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Do I Know You? Insights Into Memory for Faces From Brain Potentials

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ABSTRACT

The recognition of faces is central to human social interaction. Recordings of event-related potentials (ERPs) from the brain can shed light on the various processes that occur when a face is recognized and when knowledge related to a specific person is retrieved. ERP contrasts between processing familiar and processing novel faces offer a gateway into investigations of semantic memory for familiar persons. In particular, activity of face recognition units and semantic information units — memory representations of faces and person-related knowledge, respectively — can be indexed by specific ERPs. These potentials thus provide valuable tools for studying the cognitive and neurobiological architecture of person recognition. ERPs have also been found useful for investigating other types of memory for faces. Specifically, important insights have been derived from the study of a category of memory phenomena known as priming. Priming can be revealed in special tests when face recognition is facilitated based on prior experience. Describing the neural processes associated with memory for faces is an exciting focus of research, and future results from this line of inquiry promise to provide further knowledge about face recognition and the various types of memory that can be provoked by a human face.

INTRODUCTION

The importance of faces for social interactions can hardly be overestimated. We are surrounded by other people, and faces are a key source of information guiding our behavior towards others.[1] A vital human cognitive ability concerns identifying the person behind the face. This process comprises the perception of the face; importantly, comparisons must be made between the face and stored representations of previously encountered faces. Given the enormous number of people typically viewed in one's lifetime, it is remarkable that this quite challenging task can be performed with such apparent ease — it usually takes only a fraction of a second to recognize a familiar face. We are also able to retrieve a vast collection of other knowledge associated with a specific face seemingly instantaneously.

Face recognition involves specific neural circuits in the human brain.[2,3] Damage to certain regions of the brain, mainly within the right hemisphere, can cause a disruption of the ability to recognize faces, a syndrome called prosopagnosia.[2] The consequences for social interactions in patients with prosopagnosia are severe and call attention to the importance of face recognition.

The brain processes that occur when a perceived face provokes the retrieval of face- and person-related memories can be studied with event-related brain potentials (ERPs), measured with electrodes placed on the human scalp.[4] The high temporal resolution of ERPs allows the time course of underlying neurocognitive processes to be measured with a precision in the range of milliseconds. Additionally, the spatial distribution of ERPs across the scalp provides information about the generating sources within the brain; this information can be used, for example, to test whether two ERPs reflect similar or different neurocognitive processes.

Analyses of ERPs elicited by faces often take place within the context of contemporary theories of person recognition. One of the most influential theories about the cognitive architecture of the person recognition system (as outlined by Bruce, Young, Burton, Valentine and colleagues[5-7]) posits the following stages of face processing: structural encoding, face recognition units (FRUs), person identity nodes (PINs) and semantic information units (SIUs). Structural encoding refers to the perceptual processing of faces. An FRU is a generic representation of a familiar face that can take into account variability in viewpoint, various changeable facial features, and other visual

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variability in how the face appears in any particular image. When a familiar face is seen and the FRU of that face is activated, this will usually be followed by access to the corresponding PIN. A PIN is a multimodal representation that can also be accessed via the name of a familiar person or other meaningful cues. Successfully identifying a person is usually interpreted as an indication of sufficient PIN activation. When a person is identified, biographical knowledge about the person, for example the name or the occupation, may also be retrieved. This retrieval is thought to entail activation of SIUs. Theories on person recognition also take into account specific input routes for the variety of ways by which a person can be recognized. As simple as these schemes seem at first glance, they accord well with a vast body of evidence in cognitive psychology, cognitive neuroscience, and neuropsychology. Person recognition models of this sort explain findings concisely and elegantly, and research in this context continues to stimulate the scientific endeavor by generating new and interesting hypotheses.

In this article, we will selectively review research conducted in order to describe memory processes that occur in response to human faces (for general reviews on memory-related ERPs, see[8-14]). This review will focus on three questions. Firstly, do specific ERPs discriminate between processing specific for familiar versus newly encountered faces? Secondly, can the activity of memory representations associated with faces (FRUs, SIUs) be monitored with ERPs? Thirdly, can qualitatively different types of memory for faces (i.e., declarative and nondeclarative memory) be dissociated with ERPs?

Semantic familiarity — ERPs differentiate neural processing specific for known faces

Neurocognitive processes engaged when a familiar face is encountered and recognized can be studied by comparing ERPs to familiar faces with ERPs to unfamiliar faces. Usually famous faces are used. Because these faces have often been extensively encountered before, each face is linked to a previously stored facial representation in semantic memory, an FRU. Additional conceptual knowledge about the specific persons in question will likely also be available (e.g., information regarding names, occupations, etc.). Semantic memory is generally taken to comprise factual knowledge about the world, which can be either multimodal like biographical knowledge, or specific to modalities or domains like the visual knowledge of a known face. A hallmark of semantic memory that dissociates it from episodic memory is that semantic memory does not make any reference to the moment and circumstances — the spatiotemporal context — of knowledge acquisition.[15] Differences found between ERPs to familiar faces and ERPs to unfamiliar faces can thus reflect processes related to the successful retrieval of semantic memories for familiar faces. In practice, valuable information can thereby be gained concerning the organization of neural networks of person-specific knowledge and the time course of processing within these networks.*

A common finding is that by 400 ms after face onset, and sometimes as early as 250 ms, ERPs to familiar faces are more negative than ERPs to unfamiliar faces. This negativity generally exhibits a widespread distribution over the scalp, usually most pronounced at centro-parietal positions. This negative ERP difference relating to the retrieval of information associated with familiar faces has been called N400f or face-N400.[16-18] The N400f has been found to be expressed independent of whether or not the familiarity of faces was relevant for the task at hand, or whether or not the recognition of faces and retrieval of conceptual knowledge associated with the person behind the face was required.[17,18] In other words, N400f can be expressed incidentally in response to familiar faces. This conclusion must be qualified, however, due to the finding that when attention was diverted to a letter string presented simultaneously and overlapping the face, no N400f was found.[17] Probably, certain attentional resources must be allocated to face processing. N400f potentials also appear to be reduced for repeated presentations of faces.[17] Most interestingly, N400f was absent in a case study of a prosopagnostic patient, strengthening the interpretation that N400f is associated with semantic-memory processes for faces.[17] This interpretation finds further support in the demonstration that face inversion, which disrupts face processing and recognition, abolishes N400f.[17]

Another difference between ERPs to familiar and unfamiliar faces, the so-called P600f,[17] has been recorded around 600 ms after face onset, after the disappearance of N400f.[16-18] Similar to N400f, this positivity has been found to show a widespread distribution over the scalp with a centro-parietal maximum. P600f also shares several other properties with N400f. For example, P600f has been demonstrated when face familiarity was task irrelevant and access to conceptual knowledge associated with the specific person in question was not required.[17,18] P600f has been found to be reduced by face repetition, absent for inverted faces, and also absent in a case study of a prosopagnostic patient.[16,17] On the other hand, there is a remarkable func-

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*As a general caveat it needs to be kept in mind that a face seen before can provoke several types of memory, including semantic memory, episodic memory, and priming (see the following sections of this article for more details). Controlling for these distinct types of memory in an experimental task can be rather challenging, as has been the dissociation of ERPs associated with distinct types of memory. Moreover, the creation of semantic memory representations of a particular face arguably begins with its first presentation, so that the contrast between familiar and new faces theoretically could also reflect memory encoding.

tional difference between P600f and N400f. P600f has been found under the condition of diverted attention to overlapping letter strings presented simultaneously, a condition when N400f was absent.[17] In general, these findings parallel results obtained for the N400f and suggest a close link between P600f and semantic-memory processes for a face, either related to the facial representation or multimodal conceptual knowledge about the depicted person. Moreover, following the latter finding it could be argued that P600f may be generated automatically as long as conditions allow for face recognition to occur. Therefore, it is likely that P600f relates to semantic-memory processes for faces that are different from those that are indicated by N400f.**

In general, contrasts between ERPs to familiar (typically famous) faces and ERPs to unfamiliar faces provide promising means to study face recognition and processing of face-associated conceptual knowledge. Despite the characterization of N400f and P600f ERPs in this context, it remains an important topic for future investigation to further elucidate the aspects of semantic memory for faces indicated by these ERPs, and to specify how these ERPs relate to specific stages within face recognition models.[5-7] This knowledge should provide valuable information about the time course of processing of semantic memory for faces, and conceivably will support the application of ERP methods in the study of processing deficits pertaining to faces (e.g., perhaps in congenital prosopagnosia).

Activity of memory representations of familiar persons can be traced with ERPs — the early repetition effect/N250r and the late repetition effect/N400

Recent studies have demonstrated that processing stages within models of person recognition can be measured with specific ERPs (for a review, see[19]). Here, we focus on two prominent ERPs. Processing at the level of FRUs can be studied with the so-called early repetition effect or N250r, and processing at the level of SIUs with the so-called late repetition effect or N400. It is important to note that these ERP effects don't measure processing at these stages directly, but rather, they measure changes when such processing is repeated. These effects are revealed when ERPs to repeated (usually famous) faces are compared with ERPs to these faces presented for the first time.

With an average reference, the N250r*** consists of a positive-going amplitude modulation at frontal electrode sites and a negative-going modulation at temporal sites, which starts around 250 ms after face onset, peaks at about 300 ms and lasts for at least 100 ms.[20-24] The rationale behind linking the N250r to activity at the level of FRUs turns on at least two findings. Firstly, for unfamiliar faces, which do not have FRUs, the N250r is much smaller (perhaps reflecting a temporary FRU-like representation) or even absent.[22,23] Secondly, representations similar to FRUs exist in other visual domains, for example for words or common objects. Accordingly, when the N250r is measured in those domains, the resulting scalp topographies of the N250r have been found to be different.[21,22,25,26] Such differences are usually considered to indicate the involvement of different neurocognitive processes and one can thus infer the domain-specificity of the underlying representations. Therefore, N250r can be used to study processing at the level of FRUs, and it is also a promising tool to investigate the neural and cognitive organization of representations in semantic memory. Recently, N250r evidence prompted the hypothesis that FRUs are localized in the fusiform gyrus,[24] a specific region within a larger, distributed network implicated in face recognition by a variety of other measures.[2,3,27]

The N250r only survives a few intervening faces and has not been found after longer lags in the time range of several minutes.[28] Notably, the N250r is reduced, but not abolished when face repetitions involve different images of the same face.[24] This finding highlights a very interesting aspect of the N250r. FRUs are considered to be generic representations of familiar faces; they do not depend on one specific facial image. Therefore, any effect directly related to the activity of FRUs should not vary when different images are used for initial and repeated face presentations, as long as the faces can be identified clearly from the images. The sensitivity of the N250r to image changes hence was taken to indicate that this effect likely reflects facilitated access to FRUs when faces were seen repeatedly.[24]

Usually, the N250r is followed by the N400 (also called late repetition effect). The relationship between this ERP modulation and N400 potentials intensively studied with

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**Another study also contrasted ERPs to familiar faces with ERPs to unfamiliar faces and found support for the notion that, by doing so, semantic-memory processes for faces can be studied.[51] ERP differences of solely positive polarity were found that appeared to be present independent of task requirements (e.g., whether or not familiarity of faces was task relevant), as was the case for N400f and P600f. Interestingly, these authors suggested the separation into an early positive effect between 200 and 300 ms and a later positive effect between 300 and 450 ms. A similar polarity reversal in the N400f-time range was also observed in another study that contrasted genuinely novel faces with unfamiliar faces seen briefly once before.[55] Notably, the ERPs were referenced to mastoid electrodes in the two latter studies, whereas the studies reviewed above employed a nose reference. It is presently unclear whether factors beyond the location of the reference site might explain the differences between ERP findings from these studies.

***The terms "early repetition effect" and "N250r" have both been used to refer to the same ERP repetition effect. To complicate matters even more, neither term seems without difficulties. Repetition effects preceding the early repetition effect have been reported for faces (for example, see[20]), and the effect extends far beyond 250 ms, often with positive amplitudes at frontal electrodes.

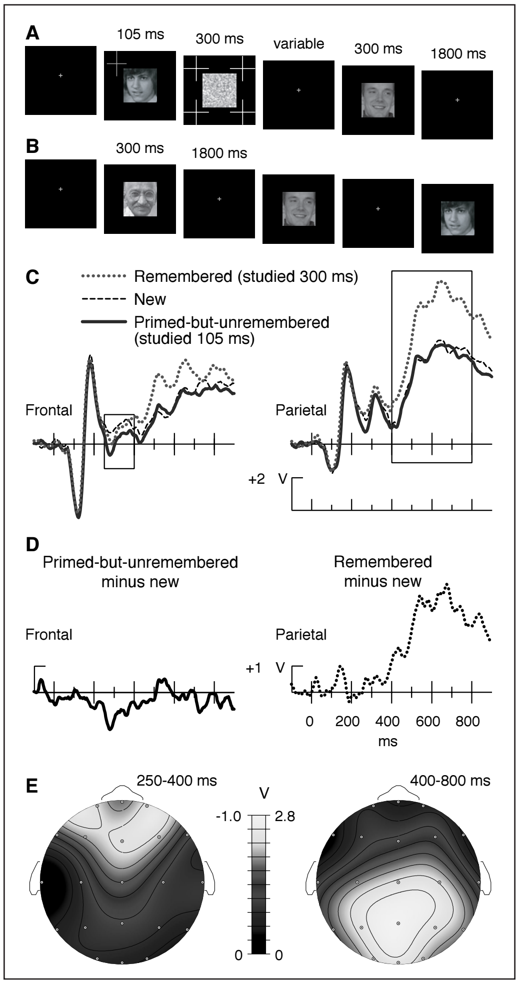

Figure 1.
An electrophysiological analysis of priming and remembering with faces (figure adapted from[42]).

A) In the study phase of this experiment, some faces were shown for 300 ms under full attention whereas others were shown for 105 ms under diverted attention. The brief faces were presented simultaneously with a yellow cross, occurring unpredictably in one of the four quadrants. Both the face and the cross were followed immediately by masking stimuli. For 105-ms faces, the task was to discriminate yellow crosses with a slightly longer vertical element from those with a slightly longer horizontal element. For 300-ms faces, the task was to remember each face. Each face was presented three times in the study phase.

B) In the test phase, the task was to discriminate faces repeated from the study phase from new faces and from famous faces. Variations on this design were used such that implicit memory tests could be run in the test phase as well. Generally, priming was found for studied faces of either type, whereas explicit memory was reliably better than chance for faces studied for 300 ms (i.e., remembered faces), but near chance for faces studied for 105 ms under diverted attention conditions (i.e., primed-but-unremembered faces).

C) ERPs recorded from midline frontal and parietal locations during the test phase for the three critical conditions. An early difference was evident for both types of studied faces (small rectangle in frontal recording), whereas a later difference was evident only for remembered faces (large rectangle in parietal recordings).

D) Difference waves computed for the ERP effect associated with priming and the ERP effect associated with remembering.

E) Topographic maps of the ERP differences associated with priming (left, maximal differences at anterior locations) and the ERP effect associated with remembering (right, maximal differences at posterior locations).

regard to verbal semantic processing is unknown and deserves further study. The same uncertainty holds for the relation of this modulation and an ERP effect found during explicit memory testing and sometimes called FN400-like old/new effect or mid-frontal old/new effect, which has been taken as an indicator of episodic familiarity (for example,[29]) or of conceptually-driven priming.[30]

The repetition-related N400 in person recognition consists of a centro-parietal positivity (or reduced centro-parietal negativity) between about 400 and 600 ms.[20-24] The N400 differs from the N250r in time course and scalp distribution, as well as in other ways. Whereas the N250r only survives a few intervening faces, the N400 can also be found after longer lags in the time range of several minutes.[28] Moreover, comparisons across domains (i.e., faces versus names/words or visual objects) revealed that the scalp topography of N400 is not domain-specific.[21,22,25,28] Notably, the N400 is also elicited when the person seen initially is different from the person seen subsequently; that is, the N400 is also invoked when the two persons are associated, for example when the name or an image of Hillary Clinton precedes the presentation of Bill Clinton's face.[23,31] All these findings indicate that the N400 in these experiments reflects changes in the processing of semantic knowledge about the depicted person.

These ERP indicators can be employed to study questions about face recognition that are difficult to address by other means. In a recent study, we investigated the recognition of familiar persons who were encountered unexpectedly.[20] Our concern was with whether face recognition occurs in a mandatory manner. To this end, ERPs were measured to unexpectedly encountered faces and to faces that participants expected to see. Both the N250r and N400 were present for the two classes of faces, indicating that familiar faces were recognized when encountered unexpectedly. Moreover, the prominent N400 for unexpectedly encountered faces showed that other person-specific knowledge was also retrieved. Though behavioral studies have provided some evidence for incidental recognition of faces and incidental access to associated semantic knowledge (for details, see[20]), ERP results from this study yielded extraordinary evidence about face recognition by indicating that the involved brain circuits (as measured by means of scalp topographies of the N250r) and their activation strengths are indistinguishable whether or not the encountered face was expected to be seen. In general, ERP research provides a powerful means to investigate person recognition including the time course of processing, which is not only helpful in elucidating the neural underpinnings of person recognition, but in the future might be proven to be invaluable in elaborating, modifying and extending models of person recognition.

Face priming — ERPs associated with nondeclarative memory are distinct from ERPs associated with declarative memory

Perceiving a face and identifying the corresponding person has very revealing consequences. When the same face is seen subsequently, these processes appear to be facilitated, resulting in faster and more accurate identification.[32] For these systematic changes to occur, a single and very brief presentation of a face is sufficient. Remarkably, such changes can nevertheless last for hours or days; priming of verbal material in one instance has been measured for a period as long as a year.[33] This priming is a form of nondeclarative (or implicit) memory.[34-36] It is important to note that nondeclarative memory comprises a variety of phenomena; here we focus on this specific example of facilitated face perception and identification. In general, however, nondeclarative memory is distinct from declarative (or explicit) memory — which comprises both episodic and semantic memory — in its functional properties and its neural implementation in the brain.[37-39] For example, level of processing during encoding[40] modulates declarative memory but has little effect on priming.[35,41] In contrast, a modality change between study and test is much more disruptive for priming than declarative memory.[34]

It is important to note that when stimuli are processed repeatedly, nondeclarative and declarative forms of memory tend to occur together. It is thus difficult to disentangle neural events associated with priming and neural events associated with episodic remembering. One approach to try to surmount this problem is to show participants a series of stimuli and ask them to decide which were encountered for the first time in the experiment and which had been seen earlier within the experiment. Some repeated stimuli may not be remembered as repeated, which usually is considered to reflect the absence of declarative memory for the prior encounter. Priming, a somewhat automatic consequence of the initial encounter, might nonetheless be present for these stimuli.

Resulting differences between ERPs to such stimuli ("misses" in a recognition test) and ERPs to genuinely new stimuli can be interpreted as indicators of nondeclarative memory when other crucial criteria are also satisfied.[29] For example, it needs to be shown that facilitated identification occurs when participants identify the stimuli in a priming test (as opposed to judging them as "repeated" or "new" in an explicit memory test). It is also important to demonstrate that the resulting ERP difference does not reflect episodic memory for repeated items that was too weak to result in a correct "repeated" response. This could be achieved by employing conditions that dissociate nondeclarative from declarative memory (e.g., level of processing or modality change). The demonstration that the ERP difference is distinct from known ERPs associated with episodic memory in terms of time course or scalp distribution could also provide supportive evidence. Notably, because trials with incorrect responses are compared to trials with correct responses, the interpretation of this ERP as a correlate of nondeclarative memory is problematic due to the confound with correctness of response. A recent investigation, however, suggests that despite this confound and hence the possible contribution from error-related brain activity, valid neural correlates of priming can be obtained in this manner.[21]

A different approach to this problem was applied in another study. We made use of an experimental condition of repeated faces that participants consistently could not remember having seen before; repeated faces nevertheless were identified faster compared to new faces in a priming test administered to other participants.[42] To achieve this behavioral outcome of priming with negligible recognition, pre-experimentally unfamiliar faces were initially presented briefly, followed by a visual mask, and with participants' attention diverted to other visual stimuli. ERPs to those primed-but-unremembered faces differed from ERPs to new unfamiliar faces in a fronto-central negativity between 250 and 400 ms (see Figure 1). This ERP does not resemble ERPs associated with remembering pre-experimentally unfamiliar faces as found within the same experiment and in other studies.[42-44] In a second experiment in which degraded faces were shown in a priming test, an ERP negativity was again associated with priming, although it showed a different time course and scalp distribution, likely in part due to the poor stimulus quality of degraded faces required in the priming test.[42]

There is widespread agreement that the type of priming under review here operates within modality- or domain-specific brain networks specialized for perceiving and identifying objects.[37,38] Indeed, consider that ERPs associated with priming of reading words tend to be positivities around 400 ms most pronounced at parieto-central or occipital sites,[21,29,45-49] whereas ERPs likely associated with face priming are small negativities around 350 ms or 650 ms at frontal, central or parietal electrode sites or fronto-temporal positivities at ~500 ms.[21,28,42,50] Yet, there may be cases in which effects are comparable across domains, such as a centro-parietal positivity around 400 ms found with faces[51] and with words.[29] Future studies will help to address the obvious differences across findings; some potentially important factors include the tasks employed and pre-experimental familiarity of faces.

Another important factor is highlighted by our recent behavioral results demonstrating that faster identification of familiar faces comprises two dissociable components, facilitation in perceptual processing (structural encoding) and facilitation in relation to FRUs/PINs, whereas repeated unfamiliar faces only showed perceptual facilitation.[52] Face priming can thus be investigated in light of these multiple components with both familiar and unfamiliar faces. We further investigated the perceptual facilitation by contrasting ERPs to repeated upright faces that were seen initially either upright or inverted, so that perceptual facilitation occurred only in the upright-to-upright condition. A left temporo-parietal positive ERP difference at 200-600 ms between the upright-to-upright and the inverted-to-upright condition implicated perceptual processing in the left hemisphere as a main source of facilitation.[53] These results brought out an intriguing divergence with traditional behavioral studies of face processing. The ERP data demonstrated a surprising left-hemispheric emphasis for perceptual facilitation, which contrasts to the advantage of the right hemisphere commonly observed for performance on tasks of face perception. Moreover, the time course of the positivity demonstrates that relevant perceptual processing extended beyond the time window when structural encoding is usually considered to occur, clearly overlapping in time with subsequent processing stages pertaining to FRUs, PINs, and SIUs as indicated by concurrent N250r and N400. This study therefore exemplifies how investigations of priming can provide valuable insights about both nondeclarative memory and the perception and identification of objects.

CONCLUSION

Many different electrophysiological phenomena can be demonstrated in association with the visual analysis of facial input, and memory influences on these responses can be observed by contrasting novel faces with faces that are familiar either because they belong to well-known individuals or because of specific personal experiences. Some of these effects reflect retrieval of information pertaining to stored semantic memory for familiar people. Specific ERPs have been associated with the activity of representations for familiar faces and for person-related knowledge. Research using these ERPs contributes to explorations of the cognitive and neural architecture of the person-recognition system. The analysis of priming-related ERPs also offers fruitful perspectives on face perception and face memory.

This review covered a sample of topics pertaining to memory for faces. Interesting research has also probed familiarity and recollection processes engaged in episodic memory for faces (for example, see[54]). In future explorations of relationships among the various ERPs and memory processes, it is crucial to take multiple types of memory into account; memory processes regularly occur together, and it can be a serious challenge to avoid mistaking one memory process for another. A continuing goal is thus to characterize the different neural events engaged in response to a face, with valid distinctions among reflections of semantic memory, episodic memory, multiple types of priming, and various processes that contribute to these memory functions.

Given the multitude of ways in which faces are important in human endeavors,[1] there are many face-processing phenomena remaining to be explored and understood. In the future, the investigation of memory for faces in healthy populations with ERPs will likely expand to many clinical populations to offer fruitful tools for examining disorders of memory and perception (e.g., Alzheimer's disease, age-related memory decline, schizophrenia, congenital prosopagnosia, post-traumatic stress disorder, Capgras syndrome).

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