Previous research suggests that attractiveness influences face memory, with poorest memory for medium-attractive faces. Moreover, women exhibit better memory than men for female faces in particular (female Own-Gender-Bias; OGB). Here we investigated for the first time whether attractiveness effects on face memory are moderated by facial and participant gender. We recorded both behaviour and Event-Related Brain Potentials (ERPs) while male and female participants memorized and subsequently recognized attractive, medium-attractive, and unattractive male and female faces. Behavioural results showed a remarkable absence of an OGB, but replicated better memory for unattractive compared to attractive faces, and poorest memory for medium-attractive faces. In a Multidimensional Face Space framework, this could reflect increased cluster density and hence increased confusability of the most frequently encountered medium-attractive faces. This interpretation was supported by findings of larger occipito-temporal P2 amplitudes (200-260 ms) for medium-attractive than both attractive and unattractive faces. The only ERP effect involving participant gender was an increased frontal positivity (300-500 ms) for medium-attractive female compared to male faces in men only, which could indicate that medium-attractive female faces are processed by men as relatively more attractive. We also observed an old/new effect with more positive ERPs to hits than correct rejections, which was similar across attractiveness conditions and participant groups. This suggests that retrieval processes reflected in the old/new effect operate independently of facial attractiveness.

Keywords: Attractiveness, Distinctiveness, Gender Typicality, Event-related Potentials, Faces

4.2 Introduction

Whereas the perception of beauty is often discussed as a matter of personal taste and aesthetics in non-scientific contexts, a substantial body of research during recent years has suggested a variety of hard-wired biological mechanisms for judging facial attractiveness (Gangestad & Scheyd, 2005). From this perspective, attractive traits and perceivers' preferences may have co-evolved to optimize reproductive fitness. Hence, attractiveness is seen as a cue for good physical condition and health (Roberts et al., 2005), correlates with oestrogen levels in women (Smith et al., 2006), and with reproductive success in men (Prokop & Fedor, 2011). Unsurprisingly, men and women alike value facial attractiveness in potential mates (Buss & Barnes, 1986; Eastwick & Hunt, 2014; Fletcher, Simpson, Thomas, & Giles, 1999; Meltzer, McNulty, Jackson, & Karney, 2014).

Facial attractiveness also impacts face memory. While earlier findings suggested that attractive faces could be more memorable (Marzi & Viggiano, 2010), more recent research suggested that unattractive faces are remembered better than attractive faces (see Wiese, Altmann, et al., 2014). An important consideration in this context is the confound of facial attractiveness with averageness vs. distinctiveness. On the one hand, facial averageness is widely considered to be an important contributing factor to perceived attractiveness (Langlois & Roggman, 1990; see Rhodes, 2006, for a review). On the other hand, this position has been challenged by the finding that morphs of highly attractive faces are perceived as even more attractive than morphs of randomly selected faces, suggesting that highly attractive faces carry traits that are systematically different from the population average (DeBruine et al., 2007). As distinctive faces are better remembered than more average faces, these conflicting views lead to different predictions for face memory (Bartlett, Hurry, & Thorley, 1984; Valentine, 1991). However, when controlling for distinctiveness, we consistently found poorer memory for attractive compared to unattractive faces (Wiese, Altmann, et al., 2014), and worst performance for medium-attractive faces (see Study 1). Taking this background into account, we tested whether attractiveness effects on face memory are further modulated by face or participant gender in the present study.

Most former studies on attractiveness effects in memory only examined participants and/or stimuli of one gender (e.g. Brigham, 1990; Fleishman et al., 1976; Light et al., 1981; Shepherd & Ellis, 1973). Importantly, however, several studies reported a so-called own-gender bias (OGB), with better memory for faces of an observer´s own gender compared to opposite-gender faces (see Herlitz & Lovén, 2013, for a review). This OGB is more consistently observed in female participants (Herlitz & Lovén, 2013) and has been interpreted to reflect enhanced individualisation of in-group faces, with gender cueing social group membership (Hugenberg et al., 2010; Wolff et al., 2014). Critically, as high attractiveness is strongly related to gender typicality (Hoss, Ramsey, Griffin, & Langlois, 2005), one might predict a particularly pronounced memory advantage for attractive relative to less attractive own- versus other-gender faces. In addition, the meta-analysis by Herlitz and Lovén (2013) reports overall more accurate face memory in females, independent of face gender. This general advantage may be functionally related to women's superior abilities in perceiving emotional expressions (Lovén, Svärd, Ebner, Herlitz, & Fischer, 2014; Montagne, Kessels, Frigerio, de Haan, & Perrett, 2005), and extended use of emotionally or - in a wider sense - socially relevant information in faces. If so, women's recognition memory should be influenced by attractiveness to a greater extent than men's — given that attractiveness is of considerable social relevance.

Yet from an evolutionary view, high gender typicality due to pronounced sexual dimorphisms of faces may be seen as a signal of opposite-sex mate quality (Rhodes, 2006). In contrast to the OGB, an evolutionary account would predict better memory for attractive opposite- relative to own-gender faces, a pattern that has indeed been reported for several non-human species (Brennan & Kendrick, 2006). Generally in line with this idea, recent research suggested that increased memory for attractive relative to unattractive male faces in female participants arises due to their romantic goals in mate selection, while more accurate memory for attractive relative to less attractive female faces putatively serves to retain details about potential rivals (Watkins et al., 2017). If attractive faces were primarily relevant in a mating context rather than in terms of social in-group/out-group categorization, face memory could be expected to be particularly good for attractive individuals of the opposite sex (in heterosexual participants).

Finally, whereas both perspectives described above assume an interaction of gender and attractiveness, one might alternatively predict that gender does not modulate attractiveness effects in face memory. The Multidimensional Face Space (MDFS) model (Valentine et al., 2015) describes cognitive representations of faces in a multidimensional space, whose dimensions correspond to physiognomic characteristics and evolve as a result of lifetime experience, promoting optimized discrimination between individual faces. While an observer's face space is normally well tuned to perceiving individual differences between regularly seen own-group faces, it is less well adapted for less frequently seen other-group faces, e.g. other-race faces (Wiese, Kaufmann, et al., 2014). We recently proposed an account of attractiveness effects on face memory based on an adapted MDFS model, assuming worse recognition performance for those faces with closely clustered mental representations due to large numbers of encountered faces of a certain type (see Study 1). Assuming that contact with people of both genders is relatively similar for men and women in most Western societies (e.g. Wolff et al., 2014), this perceptual expertise account would not predict large memory differences between male and female faces on any level of attractiveness.

Taken together, face and/or participants' gender may influence face memory due to several potential mechanisms, giving rise to a number of (partly conflicting) predictions. Since behavioural performance measures in memory experiments only reflect the final product of multiple processes, they do not easily allow for disentangling their respective contributions. In the present study, we therefore additionally recorded the electroencephalogram (EEG) and analysed event-related brain potentials (ERPs) as a measure of neuronal processing with high temporal resolution.

The earliest ERP component consistently modulated by facial attractiveness is the occipito-temporal P2, peaking around 200-250 ms after face onset. It has been suggested that P2 modulations are linked to perceived typicality of facial stimuli with smaller amplitudes for more distinctive faces (Halit et al., 2000; Schulz, Kaufmann, Kurt, et al., 2012; Schulz, Kaufmann, Walther, et al., 2012). In an earlier study, however, we found significantly smaller P2 amplitudes for attractive compared to unattractive faces matched for rated distinctiveness (Wiese, Altmann, et al., 2014). As more faces are usually rated as somewhat unattractive rather than attractive, we proposed that larger P2 amplitudes denote more commonly encountered classes of faces. Concurringly, in a more recent experiment P2 was smaller for both attractive and unattractive faces compared to very frequently encountered medium-attractive faces (see Study 1). Thus, we expect P2 attractiveness effects in the present context, with medium-attractive faces eliciting larger amplitudes.

Note that there is now evidence that different kinds of own-group biases in face memory (e.g., based on race, age, or gender as group-defining features) are mediated by different mechanisms (e.g., Wiese, 2012). Own-race and own-age faces profit from enhanced perceptual expertise compared to their other-group counterparts, and also consistently elicit larger P2 responses (Stahl et al., 2008; Wiese et al., 2008). Presuming that our participants encounter male and female faces with similar frequency, an expertise account of the P2 would predict no clear face gender effects in this component.

However, Wolff et al. (2014) found significant OGBs in both male and female participants that were accompanied by P2 modulations during learning, but only in males. The authors suggested that this P2 effect may represent a potential neural correlate of the male OGB in memory interacting with distinctiveness effects in the P2. For the present context, it is of special interest to see if similar modulations can be found when perceived distinctiveness is controlled for. If this effect would indeed be observed, the P2 may represent social in-group/out-group tagging, and own-gender faces should elicit a larger P2 mirroring results from own-race or own-age bias studies (Stahl et al., 2008; Wiese et al., 2008). Furthermore, attractive own-gender faces should elicit even larger P2 amplitudes, as they are more easily categorized as belonging to the in-group.

The occipito-temporal N250 component is a face-sensitive ERP following the P2 between about 230 and 400 ms. The N250 is known to be influenced by face learning, as reflected in larger negativity for correctly recognized old faces (hits) compared to correctly rejected (CR) new faces (Kaufmann et al., 2009). In previous experiments, we additionally observed a larger negativity for attractive compared to unattractive faces (Wiese, Altmann, et al., 2014). As attractiveness and memory effects were additive, we interpreted the effect of attractiveness in terms of an Early Posterior Negativity (EPN; Schupp et al., 2004). The EPN has similar timing and scalp distribution as the N250, but is typically thought to reflect a ‘tagging’ mechanism of motivationally relevant material that precedes more elaborate emotional processing

To the extent that the N250/EPN is sensitive to motivational relevance, we reasoned that it would be particularly important to see whether attractiveness effects on this component are moderated by face and participants’ gender. Specifically, if enhanced motivation to process social in-group faces is crucial for memory, we may expect larger N250/EPN effects to own-gender faces. Alternatively, if memory effects are crucial in a cross-gender mating context, we may expect larger N250/EPN effects to opposite-gender faces, and particularly so for attractive other-gender faces. Finally, the possibility remains that attractiveness effects on the N250/EPN are relatively independent of memory effects in this time range, and that they reflect more general processing of emotional valence and/or arousal. If so, we would expect no influences of participants' or stimulus gender on the N250 memory effect.

As in previous related research, we also examined the Late Positive Component (LPC). The LPC is a shorthand label for a family of sustained positivities which typically start around or after 300 ms after the presentation of task-relevant stimuli, and are maximal over central or parietal areas. Some authors link this response to enhanced affective processing of motivationally relevant material, and refer to it as the "Late Positive Potential (LPP)" (Schupp et al., 2000). The LPC has been demonstrated to be larger for attractive than unattractive faces (Werheid et al., 2007; Wiese, Altmann, et al., 2014), and to be larger for female than male faces in female participants (Oliver-Rodriguez, Guan, & Johnston, 1999). In another recent study, attractive opposite-sex faces elicited larger LPC amplitudes in male participants only (van Hooff et al., 2011). This latter finding could reflect enhanced intrinsic value placed on opposite-gender faces by men, (for related findings, see Meltzer et al., 2014).

In addition, hits (compared to correct rejections) generally elicit larger amplitudes over widespread areas of the scalp, an effect which is generally referred to as the old-new effect (see Rugg & Curran, 2007, for a review). In more detail, early and late portions of the old-new effect may reflect different aspect of memory, with an early part (300-500 ms) presumably reflecting familiarity-driven recognition or conceptual priming (Paller et al., 2007), whereas a late part (500-700 ms) is related to recollection. Of particular relevance, larger late old-new effects have been reported for social in-group faces, such as own-gender faces (Wolff et al., 2014), own-race faces (Stahl et al., 2010), and also own-age faces (Wiese et al., 2008), as compared to the respective out-group faces. Of note, two previous studies did not find a modulation of late old-new effects by attractiveness (Marzi & Viggiano, 2010; Wiese, Altmann, et al., 2014), while neither study assessed the combined influence of participants' and face gender.

Overall, the present study assessed, for the first time, whether attractiveness effects on memory would be moderated by face and participants' gender. In addition to performance data, we recorded event-related brain potentials that are sensitive to various factors (e.g., exposure frequency, affective processing, familiarity, recollection) related to face memory, allowing to test the aforementioned specific (and partially conflicting) hypotheses.

4.3 Methods

Participants

Twenty female participants (18 – 31 years; *M* = 21.65 ± 2.57 *SD* years; 12 singles, 7 in a relationship, 1 with undisclosed relationship status; 19 heterosexual, 1 bisexual) and 20 male participants (20 – 32 years; *M* = 24.10 ± 3.43 *SD* years; 11 singles, 8 in a relationship, 1 with undisclosed relationship status; 19 heterosexual, 1 bisexual) contributed data that were fully analysed. The data of 5 additional participants were excluded from analyses due to excessive alpha activity (2 cases) or insufficient trial numbers for ERP averaging (trials $N < 15$, 3 cases). All participants reported normal or corrected to normal vision and were right-handed as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). None of the participants reported neurological or psychiatric disorders. Participants received either course credit or monetary reimbursement after testing. All participants gave written informed consent, and the experiment was conducted in accordance with the Declaration of Helsinki and the Code of Human Research Ethics by the British Psychological Society (2014 version).

Stimuli

Six hundred faces, 300 of each face gender, rated as either unattractive (*M* = 2.466 ± 0.373 *SD*), medium-attractive (*M* = 3.518 ± 0.262 *SD*), or attractive (*M* = 4.388 ± 0.373 *SD*, all *N* = 100, respectively; see detailed rating values in Table 1) on a 6-point scale were chosen from a large stimulus pool of 1140 faces. Stimulus evaluations were carried out in an extensive rating study (see section 2.1) assessing attractiveness, two measures of distinctiveness (Wiese, Altmann, et al., 2014), gender typicality, emotional arousal and valence by means of SAM scales (Bradley & Lang, 1994), trustworthiness, dominance, and perceived age (see Figure 1). Pictures were cropped to show the face without clothing or hair line in front of a standardized black background, and scaled to 275 x 250 pixels, corresponding to viewing angles of approximately 4.6° x 4.4° at a distance of 90 cm. Luminance and contrast (without background) of individual images were equated to match the overall mean values of all original images, by employing gradation curve adjustments (mean luminance: 145 RGB units, mean contrast: 50 RGB units). Images were presented on a computer monitor, with a mean luminance of 26.84 cd/m².

Rating differences between stimulus conditions were analysed by means of Mood's median tests (for more than 2 levels) and Mann-Whitney-U tests (see Table 2). Unsurprisingly, faces of the three attractiveness conditions differed significantly with respect to attractiveness, $\chi^2(df = 2, N = 600) = 400.160$; $p < .001$; $V = 0.577$, but not deviation-based distinctiveness (see Wiese, Altmann, et al., 2014, for details and instructions), $\chi^2(df = 2, N = 600) = 5.854$; $p = .054$; $V = 0.070$. Comparing not just the three attractiveness conditions, but faces across all six conditions showed that they were successfully matched closely for deviation-based distinctiveness, $\chi^2(df = 5, N = 600) = 6.614$; $p = .251$; $V = 0.047$. Comparison of stimulus gender showed that male and female faces did not differ with respect to attractiveness and deviation-based distinctiveness — neither on the level of the entire set, all $p > .254$, nor within attractiveness conditions, all $p > .078$.

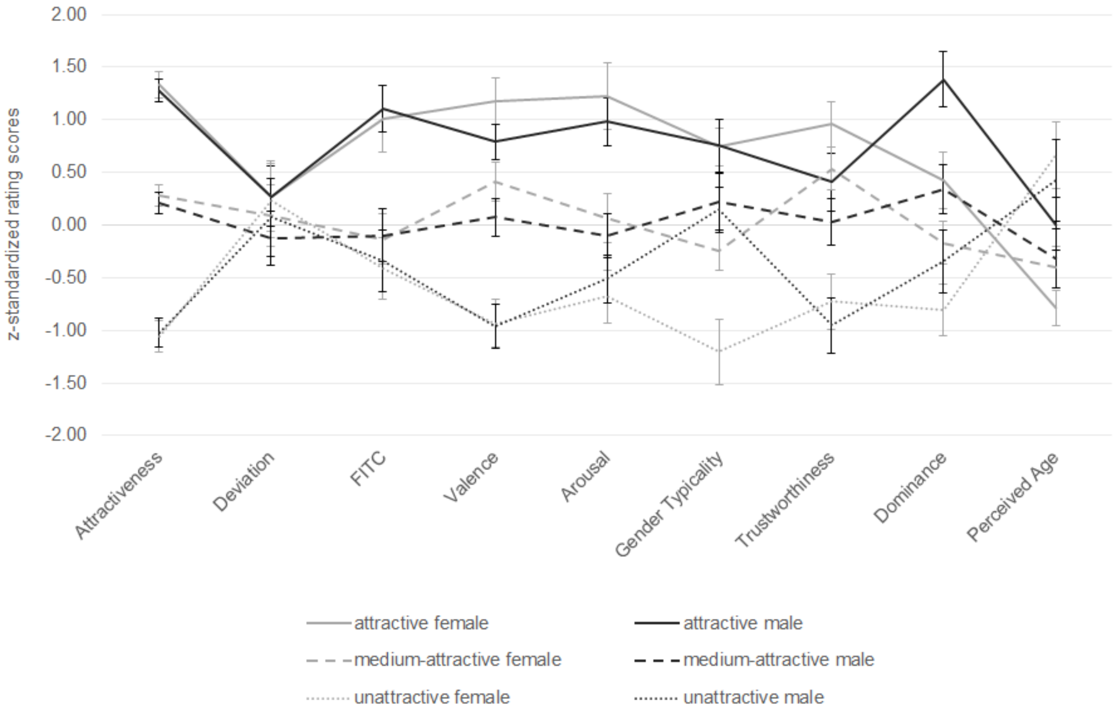

Figure 1: Differences between the mean rating values of the selected stimulus group from the mid-point of each rating scale evaluated in the rating experiment. Error bars depict standard errors of the means. FITC - 'Face In The Crowd' distinctiveness. Please refer to Table 1 for the complete overview of descriptive statistics.

Experimental Design and Procedure

Participants were seated in an electrically shielded and sound-attenuated cabin (400-A-CT-Special, Industrial Acoustics, Niederkrüchten, Germany), with their head in a chin rest approximately 90 cm away from a computer monitor. Each session began with a short practice block that was later excluded from data analysis. The main experiment consisted of 12 blocks, each divided into a study and a subsequent test phase separated by fixed breaks of 30 s duration. During each study phase 25 faces (across blocks: 50% female, equal numbers from the three attractiveness conditions) were presented in randomized order. Participants were instructed to memorize the faces and categorize them according to gender via left and right index finger key presses. Each study trial consisted of a fixation cross (500 ms), followed by a face stimulus (5000 ms) and a final blank screen (500 ms). In each of the subsequent test phases, those 25 faces shown in the preceding study phase and 25 new faces (across blocks: 50% female, equal numbers from the three attractiveness conditions) were randomly presented for 2000 ms each. As in the study phase, each test phase trial started with an initial fixation cross (500 ms) and ended with a blank screen (500 ms). Participants were instructed to indicate via left and right index finger key presses whether the faces had been presented in the preceding study phase (‘old’) or not (‘new’). Key allocation and assignment of faces to studied or non-studied conditions was counterbalanced across participants. Speed and accuracy were emphasized for all tasks.

For the study phases, mean correct reaction times (RT) and accuracies served as dependent variables. Trials were sorted into hits (correctly identified studied faces), misses (studied faces incorrectly classified as new), correct rejections (CR, new faces correctly identified as new), and false alarms (FA, new faces incorrectly classified as studied), separately for attractive, medium-attractive, and unattractive faces. Signal detection theory (Green & Swets, 1966) measures of sensitivity (*d’*) and response bias (*C*) were calculated. Statistical analyses were performed by means of paired samples t-tests and mixed model repeated-measures analyses of variance (ANOVAs), with epsilon corrections for heterogeneity of covariances performed via the Greenhouse-Geisser procedure where appropriate. Cohen’s d_{av} was calculated using the standard deviation of the difference scores between the compared measurements of the compared variables (Lakens, 2013).

EEG recording and analyses

EEG was recorded from 32 active sintered Ag/Ag-Cl electrodes using a Biosemi Active II system (BioSemi, Amsterdam, Netherlands). Note that BioSemi systems work with a "zero-Ref" set-up with ground and reference electrodes replaced by a CMS/DRL circuit (cf. http://www.biosemi.com/faq/cms&drl.htm). EEG was recorded continuously with a 512-Hz sample rate from DC to 155 Hz. Recording sites corresponded to an extended version of the 10-20-system (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, and I2).

Blinks were corrected using the algorithm implemented in BESA 5.1.8 (MEGIS Software GmbH, Berg & Scherg, 1994). The EEG was segmented from −200 until 1000 ms relative to stimulus onset, with the first 200 ms defined as a baseline. Artefact rejection was performed using an amplitude threshold of 100 µV and a gradient criterion of 50 µV. Only trials with correct responses in the study and test phases (hits, CR) were analysed. The remaining trials were recalculated to average reference, averaged according to experimental condition and digitally low-pass filtered at 40 Hz (12 db/oct, zero phase shift). Three different waveforms (study phase, hits, CR) were calculated separately for attractive, medium-attractive, and unattractive faces for both face genders. The minimum number of trials for an individual participant in any of these conditions was 15 (mean number of trials $M = 37.84 \pm 8.74$ *SD*).

Mean amplitude of the P1 (100 – 140 ms) was analysed at O1/O2, while mean amplitudes of N170 (145 - 185 ms), P2 (200 - 260 ms), and N250 (260 - 400 ms) were analysed at electrode sites P9/P10. Two additional time windows (300 – 500 ms, and 500 – 700 ms) were inspected at electrodes Fz, Cz, Pz, F3, F4, C3, C4, P3, P4, to capture the LPC and old-new effects at test.

4.4 Results

4.4.1 Behavioural results

To analyse behavioural data, repeated-measures ANOVA with the within-subject factors Attractiveness (attractive, medium-attractive, unattractive), and Face Gender (male, female) as well as the between-subject factor Participant Gender (male, female) were performed. Please see Table 3 for descriptive data. Further, see Table 4 for statistical indices of all t-tests performed on behavioural and ERP data.

During study, analysis of gender categorization accuracy revealed main effects of Face Gender ($F[1,38] = 14.353$; $p = .001$; $\eta_p^2 = .274$), and of Attractiveness ($F[2,76] = 61.368$; $p < .001$; $\eta_p^2 = .618$; $\varepsilon = .616$), as well as their interaction ($F[2,76] = 20.726$; $p < .001$; $\eta_p^2 = .353$; $\varepsilon = .621$). These findings indicated a decline in gender categorization accuracy with decreasing attractiveness for both face genders, (female faces: *M*s ± *SDs* = .98 ± .03 ms, .98 ± .03 ms, and .90 ± .07 ms; male faces: *M*s ± *SDs* = .99 ± .02 ms, .97 ± .03 ms, and .96 ± .03 ms, for attractive, medium-attractive, and unattractive faces, respectively), with the worse accuracy for unattractive female compared to male faces. No significant effects or interactions involving Participant Gender were detected (all $p > .897$; all $\eta_p^2 \leq .003$).

Analysis of gender categorization reaction times (RT) also revealed main effects of Face Gender ($F[1,38] = 5.784$; $p = .021$; $\eta_p^2 = .132$), and of Attractiveness ($F[2,76] = 27.891$; $p < .001$; $\eta p^2 = .423$), which were again further qualified by their respective interaction ($F[2,76] = 5.956$; $p = .004$; $\eta p^2 = .136$). Paired sample t-tests showed a steady increase in RT with decreasing attractiveness for female faces (*M*s ± *SDs* = 893.70 ± 33.28 ms, 926.90 ± 35.86 ms, and 965.98 ± 34.33 ms for attractive, medium-attractive, and unattractive faces, respectively). For male faces, participants responded more quickly to attractive faces compared to both medium-attractive and unattractive faces, but not differently to medium-attractive compared with unattractive faces (*M*s ± *SDs* = 880.57 ± 33.39 ms, 925.41 ± 32.79 ms, and 914.79 ± 34.71 ms for attractive, medium-attractive, and unattractive faces, respectively). The interaction arose primarily due to substantially longer RTs for unattractive female faces compared to unattractive male faces, with no differences between face genders for attractive, or medium-attractive faces. No significant effects or interactions involving Participant Gender were detected (all $p > .062$; all $\eta_p^2 \leq .079$).

At test, a repeated-measures ANOVA on *d’* revealed a main effect of Attractiveness ($F[2,76] = 35.810$; $p < .001$; $\eta_p^2 = .485$), with less accurate memory for attractive than unattractive faces, and still less accurate memory for medium-attractive than attractive faces (see Figure 2). Importantly, neither Face Gender nor Participant Gender yielded any significant main effects or interactions (all $p > .119$; all $\eta_p^2 \leq .050$).

A corresponding ANOVA on response bias measure *C* also yielded a main effect of Attractiveness ($F[2,76] = 17.621$; $p < .001$; $\eta_p^2 = .317$; $\varepsilon = .866$). Overall, all mean *C* values were positive, indicating a tendency towards conservative responses (see Figure 2), with more misses than false alarms. The attractiveness effect indicated least conservative responses for attractive faces relative to both medium-attractive, and unattractive faces. Further, medium-attractive faces were responded to more conservatively than unattractive faces. Again, neither Face Gender nor Participant Gender yielded significant main effects or interactions (all $p > .275$; all $\eta_p^2 \leq .043$).

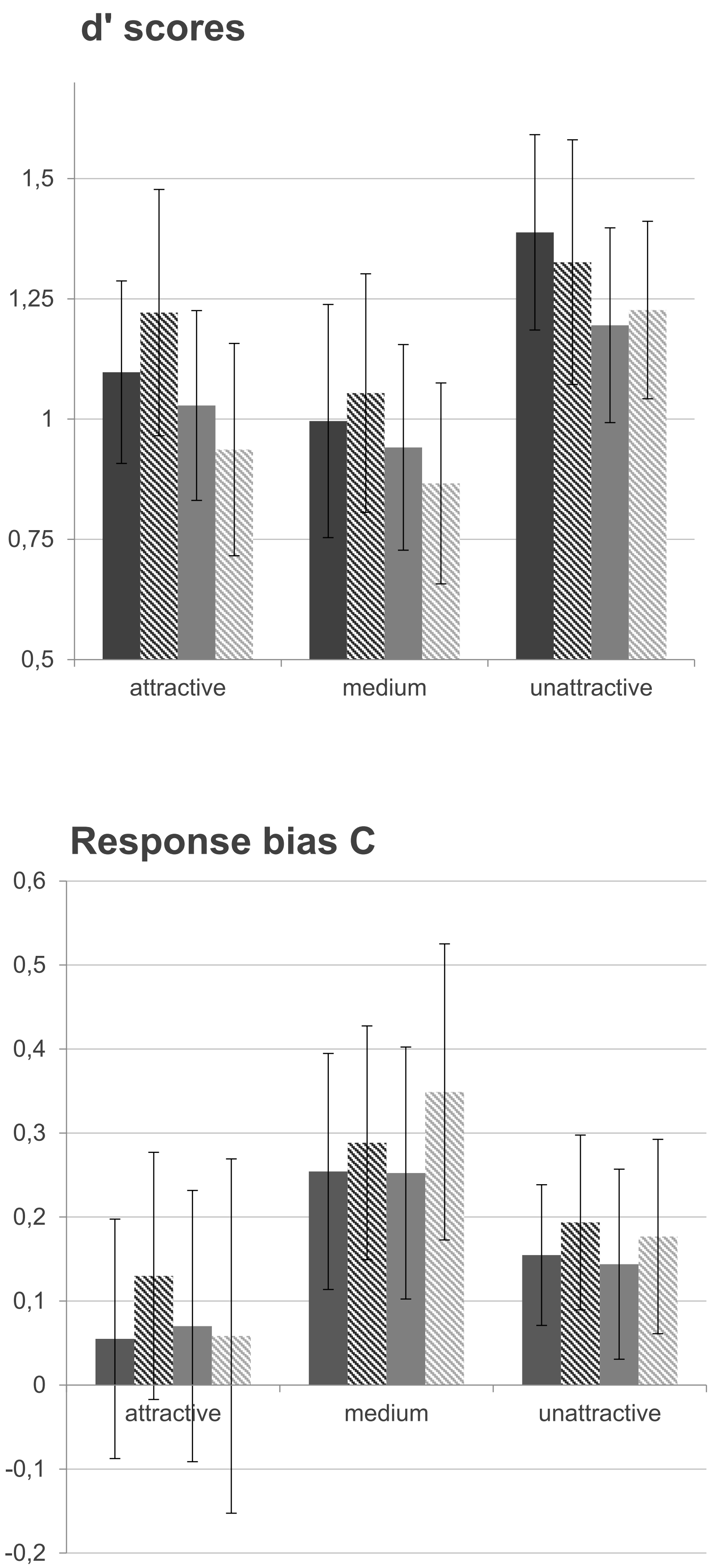

Figure 2: Behavioural measures from the recognition experiment. Error bars depict 95% confidence intervals of the mean.

To test for a potential influence of 'Face in the Crowd'(FITC) distinctiveness (in which participants indicate how likely they would spot a given face in a crowd of people, e.g.Valentine & Endo, 1992), valence and arousal ratings, and gender typicality on memory, we conducted an item analysis. A univariate ANCOVA with item d' as cases, Attractiveness as a single factor and FITC, Valence, Arousal, and Gender Typicality as covariates yielded only significant effects of FITC ($F[1,583] = 5.377$; $p = .021$; $\eta_p^2 = .009$), and Arousal ($F[1,583] = 15.789$; $p < .001$; $\eta_p^2 = .026$). Importantly, the effect of Attractiveness was still significant in this analysis ($F[2,593] = 13.727$; $p < .001$; $\eta_p^2 = .044$): memory for unattractive faces remained more accurate compared to attractive faces (adjusted mean d'-difference = 0.853; $p < .001$) and to medium-attractive faces (adjusted mean d'-difference = 0.605; $p < .001$); the d' difference between attractive and medium-attractive faces, however, was not maintained (adjusted mean d'-difference = 0.248; $p = .050$). No significant contributions were revealed from either Valence ($F[1,583] = 2.733$; $p = .099$; $\eta_p^2 = .005$) or Gender Typicality ($F[1,583] = 1.089$; $p = .297$; $\eta_p^2 = .002$).

4.4.2 Event-related potentials

ERPs Learning Phase[3]

P2. A mixed-model ANOVA with the within-subject factors Hemisphere (left, right), Attractiveness (unattractive, medium-attractive, attractive), Face Gender (male, female), and the between-subject factor Participant Gender (male, female) revealed a main effect of Face Gender ($F[1,38] = 6.694$; $p = .014$; $\eta_p^2 = .150$), indicating slightly more positive P2 amplitudes for male compared to female faces (see Figure 3). There were no significant main effects (all $p > .052$; all $\eta_p^2 \leq .095$) or interactions (all $p > .131$; all $\eta_p^2 \leq .059$) involving Participant Gender.

N250. A main effect of Attractiveness ($F[2,76] = 9.259$; $p < .001$; $\eta_p^2 = .196$) was qualified by an interaction with Face Gender ($F[2,76] = 3.387$; $p = .039$; $\eta_p^2 = .082$). Follow-up t-tests for female faces indicated that amplitudes in response to attractive faces were more negative compared to unattractive faces, but not to medium-attractive faces. Further, medium-

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[3] Please refer to the Appendix for results of P1 and N170 analyses.

attractive faces elicited more negative amplitudes than unattractive faces. For male faces, attractive faces elicited more negative amplitudes than both medium-attractive and unattractive faces (the latter comparison not surviving Bonferroni-Holm correction, however; $\alpha_{crit} = .017$). Medium-attractive and unattractive faces did not differ. There was a significant interaction between Hemisphere and Face Gender ($F[1,38] = 4.791$; $p = .035$; $\eta_p^2 = .112$), but further comparisons via t-tests between Face Gender over both hemispheres (or the other way around) did not reach significance (all $p > .103$; all $d < 0.30$). Finally, there were no significant main effects or interactions involving Participant Gender (all $p > .095$; all $\eta_p^2 \leq .072$).

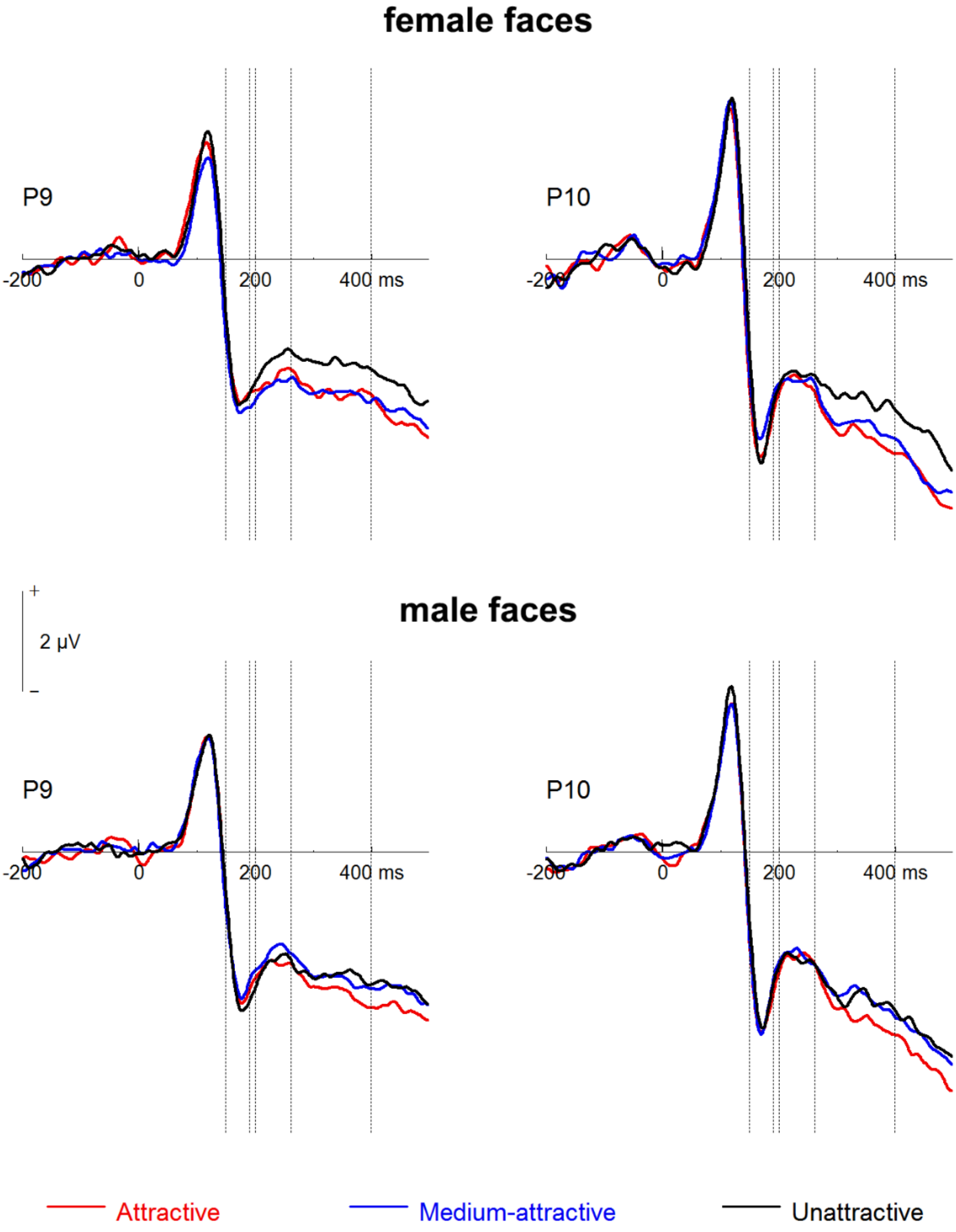

Figure 3: Grand mean ERPs from the learning phases at occipito-temporal electrodes. Dashed lines indicate the N170, P2, and N250/EPN time ranges.

Early LPC (300-500 ms). A corresponding ANOVA with the additional factors Site (frontal, central, parietal), and Laterality (left, midline, right) yielded a main effect of Attractiveness ($F[2,76] = 12.023$; $p < .001$; $\eta_p^2 = .240$), with larger amplitudes for medium-attractive compared to unattractive faces, and still larger amplitudes for attractive relative to medium-attractive faces. This was qualified by an interaction of Laterality by Attractiveness ($F[4,152] = 5.443$; $p < .001$; $\eta_p^2 = .125$), which reflected the fact that attractiveness effects were most evident over midline and left, but not right hemisphere electrodes (see Figure 4). Separate t-tests for each Laterality condition revealed larger amplitudes for attractive over medium-attractive faces over the midline only, although this effect did not survive Bonferroni-Holm correction ($\alpha_{crit} = .013$). Larger amplitudes for medium-attractive than unattractive faces were observed both over midline, and left hemisphere electrodes. Similarly, more positive amplitudes for attractive compared to unattractive faces were only present over midline and left hemisphere electrodes. There were no significant differences between Attractiveness conditions over the right hemisphere (all $p > .116$, $d \leq 0.254$; see Figure 4).

Of particular interest, we found an interaction of Site by Attractiveness by Face Gender by Participant Gender ($F[4,152] = 3.854$; $p = .013$; $\eta_p^2 = .092$). Separate ANOVAs for Attractiveness conditions yielded a significant interaction of Site by Face Gender by Participant Gender only for medium-attractive faces ($F[2,76] = 6.813$; $p = .006$; $\eta_p^2 = .152$; $\varepsilon = .689$); a significant Face Gender by Participant Gender interaction was only found over frontal sites ($F[4,152] = 8.550$; $p = .006$; $\eta_p^2 = .184$) and indicated more positive going amplitudes for female compared to male faces in men, but not in women (see Figure 5).

Late LPC (500-700 ms). A corresponding ANOVA for the time window from 500 to 700 ms yielded a main effect of Face Gender ($F[1,38] = 8.642$; $p = .006$; $\eta_p^2 = .185$), with more positive amplitudes for female than male faces. Furthermore, there was a main effect of Attractiveness ($F[2,76] = 5.240$; $p = .007$; $\eta_p^2 = .121$), with more positive amplitudes for attractive compared to both medium-attractive, and unattractive faces, which in turn did not differ. No significant main effects or interactions involving Participant Gender were detected (all $p > .069$; all $\eta_p^2 \leq .060$).

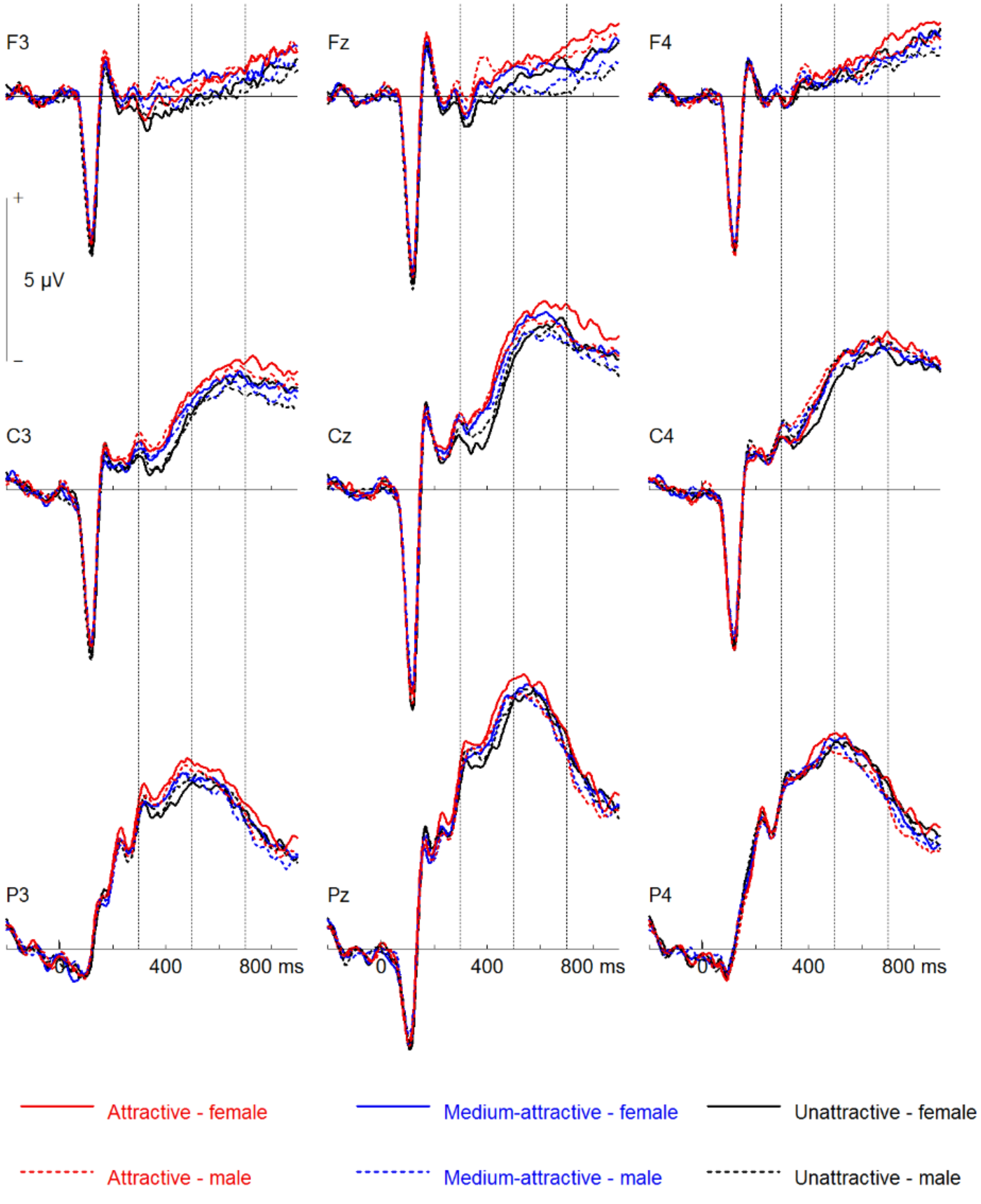

Figure 4: Grand mean ERPs from the learning phases over frontal, central, and parietal sites averaged across Participants Gender.

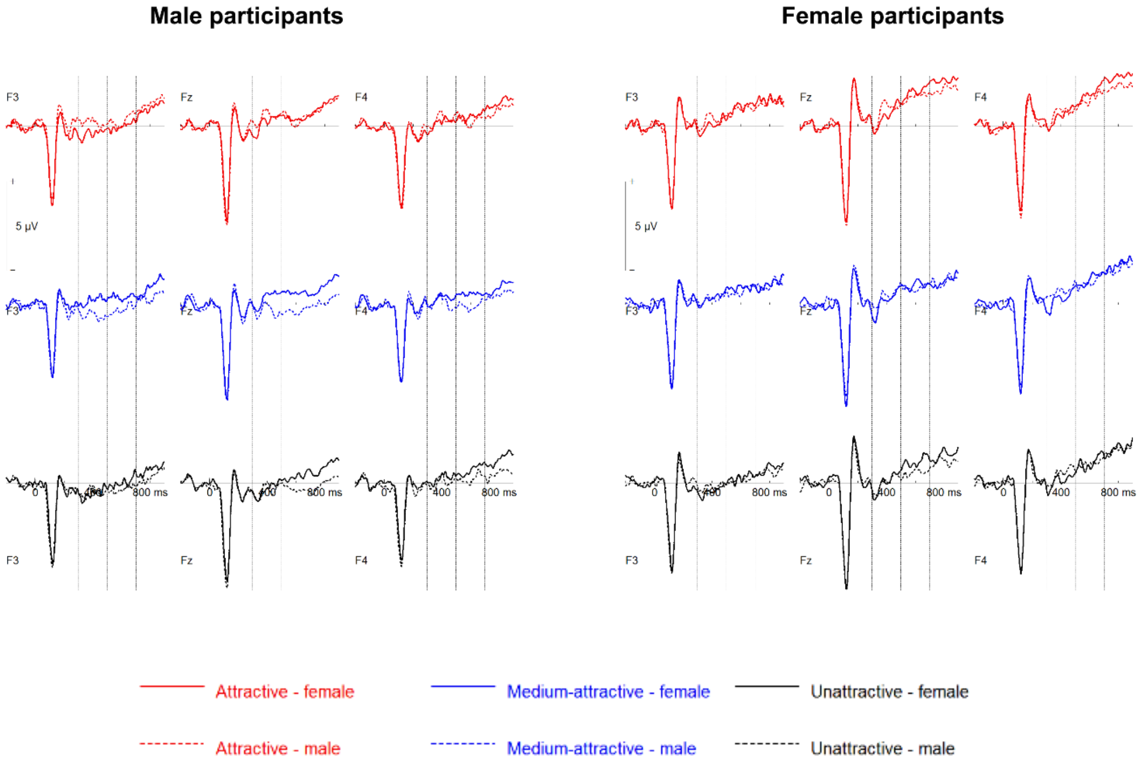

Figure 5: Grand mean ERPs from the learning phases over frontal sites.

ERPs Test Phase

P2. A mixed-model ANOVA with the within-subject factors Response Type (hits, correct rejections), Attractiveness (unattractive, medium-attractive, attractive), and Face Gender (male, female), Hemisphere (left, right), as well as the between-subject factor Participant Gender (male, female) revealed a main effect of Attractiveness ($F[2,76] = 6.004$; $p = .004$; $\eta_p^2 = .136$), indicating more positive amplitudes for medium-attractive faces compared to attractive and unattractive faces (see Figure 6). This effect was most clear over the right hemisphere, as reflected in a significant interaction between Attractiveness and Hemisphere ($F[1,38] = 3.257$; $p = .044$; $\eta_p^2 = .079$). Separate analyses per hemisphere confirmed a main effect of Attractiveness for the right hemisphere only ($F[1,38] = 7.574$; $p = .001$; $\eta_p^2 = .163$), with more positive P2 for medium-attractive faces compared to unattractive and attractive faces, which in turn did not differ.

Further, a main effect of Response Type ($F[1,38] = 40.265$; $p < .001$; $\eta_p^2 = .514$), indicating less positive P2 for hits compared to correct rejections, was further qualified by an interaction with Hemisphere and Face Gender ($F[1,38] = 5.362$; $p = .026$; $\eta_p^2 = .124$). Separate analyses per hemisphere revealed a significant interaction of Response Type and Face Gender for the right hemisphere only ($F[1,38] = 7.239$; $p = .010$; $\eta_p^2 = .157$). T-tests showed a significant effect of Response Type for female faces, but not for male faces. No significant main effects or interactions involving Participant Gender were detected (all $p > .144$; all $\eta_p^2 \leq .050$).

N250. We found significant main effects of Response Type ($F[1,38] = 16.292$; $p < .001$; $\eta_p^2 = .300$), with more negative amplitudes for hits than correct rejections, and Attractiveness ($F[2,76] = 10.246$; $p < .001$; $\eta_p^2 = .212$; $\varepsilon = .825$), with more negative amplitudes for attractive faces compared to both medium-attractive and unattractive faces. The difference between amplitudes for medium-attractive and unattractive faces did not reach the critical level of significance after Bonferroni-Holm correction ($\alpha_{crit} = 0.017$).

Moreover, there was an interaction of Response Type and Face Gender ($F[1,38] = 9.467$; $p = .004$; $\eta_p^2 = .199$), indicating larger Response Type effects for female faces. This was further qualified by a three-way interaction of Hemisphere by Response Type by Face Gender ($F[1,38] = 12.567$; $p = .001$; $\eta_p^2 = .249$), indicating a significant interaction of Response Type and Face Gender over the right hemisphere only ($F[1,39] = 15.292$; $p < .001$; $\eta_p^2 = .282$), again with significantly larger effects of Response Type for female than male faces. A three-way interaction of Hemisphere, Response Type and Attractiveness was also found ($F[2,76] = 4.809$; $p = .011$; $\eta_p^2 = .112$), but separate analyses for both hemispheres did not yield significant interactions of Response Type and Attractiveness over either hemisphere (all $p > .112$; all $\eta_p^2 \leq .055$). No significant main effects or interactions involving Participant Gender were detected (all $p > .079$; all $\eta_p^2 \leq .079$).

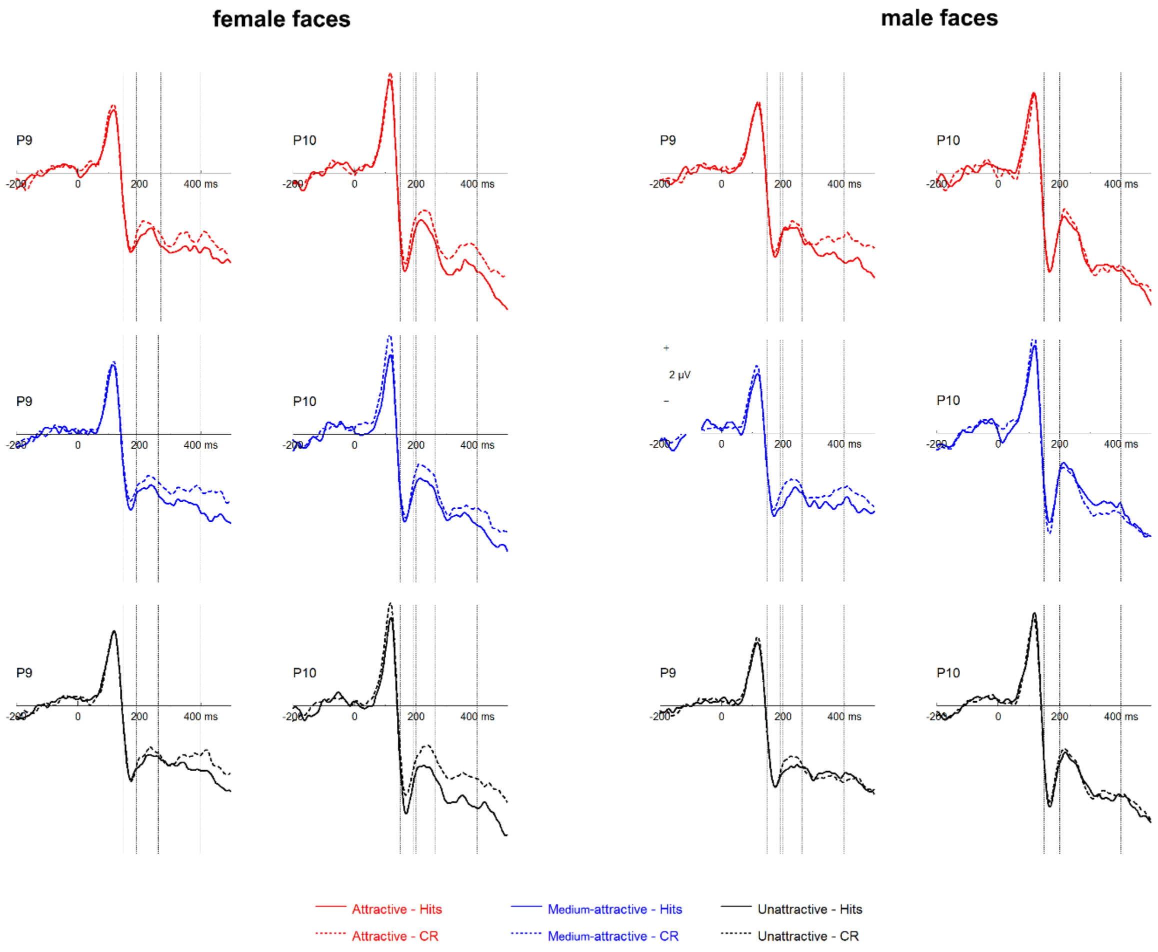

Figure 6: Grand mean ERPs from the test phases over frontal sites for male (left) and female faces (right; 20Hz low pass filtered for illustration).

Early LPC (300-500 ms). A corresponding ANOVA with the factors Laterality and Site (see above) replacing the Hemisphere factor yielded a main effect of Attractiveness ($F[2,76] = 7.504$; $p < .001$; $\eta_p^2 = .165$), with larger amplitudes for attractive compared to both medium-attractive faces and unattractive faces, which in turn did not differ. This was further qualified by an interaction of Laterality by Attractiveness ($F[4,152] = 4.017$; $p = .004$; $\eta_p^2 = .096$). Separate t-tests revealed larger amplitudes for attractive over medium-attractive faces over left and midline electrodes. Similarly, larger amplitudes for attractive than unattractive faces were observed over left, and midline electrodes. There were no significant amplitude differences between medium-attractive and unattractive faces in any Laterality condition (all $p > .725$; $d \leq 0.056$). There were also no significant amplitude differences between

Attractiveness conditions over the right hemisphere (all $p > .099$; $d \leq 0.267$). Attractiveness also interacted with Site ($F[4,152] = 2.855$; $p = .047$; $\eta_p^2 = .070$; $\varepsilon = .662$), indicating a tendency for smaller differences between attractive and medium-attractive faces over parietal compared to frontal, and central sites, though neither effect survived Bonferroni-Holm correction ($\alpha_{crit} = .006$).

Further, there was a main effect of Response Type ($F[1,38] = 29.628$; $p < 0.001$; $\eta_p^2 = .438$), with more positive amplitudes for hits than correct rejections. This was qualified by an interaction of Laterality by Response Type (F[2,76] = 5.867; p = .004; $\eta p^2 = .137$), and Laterality by Site by Response Type (F[4,152] = 4.321; p = .002; $\eta_p^2 = .102$). In short, these effects simply reflected the fact that response type effects tended to be right-lateralized over parietal sites, but not over more anterior sites.

There were also interactions of Response Type by Face Gender ($F[1,38] = 11.498$; $p = .002$; $\eta_p^2 = .232$), with larger old-new effects for female compared to male faces, and of Laterality by Response Type by Face Gender by Participant Gender ($F[2,76] = 3.229$; $p = .045$; $\eta_p^2 = .078$). Separate testing for male and female participants did not result in significant interactions of the remaining factors in either gender group. However, separate ANOVAs for each Face Gender yielded a significant interaction of Laterality by Response Type by Participant Gender only for male faces ($F[2,76] = 3.226$; $p = .045$; $\eta_p^2 = .078$). Further ANOVAs separated for Participant Gender found an interaction of Laterality by Response Type only in men ($F[2,38] = 7.347$; $p = .002$; $\eta_p^2 = .279$), indicating smaller Response Type effects for male faces over the left hemisphere compared to both midline and right hemisphere electrodes, which in turn did not differ.

We found additional higher-order interactions of Laterality by Response Type by Attractiveness by Face Gender ($F[4,152] = 2.634$; $p = .036$; $\eta_p^2 = .065$), and of Laterality by Site by Response Type by Attractiveness by Face Gender ($F[4.922,187.031] = 2.283$; $p = .049$; $\eta_p^2 = .057$), but none of the respective post-hoc tests' results survived Bonferroni-Holm corrections ($\alpha_{crit} = .006$).

Late LPC (500-700 ms). A corresponding ANOVA for the 500 to 700 ms time window yielded a main effect of Response Type ($F[1,38] = 46.119$; $p < .001$; $\eta_p^2 = .548$), with more positive amplitudes for hits than correct rejections. This was further qualified by interactions of Laterality by Response Type ($F[2,76] = 6.731$; $p = .004$; $\eta_p^2 = .150$), and Laterality by Site by Response Type ($F[4,152] = 2.956$; $p = .044$; $\eta_p^2 = .072$; $\varepsilon = .824$). In short, these effects reflected that effects of Response Type tended to be right-lateralized at frontal and central, but not parietal electrodes (see Figure 7).

An interaction of Site by Face Gender ($F[2,76] = 7.719$; $p = .001$; $\eta_p^2 = .169$) reflected larger amplitudes to female faces particularly over parietal sites. Response Type also interacted with Face Gender ($F[1,38] = 8.495$; $p = .006$; $\eta_p^2 = .183$), indicating larger Response Type effects for female compared to male faces. This was further qualified in an interaction of Site by Response Type by Face Gender by Participant Gender ($F[2,76] = 4.289$; $p = .028$; $\eta_p^2 = .101$; $\varepsilon = .745$), although separate analyses for either Site, Face Gender, or Participant Gender did not reach significance in post-hoc testing (all $p > .079$; all $\eta_p^2 \leq .134$).

Finally, a prominent main effect of Attractiveness ($F[2,76] = 12.048$; $p < .001$; $\eta_p^2 = .241$) reflected particularly small amplitudes for medium-attractive faces ($M = 3.55 \pm 1.96$ µV) when compared to both attractive ($M = 3.95 \pm 1.98$ µV) and unattractive faces ($M = 3.82 \pm 2.04$ µV), which in turn did not differ significantly. The main effect of Attractiveness was qualified by a number of less prominent higher-order interactions, which are reported below for the sake of completeness only. These included Attractiveness by Laterality ($F[4,152] = 3.946$; $p = .012$; $\eta_p^2 = .094$; $\varepsilon = .700$), Attractiveness by Face Gender ($F[2,76] = 4.901$; $p = .010$; $\eta_p^2 = .114$), Attractiveness by Laterality by Response Type by Face Gender ($F[4,152] = 2.602$; $p = .038$; $\eta_p^2 = .064$, and a five-way interaction Attractiveness by Laterality by Site by Response Type by Face Gender ($F[8,304] = 2.556$; $p = .027$; $\eta_p^2 = .063$; $\varepsilon = .644$). Post-hoc tests did not indicate different response type effects for male or female faces in the various attractiveness conditions at any electrode position (all $p > .131$; all $\eta_p^2 \leq .054$).

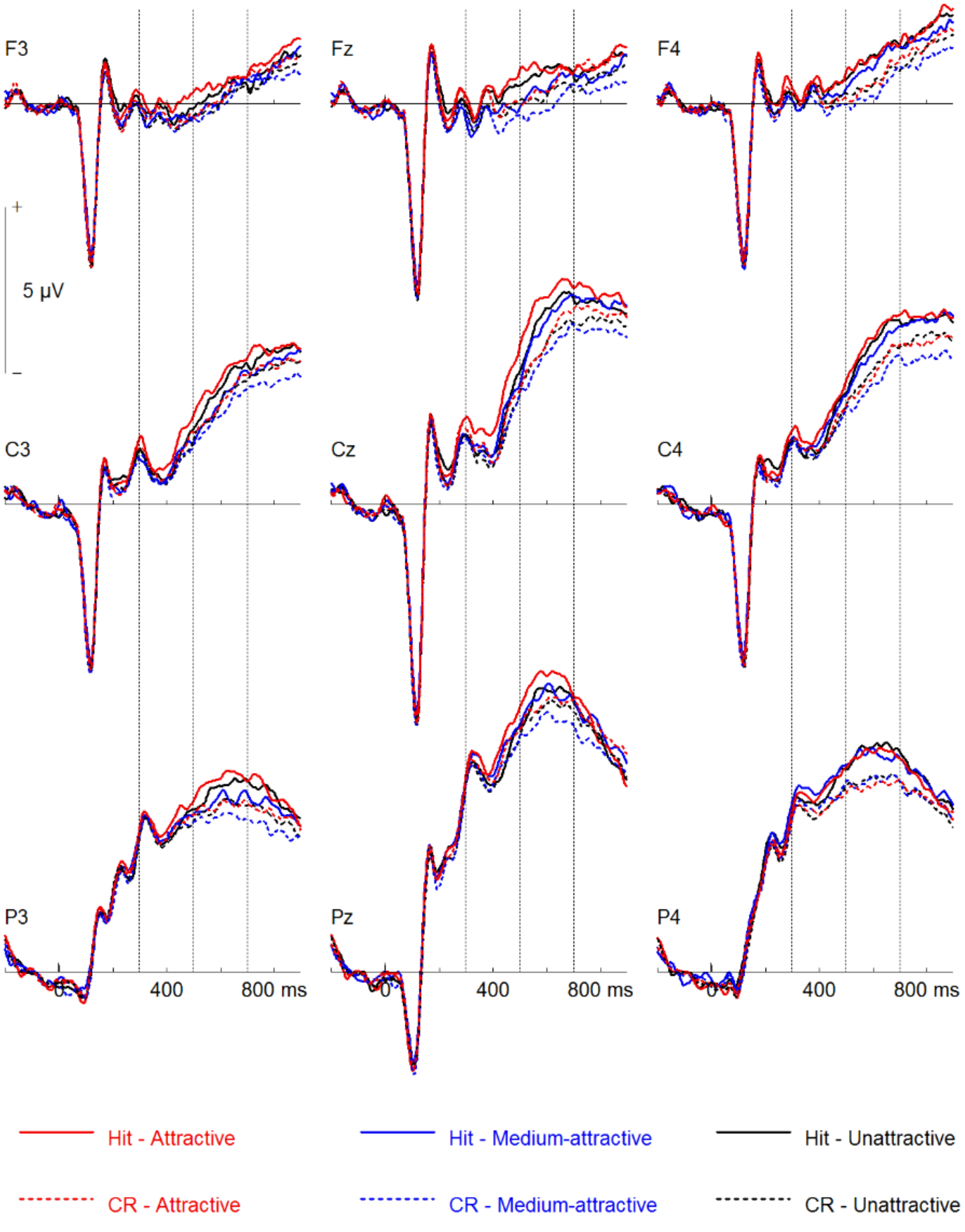

Figure 7: Grand mean ERPs from the test phases.

4.5 Discussion

Previous studies revealed a prominent effect of attractiveness on face recognition memory, with best memory for unattractive faces (Wiese, Altmann, et al., 2014), and poorest memory for medium-attractive faces (see Study 1). Here we investigated for the first time in a full-factorial design whether these attractiveness effects are further influenced by face gender, participant gender, or an interaction of both (e.g., in terms of an own-gender bias; Herlitz & Lovén, 2013). We replicated previous findings of enhanced recognition performance for unattractive compared to attractive faces with a further decline for medium-attractive faces. At the same time, we found a remarkable absence of an own-gender bias in face memory. Even more critically, we did not find any modulations of the attractiveness effect on recognition memory by either face or participants' gender.

The finding of less accurate memory for attractive compared to unattractive faces, with poorest performance for medium-attractive faces, is in line with the idea that face memory is inversely related to representational density of faces in an MDFS, as discussed in Study 1—assuming that local density is highest for the most commonly encountered medium-attractive faces. Further, density may also increase by systematic similarities in appearance, which have been well documented for attractive faces (Potter et al., 2007) and therefore may explain reduced memory for attractive relative to unattractive faces.

The difference between attractive and medium-attractive faces levelled out when emotionality ratings were taken into account as a covariate. Interestingly, the *d'*-difference between these conditions was mainly driven by high false alarm rates for attractive faces that were also reflected in a less conservative response criterion. These findings potentially indicate that participants more readily mistook newly presented attractive items with previously seen faces. Of note, infants tend to treat attractive faces as familiar even if they have never seen that particular face before (Langlois, Ritter, Roggman, & Vaughn, 1991). Such tendencies may reflect a 'warm glow-heuristic' which could be promoted by biases arising from positive emotional content (Monin, 2003).

Our current findings are hard to reconcile with socio-cognitive models (Hugenberg et al., 2010) that would assume better memory for those faces that participants are particularly motivated to remember. In terms of in-group vs. out-group biases, we found no evidence for preference of own-gender faces – not even for attractive faces for which socio-cognitive accounts would presumably predict a particularly strong OGB, as gender is very easily perceived due to increased gender typicality. More generally, as people consider attractiveness to be a socially desirable trait and more readily recognize attractive people as part of their in-group (Johnson, 1981), in- versus out-group effects should be particularly strong for attractive faces, which we did not find. Neither did we find support for an evolutionary memory benefit for attractive members of the opposite sex that would predict better memory for potential mates, i.e. attractive opposite-gender faces.

The absence of an own-gender bias in the present data is remarkable, considering the consistent finding of a relatively small effect in other studies, particularly for female participants (Herlitz & Lovén, 2013, but see Wolff et al., 2014). Numerically, women did perform slightly better for attractive and medium-attractive female compared to male faces in the current study, though this did not reach significance. It may be that the distinctiveness matching between male and female faces employed in our study attenuated the basis for the OGB. Another possibility could be related to the fact that attractiveness was a particularly salient dimension in the present set of faces, whereas gender category may have been relatively more salient in previous studies on the OGB. We speculate that relative to the present study, a more truncated range of attractiveness may have been presented in previous studies, which may have facilitated the occurrence of an OGB in the absence of other strong, socially relevant information. When, as in our case, clearly attractive and unattractive faces are presented in two thirds of the trials, this strong social signal may be perceived as more salient relative to gender in- versus out-group status. Overall, a female OGB may have been obscured by the addition of a strong attractiveness manipulation.

We did not find an overall memory advantage for women as previously reported (Herlitz & Lovén, 2013). Speculatively, men may have benefited from the current experimental context, with a higher frequency of attractive faces compared to everyday life. This may have selectively boosted their performance, thus further levelling out overall memory performance between men and women in our sample. In fact, orienting to socially relevant facial expressions in an emotional encoding task can improve men's recognition performance (Fulton, Bulluck, & Hertzog, 2015). It has been proposed that an instruction to focus on socially relevant information induces a processing style intuitively used by women, thus shifting men's processing strategy more towards perceptual detail, local features, and/or focussing on more diagnostic regions. The current experimental setting, with increased numbers of attractive faces relative to daily-life, may have encouraged similar processing strategies in women and men, and increased performance in male participants accordingly. Of relevance, it has been observed that men value physical attractiveness more than women do (Meltzer et al., 2014).

The present electrophysiological data replicated previously reported attractiveness effects in the occipito-temporal P2 (Wiese, Altmann, et al., 2014; Study 1). Specifically, attractiveness effects were more prominent during test than during learning, a finding that could relate to task factors such as more efficient processing of attractiveness at test, when no prior categorization of the faces according to gender was necessary (cf. Wiese, Altmann, et al., 2014, for a similar argument). At test, we found larger P2 amplitudes for medium-attractive faces compared to the other attractiveness conditions over the right hemisphere. Importantly, this pattern is in line with a frequency account of the P2 that predicts greater positivity in response to more commonly encountered medium-attractive faces.

Further, less positive P2 amplitudes for hits compared to correct rejections were observed for female but not male faces over the right hemisphere. As a larger negativity for hits than correct rejections was found in the subsequent N250 for both female and male faces (although more pronounced in the former condition, see below), this P2 pattern could reflect the same underlying process that may have started earlier for female faces (see discussion of the N250/EPN below).

Of note, our data do not provide support for the idea that the P2 reflects social in-group/out-group tagging or, as suggested by Wolff et al. (2014), a potential neural correlate of the OGB. Own-gender faces did not elicit larger P2 amplitudes, not even the most gender-typical, i.e. attractive faces. While this is in line with the absence of an OGB in behaviour, it does not necessarily rule out social categorization effects pertaining to memory functions for the P2 more generally (Stahl et al., 2008). The only other P2 effect of note was a larger amplitude for male compared to female faces during learning. Although prominent P2 components have been described during facial gender categorization tasks (Mouchetant-Rostaing & Giard, 2003; Mouchetant-Rostaing, Giard, Bentin, Aguera, & Pernier, 2000), we are unaware that this particular effect has been described before. In fact, Wolff et al. (2014) and more recently also Welling, Bestelmeyer, Jones, DeBruine, and Allan (2017) found larger P2 components for *female* faces in a studies that did not control for distinctiveness. To date, providing an unequivocal interpretation of these partly conflicting findings is difficult, as gender effects in the P2 are poorly understood and merit further examination.

During learning, whereas N250/EPN amplitudes for female faces were more negative for attractive and medium-attractive compared to unattractive faces, for male faces, only attractive faces elicited increased negativity compared to both medium- and unattractive faces. Although it is not entirely clear why the pattern for male and female faces was slightly different, similar attractiveness effects have been found before in Wiese, Altmann, et al. (2014). We broadly interpret these attractiveness effects in terms of an EPN component that may reflect tagging of affectively relevant material preceding in-depth emotional processing (Schupp et al., 2004). Possibly then, the increased negativity for medium-attractive female faces relates to the more positive valence ratings they received compared to male medium-attractive faces.

At test, we observed the typical finding of an increased negativity for hits compared to correct rejections, which we interpret as an enhanced N250 that reflects the transient activation of facial representations for recognition (e.g. Eimer et al., 2012; Schweinberger & Neumann, 2016). This N250 effect was larger for female than for male faces over the right hemisphere, potentially indicating more pronounced activation of such representations for female faces, independent of participant gender. Based on previous reports of an OGB in female participants (Herlitz & Lovén, 2013), one might have expected enhanced representational processing of female faces in female participants only. We speculate that the high frequency of attractive (and unattractive) faces may have prompted men to shift their processing style towards a female default strategy by focussing on emotionally relevant content during encoding (Fulton et al., 2015), possibly resulting in similar N250 response type effects in both participant groups. Nevertheless, we note that larger N250 response type effects for female compared to male faces were not paralleled by analogously larger *d'*-scores for female faces. Finally, it is remarkable that the larger N250 responses for hits than correct rejections were independent of facial attractiveness, suggesting relative independence of mnemonic and affective processing, and thus two different mechanisms driving the N250 and EPN.

During learning, we also found an attractiveness effect in the early LPC, which was largest for attractive and smallest for unattractive faces. A potentially related late positive potential has been suggested to reflect sustained emotional processing triggered by the tagging procedure reflected in the EPN (Schupp et al., 2000). Accordingly, this effect could reflect more elaborated affective processing of attractive faces during learning. Further, the early LPC time window exhibited an interaction between attractiveness, face and participant gender. More specifically, we observed an increased frontal positivity for medium-attractive female compared to male faces, but in male participants only. This effect could be reminiscent of increased frontal LPC responses in men for (attractive) opposite gender faces in a covert orienting paradigm reported by van Hooff et al. (2011), which were thought to reflect more motivated attention to attractive opposite-sex faces in men. Given that the present early frontal LPC was generally enhanced for attractive faces, we suggest that men process medium-attractive female faces as relatively more attractive then medium-attractive male faces. In the subsequent late LPC time window (500-700 ms), these participant gender effects had disappeared.

At test we found prominent but slightly different patterns of attractiveness effects for the early (300-500 ms) and late (500-700 ms) LPC time window. Specifically, the early LPC was consistently larger for attractive faces compared to medium and unattractive faces, particularly over left and midline electrodes. By contrast, attractive and unattractive faces elicited similar late LPC responses, whereas medium-attractive faces elicited smaller LPC responses compared to the other two attractiveness conditions. We suggest that only positive faces are more attended to in the early time window, but both ‘unusual’ face categories, i.e. attractive and unattractive faces, are processed more in-depth at the later stage. In both early and late LPC time windows, we found clear old-new effects with more positive amplitudes to hits than correct rejections. Importantly, old-new effects in both time segments were similar across attractiveness conditions, suggesting that the mnemonic processes reflected in both LPC time windows operate relatively independently from the processing of facial attractiveness (see also Wiese, Altmann, et al., 2014). Of note, we found larger old-new effects for female faces, independent of participant gender. Thus, familiarity and recollection-related processes may be more pronounced for female faces, but at the same time strong enough for male faces to support correct recognition.

In conclusion, the present study is the first to investigate memory effects of facial attractiveness and their potential modulation by face and participant gender. While behavioural results did not indicate an OGB, a finding of better memory for unattractive compared to attractive faces, and poorest memory for medium-attractive faces replicated earlier findings. Poor memory for medium-attractive faces could reflect increased cluster density in face space for this most frequently encountered category. In line with this interpretation, larger occipito-temporal P2 amplitudes were found for medium-attractive than both attractive and unattractive faces. Moreover, memory effects in both the N250 and the subsequent central-parietal old/new effect were clearly present, but were similar across attractiveness conditions and participant groups. We therefore propose that memory processes reflected in these ERP components are relatively independent from mechanisms mediating the processing of facial attractiveness.

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Table 1: Rating data for the stimulus set employed in the recognition experiment.

Condition	**Attractiveness**	**Deviation**	**FITC**	**Valence**	**Arousal**	**Gender Typicality**	**Trust-worthiness**	**Dominance**	**Perceived Age**
	M ± *SD*	*M* ± *SD*	*M* ± *SD*	*M* ± *SD*	*M* ± *SD*	*M* ± *SD*	*M* ± *SD*	*M* ± *SD*	*M* ± *SD*
attractive female	4.41 ± 0.33	3.25 ± 0.52	3.85 ± 0.63	5.84 ± 0.58	4.85 ± 0.74	2.05 ± 0.29	3.83 ± 0.34	3.62 ± 0.50	26.88 ± 2.24
attractive male	4.37 ± 0.27	3.25 ± 0.46	3.91 ± 0.45	5.52 ± 0.43	4.66 ± 0.54	2.06 ± 0.40	3.56 ± 0.43	4.19 ± 0.48	30.19 ± 3.28
medium-attractive female	3.55 ± 0.27	3.16 ± 0.46	3.13 ± 0.48	5.21 ± 0.49	3.98 ± 0.55	1.57 ± 0.30	3.63 ± 0.31	3.28 ± 0.37	28.48 ± 2.56
medium-attractive male	3.49 ± 0.26	3.05 ± 0.40	3.15 ± 0.51	4.92 ± 0.46	3.86 ± 0.49	1.79 ± 0.43	3.37 ± 0.34	3.58 ± 0.44	28.83 ± 3.72
unattractive female	2.45 ± 0.39	3.23 ± 0.55	2.95 ± 0.59	4.09 ± 0.59	3.43 ± 0.59	1.09 ± 0.48	3.00 ± 0.41	2.90 ± 0.46	32.91 ± 4.14
unattractive male	2.48 ± 0.35	3.15 ± 0.58	2.99 ± 0.58	4.07 ± 0.56	3.55 ± 0.54	1.76 ± 0.35	2.89 ± 0.41	3.17 ± 0.56	31.92 ± 5.13
Scale	*1 = very unattractive* *6 = very attractive*	*1 = very typical* *6 = very atypical*	*1 = very low distinctive* *6 = very distinctive*	*1 = very negative* *9 = very positive*	*1 = low arousal* *9 = high arousal*	*0 = very atypical* *3 = very typical*	*1 = very un-trustworthy* *6 = very trustworthy*	*1 = very submissive* *6 = very dominant*	*years*

Table 2: Statistics for rating differences in the stimulus set employed in the recognition experiment as tested by Mann-Whitney-U tests.

Stimulus Group	**Attractiveness**	**Deviation**	**FITC**	**Valence**	**Arousal**	**Gender Typicality**	**Trust-worthiness**	**Dominance**	**Perceived Age**
	U; *p*	*U*; *p*	*U*; *p*	*U*; *p*	*U*; *p*	*U*; *p*	*U*; *p*	*U*; *p*	*U*; *p*
Attractiveness*									
attractive vs. medium	0.000; <.001	16511.00; <.003	6387.50; <.001	8093.00; <.001	6173.50; <.001	8277.500; <.001	14331.00; <.001	10277.00; <.001	19635.00; .752
attractive vs. unattractive	0.000; <.001	17924.50; .073	5064.50; <.001	868.50; <.001	2822.50; <.001	5477.50; <.001	4002.00; <.0010	5326.50; <.001	10230.50; <.001
medium vs. unattractive	0.000; <.001	18870.0; .328	15074.0; <.001	3971.50; <.001	10569.50; <.001	14254.0; <.001	6190.0; <.001	10667.0; <.001	10380.0; <.001
									*all *df* = 398
Face gender: female vs. male °									
attractive	4789.50; .607	4863.00; .738	4533.00; .254	3394.50; <.001	4328.50; .101	4482.00; .205	3212.50; <.001	2102.00; <.001	2072.00; <.001
medium	4353.50; .114	4539.00; .260	4875.50; .761	3253.50; <.001	4501.00; .223	2735.50; <.001	2952.00; <.001	2983.50; <.001	4786.50; .602
unattractive	4861.50; .735	4500.50; .222	4674.50; .426	4896.00; .799	4279.50; .078	860.00; <.001	4050.00; .020	3564.50; <.001	4411.00; .150
									°all *df* = 198

Table 3: Behavioural data from the main experiment.

		Study phase						Test phase											
		RT			*ACC*			*d'*			*C*			Hits			CR		
		M	±	*SD*	*M*	±	*SD*	*M*	±	*SD*	*M*	±	*SD*	*M*	±	*SD*	*M*	±	*SD*
female participants																			
attractive	female	817.415	±	161.670	0.981	±	0.034	1.028	±	0.462	0.070	±	0.378	0.659	±	0.138	0.700	±	0.142
	male	816.649	±	174.301	0.987	±	0.021	0.937	±	0.517	0.058	±	0.494	0.633	±	0.186	0.682	±	0.163
	both	817.032	±	166.392	0.984	±	0.021	0.983	±	0.430	0.064	±	0.355	0.646	±	0.162	0.691	±	0.152
medium-attractive	female	867.581	±	189.839	0.976	±	0.030	0.941	±	0.501	0.252	±	0.351	0.581	±	0.127	0.741	±	0.140
	male	857.420	±	181.864	0.967	±	0.031	0.866	±	0.489	0.349	±	0.413	0.530	±	0.159	0.756	±	0.139
	both	862.501	±	182.809	0.972	±	0.026	0.904	±	0.463	0.301	±	0.342	0.556	±	0.143	0.748	±	0.139
unattractive	female	912.780	±	170.347	0.894	±	0.044	1.195	±	0.474	0.144	±	0.265	0.663	±	0.133	0.761	±	0.096
	male	851.603	±	194.052	0.961	±	0.039	1.227	±	0.432	0.177	±	0.271	0.660	±	0.129	0.774	±	0.094
	both	882.192	±	176.712	0.928	±	0.030	1.211	±	0.427	0.160	±	0.250	0.661	±	0.131	0.768	±	0.095
male participants																			
attractive	female	969.974	±	249.921	0.978	±	0.021	1.221	±	0.600	0.130	±	0.344	0.675	±	0.123	0.743	±	0.150
	male	944.492	±	242.541	0.990	±	0.015	1.097	±	0.444	0.055	±	0.334	0.683	±	0.112	0.706	±	0.123
	both	957.233	±	242.708	0.984	±	0.012	1.159	±	0.490	0.092	±	0.309	0.679	±	0.118	0.724	±	0.137
medium-attractive	female	986.220	±	258.542	0.975	±	0.022	1.054	±	0.581	0.288	±	0.326	0.589	±	0.132	0.768	±	0.140
	male	993.391	±	230.103	0.965	±	0.031	0.996	±	0.568	0.254	±	0.329	0.591	±	0.127	0.750	±	0.139
	both	989.806	±	240.391	0.970	±	0.015	1.025	±	0.546	0.271	±	0.297	0.590	±	0.130	0.759	±	0.139
unattractive	female	1019.188	±	255.515	0.898	±	0.093	1.326	±	0.596	0.194	±	0.243	0.667	±	0.141	0.793	±	0.095
	male	977.970	±	242.291	0.960	±	0.030	1.388	±	0.475	0.155	±	0.196	0.698	±	0.106	0.792	±	0.089
	both	998.579	±	245.212	0.929	±	0.046	1.357	±	0.516	0.174	±	0.188	0.682	±	0.123	0.792	±	0.092

**RT* = Reaction Times, *ACC* = Accuracy

Table 4: Statistics from the recognition memory experiment.

Behavioural data							
Study phase	**Mean difference**	**95% confidence interval**					
Accuracy (in %)		**lower**	**upper**	**t**	**df**	**p**	**d_{av}**
Attractiveness x Face Gender							
female faces:							
attractive vs. medium-attractive	.00	.00	.01	1.14	39	.263	0.15
attractive vs. unattractive	.08	.06	.11	7.05	39	.000	1.67
medium-attractive vs. unattractive	.08	.06	.10	7.49	39	.000	1.62
male faces:							
attractive vs. medium-attractive	.02	.01	.03	5.72	39	.000	0.93
attractive vs. unattractive	.03	.02	.04	4.46	39	.000	1.07
medium-attractive vs. unattractive	.01	-.01	.02	.77	39	.447	0.17
female vs. male faces							
Attractive	-.01	-.02	.00	-1.76	39	.086	0.39
medium-attractive	.01	.00	.02	1.55	39	.129	0.34
Unattractive	-.06	-.09	-.04	-4.96	39	.000	1.21
Respone time (in ms)							
Attractiveness x Face Gender							
female faces:							
attractive vs. medium-attractive	-33.21	-59.01	-7.41	-2.60	39	.013	0.15
attractive vs. unattractive	-72.29	-96.74	-47.84	-5.98	39	.000	0.33
medium-attractive vs. unattractive	-39.08	-63.34	-14.83	-3.26	39	.002	0.17
male faces:							
attractive vs. medium-attractive	-44.84	-63.16	-26.51	-4.95	39	.000	0.21
attractive vs. unattractive	-34.22	-51.24	-17.19	-4.07	39	.000	0.15
medium-attractive vs. unattractive	10.62	-6.03	27.27	1.29	39	.205	0.05
female vs. male faces							
attractive	13.12	-8.70	34.95	1.22	39	.231	0.06
medium-attractive	1.49	-24.09	27.08	0.12	39	.907	0.01
unattractive	51.20	22.86	79.54	3.65	39	.001	0.23
Test phase							
Memory sensitivity d'							
Attractiveness							
attractive vs. medium-attractive	0.11	0.03	0.18	2.80	39	.008	0.22
attractive vs. unattractive	-0.21	-0.29	-0.14	-5.58	39	.000	0.45
medium-attractive vs. unattractive	-0.32	-0.40	-0.24	-8.40	39	.000	0.65

Response bias C							
Attractiveness							
attractive vs. medium-attractive	-0.21	-0.27	-0.15	-7.31	39	.000	0.64
attractive vs. unattractive	-0.09	-0.17	-0.01	-2.22	39	.032	0.32
medium-attractive vs. unattractive	0.12	0.05	0.19	3.39	39	.002	0.44
ERP data							
Study phase	**Mean difference**	**95% confidence interval**					
N250		**lower**	**upper**	**t**	**df**	**p**	**d_{av}**
Attractiveness x Face Gender							
female faces:							
attractive vs. medium-attractive	-0.08	-0.40	0.24	-0.51	39	.617	0.04
attractive vs. unattractive	-0.63	-0.96	-0.29	-3.76	39	.001	0.30
medium-attractive vs. unattractive	-0.55	-0.89	-0.21	-3.25	39	.002	0.26
male faces:							
attractive vs. medium-attractive	-0.31	-0.55	-0.07	-2.60	39	.013	0.16
attractive vs. unattractive	-0.31	-0.58	-0.04	-2.33	39	.025	0.16
medium-attractive vs. unattractive	0.00	-0.30	0.29	-0.01	39	.990	0.00
LPC (300-500)							
Attractiveness							
attractive vs. medium-attractive	0.19	0.02	0.37	2.27	39	.029	0.12
attractive vs. unattractive	0.51	0.26	0.76	4.12	39	.000	0.31
medium-attractive vs. unattractive	0.31	0.11	0.52	3.12	39	.003	0.18
Hemisphere x Attractiveness							
left hemisphere							
attractive vs. medium-attractive	0.18	-0.04	0.39	1.67	39	.102	0.11
attractive vs. unattractive	0.59	0.32	0.85	4.53	39	.000	0.35
medium-attractive vs. unattractive	0.41	0.19	0.62	3.86	39	.000	0.23
midline							
attractive vs. medium-attractive	0.31	0.06	0.55	2.52	39	.016	0.16
attractive vs. unattractive	0.71	0.41	1.02	4.70	39	.000	0.35
medium-attractive vs. unattractive	0.41	0.16	0.65	3.39	39	.002	0.19
right hemisphere							
attractive vs. medium-attractive	0.10	-0.08	0.28	1.13	39	.267	0.06
attractive vs. unattractive	0.23	-0.06	0.51	1.61	39	.116	0.13
medium-attractive vs. unattractive	0.13	-0.13	0.38	1.01	39	.319	0.07

Site x Attractiveness x Face Gender x Participants Gender							
for medium-attractive faces over frontal sites							
female participants							
female vs. male faces	0.24	-0.24	0.72	1.04	19	.309	0.10
male participants							
female vs. male faces	-0.60	-0.95	-0.24	-3.49	19	.002	0.28
LPC (500-700)							
Attractiveness							
attractive vs. medium-attractive	0.27	0.07	0.47	2.78	39	.008	0.17
attractive vs. unattractive	0.33	0.09	0.58	2.76	39	.009	0.20
medium-attractive vs. unattractive	0.06	-0.16	0.28	0.57	39	.569	0.04
Test phase							
P2							
Hemisphere x Attractiveness							
left hemisphere							
attractive vs. medium-attractive	-0.11	-0.34	0.12	-1.00	39	.325	0.06
attractive vs. unattractive	-0.06	-0.26	0.13	-0.65	39	.522	0.03
medium-attractive vs. unattractive	0.05	-0.14	0.25	0.53	39	.597	0.03
right hemisphere							
attractive vs. medium-attractive	-0.30	-0.56	-0.04	-2.38	39	.022	0.11
attractive vs. unattractive	0.17	-0.09	0.42	1.33	39	.191	0.06
medium-attractive vs. unattractive	0.47	0.24	0.69	4.14	39	.000	0.17
Response Type x Hemisphere x Face Gender							
right hemisphere							
Hits vs. CR: female faces	-0.55	-0.79	-0.30	-4.56	39	.000	0.20
Hits vs. CR: male faces	-0.07	-0.31	0.17	-0.58	39	.564	0.03
N250							
Attractiveness							
attractive vs. medium-attractive	-0.41	-0.63	-0.19	-3.79	39	.001	0.21
attractive vs. unattractive	-0.26	-0.43	-0.08	-2.91	39	.006	0.13
medium-attractive vs. unattractive	0.15	0.01	0.30	2.14	39	.039	0.07

Response Type x Face Gender							
Hits - CR: female vs. male faces							
over both hemispheres	0.37	0.04	0.70	2.24	39	.031	0.53
right hemisphere:	0.69	0.27	1.12	3.29	39	.002	0.82
LPC (300-500)							
Attractiveness							
attractive vs. medium-attractive	0.25	0.09	0.41	3.18	39	.003	0.14
attractive vs. unattractive	0.25	0.10	0.39	3.49	39	.001	0.14
medium-attractive vs. unattractive	0.00	-0.15	0.14	-0.04	39	.965	0.00
Hemisphere x Attractiveness							
left hemisphere:							
attractive vs. medium-attractive	0.24	0.07	0.41	2.91	39	.006	0.14
attractive vs. unattractive	0.24	0.10	0.37	3.53	39	.001	0.13
medium-attractive vs. unattractive	0.00	-0.18	0.17	-0.04	39	.969	0.00
midline:							
attractive vs. medium-attractive	0.40	0.19	0.61	3.88	39	.000	0.18
attractive vs. unattractive	0.37	0.18	0.55	4.02	39	.000	0.16
medium-attractive vs. unattractive	-0.03	-0.22	0.15	-0.35	39	.726	0.01
right hemisphere:							
attractive vs. medium-attractive	0.11	-0.07	0.30	1.23	39	.224	0.06
attractive vs. unattractive	0.14	-0.03	0.31	1.69	39	.099	0.08
medium-attractive vs. unattractive	0.03	-0.12	0.18	0.35	39	.725	0.01
Attractiveness x Site							
attractive vs. medium-attractive							
frontal vs. central	0.05	-0.16	0.26	0.46	39	.651	0.07
frontal vs. parietal	0.29	-0.03	0.61	1.83	39	.075	0.43
central vs. parietal	0.24	0.02	0.46	2.25	39	.030	0.39
attractive vs. unattractive							
frontal vs. central	-0.16	-0.33	0.00	-2.00	39	.053	0.26
frontal vs. parietal	-0.07	-0.33	0.20	-0.51	39	.613	0.12
central vs. parietal	0.10	-0.11	0.31	0.93	39	.357	0.17
frontal vs. central							
medium-attractive vs. unattractive							
frontal vs. central	-0.21	-0.41	-0.01	-2.14	39	.039	0.34
frontal vs. parietal	-0.36	-0.70	-0.02	-2.13	39	.040	0.53
central vs. parietal	-0.15	-0.35	0.06	-1.46	39	.153	0.24

Laterality x Response Type x Face Gender x Participant Gender							
for male faces in male participants							
Hits - CR:							
left hemisphere vs. midline	-0.40	-0.61	-0.19	-3.95	19	.001	0.63
left hemisphere vs. right hemisphere	-0.23	-0.44	-0.02	-2.26	19	.036	0.49
midline vs. right hemisphere	0.17	-0.06	0.41	1.55	19	.137	0.30
LPC (500-700)							
Attractiveness							
attractive vs. medium-attractive	0.40	0.23	0.57	4.84	39	.000	0.20
attractive vs. unattractive	0.14	-0.04	0.31	1.61	39	.115	0.07
medium-attractive vs. unattractive	-0.27	-0.43	-0.10	-3.27	39	.002	0.13
Face Gender x Site							
female vs. male faces							
frontal	0.12	-0.09	0.33	1.19	39	.243	0.05
central	-0.18	-0.38	0.02	-1.81	39	.078	0.08
parietal	-0.31	-0.52	-0.09	-2.83	39	.007	0.13

5 STUDY 3

Will you miss me? – Attractiveness influences Dm effects during encoding parallel to later recognition performance.

5.1 Abstract

Previous studies have shown that attractive faces are less well remembered than unattractive faces, and that memory is even worse for medium-attractive faces—irrespective of distinctiveness. To investigate whether these differences in face recognition are rooted in encoding, we inspected *d*ifferences due to subsequent *m*emory (Dm) effects in terms of EEG activity during learning for later remembered vs. forgotten items. We tested memory of 20 participants for attractive, medium-attractive and unattractive faces in an old/new recognition task while simultaneously recording EEG. Memory was best for unattractive faces, followed by attractive and medium-attractive faces. For medium-attractive faces only, early Dm effects were found in the occipito-temporal P2 (200-260 ms), a component thought to reflect aspects of elaborate perceptual analysis, with larger amplitudes for subsequent hits than misses. In the N250 time range (260-400 ms), Dm effects emerged for medium-attractive and attractive faces, but not for unattractive faces. Finally, all faces yielded Dm effects in the late positive component (LPC, 500-700 ms) indicating elaborative mnemonic processing. We conclude that poorer memory performance for medium-attractive, and to a lesser extent for attractive faces, may already be rooted in early perceptual stages of encoding. Encoding of unattractive faces may be more efficient and effortless during these stages, indexed by absent Dm effects.

Keywords: Attractiveness, memory encoding, Dm effects, event-related potentials, faces

5.2 Introduction

Attractiveness reflects a pervasive social signal that is automatically assessed (Sui & Liu, 2009), and draws attention (Olson & Marshuetz, 2005). Attractiveness also impacts face memory over and above the influence of perceived distinctiveness (Bartlett et al., 1984). In a series of experiments in which we controlled distinctiveness by careful matching during stimulus selection, we found consistently better face memory for unattractive over attractive faces (Wiese, Altmann, et al., 2014), and even worse memory for medium-attractive faces (see Study 1.). Of note, stimulus and participants' gender do not have an impact on this effect, arguing against social in-group or mating motivation as driving factors (see Study 2). The present study aims to further investigate the role of attractiveness on face memory by testing whether memory differences measured at test are rooted in preceding stages of memory processing, i.e. during encoding.

Encoding – the formation of a engram during learning – relies on at least two successive neurocognitive mechanisms: 1) the transformation of sensory input into internal representations, and 2) the relay of these representations into enduring traces for later successful retrieval (Paller & Wagner, 2002). For the encoding of faces, the first of these mechanisms can be understood in terms of the Multidimensional Face Space model (MDFS; Valentine et al., 2015) – a conception of a mental storage wherein previously seen faces are encrypted along relevant dimensions reflecting perceptual characteristics of faces for later recognition – akin to an internal visual data matrix. By cumulating experience with faces, this storage system successively optimizes its dimensions to discriminate between individual identities commonly seen in daily life. Thus, our MDFS is gradually shaped to efficiently encode the most informative, i.e. distinguishing characteristics of those faces we encounter regularly.

Ideally, this encryption process should allow for easy differentiation of new identities from any previously stored exemplar. At the same time, discriminating between previously seen and novel faces is harder for similar facial representations which cluster tightly together. In line with the idea that face memory is inversely related to density of face representations in an MDFS, we previously reported a pattern of less accurate memory for attractive relative to unattractive faces, and even worse memory for medium-attractive faces. Representations of unattractive faces are distributed widely within MDFS, whereas attractive faces appear more similar to each other and thus cluster more closely together, as shown by multidimensional scaling (Potter et al., 2007). Moreover, medium-attractive faces may be particularly tightly clustered as this is by far the most frequently encountered group in everyday life (for a related discussion see Burton & Vokey, 1998). The sheer number of medium-attractive faces requires finely tuned encryption, i.e. garnering more fine-grained information for forming sufficiently distinct engrams to distinguish between new and pre-existing face representations. Thus, differentiating between identities may be relatively easy for unattractive faces, but harder for attractive and medium-attractive faces.

Of particular relevance for the present study, event-related potentials (ERPs) derived from scalp-recorded EEG provide the means to directly inspect encoding-related neural activity that differentiates between subsequently remembered and forgotten items. ERP differences between subsequent hits and subsequent misses, termed ‘*D*ifferential neural activity based on later *m*emory’, or ‘Dm’ (Paller et al., 1987), are widely distributed in scalp topography and extend over a considerable time period between 250 and 800 ms post-stimulus (Sommer et al., 1991). The scalp topography of the Dm effect elicited by faces is more posterior relative to verbal material, and is lateralized towards the right hemisphere, thus suggesting some degree of domain-specificity (Johnson Jr, 1995; Sommer et al., 1997; Sommer et al., 1991).

The magnitude of Dm appears to depend, at least in part, on the strength of the subsequent memory. For verbal material, Dm is reportedly larger when calculated on the basis of subsequent recall compared to subsequent recognition (Paller, McCarthy, & Wood, 1988). More pronounced Dm effects have also been reported for ‘deeper’ semantic encoding tasks (`Is the referent of the word a living thing?') compared to ‘shallow’ tasks (`Are the first and last letters of the word in alphabetical order?'; Paller et al., 1987). Moreover, Dm effects in later time segments (500 to 900 ms) are increased for those participants using elaborative rehearsal strategies that rely on previous knowledge, compared to those who engage in rote rehearsal such as simply repeating a word mentally (Fabiani et al., 1990; Karis, Fabiani, & Donchin, 1984). Taken together, these effects suggest that Dm is diminished for ‘easier’ tasks or ‘effortless’ processing, and increased for harder and more elaborate tasks.

In line with this suggestion, experts for certain classes of objects (e.g., cars, birds) show smaller Dm effects for expertise-domain items, while their Dm effect does not differ from novices in non-expert domains (Herzmann & Curran, 2011). Similarly, Herzmann, Willenbockel, Tanaka, and Curran (2011) found smaller Dm effects for own- relative to other-race faces in Caucasian participants, suggesting that less neural processing is required for successful encoding of own-race faces due to enhanced perceptual expertise. It is assumed that these expertise effects reflect neural efficiency also indexed by less encoding-related fMRI activation for participants demonstrating high as compared to low memory performance (Heinze et al., 2006).

Previous research has furthermore identified several consecutive ERP components reflecting a series of functional processing stages involved in face recognition (Schweinberger & Neumann, 2016). As we assume differences in the relative contribution of perceptual and affective processing for encoding attractive, medium-attractive and unattractive faces (see Study1), these differences should manifest as shifts in the relative size of Dm effects over time. For instance, the occipito-temporal P2 component, peaking at around 200-260 ms, has been implicated in the encoding of a face's second-order spatial configuration relative to a prototype (Latinus & Taylor, 2006), which may be crucial to differentiate between competing face representations at initial encoding. A recent study further established that the P2 can serve as an indicator of ongoing renormalization of the visual system following adaptation (Kloth et al., 2017). The P2 has also been interpreted to reflect perceived distinctiveness of faces (Kaufmann & Schweinberger, 2012; Schulz, Kaufmann, Kurt, et al., 2012; Stahl et al., 2008). However, we recently found increased P2 amplitudes for medium-attractive over attractive and unattractive faces, in sets that were closely matched for perceived distinctiveness. We therefore suggested that the P2 is sensitive to the frequency with which a particular face category is encountered (see Study 1). If so, the P2 may also reflect local cluster density of representations in MDFS — with larger amplitudes suggestive of higher numbers of potentially competing engrams in close 'perceptual' vicinity. In line with this idea, larger P2 amplitudes for medium-attractive faces accompanied relatively lower memory for this face category.

Previous work examining Dm effects accompanying face memory biases yielded relatively inconsistent results: In one study, Dm effects in the P2 were found to be larger for own-race compared with other-race faces, with more positive amplitudes for subsequently forgotten relative to subsequently remembered own-race faces, and the opposite pattern for other-race faces (Lucas, Chiao, & Paller, 2011). More recently, Wolff et al. (2014) report Dm effects in the P2, with more positive amplitudes for subsequently remembered versus forgotten male faces that was accompanied by an own-gender bias in recognition memory in male participants. Of note, this pattern was additionally modulated by rated distinctiveness and gender, and P2 amplitudes were generally larger for less distinctive faces. For the present purpose it will be of particular interest, whether Dm effects are still seen in the P2 when perceived distinctiveness is controlled. Taken together, the P2 may be a promising component to investigate the effortful encoding operations that are needed to generate sufficiently specific engrams against the competition of numerous pre-existing exemplars. To the extent that the P2 may be seen as a proxy measure for representational density of stored memory traces, more activation at this processing stage may be required for medium-attractive and attractive faces. Thus, we expect larger Dm effects for these categories compared to unattractive faces.

Subsequent to P2, an occipito-temporal negative deflection is observed that can reflect two functionally different ERP components. First, the so-called N250 (250-400 ms) is larger for learned or repeated relative to novel facial identities at test, and hence is thought to reflect the activation of visual memory traces of individual faces (Eimer et al., 2012; Schweinberger, Huddy, & Burton, 2004; Schweinberger et al., 2002; Tanaka et al., 2006). Second, previous studies reported more negative amplitudes in this time range for attractive relative to unattractive faces, and interpreted this effect in terms of the Early Posterior Negativity (EPN; Werheid et al., 2007; Wiese, Altmann, et al., 2014). The EPN is thought to index reflexive attention to, and an initial processing of, affective stimuli. This ‘emotional tagging’ (Schupp et al., 2007) is enlarged for emotional relative to neutral faces (Junghöfer et al., 2001; Rellecke et al., 2012; Schupp et al., 2004).

Due to the topographical and temporal overlap of N250 and EPN effects, their time range may represent a processing stage at which emotional processing and face recognition functionally interact. Notably, evidence suggests at least some contribution of affective relevance to the attractiveness effect on face memory: in two recent studies the difference in memory performance between attractive and medium-attractive faces disappeared when emotional content were taken into account (see Studies 1 and 2). Another study found a correlation between the EPN attractiveness effect during encoding and the later memory costs for attractive relative to unattractive faces (Wiese, Altmann, et al., 2014). If mnemonic and affective processing indeed interacted already during encoding, we would expect some modulation of the Dm effect in the N250/EPN window in accordance with behavioural performance differences for attractive, medium-attractive and unattractive faces.

Finally, as Dm effects for faces have been most consistently reported in the Late Positive Component (LPC; 300 to 700ms), which is maximal at parietal scalp sites (Sommer, Heinz, Leuthold, Matt, & Schweinberger, 1995; Sommer et al., 1997; Sommer et al., 1991), we expected to find a reliable Dm effect for all faces in this component. We had no specific theoretical predictions for this component related to attractiveness, and therefore did not predict prominent modulations of this LPC Dm effect by attractiveness.

Taken together, while we expected increased processing effort for medium-attractive (and, to a smaller extent, also for attractive) faces to manifest at perceptual stages reflected in the P2, Dm effects for unattractive faces should only emerge at later processing stages. To test these predictions, we conducted a recognition memory experiment for attractive, medium-attractive and unattractive faces with alternating study and test phases. Moreover, to attenuate influences of facial typicality on memory, we matched perceived distinctiveness as detailed in previous reports (see Studies 1 and 2).

5.3 Methods

Participants

Twenty participants (18 – 31 years; *M* = 21.8 ± 4.0 *SD* years; 10 female) contributed the data for this study. Six additional participants were excluded from analyses due to excessive EEG alpha activity (2 cases), or insufficient trial numbers (< 14) for ERP averaging (4 cases). All participants reported normal or corrected to normal vision and were right-handed as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). None of the participants reported neurological or psychiatric disorders. Participants received either course credit or monetary reimbursement after testing. All participants gave written informed consent, and the experiment was conducted in accordance with Declaration of Helsinki and the Code of Human Research Ethics by the British Psychological Society (2014 version).

Stimuli

Six hundred faces, 300 of each face gender, rated as either unattractive (*M* = 2.47 ± 0.37 *SD*), medium-attractive (*M* = 3.52 ± 0.26 *SD*) or attractive (*M* = 4.39 ± 0.37 *SD*, *N* = 100, respectively) on a 1-6 point scale were chosen from a large stimulus pool (described in Study 1; see detailed rating values in Table 1 of this section). Pictures were cropped to show the face without clothing or hair line in front of a black background, and were standardized in size to 275 x 250 pixels, corresponding to viewing angles of approximately 4.6° x 4.4° at a distance of 90 cm. Luminance and contrast (without background) were equated to match the overall mean luminance of all faces by employing gradation curve adjustments (mean luminance: 145 RGB units, mean contrast: 50 RGB units). Images were presented on a computer monitor with a mean luminance of 26.84 cd/m².

Rating differences between stimulus conditions were analysed by means of Mood's median tests (for more than 2 levels) and Mann-Whitney-U tests (see Table 2). As expected, faces of the three attractiveness conditions differed significantly with respect to attractiveness, $\chi^2(df = 2, N = 600) = 400.160$; $p < .001$; $V = 0.577$, but not deviation-based distinctiveness, $\chi^2(df = 2, N = 600) = 5.854$; $p = .054$; $V = 0.070$. Of note, male and female faces did not differ with respect to attractiveness and deviation-based distinctiveness — neither on the level of the entire set, all $p > .254$, nor within attractiveness conditions, all $p > .078$.

Experimental design and procedure

Participants were seated in an electrically shielded and sound-attenuated cabin (400-A-CT-Special, Industrial Acoustics, Niederkrüchten, Germany), with their head in a chin rest approximately 90 cm away from a computer monitor. Each session began with a short practice block that was later excluded from data analysis. The main experiment consisted of 10 blocks, each divided into a study and a subsequent test phase. During each study phase 30 faces (across blocks, 50% female, and equal numbers from the three attractiveness conditions) were presented in randomized order. We deliberately increased the number of study faces per block relative to our previous experiments to increase task difficulty and provoke misses at test. Participants were instructed to memorize these faces and categorize them according to gender via left and right index finger key presses. Speed and accuracy were emphasized. Each study trial consisted of a fixation cross (500 ms), followed by a face stimulus (5000 ms) and a final blank screen (500 ms). Study and test phases were separated by fixed breaks of 30 s duration. In each of the subsequent test phases, those 30 faces shown in the immediately preceding study phase and 30 new faces (across blocks, 50% female, equal numbers of attractive, medium-attractive, and unattractive faces) were presented for 2000 ms each, in randomized order. As in the study phase, each test phase trial started with an initial fixation cross (500 ms) and ended with a blank screen (500 ms). Participants were instructed to indicate via left and right index finger key presses whether the faces had been presented in the preceding study phase ('old') or not ('new'). Speed and accuracy were emphasized. Key allocation and assignment of faces to studied or non-studied conditions was counterbalanced across participants. Due to a balancing error in key allocations in two blocks in one of the experimental versions, we excluded data for those two blocks for all participants.

For the study phases, mean correct reaction times (RT) and accuracies served as dependent variables. Behavioural test phase data was analysed according to signal detection theory (Green & Swets, 1966). Trials were sorted into hits (correctly identified studied faces), misses (studied faces incorrectly classified as new), correct rejections (CR, new faces correctly identified as new), and false alarms (FA, new faces incorrectly classified as studied), separately for attractive, medium-attractive, and unattractive faces. Measures of sensitivity (d') and response bias (C) were calculated. Statistical analyses were performed by means of paired samples *t*-tests and repeated-measures analyses of variance (ANOVAs), with epsilon corrections for heterogeneity of covariances performed via the Huynh-Feldt procedure where appropriate. Cohen's d_{av} was calculated using the average standard deviation of the compared variables (Lakens, 2013).

EEG recording and analyses

EEG was recorded from 32 active sintered Ag/Ag-Cl electrodes using a Biosemi Active II system (BioSemi, Amsterdam, Netherlands). Note that BioSemi systems work with a "zero-Ref" set-up with ground and reference electrodes replaced by a CMS/DRL circuit (cf. www.biosemi.com/faq/cms/drl.htm). EEG was recorded continuously with a 512-Hz sample rate from DC to 155 Hz. Recording sites corresponded to an extended version of the 10-20-system (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, and I2).

Blinks were corrected using the algorithm implemented in BESA 5.1.8 (MEGIS Software GmbH, Berg & Scherg, 1994). The EEG was segmented from −200 until 1000 ms relative to stimulus onset, with the first 200 ms serving as baseline. Artefact rejection was performed using an amplitude threshold of 100 µV and a gradient criterion of 50 µV. Only trials with correct task responses during study were analysed. The remaining trials were recalculated to average reference, averaged according to experimental condition and digitally low-pass filtered at 40 Hz (12 db/oct, zero phase shift). During the learning phases, ERP waveforms for subsequent hits and subsequent misses were calculated based on later recognition performance at test for attractive, medium-attractive, and unattractive faces, respectively. The minimum number of trials for an individual participant in any of these conditions was 14 (mean number of trials = 37.5 ± 3.6 *SD*).

Mean amplitudes of the P1 (100 - 140 ms) were analysed at O1/O2, N170 (150 - 190 ms) at P9/P10, and P2 (200 - 260 ms), as well as N250/EPN (260 - 400 ms) at electrode sites P7/P8. The early and late LPC (300 – 500 ms, 500 – 700 ms) were inspected at electrodes Fz, Cz, Pz, F3, F4, C3, C4, P3, and P4. Below, we only report main effects and interactions containing the attractiveness or subsequent memory factors.

5.4 Results

5.4.1 Behavioural results

Please see Table 3 for an overview of descriptive data, and Table 4 for statistical indices of t-test comparisons. During learning, a main effect of Attractiveness was found for accuracy ($F[2,38] = 10.208$; $p < .001$; $\eta_p^2 = .349$) as well as reaction times ($F[2,38] = 5.173$; $p = .022$; $\eta_p^2 = .214$; $\varepsilon = .693$) in the gender categorization task. Unattractive faces were less accurately categorized according to gender than both attractive, and medium attractive faces, which in turn did not differ. Furthermore, participants categorized unattractive faces more slowly than attractive faces. Reaction times for medium-attractive faces fell in-between the other groups, and did not differ significantly from either.

At test, analyses of d’ revealed a main effect of Attractiveness ($F[2,76] = 28.526$; $p < .001$; $\eta_p^2 = .600$), with more accurate memory for unattractive as compared to both attractive faces and medium-attractive faces. Attractive faces were numerically better remembered than medium-attractive faces, but this was only seen as a statistical trend. Analyses of response bias measure C also yielded a main effect of Attractiveness ($F[2,76] = 8.340$; $p = .001$; $\eta_p^2 = .305$; $\varepsilon = .693$) that indicated less conservative responses for attractive faces, relative to both medium-attractive, and unattractive faces, which in turn did not differ.

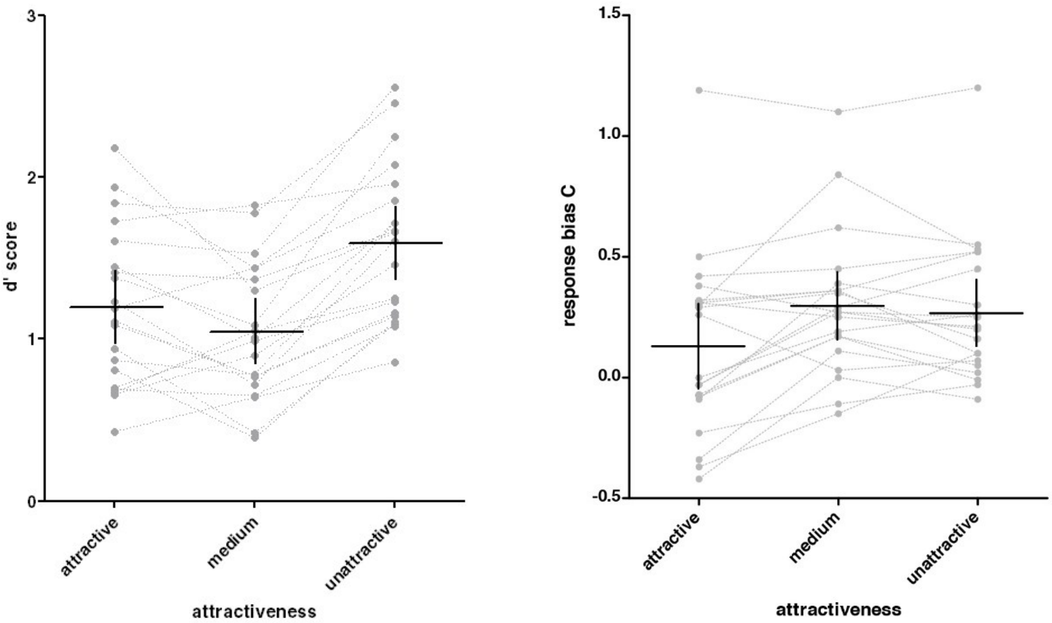


Figure 1: Behavioural measures d’ (left) and response bias C (right) from the recognition experiment. Grey dots connected by broken lines indicate data collected from individual participants. Error bars depict 95% confidence intervals.

5.4.2 Event-related potentials

P1 and N170

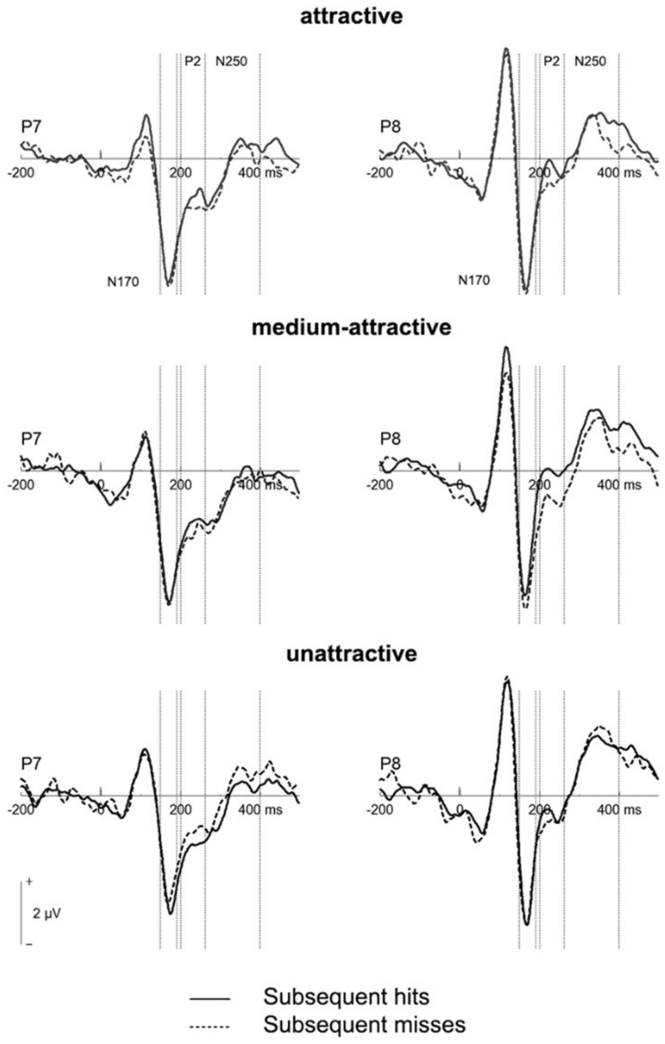
No significant results were found for these components.

P2

A repeated measures-ANOVA with the within-subject factors Hemisphere (left, right), Subsequent Memory (subsequent hits, subsequent misses), and Attractiveness (unattractive, medium-attractive, attractive) yielded a trend for a main effect of Subsequent Memory ($F[1,19] = 4.337$; $p = .051$; $\eta_p^2 = .186$), with more positive amplitudes for subsequent hits compared to subsequent misses. Importantly, there was a significant interaction of Subsequent Memory by Attractiveness ($F[2,38] = 5.658$; $p = .007$; $\eta_p^2 = .229$), indicating a larger Dm effect for medium- compared to unattractive faces, and a trend for a larger Dm effect for attractive compared to unattractive faces. The Dm effect for attractive faces was numerically smaller, yet not statistically different compared to medium-attractive faces (see Table 4, and Figure 2).

N250/EPN

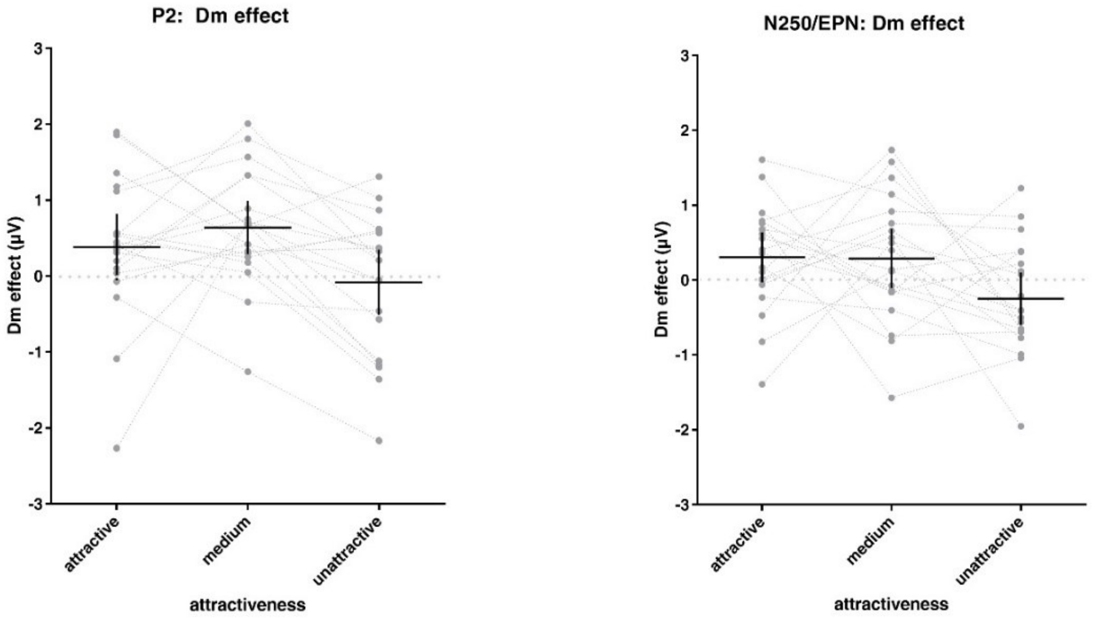
A main effect of Attractiveness ($F[2,38] = 5.712$; $p = .011$; $\eta_p^2 = .231$; $\varepsilon = .821$), with less negative-going amplitudes for unattractive faces than the other two face categories, was further qualified by an interaction of Subsequent Memory by Attractiveness ($F[2,38] = 3.335$; $p = .046$; $\eta_p^2 = .149$). *T*-tests indicated a smaller Dm effect for unattractive faces compared to both attractive and medium-attractive faces, which in turn did not differ (see Table 4, and Figure 2).



a)

Figure 2: (a) Grand mean ERPs from the learning phases of the recognition memory experiment at occipito-temporal electrodes. Dashed lines indicate N170, P2 and N250/EPN time ranges. (b) Dm effect for P2 and N250/EPN. Error bars depict 95% confidence intervals**.**

b)



Early LPC (300-500 ms)

Early and late LPC Dm effects can be seen in Figure 3, which suggests larger Dm effects over the right than left hemisphere, and also larger Dm effects at more posterior than anterior electrodes. An analysis with the additional factor Site (frontal, central, parietal) and Laterality (left, midline, right) replacing the factor hemisphere yielded a significant interaction of Subsequent Memory by Laterality ($F[2,38] = 6.097$; $p = .011$; $\eta_p^2 = .243$; $\varepsilon = .744$). *T*-tests revealed that Dm effects, with larger amplitudes for subsequent hits vs. subsequent misses, were significantly smaller over the left hemisphere compared to midline, and - to a smaller degree – to right-hemispheric electrodes, which in turn did not differ. No main effect or interactions with Attractiveness were found (all $p > .272$; all $\eta_p^2 < .065$).

Late LPC (500-700 ms)

A main effect of Subsequent Memory ($F[1,19] = 6.973$; $p = .016$; $\eta_p^2 = .268$), with larger amplitudes for subsequent hits vs. subsequent misses, was qualified by a two-way interaction of Subsequent Memory by Site ($F[2,38] = 5.573$; $p = .013$; $\eta_p^2 = .227$; $\varepsilon = .810$), indicating larger Dm effects at more posterior electrode locations. Furthermore, the effect of Subsequent Memory interacted with Laterality ($F[2,38] = 10.915$; $p < .001$; $\eta_p^2 = .365$), and was smaller over the left hemisphere compared to midline and right-hemispheric electrodes, which in turn did not differ. No main effect or interactions with Attractiveness were found (all $p > .368$; all $\eta_p^2 < .051$).

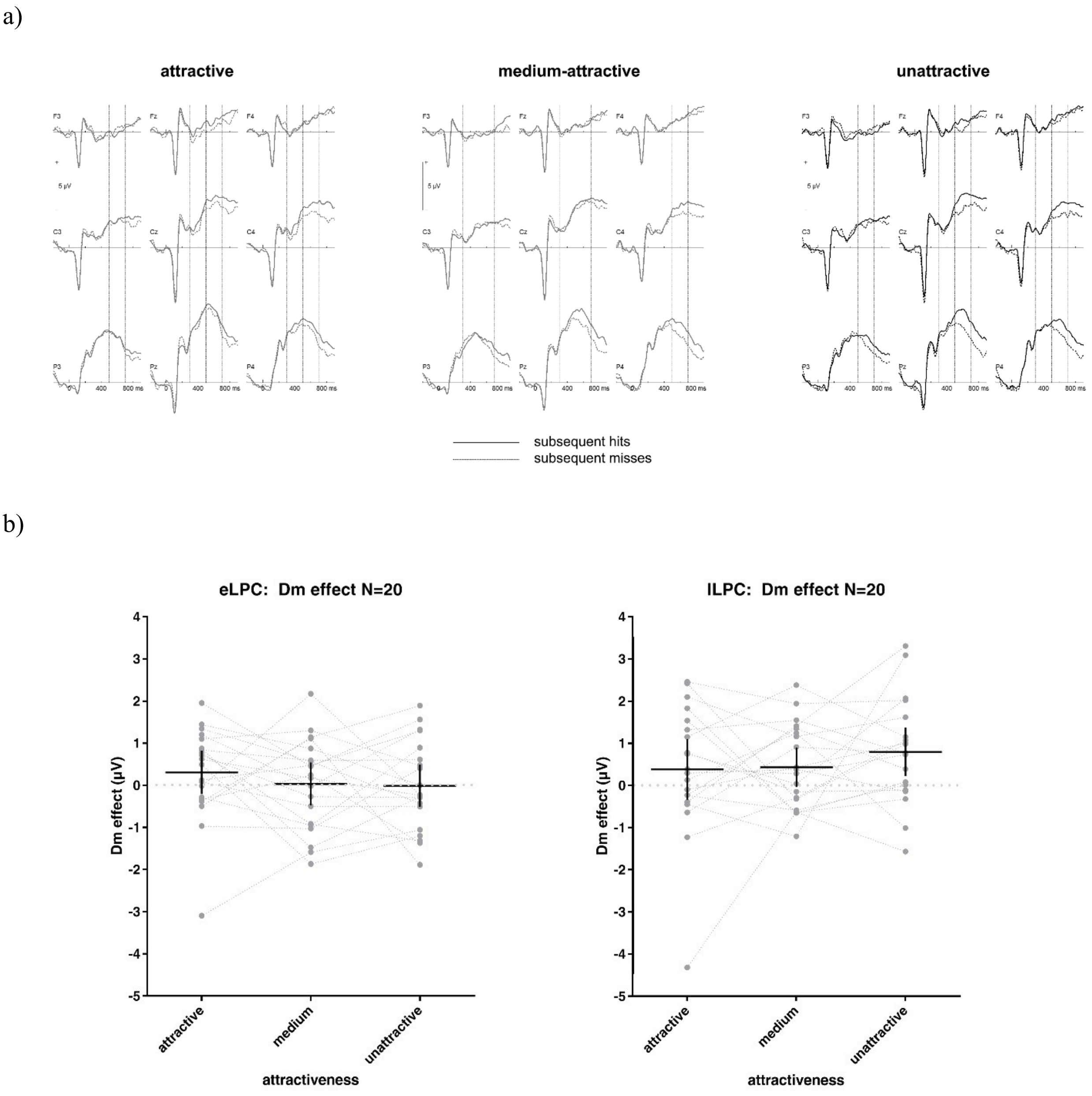


Figure 3. (a) Grand mean ERPs from the learning phases of the recognition memory experiment. Dashed lines indicate early and late LPC time ranges. (b) Dm effect for early and late LPC. Error bars depict 95% confidence intervals.

5.5 Discussion

The present paper is the first to report a neural correlate at the encoding stage for the recognition performance benefit of unattractive faces over all other attractiveness categories—a behavioural finding we have now replicated repeatedly. While previous efforts focussing on retrieval-related brain activity yielded only partly informative results, our novel findings strongly suggest that differential encoding processes are at the root of the pronounced memory effects at test. Most importantly, the memory disadvantage for medium-attractive (and to a lesser extent attractive) faces at retrieval is preceded by effortful processing at perceptual stages during encoding. By contrast, Dm effects for unattractive faces only appeared at later stages of processing. Thus, the current data suggest a cascading and nuanced contribution of perceptual, affective and mnemonic processing during encoding to the behavioural outcome in memory for attractive, medium-attractive, and unattractive faces.

Previous research on the Dm effect established that its relative magnitude depends on the difficulty and effort required for a given memory task, with easier tasks eliciting smaller Dm effects (e.g. Fabiani et al., 1990; Paller et al., 1987). On the basis of this characteristic, we inspected the relative magnitude of Dm effects for faces of varying attractiveness, in order to capture differences in processing demands across several face encoding stages. Of note, we did not find strong ERP differences for faces of varying attractiveness during the learning phases of our previous experiments, in which we did not analyse data separately for subsequently remembered versus forgotten trials. The current data suggest that a pronounced modulation of Dm effects by attractiveness may have obscured overall amplitude differences between attractive, medium-attractive, and unattractive faces.

Due to the wide-spread topography and sustained time course of the Dm effect, Friedman et al. (1996) suggested that it could either be `unitary ERP activity with a unique functional role that overlaps several ERP deflections, or it could reflect the contribution of several overlapping components, each reflecting a different function'. Our data seem to clearly support the second possibility, as we found characteristic differences in how attractiveness modulated (or did not modulate) the Dm effect across consecutive ERP time segments. Dm effects first appeared in the P2 component, most prominently for medium-attractive faces – the least-well remembered category at test. This is well in line with the proposition that behavioural memory performance is inversely related to cluster density in MDFS. It is most difficult to extract information about individual identity for those faces most densely clustered in MDFS.

The Dm effect reflects that individuation is nevertheless possible for some, but not all faces from this category. As medium-attractive faces are the most regularly encountered faces in everyday life, successful encoding of these faces necessitates forming a more detailed perceptual engram, putatively based on more fine-grained information. This may well be reflected in the face-sensitive P2, which has been connected to structural encoding (Schweinberger & Neumann, 2016), specifically the encoding of second-order spatial relations in faces (Latinus & Taylor, 2006), and renormalization of the perceptual system following adaptation to shape manipulated faces (Kloth et al., 2017) – all functionally overlapping processes critical for integration of new engrams into a pre-shaped MDFS.

The P2 Dm effect for attractive faces, while numerically smaller, did not significantly differ in size from the Dm effect for medium-attractive faces. Notably, increased representational clustering has been shown for attractive relative to unattractive faces in a multidimensional scaling study (Potter et al., 2007), in line with a similar Dm effect for attractive and medium-attractive faces in the P2. Similarly, there was only a statistical trend for a benefit of attractive over medium-attractive faces in memory. Previous reports from our lab have shown that the memory difference between medium-attractive and attractive faces abated when affective information (i.e., valence and arousal) was controlled for, suggesting that more accurate memory performance for attractive than medium-attractive faces is mainly driven by differences in affective content. This influence seems diminished in the current experiment, maybe because the increased number of attractive and unattractive identities during learning rendered affective responses less salient during encoding, and hence less efficient as potential memory cues. In line with this, we found only numerically larger Dm effects in the N250/EPN time range for attractive over medium-attractive faces, thus mirroring the pattern of behavioural results.

Of note, we did not find pronounced Dm effects for unattractive faces in P2 and N250/EPN amplitudes. This is again in line with an account of memory performance based on cluster density in the MDFS: In sparsely clustered areas, a small set of distinguishing facial characteristics may be sufficient to establish an unequivocal identity match. Whereas for attractive and medium-attractive faces elaborate processing may be required during learning, encoding of unattractive faces may be achieved by rather shallow perceptual scanning. Concurringly, no Dm effects were found for unattractive faces at these earlier stages.

In contrast to these early Dm effects which were systematically moderated by attractiveness, we found a prominent Dm effect in the late LPC which was comparable for faces across attractiveness sets. Moreover, the right-lateralized posterior scalp distribution follows the previously described pattern of sustained Dm effects for faces (Sommer et al., 1995; Sommer et al., 1997; Sommer et al., 1991). We conclude that this late processing stage is crucial for engram formation of all face categories tested in the present study, without further modulation by attractiveness. Notably, prominent Dm effect for unattractive faces were only found in this time window. This suggests that substantial processing demands for unattractive faces influence subsequent memory only at this late stage, whereas relatively easy encoding of these faces at earlier stages does not promote differential Dm effects.

These findings appear to be in some conflict with the notion of more fluent processing of attractive compared to unattractive faces (e.g. Principe & Langlois, 2012; Trujillo et al., 2014; Winkielman et al., 2006). This account predicts successful recognition of a stimulus to result from error-free and effortless, i.e. fluent processing. For the present experiment, this would predict easy processing of attractive faces, which in turn should be indexed by decreased effort and smaller Dm effects. This is in direct contradiction to the pattern of results reported here. Indeed, to the extent that smaller Dm effects indicate relative ease of processing, the opposite case could be made for increased fluency of *unattractive* over attractive faces in mnemonic tasks. It is important to note that the fluency account was mainly established in tasks requiring the recognition of broad object classes – e.g., recognizing stimuli as faces vs. objects. Such tasks arguably tap into vastly different mechanisms than those needed for individual face recognition – i.e. discriminating seen faces from new identities. Winkielman et al. (2006) proposed that processing fluency may be seen as an internal cue to familiarity. However, this cue may well serve as a faulty internal heuristic, giving rise to a 'false' sense of familiarity, as indexed by high false alarm rates, and accordingly low d' and less conservative response biases for attractive faces in the present and our previous studies (see Studies 1 and 2, and Wiese, Altmann, et al, 2014). Possibly, and as argued before (see Study 1), precisely those attributes making attractive faces easy to classify as faces may simultaneously be those making them hard to differentiate from other face identities, as indexed by the larger Dm effects for attractive over unattractive faces in the P2 and N250/EPN time window. In other words, while attractive faces may be easy on the eye, unattractive faces may be easy on the brain – at least when the task is to correctly recognize them later on.

In summary, this study reports novel findings of encoding-related neural activity during the learning of faces of varying attractiveness. Our results suggest that memory differences between attractive, medium-attractive, and unattractive faces a) are rooted in encoding, b) start to manifest at elaborative stages of perceptual processing, as reflected in the P2 and N250 ERP components, and c) are at least partly related to exemplar density in MDFS.

Acknowledgements:

We are grateful to Kathrin Rauscher for help in data acquisition, and Fabienne Windel for her support during data analysis.

Table 1: Rating data for the stimulus set employed in the recognition experiment.

Condition	**Attractiveness**	**Deviation**	**FITC**	**Valence**	**Arousal**	**Gender Typicality**	**Trust-worthiness**	**Dominance**	**Perceived Age**
	M ± *SD*	*M* ± *SD*	*M* ± *SD*	*M* ± *SD*	*M* ± *SD*	*M* ± *SD*	*M* ± *SD*	*M* ± *SD*	*M* ± *SD*
attractive female	4.41 ± 0.33	3.25 ± 0.52	3.85 ± 0.63	5.84 ± 0.58	4.85 ± 0.74	2.05 ± 0.29	3.83 ± 0.34	3.62 ± 0.50	26.88 ± 2.24
attractive male	4.37 ± 0.27	3.25 ± 0.46	3.91 ± 0.45	5.52 ± 0.43	4.66 ± 0.54	2.06 ± 0.40	3.56 ± 0.43	4.19 ± 0.48	30.19 ± 3.28
medium-attractive female	3.55 ± 0.27	3.16 ± 0.46	3.13 ± 0.48	5.21 ± 0.49	3.98 ± 0.55	1.57 ± 0.30	3.63 ± 0.31	3.28 ± 0.37	28.48 ± 2.56
medium-attractive male	3.49 ± 0.26	3.05 ± 0.40	3.15 ± 0.51	4.92 ± 0.46	3.86 ± 0.49	1.79 ± 0.43	3.37 ± 0.34	3.58 ± 0.44	28.84 ± 3.72
unattractive female	2.45 ± 0.39	3.23 ± 0.55	2.95 ± 0.59	4.09 ± 0.59	3.43 ± 0.59	1.09 ± 0.48	3.00 ± 0.41	2.90 ± 0.46	32.91 ± 4.14
unattractive male	2.48 ± 0.35	3.15 ± 0.58	2.99 ± 0.58	4.07 ± 0.56	3.55 ± 0.54	1.76 ± 0.35	2.89 ± 0.41	3.17 ± 0.56	31.92 ± 5.13
Scale	*1 = very unattractive* *6 = very attractive*	*1 = very typical* *6 = very atypical*	*1 = very lowly distinctive* *6 = very distinctive*	*1 = very negative* *9 = very positive*	*1 = low arousal* *9 = high arousal*	*0 = very atypical* *3 = very typical*	*1 = very untrustworthy* *6 = very trustworthy*	*1 = very submissive* *6 = very dominant*	*years*
Permeation coefficient r^2 (Bronstad & Russell, 2007)	r^2 = .44 ± .14 *SD*	r^2 = .16 ± .08 *SD*	r^2 = .23 ± .11 *SD*	r^2 = .29 ± .15 *SD*	r^2 = .16 ± .10 *SD*	r^2 = .79 ± .16 *SD*	r^2 = .21 ± .11 *SD*	r^2 = .25 ± .12 *SD*	r^2 = .43 ± .11 *SD*

Table 2: Statistics for rating differences in the stimulus set employed in the recognition experiment as tested by Mann-Whitney-U tests.

Stimulus Group	**Attractiveness**	**Deviation**	**FITC**	**Valence**	**Arousal**	**Gender Typicality**	**Trustworthiness**	**Dominance**	**Perceived Age**
	U; *p*	*U*; *p*	*U*; *p*	*U*; *p*	*U*; *p*	*U*; *p*	*U*; *p*	*U*; *p*	*U*; *p*
Attractiveness*									
attractive vs. medium	0.000; <.001	16511.00; <.003	6387.50; <.001	8093.00; <.001	6173.50; <.001	8277.500; <.001	14331.00; <.001	10277.00; <.001	19635.00; .752
attractive vs. unattractive	0.000; <.001	17924.50; .073	5064.50; <.001	868.50; <.001	2822.50; <.001	5477.50; <.001	4002.00; <.0010	5326.50; <.001	10230.50; <.001
medium vs. unattractive	0.000; <.001	18870.0; .328	15074.0; <.001	3971.50; <.001	10569.50; <.001	14254.0; <.001	6190.0; <.001	10667.0; <.001	10380.0; <.001

*all *df* = 398

Table 3: Behavioural data from the main experiment.

	Study phase						Test phase											
	RT			*ACC*			*d'*			*C*			Hits			CR		
Stimulus Group	*M*	±	*SD*	*M*	±	*SD*	*M*	±	*SD*	*M*	±	*SD*	*M*	±	*SD*	*M*	±	*SD*
attractive	974.53	±	327.39	0.99	±	0.02	1.20	±	0.49	0.13	±	0.38	0.67	±	0.12	0.74	±	0.15
medium-attractive	995.68	±	324.91	0.98	±	0.02	1.04	±	0.42	0.30	±	0.30	0.59	±	0.12	0.78	±	0.11
unattractive	1021.28	±	245.21	0.95	±	0.03	1.60	±	0.49	0.27	±	0.30	0.70	±	0.11	0.84	±	0.09

**RT* = Reaction Times, *ACC* = Accuracy

Table 4: Statistical indices of t-test comparisons.

Behavioural results					
Study phases	**t-value (df)**	**p-value**	**Cohen's d_{av}**	**Mean difference**	**95% Confidence Intervall**
Reaction time (ms)					
attractive vs. medium	$t(19) = 1.61$	$p = .123$	$d = 0.06$	$M_{diff} = 21.15$	CI[-6.28, 48.58]
attractive vs. unattractive	$t(19) = 4.36$	$p < .001$	$d = 0.15$	$M_{diff} = 46.76$	CI[24.33, 69.18]
medium vs. unattractive	$t(19) = 1.37$	$p = .187$	$d = 0.08$	$M_{diff} = 25.61$	CI[-13.51, 64.72]
Accuracy (%)					
attractive vs. medium	$t(19) = 1.04$	$p = .312$	$d = 0.35$	$M_{diff} = .01$	CI[-0.01, 0.02]
attractive vs. unattractive	$t(19) = 4.11$	$p < .001$	$d = 1.35$	$M_{diff} = .04$	CI[0.02, 0.05]
medium vs. unattractive	$t(19) = 2.97$	$p = .008$	$d = 1.09$	$M_{diff} = .03$	CI[0.01, 0.05]
Test phases					
d-prime					
attractive vs. medium	$t(19) = 2.02$	$p = .058$	$d = 0.34$	$M_{diff} = 0.15$	CI[-0.01, 0.31]
attractive vs. unattractive	$t(19) = 4.78$	$p < .001$	$d = 0.82$	$M_{diff} = 0.40$	CI[0.22, 0.57]
medium vs. unattractive	$t(19) = 8.35$	$p < .001$	$d = 1.21$	$M_{diff} = 0.55$	CI[0.41, 0.69]
Response bias C					
attractive vs. medium	$t(19) = 3.49$	$p = .002$	$d = 0.49$	$M_{diff} = 0.17$	CI[0.07, 0.27]
attractive vs. unattractive	$t(19) = 2.83$	$p = .011$	$d = 0.40$	$M_{diff} = 0.14$	CI[0.04, 0.24]
medium vs. unattractive	$t(19) = 0.94$	$p = .357$	$d = 0.10$	$M_{diff} = 0.03$	CI[-0.04, 0.10]

ERP results (µV)					
Dm effect (hits vs. misses)					
P2	**t-value (df)**	**p-value**	**Cohen's d_{av}**	**Mean difference**	**95% Confidence Intervall**
attractive vs. medium	$t(19) = 1.06$	$p = .302$	$d = 0.31$	$M_{diff} = 0.26$	CI[-0.25, 0.77]
attractive vs. unattractive	$t(19) = 1.94$	$p = .067$	$d = 0.50$	$M_{diff} = 0.47$	CI[-0.04, 0.97]
medium vs. unattractive	$t(19) = 4.50$	$p < .001$	$d = 0.87$	$M_{diff} = 0.72$	CI[0.39, 1.06]
N250/EPN					
attractive vs. medium	$t(19) = 0.44$	$p = .665$	$d = 0.16$	$M_{diff} = 0.12$	CI[-0.42, 0.65]
attractive vs. unattractive	$t(19) = 3.25$	$p = .004$	$d = 0.96$	$M_{diff} = 0.66$	CI[0.25, 1.07]
medium vs. unattractive	$t(19) = 2.14$	$p = .046$	$d = 0.67$	$M_{diff} = 0.54$	CI[0.03, 1.06]
Early LPC					
left vs. midline	$t(19) = 4.84$	$p < .001$	$d = 0.50$	$M_{diff} = 0.41$	CI[0.23, 0.59]
left vs. right	$t(19) = 2.10$	$p = .050$	$d = 0.39$	$M_{diff} = 0.33$	CI[0.00, 0.66]
midline vs. right	$t(19) = 0.68$	$p = .505$	$d = 0.10$	$M_{diff} = 0.08$	CI[-0.17, 0.34]

Late LPC					
Site					
frontal vs. central	$t(19) = 2.41$	$p = .026$	$d = 0.50$	$M_{diff} = 0.54$	CI[0.07, 1.01]
frontal vs. parietal	$t(19) = 2.63$	$p = .017$	$d = 0.71$	$M_{diff} = 0.77$	CI[0.16, 1.38]
central vs. parietal	$t(19) = 1.28$	$p = .218$	$d = 0.20$	$M_{diff} = 0.23$	CI[-0.15, 0.60]
Laterality					
left vs. midline	$t(19) = 4.94$	$p < .001$	$d = 0.71$	$M_{diff} = 0.70$	CI[0.40, 1.00]
left vs. right	$t(19) = 3.27$	$p = .004$	$d = 0.63$	$M_{diff} = 0.61$	CI[0.22, 1.00]
midline vs. right	$t(19) = 0.59$	$p = .564$	$d = 0.09$	$M_{diff} = 0.09$	CI[-0.24, 0.42]

6 GENERAL DISCUSSION

6.1 Overview

This thesis describes an experimental series wherein the influence of attractiveness on face recognition memory was systematically studied. By employing careful stimulus control, and a similar experimental paradigm, this series provides the most coherent and stable results in this field to date. Strikingly, a memory benefit for unattractive faces over attractive and, to an even greater degree, also over medium-attractive faces was found in all experiments. Further, memory differences at test were linked to differential P2 modulations throughout this series, suggesting a relevant contribution of mechanisms reflected in this component to the memory outcome (discussed in more detail below).

Study 1 inspected the functional relation of attractiveness on face memory by including a medium-attractive face group to the paradigm. It established that attractiveness impacts memory non-linearly when perceived distinctiveness is controlled. Substantially lower memory for medium-attractive faces was found. Inspection of neural correlates suggests contributions of several mechanisms, including perceptual processing implicated in the P2, and affective processing in the N250/EPN and LPC. Of particular relevance, the least-well remembered group, i.e. medium-attractive faces, yielded increased P2 amplitudes at test.

Study 2 was designed to test conflicting suggestions on the influence of gender on the attractiveness effect, i.e. socio-cognitive accounts, adaptive memory derived from an evolutionary framework, and representational density. There was no significant impact of face and/or participant gender on the effect of attractiveness on face memory, arguing against socio-cognitive and adaptive memory assumptions. ERP analyses indicated increased frontal LPC amplitudes for medium-attractive faces selectively for male participants. This may tentatively indicate a shift in processing style in men towards the female default mode, possibly triggered by the frequent presentation of motivationally relevant attractive faces in the paradigm.

Study 3 focused on encoding-related brain activity that precedes the differential memory for attractive, medium-attractive, and unattractive faces. Memory was again worst for medium-attractive faces, and a pronounced Dm effect in the occipito-temporal P2, probably indicating effortful encoding at this perceptual stage compared to the other face categories. Overall, these findings argue in favour of perceptual accounts and the impact of representational density and—to a lesser extent—some contribution of emotional processing to attractiveness effects on recognition memory.

6.2 Critical reflection: Theoretical implications and integrative discussion

The series of experiments in this thesis presents the most stable pattern of results in a long line of research trying to investigate the influence of attractiveness on face recognition memory. In what now comprises four separate data sets (including the data presented in Wiese, Altmann, et al., 2014), participants always remembered unattractive faces more accurately than the other face groups. This finding is highly robust, was found across different stimulus sets, and does not seem driven by perceived distinctiveness (as this was matched between conditions), or affective content (as this was statistically controlled by means of analyses of covariances), or influences of either participant's or face gender (as inspected in Study 2). Notably, medium-attractive faces were least well remembered throughout the study series. Further, the benefit for attractive faces over them seems to be largely driven by affective content, as indicated by the item-analyses reported for Studies 1 and 2. The following paragraphs will shortly discuss implications of these findings for the accounts presented in the introduction.

6.2.1 Socio-cognitive account

The present data are not in line with assumptions from socio-cognitive accounts that predict better memory for motivationally relevant faces. As detailed before, attractive faces are more readily perceived as in-group members (Johnson, 1981). They are also motivationally more relevant in terms of explicit emotionality ratings: attractive faces are seen as both more positive and more arousing than the other face groups. This is also seen throughout the experimental series in neuronal markers of affective processing for motivationally relevant material. Specifically, attractive faces yielded consistently more negative EPN amplitudes than unattractive faces in the ERP data of all four experiments. Hence, people should have been inherently more motivated to memorize them in terms of social cognition. However, attractive faces were consistently less well remembered than unattractive faces. Similarly, yet in the context of the ORB, Wan, Crookes, Reynolds, Irons, and McKone (2015) report that level of contact and thus perceptual expertise best predicts the own-race bias rather than socio-motivational factors. Further, they report that the memory bias for own-race faces persists even though participants are more motivated to process the more difficult, i.e., other-race faces. These results also argue against social–motivational theories (e.g. Hugenberg et al., 2010).

Furthermore, socio-cognitive accounts predict own-gender biases, particularly when gender is easily perceived—as is the case in attractive faces high in hormone-facilitated sexual dimorphism. However, no such effects were found in the present studies. It is possible that matching for distinctiveness removed gender cues in faces, and thus a potential foundation of the OGB (also discussed in section 4). However, gender typicality was indeed increased in the stimulus pool used in the current work—even after distinctiveness matching[4]. Hence, own-gender faces should have been remembered better in Study 2. This was not seen in d' scores, however. Notably, the OGB is generally small and not consistently found in the literature (see Herlitz & Lovén, 2013, for a meta-analytical review). There was also no convincing evidence of own-group biases on a neural level. While old-new effects were consistently present in Studies 1 and 2 of this thesis, as well as in Wiese, Altmann, et al. (2014), they did not stably interact with either attractiveness or participants' gender. Taken together, the current results are not well explained by socio-cognitive accounts, and even contradict them to some extent.

6.2.2 Evolutionary account

Adaptive memory frameworks assume that human memory is geared towards retaining survival- and fitness-relevant information (Nairne et al., 2008; Nairne et al., 2007). Thus, they would predict better memory for faces of potential mates and rivals. In that sense, attractive faces—that potentially either bear the promise of fit offspring or are a threat to mating resources, should be best remembered. This is not seen in the current data. In fact, attractive faces are consistently less well remembered than unattractive faces, a finding that is not easily explained in terms of adaptive memory.

It is possible that matching for distinctiveness may again have removed relevant cues to adaptive fitness in faces, and thus the current results may not hold in a natural setting. This is unlikely, however, as the selected face groups were maximized for differences in

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[4] While the perceptual basis of this difference after matching is presently unclear, enhanced sexual dimorphism in attractive faces on an average group level cannot entirely be ruled out as a source. Matching for perceived distinctiveness likely prevented inclusion of faces with extreme markers of femininity or masculinity. These, however, should only be present in some individual faces. Excluding them attenuates large differences of sexual dimorphism between groups, but may not necessarily remove them entirely. Notably, gender typicality only moderately correlated with attractiveness in the rating study (ρ [1100] = .57; $p < .001$), thus suggesting a limited portion of shared variance that could have been be affected by matching for distinctiveness. Even more strikingly, deviation-based distinctiveness and gender typicality were not significantly related at all despite the large sample (ρ [1100] = -.06; $p = .06$). Thus, the likelihood of sampling biases in the stimulus material due to the matching procedure seems acceptably low.

attractiveness—arguably a highly relevant dimension for evaluating potential mates and rivals. However, the presented faces in the current experimental series were not rated for perceived health, another survival-relevant information. It may be argued that an unattractive face signals ill health and thus bear the threat of contagion. Infection avoidance by shunning sick individuals is a reasonable strategy to increase likelihood of survival. Nevertheless, it seems unlikely that health signals affected the current results. For one, the link between perception of facial health and attractiveness is—somewhat counterintuitively—neither very close nor particularly robust as suggested by a recent and comprehensive study (Foo et al., 2017): Most findings linking attractiveness and perceived health rely strongly on surface cues, i.e. facial skin colour, yet skin colour did not predict attractiveness in men nor in women. Contradictory to this, carotenoid-based skin colouration has been found to increase perceived attractiveness in a study inspecting the influence of subtle colour shifts by means of digital image manipulation (Lefevre & Perrett, 2015)[5]. The results by Foo et al. (2017) suggest, however, that this influence maybe rather small and loose its impact when other, more salient factors are available for attractiveness judgments in natural faces. Thus, despite current interest in the literature, colour cues to health may play a limited role in judging attractiveness. Further, faces in the current stimulus pool were carefully prepared by means of Gradation Curve Adjustments of histograms. In this procedure, gross deviances between global distributions of RGB values in the images are levelled out to adjust overall pictorial luminance and contrast. Thus, variations in colour, although not strictly controlled, should be relatively subtle between face groups.

Further, all face groups were matched for perceived deviation-based distinctiveness. Arguably, indicators of severe ill health would also increase distinctiveness. Thus, distinctiveness matching should limit this influence. Most importantly, avoidance behaviour of potentially infectious stimuli should result from negative valence and increased arousal. While unattractive faces are indeed viewed less favourably—and evaluated as slightly negative in SAM ratings of this stimulus pool—this did not also coincide with increased arousal. In fact, unattractive faces were rated as affectively less arousing than other faces (see next section for

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[5] Note that some of these authors in a related and more recent publication do not discuss the link of attractiveness and health due to the inconsistencies in the literature: “It should be noted that, although perceived attractiveness is often thought to be a proxy for apparent health, some studies have failed to find a relationship between attractiveness and health […]. Therefore, for brevity and clarity, within this review perceptual studies were limited to those specifically investigating perceived health and not attractiveness.” (p.1, Henderson, Holzleitner, Talamas, & Perrett, 2016).

a more detailed discussion). Taken together, evolutionary accounts as such do not sit easily with the current pattern of results.

6.2.3 Emotional memory account

As detailed in the general introduction, emotional memory accounts suggest better memory for affectively relevant material. At first sight, the pattern of better memory for attractive and unattractive faces over affectively neutral, medium-attractive faces could be explained by a combination of positivity and negativity biases (see section 3). SAM ratings of valence indeed showed attractive faces as more positive and unattractive faces as more negative than medium-attractive faces.

Indeed, the difference in memory between attractive and medium-attractive faces disappeared when valence and arousal ratings were accounted for in the item analyses in Studies 1 and 2. Thus, the benefit for attractive over medium-attractive faces seems driven by the positive affect elicited by the former group. Interestingly, participants committed more false alarms for attractive faces in all experiments. This was also reflected in a consistently less conservative response criterion C for this face category. This matches reports of a ‘warm glow heuristic’ of familiarity, also used to explain differences in memory for emotionally expressive faces (Monin, 2003). Based on a study of recognition memory for facial expressions, Johansson et al. (2004) propose that emotional content may indirectly affect recognition performance by influencing criterion setting mediated by the prefrontal cortex (PFC; e.g. Miller, Handy, Cutler, Inati, & Wolford, 2001). Affective content of faces may hamper the execution of general control functions in the PFC that normally ensure task-relevant processing. Hence, the maintenance of these control mechanisms might be temporarily suppressed, resulting in a less conservative response criterion for emotionally arousing material.

Several aspects of the current data sets, however, cannot be accounted for by valence biases. First, the observed rating differences were moderate, and only ranged around (±) one rating point on a 9-point-scale. Emotional memory differences are usually described for more extreme stimuli, such as erotic imagery, pornographic material, or depiction of severe violence or mutilation (e.g. Kaestner & Polich, 2011). Notably, unattractive faces were neither particularly negative in these terms, nor very arousing. It is unlikely that they are perceived just as negatively or as threatening as to explain their memory benefit by emotional saliency. Inspection of ERPs also does not suggest increased affective processing of these faces. In the majority of analyses in this thesis (with one notable exception in the late LPC in Study 2), both EPN and LPC responses to unattractive faces were consistently diminished compared to attractive faces, and also diminished or of at least equal size to medium-attractive faces. Hence, there was no evidence found in the current data that increased affective processing boosted performance for unattractive faces. In fact, the benefit of unattractive faces persisted in all item analyses even when both arousal and valence were accounted for. Taken together, differences in emotional content explain only a part of the d' pattern. In the present data, they do not well explain the memory difference between unattractive faces and the other face categories that has now consistently been reported in four experiments.

6.2.4 Perceptual accounts: Representational clustering

As detailed in the introduction, high local density of facial representations within the MDFS can result in high inter-item confusion. This should result in a high false alarm rate, and thus low memory as indexed by d'. This pattern was indeed observed throughout the experimental series for both attractive and medium-attractive faces compared to unattractive faces. This is in line with the assumption that both attractive and medium-attractive faces are more densely represented within the MDFS. To the author's knowledge, this is the only account that predicts higher memory for unattractive over other faces.

Strikingly, the size of the Dm effect in the P2 was exclusively decreased for unattractive faces in Study 3. As noted before, the relative size of the Dm effect depends partly on the required effort during encoding, and increases for difficult tasks (Fabiani et al., 1990; Paller et al., 1987; Paller & Wagner, 2002). Thus, the memory disadvantage for medium-attractive, and—to a numerically lesser extent—for attractive faces at retrieval is preceded by more effortful processing at perceptual stages during encoding captured in the P2. This is well in line with the assumption that the P2 is connected to processing of perceptual information of incoming faces in relation to already stored representations, i.e. a P2 account of cluster density (see section 3). If an incoming face's dimensional values are similar to previously seen faces—due to a number of pre-existing representations in a similar region of the MDFS—the cognitive system needs to extract and store more detailed information in order to encode a sufficiently idiosyncratic representation for later recognition. This increased mental effort may be represented in the increased P2 for subsequent hits during encoding of medium-attractive and attractive faces.

Similarly, accessing and matching these representations may also require more perceptual effort during retrieval which in turn may explain the increased amplitudes for medium-attractive faces in the test phases of Studies 1 (over the right hemisphere) and 2. Notably, the larger P2 amplitudes for unattractive over attractive faces seen in Wiese, Altmann, et al. (2014), were not replicated in the current experiments. The specific reasons for this are currently unclear, but may likely be related to the changes in the experimental setup. For instance, the inclusion of medium-attractive faces that bridged the larger gap in attractiveness changed several factors i.e. lengthening of the test procedure and thus higher need for sustained task attention, or general increase in mental load, stronger interference of previous experimental blocks. These differences could play into the different findings. Speculatively, the differences in the P2 between unattractive and attractive faces, both affectively valenced groups, are more strongly influenced by processes captured in the EPN. It is possible that increased affective processing for these groups described for the N250/EPN time range may overlap with P2-related activity in these two groups. This may have played more strongly into the pattern reported in Wiese, Altmann, et al. (2014) in absence of medium-attractive faces.

Taken together, representational clustering currently seems to be the only account that predicts the stable pattern of behavioural results obtained in the current experiments. While some conflicting ERP findings need to be addressed by future work, the larger Dm effect during encoding and the increased activity during retrieval in the P2 for medium-attractive faces—the least well remembered group—point to a relevant contribution of perceptual processing to the attractiveness effect in face memory.

6.3 Further discussion of selected aspects

6.3.1 Attention and attractiveness in face memory

Some evidence suggests that other face memory biases, e.g. own-race bias, are at least partly driven by differences in allocating attentional resources (Hills & Lewis, 2006; Zhou et al., 2015; Zhou, Pu, Young, & Tse, 2014). The opposite, however, has been reported in the case of the own-age bias (Neumann, End, Luttmann, Schweinberger, & Wiese, 2015). Relevantly, while attractive faces capture attentional resources (Maner et al., 2003; Sui & Liu, 2009), this does not boost memory accuracy (Silva, Macedo, Albuquerque, & Arantes, 2016). A recent study further found a dissociation between attention capture and later memory for attractive faces: while women attend more to attractive men, they do not remember them better—not even when their attention for attractive males peaks during ovulation (Anderson et al., 2010). This further argues against an evolutionary explanation for the current data. There is no evidence of a gender difference in memory in the current data similar to this attentional bias.

Further, it is unlikely that better memory for unattractive, i.e. negatively valenced faces, arises due to attention to their affective content. There is evidence that even patients with attention geared towards negative info in faces, i.e. social anxiety patients, still exhibit a positivity/happy-face bias in memory (Hagemann et al., 2016). Taken together, it seems unlikely that attentional differences are a factor underlying the current pattern. To test this, however, future research may directly manipulate attentional resource allocation during encoding similar to the procedure of Neumann et al. (2015).

6.3.2 Perceptual fluency and memory for attractiveness

Accounts of perceptual fluency assume that our perceptual system handles some stimuli more efficiently, i.e. quicker and more accurately, than others (Winkielman & Cacioppo, 2001; Winkielman et al., 2006). It has been suggested that such ‘fluent’ processing is engaged for stimuli that are good representations of their class, i.e. high in prototypicality. In a similar vein, attractive faces have been assumed to be more prototypical, i.e. more face-like, than less attractive faces as they are dimensionally more average (Principe & Langlois, 2011, 2012; Trujillo et al., 2014; Winkielman et al., 2006). Further, fluent processing is assumed to be associated with positive affect, thus rendering stimuli ‘visually pleasing’ (Winkielman & Cacioppo, 2001). Indeed, the same authors even propose that the perception of facial attractiveness itself results from the fluent processing of attractive versus less fluent processing of unattractive faces.

As discussed in Winkielman et al. (2006), fluent processing is typically error-free and thus should result in successful recognition of a stimulus. Support for this is usually cited from studies reporting improved performance for attractive faces in gender categorization, or face/non-face decision tasks (e.g. Trujillo et al., 2014). This, however, may not hold true for a more elaborate mnemonic face recognition task as employed in the current paradigm. The memory scores obtained in all experiments indicate more error-prone performance for attractive faces, resulting in low d’ scores. While it may be true that attractive faces are processed fluently in terms of speed for object classification, this type of processing may still not be very helpful for within-class discrimination. This, however, is crucial when correctly recognizing a previously seen face and rejecting newly presented identities. In other words, those attributes making attractive faces easy to classify for gender may simultaneously be those making it hard to differentiate them from other faces, as detailed in the account of representational clustering.

6.3.3 Absence of gender effects – converging (neuro)physiological evidence

The absence of gender effects in Study 2 seems remarkable, especially since both socio-cognitive and evolutionary accounts predict at least some interaction. It is possible that the experimental design lacked statistical power to detect significant gender effects. However, a post-hoc power analysis in the present data for the OGB in women—the most stably reported finding in the OGB literature (Herlitz & Lovén, 2013)—revealed that on the basis of the effect size for the mean d' difference between male and female faces observed in the present study ($d_{av} = .12$), an excessive *N* of approximately 422 women would be needed to obtain statistical power at the recommended .80 level following Cohen (1988).

There is some converging evidence that may help to explain the absence of gender effects in the present context. For one, there is high agreement between the sexes on explicit ratings of facial attractiveness, suggesting men and women perceive facial attractiveness similarly (Hahn & Perrett, 2014). Ishai (2007) reports that not even sexual preference for a particular gender impacts explicit attractiveness ratings. Hahn and Perrett (2014) further point out that there is surprisingly limited evidence of gender differences in motivational aspects of attractiveness-related activation in the neuronal reward circuitry, and cite several studies that do not find any evidence of gender differences in responses to facial attractiveness (e.g. Chatterjee, Thomas, Smith, & Aguirre, 2009; O'Doherty et al., 2003). Thus, men and women process attractiveness similarly as measured by activity in core and extended systems, including the ventral circuitry for processing of reward value.

The few consistently described gender differences appear in the higher-order processing of reward-related decisions in the OFC and in the medial prefrontal cortex (mPFC; Hahn & Perrett, 2014). On this level, implicit neuronal activation and explicit judgments for attractiveness differ. While OFC activation has generally been found to increase with enhanced attractiveness, there is some evidence of participant gender differences when additionally considering face gender. Women, but not men, show increased activation of the NAcc in response to attractiveness of same-sex faces (Kim & Cabeza, 2007). Further, OFC activation in both homo- and heterosexual participants of either gender increases only for attractive faces of their preferred gender (Ishai, 2007). For opposite-sex faces, both men and women exhibit greater neural activity in response to attractive faces than unattractive faces (Kim & Cabeza, 2007). Men, however, show a stronger effect in the OFC and mPFC than do women (OFC: Cloutier et al., 2008; mPFC: O'Doherty et al., 2003).

Notably, Winston et al. (2007) observed a larger response to attractiveness in men compared to women in the ACC. As the ACC is involved in generating and monitoring internal autonomic states (Critchley, 2004; Critchley, Elliott, Mathias, & Dolan, 2000; Teves, Videen, Cryer, & Powers, 2004), the authors suggest that men change their internal state upon presentation of attractive faces. Of interest, pupillometry data in Winston et al. (2007) similarly showed larger pupil dilations for attractive faces only in men, but not in women. This further points to a larger arousal-related response to attractive faces in men. If so, this could likely also shift men’s face processing style towards the ‘female default mode’, i.e. focusing on emotionally relevant material, as discussed in Study 2 of this thesis.

6.3.4 Diminished P2 amplitudes – task and sampling

Generally, the size of the P2 seemed relatively diminished compared to other reports throughout the current experimental series. In Study 3, it was further slightly shifted to more parietal sites than usual. This may well be due to a) the comparatively demanding task, and b) the inclusion criteria for Dm inspection. Encoding may be more effortful for perceivers with either generally low recognition abilities, lack of expertise for a specific group of faces (Wiese, Kaufmann, et al., 2014), or high error rates due to transient random factors (e.g. lack of sleep, less motivation etc.). Thus, by targeting erroneous encoding, inclusion criteria in Study 3 may have sampled a participant group with diminished performance and potentially a different processing style compared to those described in other experiments. It may well be that only those participants who displayed either transitory or habitually bad face recognition skills commit enough recognition errors, i.e. misses, to reach sufficient trial numbers. Indeed, as ERP averaging requires a minimum of 15 trials per condition, some high-performing participants had to be excluded in Study 3 as they did not meet the minimum trial number criterion for subsequent misses. It may be of particular interest to test whether the P2 may be generally diminished in ‘bad’ versus ‘good’ recognizers. If so, this would further point to the crucial involvement of the underlying mechanisms in the P2 for face recognition memory. Potentially, participants may have also recruited slightly different, more anterior neural networks than usual to compensate for the increased task requirements.

6.3.5 The adapted MDFS – towards a more flexible view

As discussed in the introduction and throughout this thesis, the original proposition of the MDFS probably does not well describe the nature of facial information storage. This is only partly due to its vagueness concerning underlying dimensions. More importantly, though, and as well criticized by Burton and Vokey (1998), the proposition of a densely clustered central region of the MDFS does not match empirical ratings of perceived distinctiveness, termed the 'face space typicality paradox'. Burton and Vokey (1998) show that most faces fall into medium-distance from the mathematical origin when more than two dimensions are taken into account. This gets more relevant the more dimensions are considered.

Burton and Vokey (1998) fail to acknowledge, however, that it is quite unlikely that our brains constantly use the entirety of visual dimensions contained in faces. In other words, it would not be a parsimonious solution to use all available information contained in facial images for all tasks and instances. Depending on task, circumstance, stimulus, and individual ability, very different sets of dimensions may be used by our mnemonic system. It is quite likely that our perceptual system refers not to the complete set of available information for memory encoding and later retrieval, but rather retains and retrieves only the necessary amount of information for solving a given task. For example, it would not be very efficient and hence a waste of resources to remember the only man in a group of women by means of eye-colour, rather than his beard. In terms of the current research, it may not be necessary to encode sixty or more dimension values for memorizing an unattractive face if maybe two or three already suffice to create a recognizable engram. On the other hand, a small number of generally used dimensions may not yield a distinct representation for a medium-attractive face. More detailed, relational, elaborate information needs to be extracted to enable unequivocal recognition.

This flexible usage of dimensions is more in line with the idea that the brain allocates its resources for mental operations economically (e.g. Goldfarb & Henik, 2014). That is not to say that this mechanism is failsafe. It is quite likely that our cognitive apparatus is not very adapt to select the most suitable dimensions for a given tasks, additionally hampered by top-down influences such as heuristical thinking, situational factors like tiredness and stress, or task demands like time restraints and memory load. These differences may well explain the disparity between meta-memory ratings and actual memory performance, as seen for attractive faces. Meta-mnemonic judgments are notoriously unreliable. O'Toole et al. (1998) found a correlation with actual memory performance of only $r = .19$. In the case of attractive faces, we may be inclined to think that we will be able to remember them as they are thought and perceived to stand out in the crowd (as indexed by increased FITC ratings). Although sufficiently distinct information to remember a given face may have been collected to reject a large majority of other faces, recognition may still fail due to large inter-item similarity within this group.

6.4 Limitations and outlook

It is not entirely clear what matching for distinctiveness implies for perceptual differences within and between the groups of attractive, medium-attractive, and unattractive faces. The adapted model in Figure 1, section 1.4.1 of this thesis only serves as a crudely simplified illustration. Thus, the assumption of local clustering is still very much only an assumption. Quantifying this hinges on two aspects: a) measuring perceptual similarity on an image level, but more importantly, b) identifying relevant dimensions that are extracted from facial stimuli for each class of faces. This can potentially be remedied in future work. Several approaches are discussed below.

The Dm effects in the P2 in Study 3 indicate that perceptual processing at encoding is indeed different for attractive, medium-attractive, and unattractive faces. To gain converging evidence, it may be of interest to adapt similar experimental setups for fMRI studies. In a study inspecting illusionary memory, hippocampal activity during encoding predicts subsequent retrieval with high confidence (Kim & Cabeza, 2007). Similarly, Dm effects can also be inspected in the BOLD signal (Paller & Wagner, 2002). It would be informative to see if the memory differences for attractive, medium-attractive, and unattractive faces are similarly reflected in differential activity of regions engaged in perceptual analysis of faces and facial attractiveness (as described in Hahn & Perrett, 2014).

To directly capture perceptual similarity, it would be possible to use multidimensional scaling methods for attractive, medium-attractive, and unattractive faces, similar to the approach by Potter et al. (2007). Further, principal component analysis (PCA)-based approaches (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 face identity (see also Jenkins et al., 2011). Similar image processing techniques may elucidate the underlying image properties of differences in perceptual processing described in this thesis.

Very recently, Chang and Tsao (2017) described a neuronal face space code derived from cell recordings in the inferior temporal cortex of macaque monkeys with specialized face patch neurons for shape dimensions (middle lateral [ML] / middle fundus [MF] cells) and for appearance, i.e. luminance/texture/reflectance dimensions (anterior medial [AM] cells). This work provides evidence that the primate brain needs only about 200 neurons to uniquely encode any face, with each neuron encoding a specific dimension, or axis, of facial variability. In a second step, they developed an algorithm to decode unseen faces based on these neural responses recorded from these cells by means of neuronal network computations. Intriguingly, even fewer dimensions (~50) are needed to convincingly code facial identity, and that this is achieved by simple linear algebraic computations. This work, in the authors' opinion, is the most convincing evidence of now that the dimensional coding suggested by Valentine et al. (2015) is in fact manifested on a neuronal level in the primate brain.

By using this algorithm, it would be well possible to simulate the neuronal activation pattern for attractiveness. Notably, it would be interesting to test the findings of Said and Todorov (2011), namely that average activation of shape-coding MF/ML neurons coincides with higher attractiveness ratings, yet more extreme responses in AM cells coding for texture cues are preferred. In principle, this could also provide means to quantify processing demands for encoding of different faces. By reversing this algorithm, it may be possible to simulate the cell activation pattern required for successful encoding of attractive, medium-attractive and unattractive faces. This may well give us a perceptually clearer understanding of the summative neuronal response captured in ERP Dm effects. Putatively, this perceptual space code could also be used to generate biologically plausible faces—both in terms of appearance as well as processing, and thus overcome limitations of current methods in digitally created face stimuli. If so, it could even be possible to simulate and then match for differences in processing demands—and thus more directly test and manipulate assumptions from representational clustering.

Potentially, creating similar algorithms based on single-cell data recorded intracranially from e.g. lesioned, inexperienced, or otherwise low-ability individuals could also help to further understand and simulate faulty face recognition. This may bear the potential of designing compensating training for both recognition deficits and memory biases. As these combined insights from computational and biological neuronal networks are still at incipient stages, implementation of such approaches still requires additional work and research. Of interest, it may be possible to simulate modulating influences on the face processing system's responses by adding insights from functional MRI and EEG analyses.

6.5 Conclusion

Taken together, the current set of experiments describes a robust effect of attractiveness on recognition memory, with highest performance to unattractive faces, followed by attractive faces, and lastly medium-attractive faces. This attractiveness effect on recognition memory may be best explained by a combining influence of representational density—potentially accounting for the memory decrease of attractive and medium-attractive compared to unattractive faces—and a further contribution of affective content—increasing performance for attractive over medium-attractive faces. These mechanisms are rooted at early perceptual stages of encoding, and do not consistently interact with retrieval-related processing. Future work should directly point to measuring and/or manipulating representational clustering of faces to corroborate these findings.

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APPENDIX

Table 1: Rating study – dimensions and written instructions.

Dimension	German instruction
Attractiveness	*Bitte bewerten Sie die Attraktivität der nun folgenden Gesichter auf einer Skala von 1 bis 6 wie angegeben.* 1 = sehr unattraktiv 2 = unattraktiv 3 = eher unattraktiv 4 = eher attraktiv 5 = attraktiv 6 = sehr attraktiv
Distinctiveness assessed by two instructions **(see Wickham & Morris, 2003, for methodological discussions; Wiese, Altmann, et al., 2014)**	
Deviation-based distinctiveness	*Schätzen Sie bitte ein, wie durchschnittlich bzw. untypisch das Gesicht ist. Geben Sie dazu an, wie stark das Aussehen des Gesichts in irgendeiner Weise von anderen, Ihnen bekannten Gesichtern abweicht. Bitte nutzen Sie dafür eine Skala von 1 bis 6.* 1 = sehr typisch 2 = typisch 3 = eher typisch 4 = eher untypisch 5 = untypisch 6 = sehr untypisch

Face-in-the-Crowd (FITC) distinctiveness

Beurteilen Sie bitte die Distinktheit der Gesichter auf einer Skala von 1 bis 6.
Fragen Sie sich dazu, wie leicht Sie das jeweilige Gesicht in einer Gruppe von Menschen (z.B. am Bahnhof auf dem gegenüberliegenden Gleis) entdecken würden. Umso distinkter ein Gesicht ist, desto wahrscheinlicher ist es, dass es Ihnen in dieser Gruppe von Gesichtern auffällt.

1 = sehr wenig distinkt
2 = wenig distinkt
3 = eher wenig distinkt
4 = eher distinkt
5 = distinkt
6 = sehr distinkt

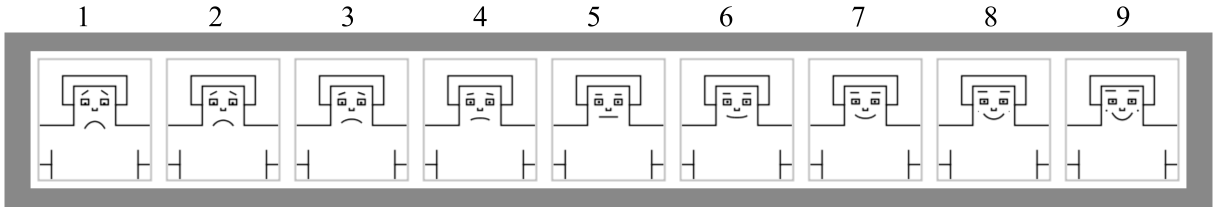
Affective content: measured by Self-Assessment Mannequins **(Bradley & Lang, 1994)**

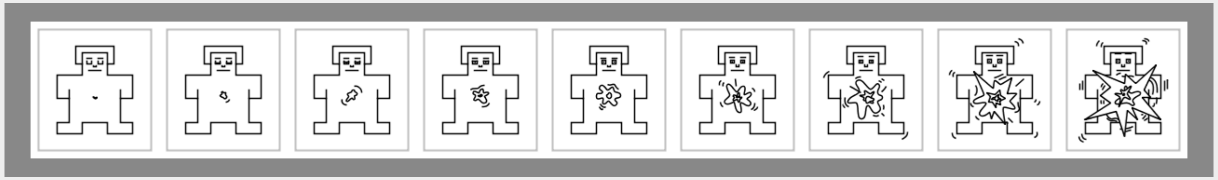
Valence

Bitte bewerten Sie im Folgenden, wie Sie sich beim Betrachten der präsentierten Gesichter fühlen. Wählen Sie dabei anhand der unten abgebildeten Skala das Portrait, das am ehesten Ihrem persönlichen Gefühl entspricht.

Achtung: Bitte bewerten Sie NICHT, welche Emotion das jeweilige Gesicht zeigt. Bewerten Sie Ihre eigene emotionale Reaktion.

Bitte geben Sie an, welche Art von Emotion Sie beim Betrachten dieses Gesichts empfinden.



Arousal	*Bitte bewerten Sie im Folgenden, wie stark Sie das Betrachten der präsentierten Gesichter emotional erregt. Wählen Sie dabei anhand der unten abgebildeten Skala das Bild, welches am ehesten der Stärke Ihres Gefühls entspricht.* *Bitte beachten: Wir verstehen unter emotionaler Erregung die Stärke jeder Art von emotionaler Reaktion, nicht nur (aber auch) sexuelle Erregung.* *Bitte geben Sie an, welche Art von Emotion Sie beim Betrachten dieses Gesichts empfinden.* 1 2 3 4 5 6 7 8 9 
Gender typicality	*Bitte bewerten Sie die Weiblichkeit/Männlichkeit der nun folgenden Gesichter auf einer Skala von 1 bis 7 wie angegeben.* 1 = sehr männlich 2 = männlich 3 = eher männlich 4 = androgyn 5 = eher weiblich 6 = weiblich 7 = sehr weiblich
Trustworthiness	*Bitte bewerten Sie nun, wie vertrauenswürdig die nun folgenden Gesichter auf Sie wirken, auf einer Skala von 1 bis 6 wie angegeben.*

	1 = sehr unvertrauenswürdig 2 = unvertrauenswürdig 3 = eher unvertrauenswürdig 4 = eher vertrauenswürdig 5 = vertrauenswürdig 6 = sehr vertrauenswürdig
Dominance	*Im Folgenden sollen Sie die Dominanz der gezeigten Gesichter einschätzen.* *Eine dominante Person sagt anderen Leuten, was sie zu tun haben, wird respektiert, ist einflussreich, und häufig eine Führungsperson; submissive Personen sind nicht einflussreich, bestimmend oder durchsetzungsfähig und werden meist von anderen gelenkt oder gar bevormundet.* *Bitte bewerten Sie wie dominant die nun folgenden Gesichter auf Sie wirken, auf einer Skala von 1 bis 6 wie angegeben.* 1 = sehr submissiv 2 = submissiv 3 = eher submissiv 4 = eher dominant 5 = dominant 6 = sehr dominant
Perceived age	*Bitte schätzen Sie das Alter der nun folgenden Gesichter in Jahren mit Hilfe der Zifferntasten von 10-99.*

EHRENWÖRTLICHE ERKLÄRUNG

Ich erkläre hiermit, 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 Kennzeichnungen übernommen habe und alle benutzten Quellen und Hilfsmitte in der Arbeit angegeben habe. Insbesondere habe ich keine Hilfe eines Promotionsberaters in Anspruch genommen. Bei der Auswahl, Auswertung und Schriftlegung des Materials haben mich meine Betreuer und Korrekturleserinnen 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. Ich erkläre weiterhin, dass ich diese Dissertation noch nicht als Prüfungsarbeit für eine staatliche oder andere wissenschaftliche Prüfung, oder eine gleiche, eine in wesentlichen Teilen ähnliche oder eine andere Abhandlung bei einer anderen Hochschule bzw. anderen Fakultät als Dissertation eingereicht habe. Ich versichere, nach bestem Wissen die reine Wahrheit gesagt und nichts verschwiegen zu haben.

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