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The neural dynamics of familiar face recognition

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ABSTRACT

Humans are highly efficient at recognising familiar faces. However, previous EEG/ERP research has given a partial and fragmented account of the neural basis of this remarkable ability. We argue that this is related to insufficient consideration of fundamental characteristics of familiar face recognition. These include image-independence (recognition across different pictures), levels of familiarity (familiar faces vary hugely in duration and intensity of our exposure to them), automaticity (we cannot voluntarily withhold from recognising a familiar face), and domain-selectivity (the degree to which face familiarity effects are selective). We review recent EEG/ERP work, combining uni- and multivariate methods, that has systematically targeted these shortcomings. We present a theoretical account of familiar face recognition, dividing it into early visual, domain-sensitive and domain-general phases, and integrating image-independence and levels of familiarity. Our account incorporates classic and more recent concepts, such as multi-dimensional face representation and course-to-fine processing. While several questions remain to be addressed, this new account represents a major step forward in our understanding of the neurophysiological basis of familiar face recognition.

1. Introduction

Imagine you are in the queue at the cashier in your local supermarket, and you turn around looking at the person behind you, realising that you know him/her. Arguably, what you will do next critically depends on who exactly this person is. Is it one of your close friends, known to you for many years? Is it a colleague you have first met a few weeks ago, and only a few times since? Is it this man who sometimes takes the same bus as you when you go to work in the morning? Or is it maybe somebody you know only via media coverage (newspapers, social media etc.), such as a local politician? While in the case of your friend, you may enthusiastically greet her/him and engage in a friendly chat, your response to the barely known colleague will presumably be more reserved, and you may decide to not show any signs of recognition towards the man from the bus or the local politician. What is the basis for this?

In all these cases, your brain has a visual long-term memory representation of the other person's face, the activation of which is the basis for recognition (Young and Bruce, 2024). In case of highly familiar faces, this representation is *image-independent*, meaning that its activation does not depend on the specific conditions in which you encounter the face.[1] You may have never seen your friend in this particular context of the supermarket, yet you have no problem recognising her/his face in new situations, under different lighting, from different viewpoints, and even after a few years have passed and she/he has become somewhat older. We have seen the faces of people we know well in many different circumstances. We therefore know about the range of possible variations in their appearance. However, this is not the case for less well-known people (Young and Burton, 2018). Therefore, face representations will be more refined for the faces we know better (Kramer et al., 2018). Less well-known faces can be difficult to recognise because they appear very different in changing conditions (Jenkins et al., 2011), resulting in a higher potential for error when trying to recognise them.

But this risk for error is presumably not the only reason you are more likely to engage in an interaction with the more familiar people in the example above. While you can access a variety of information about your friend, including the type of meal she/he might cook given the items in her/his basket, or when you have last been invited over for dinner, you possess much less biographical and semantic information about your colleague, and only very little about the man from the bus.

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[1] Please note that it may well be the case that some instances (e.g. a ¾ view in good lighting) are recognized more *efficiently* than others (e.g. a profile view in bad lighting). However, a wide range of images is usually effective at activating face representations of well-known individuals (e.g. (Jenkins et al., 2011).

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Moreover, while you may strongly agree or disagree with your local politician's views, you are unsure about how she/he would respond to a direct approach in the supermarket and this may lead you to decide that this is not the right time and place.

Face and person recognition arguably mainly serves the purpose of preparing us for interactions with others. While this may appear intuitively plausible, it is all the more surprising how little this basic premise has impacted neuroscientific research. Recent years, however, have seen a substantial change in this regard. In this review, we will discuss recent findings, mostly from EEG studies, on face recognition and the subsequent stages leading up to a potential interaction with a person. We will start with a brief description of the relevant theoretical background before summarizing a traditional ERP-based model of face recognition and the challenges it has faced in recent years. In the main part, we will then discuss recent uni- and multivariate electrophysiological work in relation to these challenges. We will conclude by integrating and reformulating the theoretical account, and by pointing out open questions and important areas for future study.

2. Basic concepts

The hallmark of human face recognition is its image-independence, typically operationalised as the accurate and efficient identification of a known face from highly variable images (Burton et al., 2016; Kramer et al., 2018;Young and Burton, 2017). For unfamiliar persons, however, performance is often error-prone (Bruce et al., 1999; Burton et al., 1999; Jenkins et al., 2011). As will be discussed in detail below (see Section 5), the critical difference between familiar and unfamiliar face recognition lies in the fact that the former is based on detailed long-term representations (Burton et al., 2011), while such representations are not or only partly developed for less familiar and unfamiliar faces. Recognition of unfamiliar faces relies on the representation of one (or few) specific picture(s) or instance(s) and therefore cannot be image-independent (Hancock et al., 2000). A cognitive neuroscientific understanding of familiar face recognition therefore will have to identify the neural processes associated with the implementation and operation of image-independent face and person representations.

Before discussing empirical work, we first clarify some terminology. Specifically, the concepts of familiarity, recognition, and identity, as well as the distinction between face and person recognition, need to be defined.

2.1. *Familiarity*

The term familiarity occurs in at least two different contexts in the psychological and cognitive neuroscience literature. Episodic memory researchers, and particularly proponents of dual-process accounts (Rugg and Curran, 2007; Yonelinas, 2002), contrast "familiarity" with "recollection". Here, the former is understood as reflecting a vague feeling of having encountered an item (a word, a face, etc.) before, even though no specific information about the where and when, or other specific circumstances, are available. In face recognition research, on the other hand, familiarity is typically assumed to arise from the activation of a visual representation of a known face (Bruce and Young, 1986; Burton et al., 1990). Similar to its use in episodic memory research, familiarity does not signal specific contextual or other information associated with the face.

Critically, familiarity in episodic memory studies typically refers to whether an item has been encountered in an earlier phase of the experiment. For instance, the word "car" may elicit a feeling of familiarity if it was seen in an earlier learning phase, but the very same item may not elicit familiarity if it is presented as a novel item at test. In other words, the identical stimulus may or may not elicit a familiarity signal (Rugg and Yonelinas, 2003). By contrast, in typical familiar face recognition experiments, personally familiar or famous faces are presented intermixed with faces the participants has never seen before. Here, the accuracy of a familiarity response is independent of whether a face/person was seen during the experiment before but depends on whether a stimulus represents a face/person already known from outside the context of the experiment. While this difference between memory and face recognition experiments may first appear to be merely a question of experimental detail, it is in fact fundamental, because the underlying neural representations are different in a critical way. In the memory case, even though specific details are not remembered, the activation of the representation (e.g. of the word "car") becomes activated not because the participant has a long-term representation of what a car is, but because the item was seen earlier in the experiment. In face recognition, however, the representation that gives rise to the familiarity signal will respond whenever an appropriate stimulus is perceived, independent of specific instances or episodes.

Face familiarity has been examined in numerous studies using various cognitive neuroscientific techniques. Human fMRI research has traditionally suggested that regions in the lateral fusiform gyrus are particularly relevant (Gobbini and Haxby, 2007; Haxby et al., 2000), while more recently the view that a whole "core" network of brain regions is important for the processing of familiarity has emerged (see e.g. (Kovacs, 2020). Moreover, recent studies using single-cell recordings in monkeys have identified patches in the temporal pole (Landi et al., 2021), as well as the anterior medial temporal lobe (She et al., 2024) to differentiate between familiar and unfamiliar faces. Of note, many of these studies have not tested image-independent familiarity effects (for notable exceptions, see e.g. (Davies-Thompson et al., 2009); (Weibert et al., 2016).

2.2. *Recognition*

Following from the above, we can define familiar face *recognition* as a sufficiently strong activation of a long-term visual representation containing information about what the face of an individual person looks like. If the familiarity signal reaches a specified threshold, it establishes the perceived face as a specific individual, and at this point the face is assumed to be recognised (see e.g. (Burton et al., 1990). This recognition process is highly reliable for those faces that have image-independent long-term representations, but not for those we have only seen a few times before. Corresponding to our limited experience with these latter faces, their representations can only contain limited information and are accordingly more image-dependent (Kramer et al., 2018). In instances with insufficient overlap with previous encounters, weaker familiarity signals may leave the observer uncertain, and accordingly the face is not unambiguously recognised.

It is worth noting that evidence for implicit or covert forms of face recognition exists. In cases of acquired prosopagnosia (e.g. (Barton, 2008); (Behrmann et al., 2011), individuals show (relatively) selective deficits in face recognition after brain injury, while (most) other cognitive abilities are spared. This is unlike cases of e.g. Alzheimer's Disease, in which a face recognition deficit is usually combined with wider cognitive impairment. Studies have shown that, while explicit and conscious recognition of faces may be absent, people with prosopagnosia can still exhibit signs of implicit recognition of familiar faces, for instance in the form of skin conductance responses (Bauer, 1984). Together with other findings in people with Capgras delusion who lack this response, this has prompted some authors to postulate separate pathways to cognitive versus affective aspects of recognition (Ellis and Lewis, 2001; Ellis et al., 1997; Schweinberger and Burton, 2003). Crucially, such models propose that cognitive and affective aspects of face recognition are based on the same visual representations.

2.3. *Visual identity*

From the above outlined theoretical perspective (which will be revisited later in this review), recognising a face as familiar (as opposed to unfamiliar) and recognising an individual facial identity (my friend

Jack's face) is based on the same underlying representation. Faces always represent individual people, and accordingly their visual representations are also specific to the individuals. If a face is recognised as familiar, this is based on the activation of the representation of an individual facial identity. Because other familiar faces look different, their representation will not become (sufficiently) activated (e.g. my friend David's representation is not activated when I see my friend Jack).

As described above, the memory literature uses the term familiarity as a mere "feeling of knowing", and one might assume a similar mechanism for the feeling that a face is familiar without being able to identify a specific person. However, in face recognition, a "feeling of knowing" a person ("I know that I know this face …") is conceptualized as a failure of accessing post-perceptual person-related information (see Hanley and Cowell, 1988; see also next section).

2.4. *Face versus person recognition*

In most real-life cases, face recognition does not provide us with enough useful information for our social interactions. We need to know who the person in front of us is, and not just that we know the person. Accordingly, once a face is recognised as familiar, we need to access further person-specific information. This information entails episodic memories (e.g. that you went to dinner to your friend's house last Friday and talked about politics), semantic knowledge (e.g., what food your friend likes, that your friend holds slightly conservative views), and affective information (e.g. you like your friend, but you slightly dislike their partner). While we hold such information for each familiar person, the specific content partly overlaps between individuals (Burton et al., 1990). Moreover, such information can be accessed not only via a person's face, but also, for instance, via their voice (e.g. Lavan and McGettigan, 2023) or their (heard or read) name. It is *post-perceptual* and can be accessed via different stimulus domains and modalities. We will call the successful activation of such information *person* recognition, as opposed to face recognition.

3. Previous EEG/ERP studies

3.1. *Previous ERP work and the serial face recognition model*

How are the processes related to these concepts reflected in the human EEG? Previous work on event-related brain potentials (ERPs) has led to the development of a *serial face recognition model* (Schweinberger and Burton, 2003), and we briefly review this model and its development here as a starting point, before presenting a more advanced view in Section 5, which integrates the more recent findings discussed below. Here, serial is not meant in a strict sense, as the model allows for overlapping processes and feedback loops from later into earlier processing stages (Herzmann et al., 2004; Schweinberger and Neumann, 2016). However, it does assume a broadly serial architecture, and that output from an earlier stage is passed on to subsequent stages, which then process the incoming information further.

ERPs reflect transient voltage changes in the human electroencephalogram that are time-locked to an event such as the presentation of a stimulus. They reflect summed post-synaptic potentials and are therefore a direct measure of brain activity (e.g. Jackson and Bolger, 2014). The presentation of faces results in a typical ERP waveform, consisting of a series of positive and negative deflections at occipito-temporal electrode sites (see Fig. 1). While earlier ERP peaks (i.e. the C1) are observed in experiments contrasting upper and lower visual hemifield stimulation (Clark et al., 1995; Qin et al., 2022), the first peak typically measured in face recognition experiments is the P100. It is observed for any visual stimulus (i.e., it is not particularly sensitive to faces) and reflects the processing of low-level stimulus characteristics such as luminance or contrast (see top left box in Fig. 1). Subsequent components, however, have been associated with specific perceptual and/or cognitive processing stages which (given sufficient familiarity) eventually result in face and person recognition (Schweinberger and Burton, 2003; Schweinberger and Neumann, 2016).

Although important earlier work exists (e.g., Bötzel and Grüsser, 1989; Jeffreys and Tukmachi, 1992), the probably best known face ERP paper has been published by Bentin and colleagues in 1996 (Bentin et al., 1996), which demonstrated substantially more negative amplitudes for faces relative to other visual stimuli at occipito-temporal channels at a latency of approximately 170 ms (see upper right box in Fig. 1). The sensitivity of this N170 component to differentiate between faces and other visual stimuli is seen as an established finding by most (for reviews, see Eimer, 2011; Rossion and Jacques, 2008) but not all researchers (Thierry et al., 2007). Interestingly, the N170 has been shown to be very similar for familiar and unfamiliar faces (Alzueta et al., 2019; Andrews et al., 2017; Bentin and Deouell, 2000; Eimer, 2000; Tanaka et al., 2006). Consequently, it is typically interpreted as reflecting the detection of a face-like stimulus,[2] or its structural encoding (Eimer, 2011; Schweinberger, 2011), and therefore perceptual stages prior to the processing of individual identity.

Processes reflected in the occipito-temporal P200, which immediately follows the N170, seem to be related to matching the presented stimulus to a prototypical, or average face. Specifically, it has been shown that the P200 is sensitive to the similarity of a face with an average across multiple identities (see middle left box in Fig. 1), and that this sensitivity is similar for familiar and unfamiliar faces (Wuttke and Schweinberger, 2019). Kloth, Rhodes and Schweinberger (Kloth et al., 2017) have further observed the P200 amplitude to increase from trial to trial across different consecutive faces which shared a uniform spatial distortion (i.e., compression or expansion), paralleling the perceptual impression that consecutive distorted faces look more and more "normal". As this effect was observed for unfamiliar faces, it seems to reflect a perceptual processing stage rather than affecting the long-term representations of individual faces. Accordingly, the P200 seems to reflect the perceived distance of the stimulus to a prototypical face, or distance-to-norm (DTN), with respect to a face's spatial configuration (for a review, see Schweinberger and Neumann, 2016).

In contrast to the earlier time windows discussed above, highly consistent ERP effects observed in the subsequent N250 time range are related to facial familiarity. A first set of studies has not directly compared familiar and unfamiliar faces, but has used immediate repetition priming (Begleiter et al., 1995; Schweinberger et al., 1995). In these experiments, a target face is preceded by another (prime) face, which can be either the same face or the face of a different person. Targets in the repeated condition elicit a more negative waveform relative to non-repeated targets at occipito-temporal channels with an onset around 200–220 ms and a peak between 250 and 350 ms after stimulus onset (see bottom right box in Fig. 1). This N250r (r for repetition) is larger for familiar than unfamiliar faces (Begleiter et al., 1995; Herzmann et al., 2004; Pfütze et al., 2002; Schweinberger et al., 1995). It has been shown to be partly image-dependent, i.e. it is bigger when the same image rather than different images of the same person are repeated (Schweinberger et al., 2002). Critically, however, the N250r for familiar faces is still observed when facial identity is repeated but prime and target images are different (Bindemann et al., 2008; Schweinberger et al., 2002; Wiese et al., 2019; Wiese et al., 2024), and this (smaller)

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[2] Work using saccadic response times has reported earlier face detection (Crouzet et al., 2010). In this study, minimum response times, reflecting the earliest 10 ms bin in which correct saccadic responses towards a target face were significantly more likely than incorrect ones, were observed between 100 and 110 ms, while mean response times ranged between 138 and 154 ms. We note that the N170 is an average response, so should probably be compared to the mean responses in Crouzet et al. (Crouzet et al., 2010). Moreover, while the N170 peaks between 150 and 170 ms, differences between faces and non-face stimuli typically emerge earlier, and timing may therefore not be that dissimilar to the mean response time in saccadic response tasks.

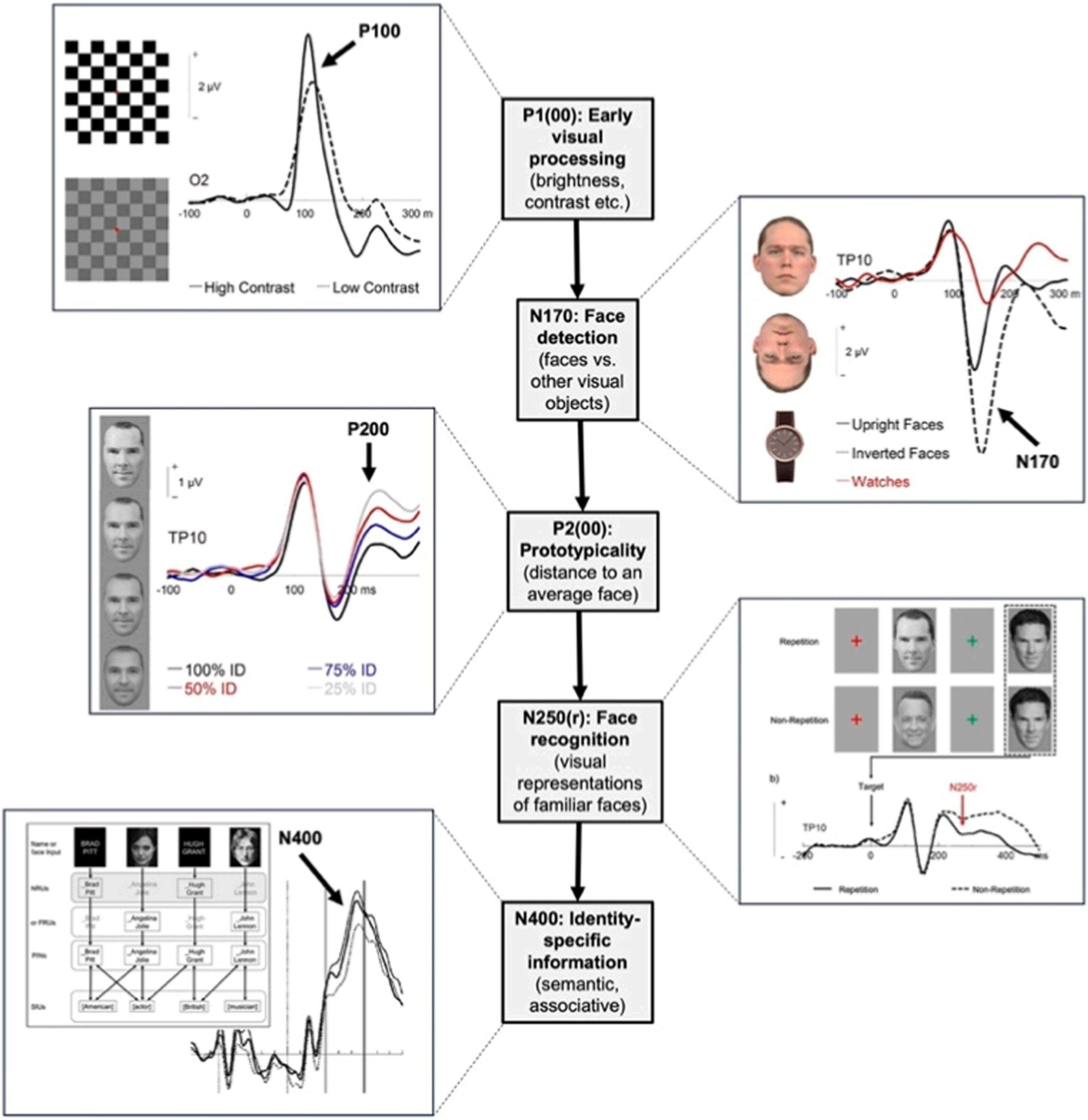

Fig. 1. The serial ERP face recognition model. Separate processing stages ("early visual processing", "face detection" etc.) are linked to specific ERP components (P100, N170 etc.). Although more recent models allow for considerable overlap between time ranges, the architecture is basically serial in the sense that some form of output from an earlier stage is passed on to subsequent stages, which then process the incoming information further.

N250r effect is therefore image-independent. Interestingly, while it has been repeatedly demonstrated for familiar faces, no such image-independent N250r is observed for completely unfamiliar faces (Zimmermann and Eimer, 2013). We therefore conclude that the image-independent N250r reflects facilitated access to visual long-term representations of familiar faces.

Other experiments have directly contrasted ERPs for familiar and unfamiliar faces. These experiments have reported more negative amplitudes for familiar than unfamiliar faces at occipitotemporal channels from approximately 200 ms onwards (Bentin and Deouell, 2000; Gosling and Eimer, 2011; Saavedra et al., 2010), which may reflect the activation of a visual long-term representation of a familiar face. In line with this interpretation, this N250 familiarity effect has been shown to build up when learning the face of a previously unfamiliar person. Earlier work has conflated picture with face learning (Tanaka et al., 2006), but has shown that the N250 effect only occurred when participants were trained on individuation of face images (discriminating person A from person B, C, or D) rather than categorization (discriminating African American from Hispanic faces; Tanaka and Pierce, 2009). Moreover, subsequent studies have shown learning effects in the N250 even when participants were tested with images different from those used during learning (Andrews et al., 2017; Kaufmann et al., 2009).

Finally, while the N250(r) reflects visual recognition, subsequent ERP effects have been shown to represent access to information about *people* rather than faces (Schweinberger and Neumann, 2016). First, self-priming (or cross-domain repetition priming) experiments present familiar target faces which are preceded by a written name (or vice versa), and the identity can be either the same or different. These experiments have shown no N250r, while at the same time N400 effects emerge, with more positive amplitudes for identity repetitions relative to non-repetitions at centro-parietal electrode positions between approximately 300 and 600 ms (Pickering and Schweinberger, 2003; Wiese et al., 2017). Secondly, similar N400 effects (and no N250r) have been demonstrated when targets are preceded by different identities that are either semantically related or associated as compared to unrelated primes (Schweinberger, 1996; Schweinberger et al., 1995; Wiese and Schweinberger, 2011; Wiese and Schweinberger, 2015; see bottom left box in Fig. 1). Accordingly, the N400 is typically interpreted as reflecting access to the semantic knowledge we hold about a specific person. Finally, face recognition memory experiments have shown more positive amplitudes for correctly remembered relative to new faces at parietal electrodes in a similar time range (Curran and Hancock, 2007; MacKenzie and Donaldson, 2007; Wiese and Schweinberger, 2018; Yovel and Paller, 2004). Such old/new effects are typically interpreted as reflecting episodic memory.

3.2. Limitations of previous ERP work

The above-described studies have provided important information for our understanding of human face recognition. However, they have usually failed to test several important aspects. First, most of these studies have used a single image per identity. Arguably, they have therefore not examined the most important characteristic of familiar face recognition - its image-independence. Critically, the issue of image-independence does not reflect a minor methodological refinement – it lies at the very heart of familiar face recognition. We will review current studies on image-independence in face recognition in Section 4.1.

A second shortcoming of previous work is related to the common dichotomy contrasting familiar with unfamiliar faces (Bentin and Deouell, 2000; Gosling and Eimer, 2011; Saavedra et al., 2010; Schweinberger et al., 1995). In real life, familiarity is a continuum, as we know faces (and people) to varying degrees, ranging from only just briefly met to near life-long acquaintances. Relatedly, we know faces and people from different contexts. We recognise the people we see regularly in the street without knowing much about them. By contrast, we usually have rich semantic, episodic, and affective information about the people we know well. We know some faces from real life, while we know the faces of others (such as famous actors, musicians, or politicians) only from exposure to various media sources. While both behavioural and neuroimaging studies have shown advantages for personally familiar over famous faces (e.g., Ramon and Gobbini, 2018), it remains unclear whether such differences stem from qualitatively different types or quantitatively more or less detailed representations. In other words, it is unclear whether the serial model (Fig. 1) needs to be refined to include different *levels* or *types* of representations. We will discuss recent studies related to this issue in Section 4.2.

Third, in line with the real-life observation that it seems impossible to *not* recognise a highly familiar face, the serial model assumes that, given sufficient activation levels at a specific processing stage, subsequent stages are automatically triggered. The question of how automatically faces are recognised has been investigated in ERP studies before (Neumann et al., 2011; Neumann and Schweinberger, 2008). These experiments, however, have used image repetition and it is therefore unclear to what extent their findings transfer to image-independent recognition. We will re-visit the question of automaticity in Section 4.3.

Fourth, ERP evidence on the domain-specificity of familiar face recognition is mixed. While a previous experiment (Schweinberger et al., 2004) suggested that the N250r is exclusively observed for faces, others found that familiar buildings show similar ERP repetition priming (Engst et al., 2006). Again, neither of these previous studies has used image-independent priming. We note that whether familiar faces are represented differently from other individually familiar stimuli (such as familiar objects or scenes) does not per se explain the processes underlying familiar face recognition. However, since the recognition of both individual faces and other visual objects requires image-independence (as we arguably don't see *any* visual stimulus under precisely the same conditions again), it appears relevant to examine similarities and differences of the underlying neural processes (see Section 4.4.).

A fifth limitation directly relates to the ERP methodology: Traditional ERP work typically thinks in "components", often defined by time-windows. This is far from how the brain actually works (i.e., continuously, parallel and recurrent). Moreover, ERP studies typically average large numbers of trials together to enhance signal-to-noise ratio. While this may be applicable for testing familiarity effects, it can make the separation of *identity*-specific signals difficult as ERPs in familiarity-based experiments average neural signals coding for many different identities together. To overcome this problem, several studies applied stimulus selective adaptation and priming paradigms. These paradigms exploit the fact that repetitions (of e.g. facial identities) lead to selectively reduced neural signals (Grill-Spector et al., 2006; Grill-Spector and Malach, 2001; Grotheer and Kovacs, 2016). Similar to related fMRI work (Davies-Thompson et al., 2009; Lee et al., 2022; Weibert et al., 2016), the manipulation of facial identity combined with the measure of release from adaptation can reveal which ERP components are sensitive to identity (Walther et al., 2013; Walther et al., 2013). However, the application of multivariate pattern analysis (MVPA) techniques (Haxby et al., 2014; Haxby et al., 2001) to electrophysiological data (Grootswagers et al., 2017; Kaplan et al., 2015) allows to test for the available identity information in the EEG signal without averaging across trials (for potential limitations, see Dubois et al., 2015). For an MVPA analysis, typically, the EEG data is split into a training and test subset. MVPA then uses a machine learning classifier algorithm to extract information from the training dataset and attempts to classify trials of the test set iteratively. If the performance of the classifier algorithm is significantly better than chance, this indicates the presence of category information in the EEG data (Grootswagers et al., 2017). While univariate ERP studies, in combination with repetition priming or adaptation techniques, *can* reveal identity specific processing, its continuous and trial-based nature makes MVPA ideal for testing such processes in finer details (see Section 4.5).[3]

Finally, the serial model has been challenged more fundamentally by the claim that a distinction between perceptual and representational processing stages is not necessary (Caharel and Rossion, 2021; Rossion and Retter, 2020). According to this view, face perception and recognition reflect the "accumulation of neural evidence" within the same "neuro-functional system" rather than reflecting two, at least partly separable processing stages. Face recognition is considered as a single continuous processing of face familiarity, with richer representations (for more familiar faces) producing earlier onsets. Theoretically, it is unclear to us how it is possible to determine whether a perceived face is familiar or unfamiliar without a long-term representation of what particular familiar faces look like. Empirically, because of its claim that the onset of familiarity effects depends on the level of familiarity and that superordinate category (i.e. face versus different visual object) and familiarity information is processed by the same neural mechanisms, the account argues that familiarity effects, and particularly differences

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[3] Please note that some articles have also tested face processing with other trial-based electrophysiological methods, such as trial-based time-frequency analysis, and that these studies have reported familiarity-specific activities in the theta, alpha, beta, and gamma bands (e.g. (Guntekin and Basar, 2014); (Herweg et al., 2020).

between personally familiar and unfamiliar faces, are already observable in the N170. We will return to this claim in Section 4.6.

4. New insights into the temporal dynamics of familiar face and person recognition

4.1. Image-independent recognition of familiarity

As outlined above, probably the greatest restriction of most previous ERP work is the strong focus on picture rather face/identity-based effects. To overcome this limitation, researchers at Durham University (Durham group) have contrasted the processing of multiple ambient images of highly familiar and unfamiliar identities. In our initial experiment (Experiment 1; Wiese et al., 2019), we presented participants with 25 highly variable images of each of two highly familiar identities (close friends, relatives) and of each of two unfamiliar faces (for example stimuli, see Fig. 2a). Experiments were tailored to individual participants by using stimuli that were idiosyncratically familiar. Participants were then tested in pairs, and familiar faces for Participant 1 in each pair were used as the unfamiliar faces for Participant 2 and vice versa. Accordingly, across participants, stimuli in the familiar and unfamiliar conditions were identical, therefore excluding the possibility that any observed difference is related to properties of the images themselves.

This experiment yielded a strong N250 effect for personally highly familiar relative to unfamiliar faces, starting 200 ms after stimulus onset and peaking between 200 and 300ms (right panels in Fig. 2a). Unexpectedly at the time, an additional substantial increase in the familiarity response was found in the subsequent time range (400–600ms). This Sustained Familiarity Effect (SFE) had a very similar scalp distribution to the N250 and decreased with image repetition, i.e. across the four blocks of the experiment. Moreover, using a bootstrapping approach to single-trial data, we were able to reliably demonstrate the SFE in 17 out of 20 participants (85 %). In a control experiment, which used the same

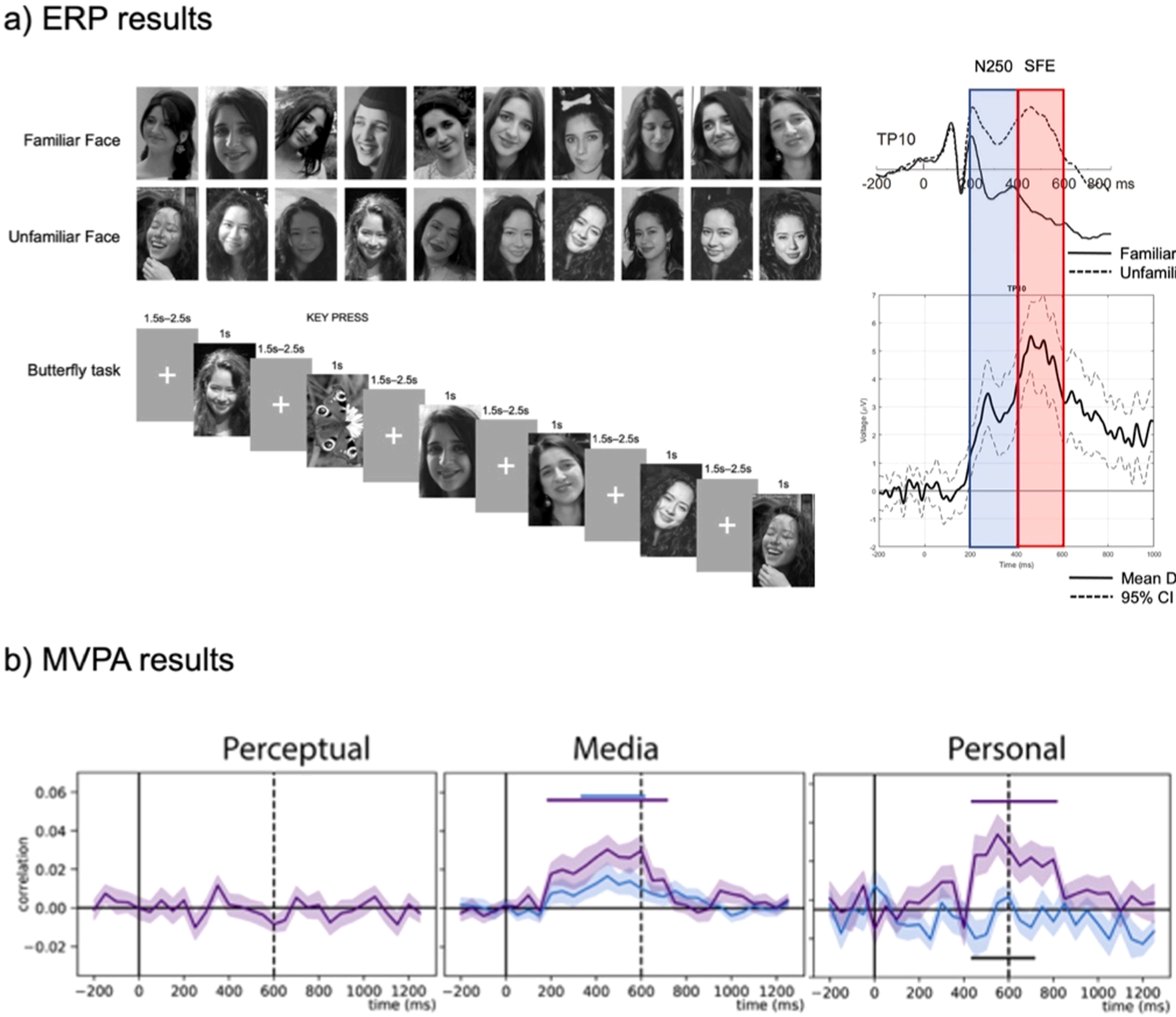


Fig. 2. a) Left: example ambient images and basic trial structure for the ERP experiments described in this section. Faces are presented with explicit consent of the depicted persons. Right/top: Grand average event-related brain potential for familiar and unfamiliar faces at right temporal electrode TP10. Right/bottom: Mean difference (unfamiliar – familiar) and 95 % confidence interval (CI). Blue and red shaded areas reflect the N250 and SFE time windows, respectively. **b)** Neural representations of face familiarity. Results of the representation similarity analysis (for details see text). Y axis represents the average correlation between the neural and the familiarity model representation dissimilarity matrixes across participants and for each time point separately. Left panel: after perceptual familiarization. Middle and Right panels: before (blue) and after (purple) media and personal familiarizations, respectively. Horizontal lines indicate statistical significance (p=0.05, corrected for multiple comparisons across time). Shaded regions represent SEM. Dashed vertical line represents the stimulus offset. Figure is generated from the data of and is similar to that of Ambrus et al. (Ambrus et al., 2021).

images for a new group of participants (i.e., all faces were unfamiliar), no false positive familiarity responses were detected. Finally, in a third experiment, we replicated the SFE for personally highly familiar faces, while substantially smaller effects were observed for personally, but less familiar faces (lecturers), and for celebrities selected by the experimenters. Independent of these experiments, a similarly prominent late posterior ERP response (400–800 ms) to facial familiarity was also seen in a study conducted at Jena University (Wuttke and Schweinberger, 2019).

A different series of studies conducted at Jena University (Jena group) tested the neural dynamics of familiar face recognition using MVPA. In one experiment (Ambrus et al., 2021), participants were familiarised with two, previously unknown persons in real life interactions. Data obtained for highly variable "ambient" face stimuli of the familiarized persons was compared to those of two randomly selected unknown persons in pre- and post-familiarization EEG sessions. As expected, in the pre-familiarization phase no familiarity information could be detected in the signal. After familiarization, however, strong and long-lasting familiarity information was found, peaking between 450 and 850 ms (right panel in Fig. 2b), similar to the time-window of the above-described ERP-based SFE. These findings are also similar to MVPA results of other groups, who also found generic familiarity effects in MEG (Dobs et al., 2019) and EEG signals (Bayer et al., 2021; Karimi-Rouzbahani et al., 2021), starting at 200 ms and peaking at around 400 ms.

While these results arguably reflect image-independent familiarity effects, they do not directly show the importance of within-person variability. If nearly any picture of a familiar face triggers the respective representation, why not just pick a single image? First, such an approach conflates picture and face recognition, as we may recognise a lesser-known face from a very typical single picture, but not from highly variable images. Second, using a single (or a small number of) image(s) per identity often leads to substantial stimulus repetitions (e.g. Caharel et al., 2005; Tanaka et al., 2006). Such repetitions will inevitably result in remembering and recognising a particular image, which is different from true (image-independent) face recognition and should therefore confound facial familiarity responses.

The Durham group has empirically tested this prediction. When a single image of a facial identity was repeated 50 times, both the N250 effect and the SFE were substantially reduced relative to the singular presentation of 50 different images of a face (Wiese et al., 2022). Specifically, the effect size of the N250 effect was about half in the single image (Cohen's $d = 0.32$) relative to the image variability condition ($d = 0.70$). Similarly, repetition of the same image relative to the singular presentation of multiple ambient images clearly reduced the SFE (from $d = 1.05$ to $d = 0.76$). As only one stimulus was presented in the single image condition, one might argue that this particular image may have been particularly difficult to recognise. However, individually familiar identities (and therefore different images) were used for different participants, and images were provided by the participants themselves. It appears highly unlikely that participants systematically picked single images that were more difficult to recognise than the average of the 50 different pictures (which contained unusual viewing angles and pictures with lower resolution). In summary, both the N250 effect and the SFE are not only detectable when tested with high stimulus variability, they are actually *increased* under these conditions – a noteworthy difference to the N250r as the main previous ERP marker of face recognition.

4.2. Levels and types of familiarity

People are not dichotomously familiar or unfamiliar to us – we know them more or less well. As discussed above, initial results from the Durham group (Experiment 3 in Wiese et al., 2019) suggested a clear N250 effect and SFE for highly personally familiar faces, but substantially reduced effects for lesser-known faces, and nearly no effects for two celebrities selected by the experimenters. These results seem partly at odds with the MVPA results of the Jena group. Ambrus et al. (Ambrus et al., 2021) measured the emerging familiarity information across three conditions by comparing pre- and post-familiarization data (Fig. 2b). Participants were exposed either to a brief perceptual familiarization (modelling typical old/new paradigms of memory research), to extensive several weeklong media familiarization, or to real-life personal familiarization. On the one hand, the resulting MVPA data suggests that the degree and method of familiarization impacts face familiarity representation profoundly. The representation of familiarity was observed to be far stronger after personal when compared to media and perceptual familiarization methods. On the other hand, media familiarization, unlike the results of Wiese et al. (Wiese et al., 2019) regarding famous faces, led to a reliable representation of face familiarity, specifically over the temporal cortex and after 400 ms post-stimulus. A clear difference between studies lies in the fact that the Durham group used the faces of two UK Royalties but did not test their actual familiarity, while the Jena group used an intensive familiarization procedure which engaged participants in identity-specific media consumption. The more recent and controlled nature of media familiarization may explain the enhanced familiarity signal of the MVPA when compared to the initial ERP study.

These observations triggered the question whether ERP familiarity effects based on multiple ambient images would really only be observable for personally familiar faces (as implied by the initial ERP results), or also for media-based familiarity (as suggested by the MVPA data). In a series of experiments (Wiese et al., 2022), the Durham group repeatedly found clear N250 effects and SFEs for well-known and liked celebrities (the participants' favourite singers, actors etc.), while smaller and less clear effects were observed for lesser-known and disliked celebrities, as well as for random celebrities (e.g. some other participant's favourite celebrity). In an additional experiment, the largest familiarity effects were observed for the participants' own faces, arguably the best-known face. Crucially, timing and scalp-distribution of both the N250 and SFE were highly similar, which provides no evidence for the suggestion of different representations for different types of familiar faces. At the same time, familiarity effects became smaller with decreasing levels of familiarity (see Fig. 3a), suggesting quantitative rather than qualitative differences for the various familiar faces tested in these experiments.

Following a similar line of thinking, the Jena group developed a measure to estimate the degree of face familiarity as well as the correlation between its behavioural and neural indicators (Li et al., 2022). First, a behavioural mnemonic familiarity index (MFI) was established (Fig. 3b), including both subjective familiarity ratings and an explicit memory score, reflecting successfully recalled episodes and events, for a broad range of celebrities. Next, a subset of these celebrities was selected, covering as much of the familiarity spectrum as possible. Moreover, the participants' own face, three highly personally familiar faces (family members or close friends), and three unfamiliar controls (Hungarian celebrities) were added. EEG responses to highly variable ambient images of this stimulus set were measured and correlated with the behavioural MFI as a function of time. This analysis revealed a significant correlation of decoding performance with MFI from 200 ms to 1100 ms, peaking at around 450 ms (Fig. 3b). This suggests that the degree of familiarity affects neural processing from a relatively early time-period (in line with the N250 familiarity effects observed by the Durham group) but extends well beyond this (in line with the SFE results described above).

Next, the Jena group tested whether own, personally familiar, and famous faces are processed qualitatively differently, or, in other words, whether the observed representation of the degree of familiarity was driven more strongly by personally familiar when compared to celebrity faces or not. Therefore, we performed the same correlational analysis again, but excluded trials in which own- or personally familiar faces were presented. In this case (Fig. 3b, right panel, orange line), we observed a later onset (400 ms) and peak (550 ms), as well as a substantially shorter period (until 670 ms) during which familiarity information was present. At first sight, one might be tempted to interpret

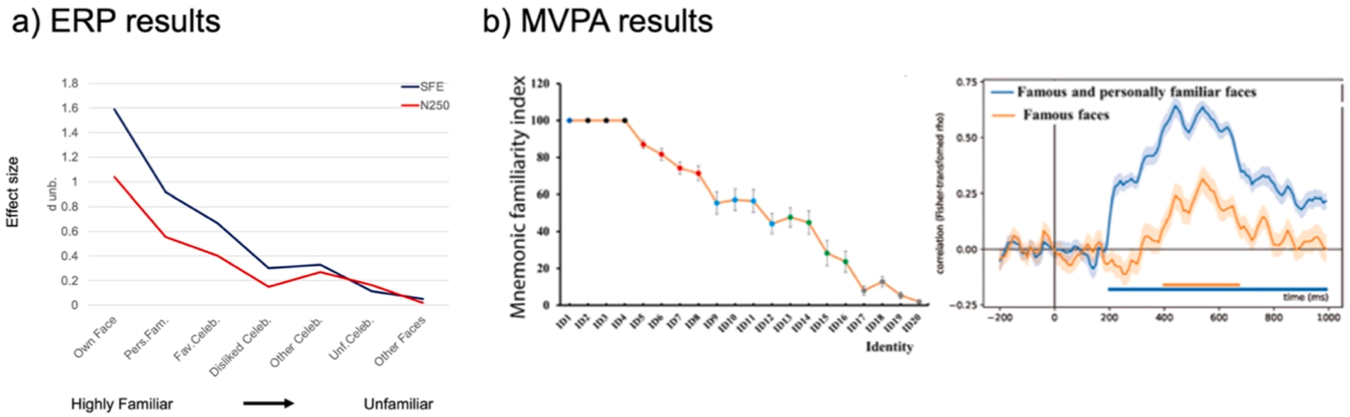


Fig. 3. a) Effect sizes of different categories of faces when compared to completely (non-famous) unfamiliar faces (Wiese et al., 2022). Note the steady decline in familiarity effects for both the N250 and SFE with decreasing levels of familiarity. b) Left panel: The average mnemonic familiarity index (MFI) across participants, for twenty identities separately. Vertical bars denote SE. Right panel: Neural representation of face familiarity. The average correlation of the familiarity information in the neural signal with the behavioural MFI across participants, for each time-point separately. Blue line represents the correlation across the 20 presented identities, including unfamous, famous and personally familiar faces. Orange line represents the same correlation, but without the personally familiar faces (dark blue and black on the left panel). Horizontal lines indicate statistical significance ($p < .05$, corrected for multiple comparisons across time). Shaded ranges represent SEM.

these findings as showing that the earlier components (from 200 to 400 ms) depend on the type of familiarity, and that they are specific to personal familiarization (see Ambrus et al., 2021; Dobs et al., 2019). However, as personally familiar faces in this study were also more familiar than famous faces, it is not straightforward to separate type from degree of familiarity, and accordingly the results of this study do not represent a strong argument for qualitatively different representations.

To further test the generalizability of familiarity effects across the type of familiarization, the Jena group took advantage of the fact that, for MVPA, the training data of the machine learning algorithm can (and should) be independent of the testing datasets. Accordingly, the classifier algorithms can be trained on the data of one participant, obtained from one experiment, and tested on the data of another participant and experiment. If such cross-participant and cross-experiment MVPA returned significant decoding performances, then neural activation patterns would be shared across participants and experiments (Kaplan et al., 2015). For this end, the classifier algorithm was trained to differentiate between the familiarized and unfamiliar trials from one of the three experiments (perceptual, media, or personal familiarization experiment) of Ambrus et al. (Ambrus et al., 2021) and tested on data of the other two (Dalski et al., 2022). Despite having different stimuli, participants, and types of familiarisation, significant familiarity information was found over central and posterior electrode sites between 270 and 630 ms post-stimulus. This further supports the conclusions that processing within this time-window is independent of the type of familiarization.

While the ERP experiments reported above demonstrate that both the N250 effect and the SFE are sensitive to the degree of familiarity, further experiments from the Durham group have examined the minimum amount of exposure sufficient to get reliable image-independent familiarity effects (Popova and Wiese, 2023). Participants met a pre-experimentally unfamiliar person in a real-life interaction, followed by an EEG test session in which multiple ambient images of the newly learnt identity and of a completely unfamiliar person were presented. Critically, across a series of experiments, the length of the interaction was varied. The results show that ten but not five minutes of real-life exposure were sufficient to elicit a reliable N250 familiarity effect. Moreover, an additional 20 minutes of interaction (i.e., a total exposure of 30 minutes) did not result in a larger N250 effect. A further study showed that the N250 effect from a ten minutes interaction is still evident after 24 hours (Wiese et al., 2024). Interestingly, no SFE, in the sense of an increased familiarity response following the N250 time range, was observed in these experiments. It thus appears as if ten minutes of real-life interaction are sufficient to establish an initial visual representation, whereas the processes reflected in the SFE (see below) do not seem to be sufficiently developed.

In line with these results, both cross-sectional and longitudinal studies on long-term learning show how the N250 and the SFE build up over the time course of knowing a person. First, given regular contact, both effects are significantly larger after 14 relative to two months of familiarity, while knowing a person for 26 months does not result in a further increase (Popova and Wiese, 2022). It therefore appears as if the first year is critical for the development of both the N250 effect and the SFE. Second, however, the developmental trajectory of the two effects within this first year appears to be different. The N250 effect was observed to build up over the first five to eight months of getting to know a person, while the SFE did not increase significantly within this time range (Popova and Wiese, 2023). While these initial results seem promising, clearly more work on real-life learning is necessary, for instance taking duration and the meaningfulness of interactions into account.

In sum, the experiments discussed in this section have not revealed any clear-cut evidence for qualitatively different *types* of familiarity. At the same time, both MVPA and ERP familiarity effects become larger with increasing *levels* of familiarity. This latter conclusion is supported by both studies examining different categories of known identities and learning experiments, covering a time range of several minutes to more than two years of knowing a person.

4.3. *Robustness to task and top-down processes/automaticity*

Familiar face recognition is often assumed to be automatic (Yan et al., 2017; Young and Burton, 2018). Classic as well as more recent definitions state that automatic processes (i) are fast, and do not depend on (ii) conscious awareness, (iii) attentional resources, or (iv) intention or voluntary control (Logan, 1988; Moors, 2016; Posner and Snyder, 1975; Shiffrin and Schneider, 1977). According to this definition, if familiar face recognition really was automatic, its ERP markers should not depend on the task at hand or the availability of processing resources. In line with this idea, previous work has shown a clear N250r independent of task demands (Martens et al., 2006; Schweinberger et al., 2004) or perceptual load (Neumann et al., 2011; Neumann and Schweinberger, 2008). Moreover, testing the conscious awareness aspect of automaticity, an N250 familiarity effect has been reported in participants with developmental prosopagnosia (Eimer et al., 2012), suggesting that overt recognition is not necessary to elicit the effect. This finding can be explained by sub-threshold activations of face representations (Burton et al., 1991; Schweinberger and Burton, 2003), assuming that familiar face representations can be activated sufficiently to elicit an ERP familiarity effect, but not strongly enough to allow for conscious awareness. However, these findings are based on image repetition or recognition of single images, and it remains unclear whether image-independent effects show similar characteristics.

In a recent study (Wiese et al., 2022), the Durham group examined ERPs in implicit (butterfly detection; Experiment 1) or explicit familiarity tasks (familiarity judgments; Experiment 2) and observed highly similar effects (N250: d = 0.70 in Experiment 1, d = 0.71 in Experiment 2; SFE: d = 1.05 in Experiment 1, d = 0.98 in Experiment 2). Moreover, ERP familiarity effects were also observed when participants were instructed to conceal their familiarity with a given identity, i.e., when participants were asked to "lie" about knowing someone (Experiment 3). However, in contrast to the N250, the SFE was less reliably detected in individual participants in the "concealed" relative to the "acknowledged familiarity" condition, which suggests some level of voluntary control over the effect.

In a collaboration between the Durham and Jena groups, the role of task instructions was further tested by re-analysing this dataset using MVPA (Dalski et al., 2022). The results confirmed the task-independence of the familiarity signal, as both implicit and explicit familiarity tasks led to a robust familiarity effect starting from 200 ms and lasting until 1000 ms post-stimulus. Also, the different task and instruction modulation of the early (200–400 ms) and later (400 ms-) time-windows was confirmed by this analysis – as only the later component reflected conscious efforts to conceal knowledge.

In a further study, the Durham group examined whether ERP familiarity effects depend on processing resources (Wiese et al., 2019). Here, letter strings were superimposed over highly personally familiar and unfamiliar faces, and participants were asked to report whether each string either contained an "X" or an "N" (see Jenkins et al., 2002; Lavie et al., 2003). While in a first experiment, four different letters were presented ("high load"), four "Xs" or "Ns" were presented in Experiment 2 ("low load"; see Fig. 4). We observed clear N250 effects in both experiments, which were highly similar in timing and size, and clearly comparable to effects observed in previous experiments. At the same time, the SFE was substantially reduced relative to previous studies. This was particularly pronounced in the "high load" condition, while a somewhat increased SFE was observed in the "low load" condition. It appears that distraction had no detectable effect on the N250, while the SFE was increasingly affected by reduced processing resources.

In conclusion, both ERP and MVPA results suggest that early and later familiarity effects respond differently to task demands. Effects in the 200–400ms time window seem remarkably robust to such manipulations, while later effects are not. These results point to a high degree of automaticity for earlier MVPA/N250 effects, while the later MVPA effects and the SFE appear to require processing resources and are more under voluntary control.

4.4. Domain-specificity of familiarity effects

In a series of experiments testing the recognition of personally familiar as compared to unfamiliar faces, animals, indoor scenes, and objects (Wiese et al., 2023), the Durham group demonstrated clear differences in the timing and scalp topography of familiarity effects for different stimulus classes between 200 and 400 ms (see Fig. 5a). At the same time, highly similar right occipito-temporal familiarity effects were observed from 400 to 500 ms onwards, suggesting the occurrence of an SFE for all tested stimulus categories. It therefore appears that the SFE does not reflect processes that are specifically targeted at faces (or people).

In an independent experiment, the Jena group tested whether MVPA familiarity effects are specific to faces or reflect a shared domain-general recognition process. Klink and colleagues (2023) used personally familiar and unfamiliar faces and scenes. MVPA revealed that familiarity is similarly decodable from the EEG data for faces and scenes from around 200 ms onwards (Fig. 5b). Importantly, in line with the above ERP results, familiarity information appeared earlier for faces when compared to scenes. Moreover, familiarity information generalised well

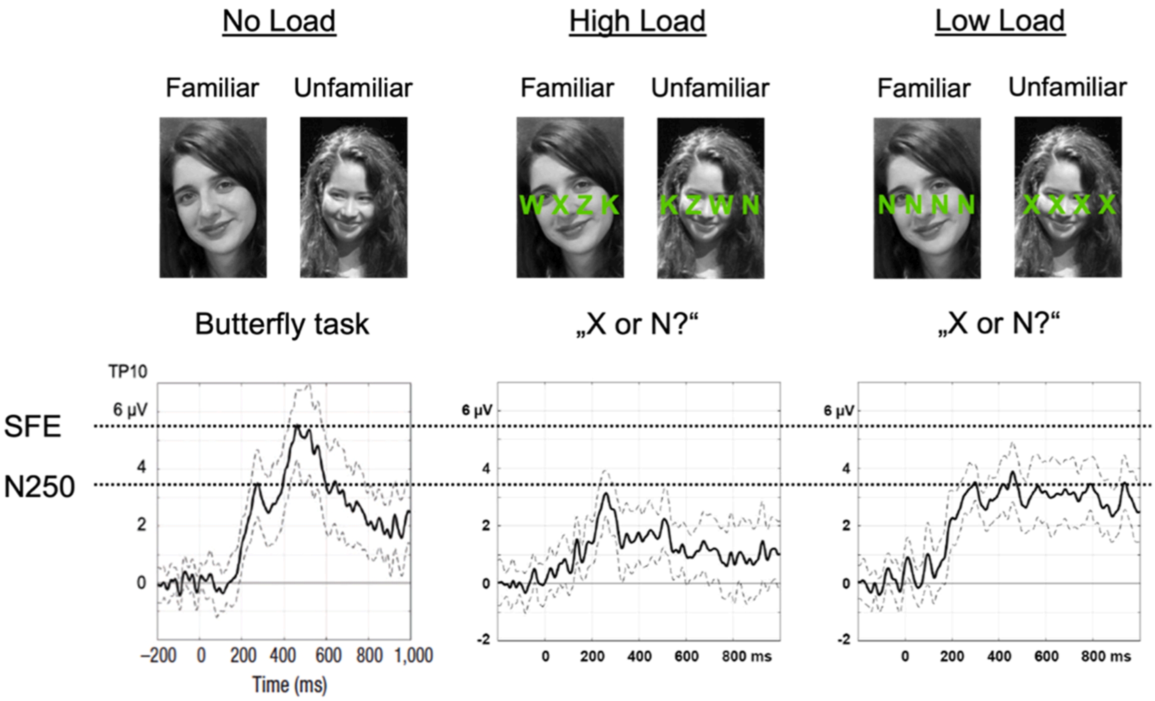
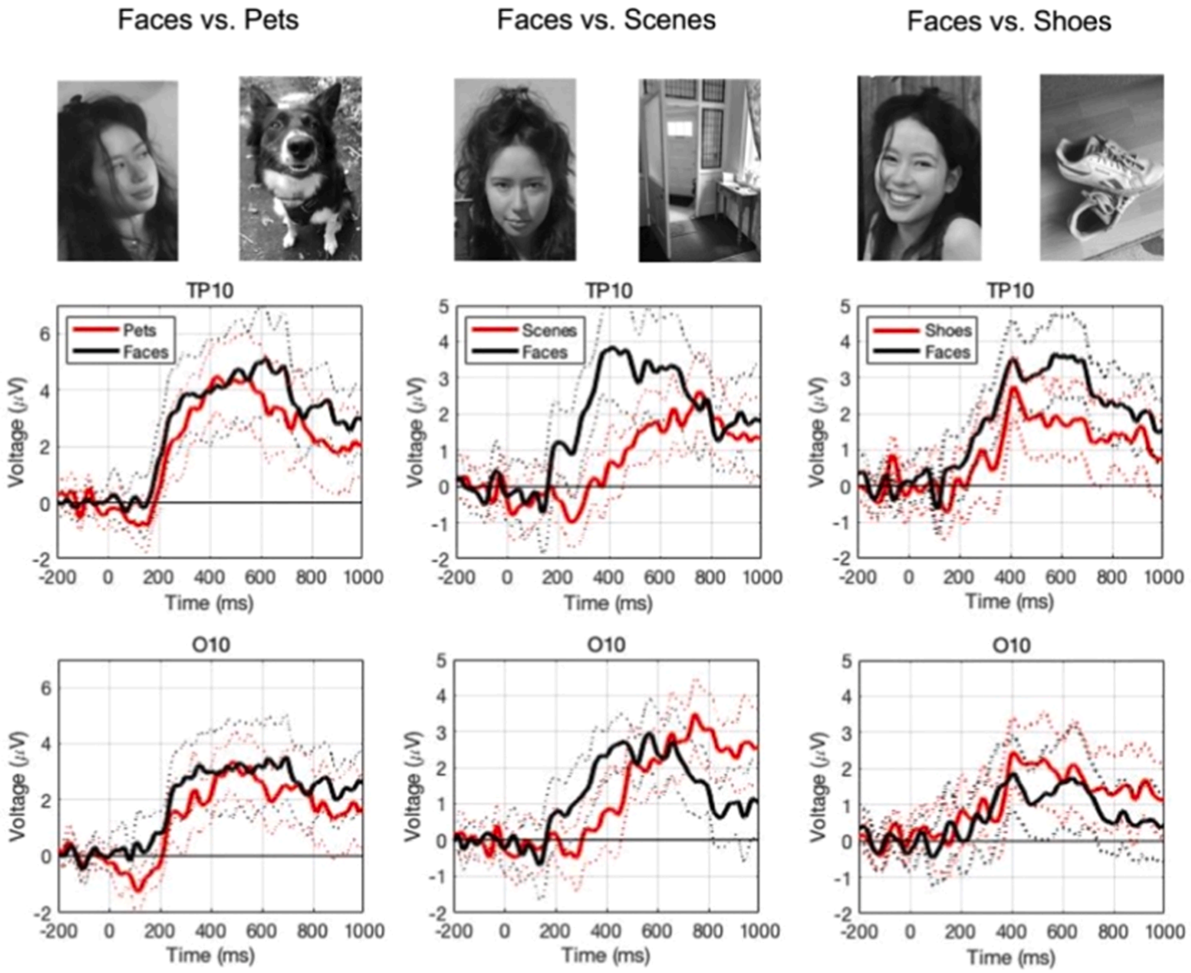


Fig. 4. Top: Illustration of the butterfly detection and XN tasks as used in Wiese, Tüttenberg et al. (Wiese et al., 2019) and Wiese, Ingram et al. (Wiese et al., 2019). Bottom: Difference curves (unfamiliar – familiar conditions, +/- 95 % CI), demonstrating highly similar N250 effects across tasks and load manipulations, as well as substantially reduced SFEs in the XN tasks, and particularly in the high load condition.

a) Faces vs. other visual stimulus categories – ERP results



b) Faces versus scenes – MVPA results

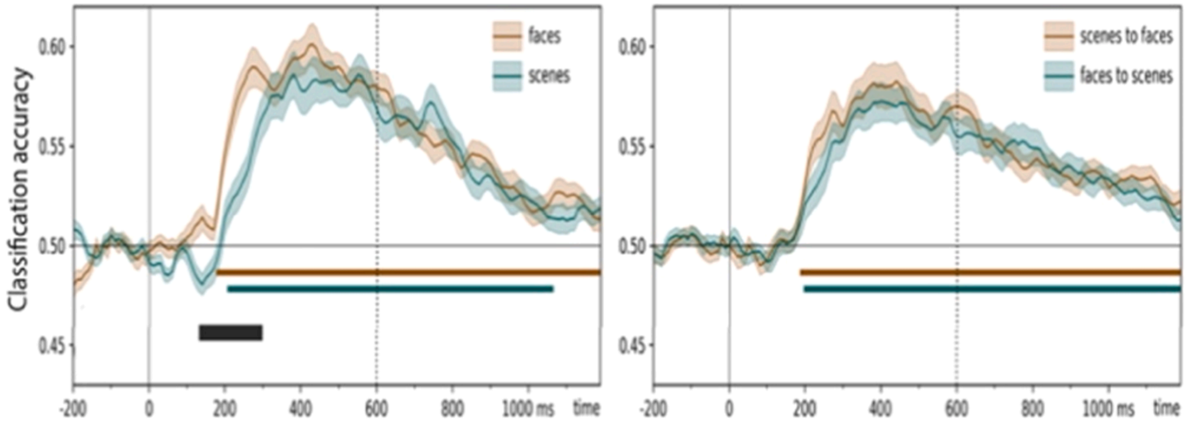


Fig. 5. a) Example ambient images and ERP difference curves (unfamiliar – familiar) for faces as compared to other visual categories (pets, scenes, and objects) at right-hemispheric temporal electrode TP10 as well as occipital electrode O10. b) Time-resolved, leave-one-subject-out classification of familiarity. Classifiers were trained to categorize ERPs for familiar and unfamiliar stimuli. Left panel: Within-category classification. Training and testing for familiarity was performed within the same stimulus category. Right panel: Cross-category classification. Training and testing for familiarity was performed on different stimulus categories. Two-sided cluster permutation tests, $p < .05$.

across stimulus categories, suggesting domain-generality, particularly of the later parts of the effect.

4.5. Image-independent representation of identity

Previous studies have used MVPA to evaluate the temporal dynamics of unfamiliar face identity processing (Nemrodov et al., 2019; Nemrodov et al., 2016; Vida et al., 2017). As discussed above, familiarity and identity processing for familiar faces are assumed to be based on the same underlying long-term representations, which are not available for unfamiliar faces. However, given sufficient similarity between images, "identity"-based effects may also arise for unfamiliar faces, as images of the same identity are likely to be perceptually more similar to each other relative to pictures of a different identity. Studies using unfamiliar faces have unanimously examined identity representations across changes in emotional expression and found them to emerge relatively early, within the first 200 ms after stimulus onset. As variability across images of the same identity was very limited in these studies, it appears plausible that at least the early part of these effects reflects low-level visual feature-based discrimination.

The Jena group tested the neural dynamics of identity representations by using highly variable images of very familiar celebrities (Ambrus et al., 2019). Image-independent representation of facial identity emerged very fast, shortly after 100 ms post-stimulus onset (Fig. 6). These results corroborate Dobs et al. (Dobs et al., 2019) who used MEG to measure the temporal course of face perception. Using famous faces, they similarly found identity information from approximately 90 to 400 ms. Again, it seems likely that very early (presumably <200 ms) effects reflect low-level stimulus features (see below).

The Jena group has also tested how experimental familiarization affects face identity representations. In the Ambrus et al. (Ambrus et al., 2021) study, using perceptual, media and personal familiarization experiments, identity information was found from approximately 200 ms until 1300 ms, largely independently of the type of familiarization. However, this identity-specific information was not significantly different pre- and post-familiarization. This suggests that this prolonged identity representation is largely independent of learning and may reflect the physical similarity of pictures of the same faces, allowing for incidental and familiarity-independent identification. This may be seen as an initial phase in the acquisition of genuine representations of face identity (Johnston and Edmonds, 2009). However, as it is independent of familiarity, the process described here does not reflect the activation of a newly-established face representation.

A potential explanation of why Ambrus et al. (Ambrus et al., 2021) did not find enhanced identity representations after experimental familiarization may be that the applied familiarization was not sufficient to generate robust identity signals. For this reason, the activation of pre-experimentally existing identity-specific representations of famous and personally familiar faces was tested (Kovacs et al., 2023). This was achieved by reanalysing the data of Li et al. (Li et al., 2022), which is based on the presentation of multiple ambient images of own, personally familiar, and famous faces. This analysis showed that identity information between 100 and 200 ms is relatively independent of familiarity levels, while it is determined by the degree of familiarity between 200 and 400 ms (see Fig. 7). Further, these results again argue for similar identity representations for famous and personally familiar faces.

4.6. A single representation for perception and recognition?

As discussed above, Caharel and Rossion (Caharel and Rossion, 2021) have suggested that the distinction between perceptual and mnemonic representations in face recognition is not necessary. Empirically, the argument is built on the assumption of familiarity effects occurring already in the N170 time range (with larger amplitudes for familiar relative to unfamiliar faces). Of particular importance, according to this view, the onset of ERP familiarity effects should depend on the level of familiarity, and familiarity effects in the N170 should therefore particularly occur for personally highly familiar faces.

Based on the research program outlined in previous sections, the Durham group is in a good position to test this claim. By now, 14 data sets using the basic paradigm illustrated in Fig. 2, with a total of 288 participants, have been collected. Critically, however, a mini meta-analysis on this data has not found any evidence for the suggestion of larger N170 amplitudes for personally familiar faces, neither when

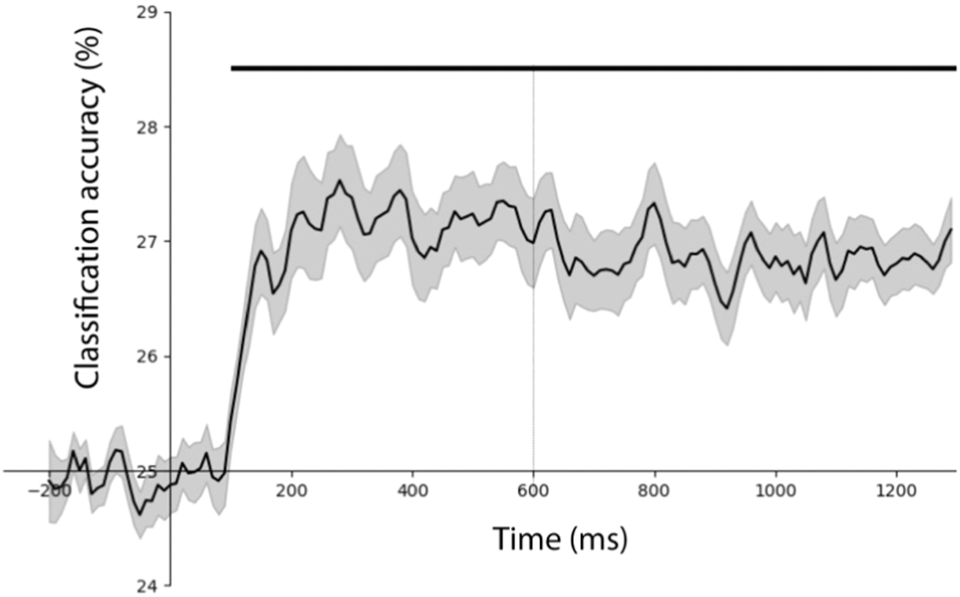


Fig. 6. Time-resolved mean identity classification accuracy for four famous identities across all participants. The classification analysis was conducted according to a leave-one-stimulus-out cross validation logic. For each participant in every time-point, linear discriminant analysis classifiers were sequentially trained on different images of all four famous identities (e.g. images #1 to #9 of Heidi Klum, Leonardo Dicaprio, Till Schweiger, and Angelina Jolie) and tested on the left-out image of one identity (e.g. AJ image #10), leading to a chance level of 25 %. Identity information emerges at 110 ms (peak at 280 ms, Cohen's d = 1.23) and persists throughout the epoch. Black horizontal line denotes statistically significant difference from chance (25 %), p<0.05 FDR-corrected for multiple comparisons). Shaded area denotes standard errors of the mean. Vertical grey line signals stimulus offset. Figure is modified from Ambrus et al. (Ambrus et al., 2019).

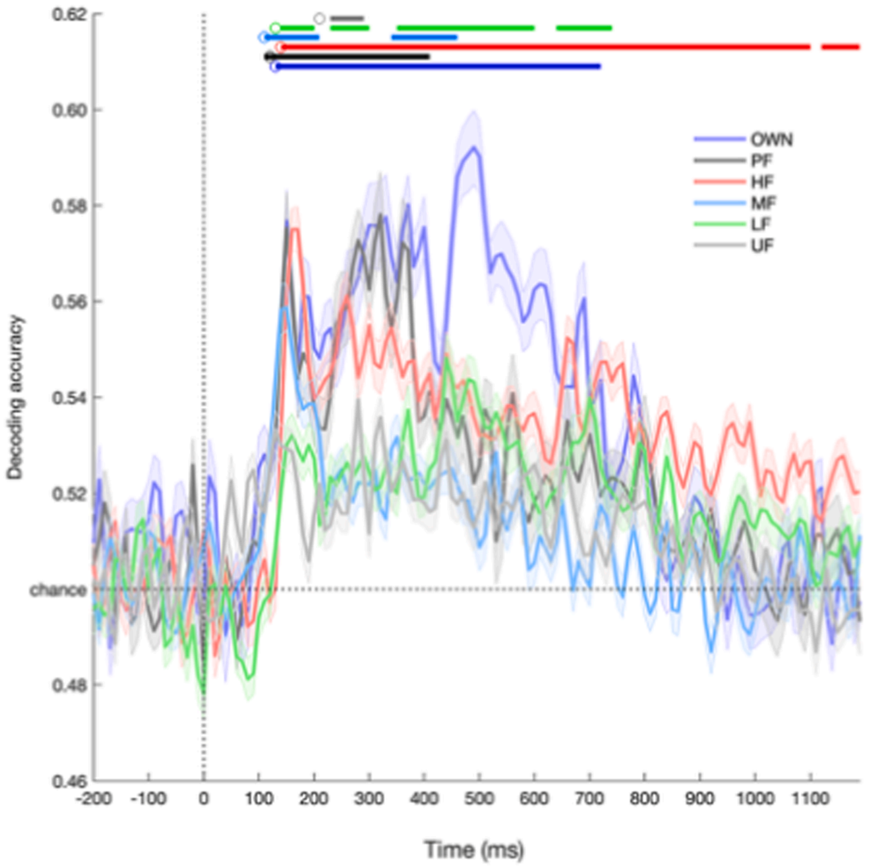


Fig. 7. Average time-resolved decoding accuracies across participants, separately for the faces having different degrees of familiarity as a function of time. Horizontal lines denote temporal clusters with significant decoding accuracies (10,000 two-sided cluster-based permutations against chance, p <.05). OWN, participants' own face; PF, personally familiar faces; HF, highly familiar celebrity faces; MF, medium familiarity celebrity faces; LF, low familiarity celebrity faces; UF, unfamiliar faces. Dotted horizontal line signals chance level.

analysing electrodes TP9/TP10 (where maximum familiarity effects occur in later time ranges) nor at electrodes P7/P8 (which are commonly analysed in N170 research; see Fig. 8). Only one out of 14 data sets revealed a significant effect (in the TP9/TP10 analysis only) but in the direction opposite to the expected one. The analysis further shows that any potential non-significant N170 familiarity effect is very small (with an estimated overall effect of 0.03 μV at TP9/TP10, see red diamond in Fig. 8) and might well point in the opposite direction. It seems possible that larger N170 familiarity effects occur under different experimental circumstances (e.g., Jacques and Rossion, 2006; Johnston et al., 2016). However, the specific conditions used in the present paradigm seem to be more naturalistic than those in most other studies. We conclude that under these conditions, the N170 does very consistently not show the suggested effect. By contrast, corresponding mini meta-analyses of the N250 and SFE time ranges revealed highly consistent and substantial effects, with the latter being clearly larger than the former.

5. Synthesis and integration: A revised model of face recognition

The above review suggests that the processes leading up to face and person recognition can be divided into three phases (see Fig. 9): an early visual processing stage (Section 5.1), a domain-sensitive processing stage during which familiarity emerges (Section 5.2), and a domain-general post-perceptual processing stage (Section 5.3). The latter two phases can be seen as broadly analogous to the core and extended systems hypothesised in previous models (Gobbini and Haxby, 2007; Haxby et al., 2000; Kovacs, 2020).

5.1. *Early visual processing*

MVPA work suggests a very early period relevant to the processing of identity from faces (Dobs et al., 2019; Kovacs et al., 2023), starting between 50 and 110 ms and lasting until around 200–250 ms. This effect overlaps with the processing of low-level stimulus characteristics, is largely independent of the degree and type of familiarity, and also occurs for unfamiliar faces. We interpret such effects as an early feed-forward sweep of identity processing, which may allow for an incidental representation of facial identity, based on low-level, idiosyncratic features even if the person is practically unknown.

However, it is important to point out what exactly this "early sweep" signals to the recipient. As studies reporting such effects typically use a handful of different images per face, early "identity" effects seem to indicate that pictures of the same person are more similar to each other than to pictures of a different person, and this is presumably based on the processing of local low-level image characteristics (e.g., one person may have blonde hair and very large eyes while others don't). Attempts to control low-level properties (e.g. Willenbockel et al., 2010) are unlikely to mitigate these effects, because such manipulations are performed on the whole image and do not eliminate local feature differences. More fundamental to the issue of stimulus similarity, a shortcoming of current approaches is that while they may provide a metric for physical similarity, they universally fail to provide a metric for *perceptual* similarity. Arguably, however, perceptual (not physical) similarity is key to mental representations (e.g., Edelman, 1998).

One promising method to solve the problem of how perceptual similarity is reflected in neural representations is provided by machine learning algorithms. Recent studies show that deep neural networks

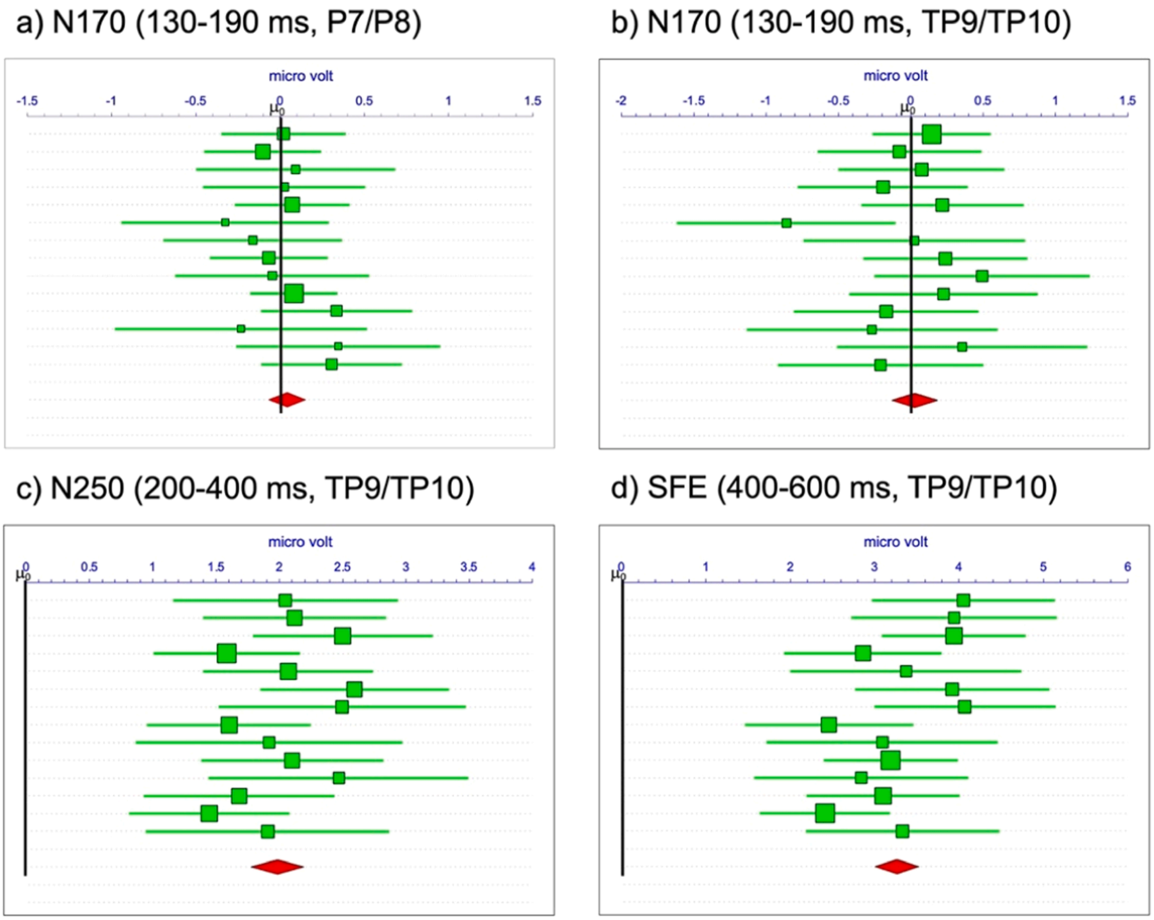


Fig. 8. Mini meta-analysis of 14 data sets comparing unfamiliar and highly personally familiar faces in (a) the N170 at P7/P8 (random effects = 0.04 μV, 95 % CI [-0.06, 0.15]), (b) N170 at TP9/TP10 (random effects = 0.03 μV, 95 % CI [-0.13, 0.18]), (c) the N250 at TP9/TP10 (random effects = 1.98 μV, 95 % CI [1.78, 2.19]), and (d) the SFE at TP9/TP10 (random effects = 3.29 μV, 95 % CI [2.97, 3.61]). Data stems (top to bottom in each panel) from (Wiese et al., 2019), Experiments 1 and 3 (Wiese et al., 2022), Experiments 1, 2, and 4 (Wiese et al., 2022), Experiments 1 and 2 (Popova and Wiese, 2022), Groups 1, 2, and 3, (Wiese et al., 2023), Experiments 1, 2, and 3, as well as an as yet unpublished data set. Note that we did not include data sets in which face stimuli were not fully visible and participants were distracted or instructed to conceal familiarity (see Wiese et al., 2019; Wiese et al., 2022, Experiment 3).

(DNN) develop similar properties to the brain (Dobs et al., 2022; Grossman et al., 2019; Kanwisher et al., 2023; van Dyck and Gruber, 2023; Wang et al., 2022). Indeed, a recent study found that the representational distances among face pairs in a state-of-the-art DNN correlate well with the perceived similarity of human observers (Jozwik et al., 2022), signalling the benefits of applying DNNs to human perceptual problems (see also Jiahui et al., 2023).

In conclusion, this "early sweep of identity" neither signals whether we know the face or not, nor any additional information about who the person is. Returning to the example from the introduction, the person behind us in the supermarket queue would probably not be recognised based on the processes discussed in this section.

5.2. *Domain-sensitive processing/core system*

The next stage, broadly spanning the time period from 150 to 300–400ms, is domain-sensitive in the sense that processing appears to differ for faces as compared to other visual stimuli. We do not hold strong views on whether *any* non-facial stimuli can elicit precisely the same processes, and we consider this question as orthogonal to the present purposes. A more specific account of this time range is illustrated in the middle part of Fig. 9. We very broadly base the suggested processes on the multi-dimensional face space (MDFS) model (Valentine, 1991; Valentine and Endo, 1992). Here, the multiple dimensions of the space code 3D shape and surface reflectance characteristics of faces. While only two dimensions are presented in the figure, an actual face space will contain many more. As the dimensions code physical facial characteristics, more similar faces will be represented closer to each other. This basic architecture appears realistic, given the discovery of a similar coding system in the primate brain (Chang and Tsao, 2017; She et al., 2024) as well as artificial networks (Jozwik et al., 2022).

Critically, in contrast to MDFS, in which faces are represented as single points, the present account incorporates image-independence and varying degrees of familiarity by representing each familiar facial identity as a multidimensional sub-space carved out by natural image variability for an individual identity (green circles in Fig. 9; also see Burton et al., 2011; Tanaka et al., 1998). Different instances, as well as an average of a specific identity (Burton et al., 2005; Burton et al., 2016), are stored within each sub-space (see lower part of Fig. 9), and faces can therefore vary in appearance while still being recognised as belonging to the same person. Moreover, more familiar faces have larger representations, containing more instances, which accounts for varying levels of familiarity.

Given this basic architecture, we can understand the process of face recognition as follows: When a face is perceived, a perceptual representation of the stimulus (red circles in Fig. 9) is formed in the brain. This perceptual representation is initially broad and becomes more fine-grained with increasing time, reflecting the results of gradually more detailed processing. The initial broad perceptual representation reflects a basic face template (two eyes above a nose above a mouth). All

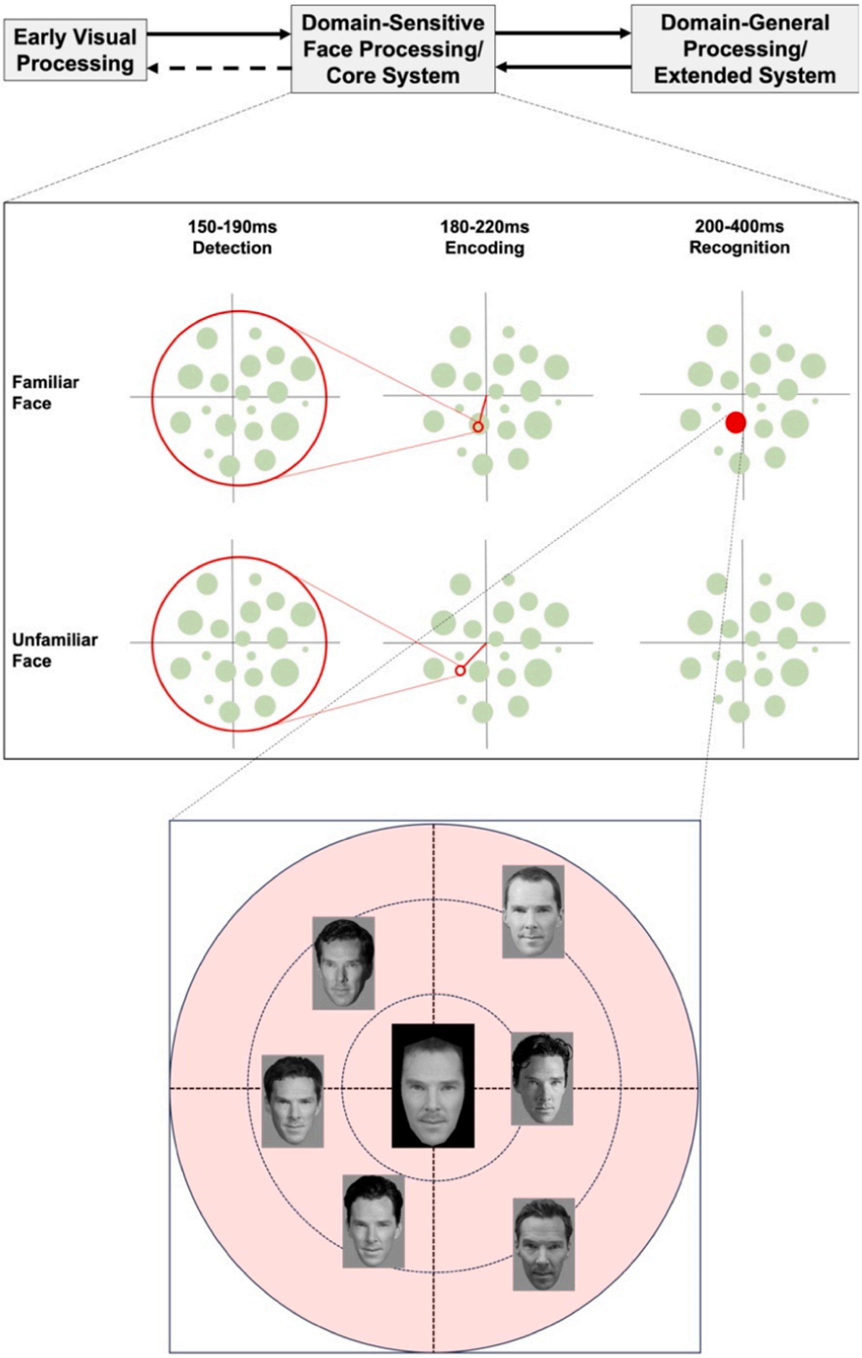


Fig. 9. A revised EEG-based model of face recognition, see text for details. Top level: Neural processes involved in face recognition can be broadly divided into three stages, early visual processing, domain-sensitive, and domain-general processing. Middle: Stored representations of known faces (green circles) are arranged in a multidimensional space, with more similar faces being represented closer to each other. More familiar faces are represented as larger circles, less familiar faces as smaller circles. A perceptual representation of the face stimulus is created which is initially coarse (red circle in 150–190ms time window) and therefore matches all stored representations of known faces. While this stage allows a categorisation of the stimulus as being a face (and not a different visual object; face detection), recognition of individual identity is not possible yet. The perceptual representation is increasingly refined during the encoding stage (small red circle in the 180–220ms time window) and matches a stored representation in case of a familiar face but not in case of an unfamiliar face (i.e. the red circle falls on a green circle in the upper but not in the lower panel). Encoding is conducted relative to a norm in the centre of the space. In case of a match, the respective representation becomes activated (red circle in the 200–400ms time window) and an individual face is recognised. Bottom level: illustration of an individual long-term representation, containing both an average of the respective individual face at the centre and specific instances.

familiar face representations match this basic description and therefore fall within the circle. The resulting information at this stage is that the stimulus is indeed a face, and not a different visual object, and the electrophysiological correlate of this process is the N170.

Over time, details about the 3D shape and surface reflectance information of the perceived face are accumulated. This gradually refines the perceptual representation (i.e., the red circle gets smaller) and moves it into a more specific part of the space. Importantly, even if substantially refined, the perceptual representation does not become point-like. Similar to MDFS, we assume that no perceptual representation is a perfect copy of the original stimulus, and that a degree of uncertainty is therefore coded into it, which may vary depending on viewing conditions etc. The P200 seems to partly reflect this process of refining the perceptual representation, as it codes the distance to the norm, or origin of the space. This is illustrated in Fig. 9 (middle column) as the distance between the red circle and the origin of the space (depicted by the red line). Critically, in case of a perceived familiar face (top row), the red circle is projected onto an already existing (green) long-term representation, while in the case of a perceived unfamiliar face (bottom row), the circle falls into an unoccupied part of the space, as a face representation with these specific parameter values does not exist. In case of a match between the perceptual and long-term representation, the individual long-term representation becomes activated, resulting in a familiarity signal. This signal is measured as a more negative waveform in the N250 and as the familiarity signal between 200 and 400 ms in MVPA studies.

In contrast to previous models (see Fig. 1), this account explains why recognition should be easier for more familiar faces, as well-known faces will have more detailed long-term representations, which are in turn more likely to match a perceptual representation. As an analogy to familiar face representations based on exemplars (Burton et al., 2016), one might think of folders on a computer, each containing images of a specific face. Better known faces have larger folders with more images, and lesser-known faces have smaller folders with fewer images. It follows that, in the case of lesser-known faces, which are represented only incompletely, a particular instance may not be represented within a given individual sub-space. Accordingly, highly familiar faces are more likely recognised from a wide range of images than less familiar faces as their representational sub-spaces are larger, and the probability of relevant facial information being projected onto them is higher.

Importantly, this account does not assume that processing at a given stage needs to be complete before information is passed on, and accordingly stages overlap (see timing information in Fig. 9). For example, in the case of more familiar faces, recognition may be achieved earlier, because even a less refined (or broader) perceptual representation already allows for the unambiguous activation of the specific long-term representation. The assumption of overlap between processes explains the empirical finding of beginning familiarity effects in the 200–400 ms time window in MVPA data (Li et al., 2022) or in the P200 time range with highly personally familiar faces (Wiese et al., 2019) and is more generally in line with the idea of using the available information in real-time.

Returning to our supermarket example, at the end of this processing stage, we know that we know the person behind us. Depending on how familiar this person is, the familiarity signal that forms the basis for this knowledge will vary in strength. However, at this stage, we do not have any further person-related information, access to which will strongly influence our decision about whether or not to approach the person.

5.3. Domain-general processing/extended system

The time range starting at 300–400 ms is usually associated with access to post-perceptual person-related information, such as semantic, episodic, or affective information. This stage is domain-general, in the sense that it can be accessed not only via faces, but also from other stimuli carrying identity information, and similar information may be represented for personally familiar objects or scenes (Klink et al., 2023; Wiese et al., 2023). While we clearly need such information to interact with people in real life, systematic research in this area is still relatively sparse. However, in addition to the classic ERP markers of semantic and episodic memory within this time-window, the SFE and MVPA findings might well represent additional neural correlates of this stage. The SFE overlaps in time with the N400 and old/new effects but has a clearly different scalp-distribution. While the latter effects are typically maximally observed at central and parietal electrodes, the SFE is maximal at occipito-temporal channels. Similarly, MVPA shows that familiarity effects in this time-window have occipito-temporal maxima.

As noted above, in case of the successful recognition of a familiar face, the domain-sensitive stage results in the activation of an individual face representation reflected in the 200–400 ms time window. As the scalp-distributions of the N250 effect (200–400 ms) and the subsequent SFE (400–600 ms) are highly similar, it seems plausible that the underlying processes are related. They are, however, not identical, as the two effects respond differently to degrees of familiarity (Popova and Wiese, 2022; Popova and Wiese, 2023; Popova and Wiese, 2023). Moreover, it is possible to observe an N250 effect without an SFE (Popova and Wiese, 2023; Wiese et al., 2019), and an SFE without the typical face N250 (Wiese et al., 2023). The results of the MVPA studies generally agree with a separation of processing reflected in the N250 and SFE time-windows. Here, an earlier familiarity effect (after 200 ms) was sensitive to different categories or levels of familiarity, while the peak of the available familiarity information (between 400 and 600 ms) was similar for personally familiar, famous as well as experimentally familiarized faces (see Section 4.2).

Given that processing of episodic and semantic information takes place in this time range, it appears plausible that such information feeds into an evaluation process signalling *relevance* of the perceived stimulus. Such relevance might be related to a potential upcoming interaction (with a person), or action (with a scene or object), or may more generally reflect significance to the self (as in own-face recognition, or in recognition of close relatives or loved-ones; for a related discussion, see Wiese et al., 2023). The SFE and MVPA effects between 400 and 600 ms may reflect this evaluative process.

This interpretation is in line with the finding that the SFE strongly depends on processing resources (Wiese et al., 2019). When participants are distracted from the familiar face by the task at hand, the face will clearly not be immediately relevant, and the SFE is substantially reduced. Moreover, people we have only just met do not elicit a clear SFE (Popova and Wiese, 2023), and the effect only slowly builds up over approximately the first year of knowing a person (Popova and Wiese, 2022). If only little is known about a person, any potential interaction cannot be based on substantial background information. It thus appears that the relevance signalled by the SFE reflects a slowly (over several hundred milliseconds) occurring and slowly (over many months) developing process, which depends on the degree of familiarity. This may complement other, fast-acting, amygdala-driven mechanisms that signal relevance in the sense of a potential immediate threat (Morris et al., 1996; Morris et al., 1999).

In conclusion, familiar face recognition arguably mostly serves the purpose of preparing a social interaction. We have to identify a face as a known person, access information about this person, and then weigh this information for its relevance. It may be this latter process that will make us cheerfully greet our close friend in the supermarket queue, while we may decide to give a hesitant and half-hearted nod to the person who may or may not be the man from the bus.

6. Outlook and Open Questions

This article has developed a number of positions on important theoretical questions in face recognition research based on recent empirical findings. However, and almost inevitably, a similar number of questions remain unanswered.

First, following a long tradition in cognitive research (Bruce, 1983; Bruce and Young, 1986), we have throughout this review insisted on differentiating familiar face recognition from picture recognition, and that representations underlying the former need to be image-independent. However, we have not touched upon the question about what kind of information is stored within these representations. While it seems clear now that so-called second-order configural information plays a minor role at best for familiar face representations (Burton, 2013; Burton et al., 2015), and that surface reflectance (texture) information is more important (Itz et al., 2017; Itz et al., 2014), the extent to which surface reflectance and 3D shape information are represented for each face is not precisely known (see also Russell et al., 2007). Furthermore, while not necessarily mutually exclusive, it is unclear to what extent information is stored in an exemplar-based or average-based format (Burton et al., 2005; Burton et al., 2016). Future studies will hopefully use image-independent recognition experiments to examine these questions.

Second, building on the MDFS framework (Valentine, 1991), we have argued that more similar facial identities will be located more closely to each other in "face space". The question of similarity, however, becomes complex when taking within-person variability into account. On the one hand, familiar face representations need to be wide enough to allow for recognition from highly variable images. On the other hand, they need to be restrictive enough to prevent intrusions from images of other known or unfamiliar identities, potentially leading to false positive recognition. It therefore seems important to examine how sensitive face recognition processes are for more or less "typical" exemplars of a given facial identity, and to what extent false identifications become more likely when a particular stimulus is projected onto the "edge" rather than the centre of a representation. The application of DNNs can be useful for testing various levels of invariances and similarities for faces (for a review, see Grill-Spector et al., 2018).

Third, interest in individual differences in face perception and recognition has substantially increased over the last decade (e.g. (White and Burton, 2022). However, the majority of this research focuses on unfamiliar face processing, which is highly relevant for applied fields (Phillips et al., 2018; Robertson et al., 2016; White et al., 2014). At the same time, most people recognize familiar faces accurately and without apparent effort. While it may therefore appear that no substantial individual differences exist for familiar face recognition, we note that (i) impaired familiar face recognition is a highly prominent everyday-life problem in developmental prosopagnosia (e.g. Duchaine and Nakayama, 2006), and that (ii) at-ceiling accuracy in the wider population does not preclude differences in efficiency (e.g., (Wilhelm et al., 2010). In addition, it seems plausible that differences in real-life and long-term face learning exist, with so-called super-recognisers (Ramon et al., 2019; Russell et al., 2009) needing substantially less exposure to become familiar with new faces.

Initial evidence indeed suggests that electrophysiological markers of face perception derived from fast periodic visual stimulation (Xu et al., 2017) or MVPA (Mares et al., 2023) could be related to face recognition skills. Moreover, a recent study (Schroeger et al., 2023) compared distance-to-norm effects in the P200 and familiarity effects in the N250 between high and low performers in face recognition tests. The findings suggested important roles of efficient norm-based coding and robust familiar face representations for good face recognition skills. Overall, neural correlates of face recognition skills are an emerging field, and one which calls for more systematic study and cross-method comparisons (including MVPA and DNNs).

Finally, insufficient research effort has as yet gone into the examination of the neural processes underlying person as opposed to face recognition. While earlier studies reviewed above have examined the activation of semantic and episodic person knowledge, more recent findings point to an integrational process, boosting the activation of visual face representations via feedback from post-perceptual processing stages (Wiese et al., 2019). This integration may well involve medial temporal lobe structures, as "concept cells" in this brain region (such as the "Jennifer Aniston neuron") have been observed to respond to both highly variable face images and written names of specific identities (Quiroga et al., 2005). More recently, Tyree and colleagues (Tyree et al., 2023) found a group of neurons in the hippocampus of marmosets which showed modality-independent (face and voice) identity representations. Finally, recent human single-cell data suggests that the temporal pole plays an important role in the integration of personally familiar faces with higher-order, person-specific conceptual information (Deen et al., 2024).

In conclusion, we believe that the research outlined in this paper, and the theoretical positions we have derived from it, form an important step forward in our understanding of the cognitive and neurophysiological processes underlying familiar face recognition. At the same time, substantial work is necessary to close the still existing knowledge gaps. We are excited about continuing our work on what we believe are the critical research questions in face and person recognition, and we hope to have stimulated others to think (and be excited) about these questions as well.

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