Research report

N400-like potentials elicited by faces and knowledge inhibition

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Abstract

Within the theoretical framework of reference, the brain errs in processing complex stimuli, such as faces. Thus, these stimuli not only activate accurate representations but also inaccurate representations corresponding to known persons who resemble the face stimulus, and hence knowledge about these known persons. Since more errors are made in processing unfamiliar than familiar stimuli, these inaccurate activations are assumed to be more frequent, and/or more intense, with unknown than with known faces. Moreover, top-down mechanisms favor representations of stimuli that are congruent with the context, and representations of known persons, even if inaccurate, receive an additional amount of activation in contexts wherein known faces are expected. Inaccurate representations have to be inhibited to achieve accurate recognition. Thus, more inhibition would be required for unknown than for known faces, and in contexts wherein known faces are expected. The aim of the present work is to study the hypothesis that the N400 component of the event-related potentials (ERPs) reflects the inhibition of knowledge, and to see whether this hypothesis accounts for the N400-like potential elicited by faces. To achieve that goal, ERPs to known and unknown faces were recorded while the richness in known faces of each experimental block, and thus the expectancy for known faces, was manipulated. Consistent with the hypothesis, the amplitudes of the N400-like components were greater in conditions where more inhibition was required, i.e. for unknown rather than for known faces, and in the context of the block rich in known faces. This context effect was larger for unknown than for known faces.

Keywords: Event-related potential; N400; N400-like; Face; Context; Knowledge; Inhibition

1. Introduction

The event-related potentials (ERPs) elicited by faces include a negative potential resembling the N400 component elicited by words ([16,19,34] for reviews) since this potential peaks around the same latency, i.e. 450 ms post-onset, and since its amplitude can also be reduced by semantic priming [3,12,54]. Indeed, the amplitude of the N400-like potential elicited by the face of a known politician, for instance, is smaller when its presentation has been preceded by the face of another known politician [3] than when preceded by the face of a known person belonging to a different semantic category (e.g. an actor, a sport star, etc.).

One of the most quoted hypotheses about the functional significance of the N400 component is based on this semantic priming effect [5,22,23,48]. Accordingly, the component indexes the activation within semantic networks [32,33]. Thus, the large amplitude of the N400s elicited by a word (e.g. DOCTOR) that has been preceded by a stimulus that is not semantically associated (e.g. SOCKS) can be interpreted as reflecting the large activation that occurs when preceding stimuli did not activate semantically appropriate representations. Conversely, the small amplitudes of the N400s elicited by the same word when it is primed by a semantic associate (e.g. NURSE) reflects the small amount of activation that is necessary when the preceding stimulus already carried on a part of the appropriate activation. Similarly, the large N400-like amplitudes to faces preceded by the face of a semantically unrelated person could reflect the large amount of semantic activation required when the preceding stimuli did not activate semantically appropriate representations.

However, the semantic priming view of N400 has been challenged by several other hypotheses, including that of the semantic mismatch [11,21,42,46]. This alternative hy-
hypothesis is based upon the fact that physical mismatches elicit negative ERP components peaking around 200 ms post-onset, the N2s, and upon the idea that ‘... semantic information processing generally takes longer than most types of physical processing’. Hence, N400s are viewed as a type of delayed N2 components that index the semantic mismatch generated by the adjacent presentation of semantically unrelated words (e.g. SOCKS DOCTOR).

Koyama et al. [30] proposed another alternative hypothesis that associates N400s with decision-making processes. Their study included experiments in which N400s were recorded in response to target Kanji words and pseudo-Kanji words (i.e. meaningless line drawings which looked like Kanji ideograms) in three different prime conditions: a related condition where targets were preceded by semantically related prime words; a neutral condition where the prime consisted of a drawing that pictured a pair of two concentric circles; and an unrelated condition where primes were words semantically unrelated to the targets. Half (200) of these targets were real words, the other half were pseudo-words, and subjects had to perform a lexical decision task (i.e. to decide whether the targets were or were not real Kanji words). As in other similar experiments, the classical effect of semantic priming on reaction times was found, i.e. the responses were performed more quickly for target words in the related than in the neutral condition. On the other hand, subjects took longer to respond to unrelated targets than to neutral targets. Prolonged decision-making processes were proposed to account for these longer reaction times since they were observed in the conditions which violate the dominant associations. Indeed, in the experiment, unrelatedness was associated with the non-word response in the majority of cases, i.e. in 160 out of 200 trials. Thus, the correct decision was likely to be more difficult to make for unrelated targets which were real words. Since N400 amplitudes were, as reaction times, greater in the unrelated than in the neutral conditions, and since no significant N400 amplitude differences were recorded between targets of the related conditions and targets of the neutral conditions, the authors also associated N400 amplitude with the prolonged decision-making process.

However, none of the previously described views can account for all of the N400 observations. The semantic activation and the semantic mismatch views, for instance, do not make sense of the word frequency effect, i.e. of the smaller N400 amplitudes to unprimed words of high than to unprimed words of low frequency of occurrence in the language [50,55,57]. Indeed, there is no reason frequent words should induce less activation in semantic network(s), or induce smaller mismatches than infrequent words. As for the decision-making process view, it does not account, for instance, for the large amplitudes of the N400s elicited in situations where subjects were not required to make any decision (e.g. [58]).

The aim of the present study was to test another hypothesis about N400. This hypothesis stipulates that the component amplitude is generated by the inhibition of knowledge 1 which is not compatible with the meaning of the eliciting stimulus in its context [13]. According to this knowledge inhibition hypothesis, or N4KI hypothesis, the large amplitudes of the N400s elicited by words, such as DOCTOR, when preceded by semantically unrelated words, such as SOCKS, reflect the inhibition of knowledge activated by these unrelated words. Conversely, small N400 amplitudes elicited by the same words when preceded by semantically related words, e.g. NURSE, reflect the small amount of knowledge inhibition performed when preceding stimuli activated knowledge that is mostly compatible with the eliciting stimulus.

The N4KI hypothesis stipulates that N400 amplitude reflects the inhibition of any type of incompatible knowledge, not only incompatible knowledge activated by preceding stimuli, but also incompatible knowledge activated by the eliciting stimulus itself via inaccurate representations. Indeed, according to many word-processing models [4,17,29,37,38,40,41], word presentations activate both accurate representations and inaccurate representations of words that physically resemble the stimulus word. The presentation of the word BRIBE, for instance, activates not only the representation of BRIBE but also that of BRIDE 2. Hence, knowledge corresponding to these inaccurate words can also be activated. Since physically similar stimuli are usually not semantically similar stimuli, this knowledge is not compatible with the one activated through the accurate stimulus representation. Thus, within the N4KI hypothesis framework, it will be inhibited and responsible for an N400 activity 3.

Since more errors, and hence more inappropriate knowledge activations, are made when processing low-

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1 The concept of knowledge used here has been adapted from that of person’s identity nodes (PINs) included in models of person recognition such as that of Bruce and Young [7]. These models stipulate that once the recognition unit for the face of a person (or the recognition unit for the person’s voice) has been activated, knowledge about the person and the contexts wherein he or she had previously been encountered, is, usually automatically and irrepressibly, activated. Similarly, the activation of a visual or auditory word representation would induce the activation of knowledge. Such knowledge is viewed as elementary blocks used to build representations of situations [29].

2 Such activations are covert, i.e. not correlated with any phenomenon of awareness of the resembling stimuli and, similarly, to other types of inappropriately activated representations [18,56], inaccurate representations are inhibited [10,53], except when an explicit error occurs, e.g. when BRISE is mistaken for BRIDE.

3 Thus, although, the ‘usual way’ of producing incompatibility in N400 studies is the sequential presentation of two unassociated stimuli [5,48,22], the N4KI hypothesis stipulates that a semantic incompatibility can be generated by a single stimulus and, thus by a single presentation. Interestingly, Anderson and Holcomb [1] recently published a study showing that N400s effects between semantically associated and unassociated prime-target word-pairs can be obtained even when prime and target words both occur in a single visual presentation.
than high-frequency items [20,51], the N4KI hypothesis can account for the fact that N400 amplitudes are greater for infrequent than frequent words [50,55,57]. Consistent with this account of the frequency effect, N400 amplitudes to low-frequency words, such as BRIBE, have been found greater than to equally low-frequency words, such as SIGNAL, which do not orthographically resemble other words as much [14,15].

The aim of the present study was to further assess the N4KI hypothesis and to determine whether it can also account for the N400-like component generated by faces. To achieve this goal, we examined the amplitudes of the N400s elicited by known and unknown faces during a ‘fame decision task’. It was assumed that unknown faces would require more knowledge inhibition, and hence elicit larger N400 activities than known faces. Indeed, like infrequent words (and pseudo-words), unknown faces are stimuli that the brain is not used to process, and for which it is thus more likely to err. Unknown faces should then be more likely to activate representations corresponding to similar stimuli (i.e. to faces of resembling known persons) and hence to activate incompatible knowledge.

According to several models of word processing ([45], representations that are congruent with the context receive, via top-down mechanisms, an additional amount of activation, whether these representations are accurate or not 2. Extended to faces, this means that the representations corresponding to known faces which resemble the face stimulus receive an additional amount of activation in contexts where known faces are expected. Therefore, incompatible knowledge that correspond to these known persons 5, is more likely to be activated. Under these conditions, N4KI hypothesis predicts an additional N400 activity, since more inhibition would be required.

In order to test this prediction, the expectancy for known faces was manipulated by using blocks of stimuli containing different percentages of known faces. Block A, rich in known faces, included 67% of these stimuli and only 33% of unknown faces. Block B was neutral and included 50% of known and 50% of unknown faces. Block C was poor in known faces, including only 33% of these stimuli and 67% of unknown faces. N400-like amplitudes to known and to unknown faces were expected to be larger in the context of the block A than in other blocks, and this effect was expected to be larger for unknown than for known faces. Indeed, for unknown faces, the additional amount of activation only affects representations that have to be inhibited, while, for known faces, it also (and probably mainly) affects the accurate representations, given that these latter representations are congruent with the context rich in known faces. Thus, it is especially for unknown faces that contexts rich in known faces should lead to a greater inhibition.

Manipulating context by varying the percentage of each category of stimuli induces the classical effect of probability on the amplitude of the ERP component that is adjacent to the N400, viz. the P3 [28]. Indeed, Kutas et al. [31] have shown that such category variations induce large P3 effects, just like the manipulation of the probability of occurrence of one stimulus. Given that such effects were likely to create a problem for the interpretation of the results since N400 and P3 components overlap, intertrial intervals (ITIs) of four s were chosen because the results of recent studies [39,44] suggest that, when ITIs equal or are longer than 4 s, both frequent and rare stimuli elicit large P3s, and the classical effects of probability on P3 disappear.

In sum, famous known and unknown faces were presented to subjects who were asked to decide whether or not each face was that of a famous person that he or she knew. The predictions drawn from the N4KI hypothesis were: (a) that the N400-like amplitudes should be greater for unknown than for known faces; (b) that these amplitudes should be larger in the contexts of the block A, rich in known faces; and (c) that this block effect should be larger for unknown than for known faces.

2. Materials and methods

2.1. Subjects

The subjects were six males and six females between 20 and 30 years of age who watched French television at least 3 h a week. They were all right-handed, had normal (or corrected to normal) visual acuity, reported being free of

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4 Potter et al. [42] have shown that non-words (e.g. dack) and anomalous words (e.g., deck) are misread as appropriate words (e.g. deck) in the context of sentences that biases their processing toward the meaning of their orthographic neighbor word (e.g. ‘The child fed the deck/deck at the pond’). These authors although showed that the bias was greater for non-words than for words, and thus for stimuli that the brain is not trained to process than for stimuli for which it is trained. They show how such misidentification can be accounted for by an additional amount of activation to context congruent stimuli. For faces, such an additional amount of activation provide a way to account for the strong effect of context on misidentifications. Such an effect, noticeable in everyday life, has been quantified in the Young, Hay and Ellis’ [59] study which reported that for 33% of the misidentifications of an unfamiliar face as a familiar person, subjects reported they ‘would definitely have expected to meet the person they had thought they had encountered at that time and place’.

5 The concept of knowledge used here has been adapted from that of persons identity nodes (PINs) included in models of person recognition such as that of Bruce and Young [7]. These models stipulate that once the recognition unit for the face of a person (or the recognition unit for the person’s voice) has been activated, knowledge about the person and the contexts wherein he or she had previously been encountered, is, usually automatically and irrepressibly, activated. Similarly, the activation of a visual or auditory word representation would induce the activation of knowledge. Such knowledge is viewed as elementary blocks used to build representations of situations [29].
neurological or psychiatric disorders and had at least undergraduate degrees.

2.2. Stimuli

Stimuli consisted of 160 color slides portraying a front view of different faces, chosen from the archives of two major French press agencies (Agence Gamma and Cipa Press). Half were men, and half were women. In order to reduce automatic semantic priming from one face to the next [8], the faces were taken from different categories, including politicians, pop stars, sports stars and actors, in approximately equal numbers, and, in the experiment, the category to which two adjacent known persons belonged was never the same. Eighty of the faces belonged to people well known to French citizens (known faces) and 80 of them belonged to celebrities from other western countries and unknown to French citizens (unknown faces). Both classes of stimuli (known and unknown faces) looked equally ‘famous’ since they had the same general presentation and were both professionally photographed (thus increasing the likelihood that unknown faces activate representations of famous known persons). Unlike other previous face experiments, slides of known faces were selected from unpublished slides that did not show the person in a typical pose. This was done to reduce the likelihood that the subject would respond based on an immediate feeling of familiarity which would have introduced large differences between the processing of known and unknown faces. The slides were rephotographed in order to standardize, as much as possible, brightness, contrast, and dimensions of the face, and to ensure that the eyes were at the same height on the slides. These new 160 stimuli were then divided into two matched sets, each of which included 40 known and 40 unknown faces. They will be referred to as the first and the second set.

The first set was duplicated twice, in order to have a total of three exemplars of it. One of these exemplars of the first set was put in each of the three blocks (A, B and C). The 40 slides of known faces of the second set were then added to block A, in order to increase its richness in known faces. This block thus included a total of 120 slides, 80 (40 + 40) known and 40 unknown faces, resulting in a high (67%) percentage of known faces, and a low (33%) percentage of unknown faces. The 40 unknown faces of the second set were added to block C, in order to decrease the proportion of known faces. Block C thus included a total of 120 slides, 40 known and 80 (40 + 40) unknown faces, resulting in a low (33%) percentage of known faces and a high (67%) percentage of unknown faces. Block B was left unchanged and thus included a total of 80 slides, 40 known and 40 unknown faces, resulting in the medium (50/50%) percentage conditions. Subjects were divided in three groups of four. The order of the presentation of the blocks in the first group was ABC, in the second group: BCA, and in the third group: CAB.

2.3. Procedure

Subjects sat in a comfortable chair in a sound-attenuated room, and were told to stare the center of a screen (1.50 m away) during the presentation of each rack of 40 slides. They were asked to wait for two s after each slide had disappeared before blinking. Each face subtended a visual angle of 5°, and was displayed for a 400 ms duration, in order to ensure that the processing would be completed, and that the hypothesized inhibition could occur. The time interval between adjacent stimuli was systematically jittered and varied between 3.5 and 4.5 s.

Subjects had to respond as quickly and as accurately as possible by moving their right index finger above two electrical cells, toward the right for known faces and toward the left for unknown faces. They were asked not to try to recall names but to respond as soon as they were sure they had seen the person before.

During the debriefing session, subjects were shown the unknown faces for which they had given the motor response corresponding to known faces and asked if they had actually recognized a known person. If so, they were asked who that person was. This question revealed that among the famous persons of other western countries used as unknown faces, none were correctly recognized. These trials were counted as false recognitions since subjects mistook these faces for those of persons who were famous in France. The subjects were also shown the known faces for which they had given the motor response corresponding to unknown faces. When they did not know the face of the famous person, the trial was included in the unknown face trials (this happened for two or three faces for each subject). When they knew the face of the person but did not recognize it on the particular slide used in the experiment, the trial was counted as an unrecognized known face trial but excluded from the ERP averaging.

2.4. Data acquisition and processing

Reaction times (RTs), number of errors and ERPs were computed for the slides of the first set only. ERPs were recorded with a longitudinal and a transverse branch of electrodes placed according to the 10–20 system [24]. The longitudinal branch included 6 equidistant leads (10% of the inion-nasion distance): Oz, POz, Pz, CPz, Cz and FCz. The transverse branch crossed the longitudinal branch at Pz, and included 5 equidistant leads which covered parietotemporal regions and were termed: P4, PP4, Pz, PP3 and P3. Linked earlobes were used as a reference. Vertical and horizontal eye movements were monitored by 2 separate EOG bipolar recordings of electrodes placed above and below the right eye for vertical movements and at the outer canthi for horizontal eye movements. Rejection of artifacted trials was done off-line and manually by examining the printed EEG for each trial. EOG and EEG were amplified with a 2 s time constant and an upper half
amplitude cutoff at 50 Hz; signals were digitized on line by a PDP 11/60 computer at a sampling rate of 125 Hz. ERPs were calculated off-line, between 0 and 1200 ms after the onset of each slide with a 200 ms prestimulus base line.

The correct response trials were grouped according to the category of the stimulus (known or unknown). The measures were the average amplitude within time windows centered on each wave peak, 240–300 ms for the N270 wave, 350–500 ms for the N450 wave, and 500–700 ms for the P600 wave. MANOVAs with familiarity (known/unknown), richness in known faces (blocks A, B and C) and electrodes as factors were used for testing the level of significance of the effects [35]. For each time window, MANOVAs were run for the longitudinal and for the lateral montages. Thus, for this latter montage, the electrode factor corresponded to hemispheres. MANOVAs with a restricted number of factors were used for posthoc analyses when at least one of the factor had more that two levels. When no factor had more than two levels, ANOVAs were used.

3. Results

3.1. Behavioral results

3.1.1. Debriefing session

When presented again with the slides that were used in the experiment, subjects appeared to remember quite well what happened during the presentation of many of the faces. All subjects reported that the task was slightly difficult. Most of them (10 out of 12) reported that a few times (four times on average) they based their response on the basis of vague resemblances.

3.1.2. RTs

Table 1 shows the RTs to known and unknown faces for the different blocks. The 2-way MANOVA, including familiarity (known and unknown faces) and block as factors, revealed that there was a tendency for known faces to be responded to faster than unknown faces, $F_{1,11} = 3.15$, $0.1 < P < 0.05$. There was no significant effect of block, $F_{2,22} = 0.76$, nor was there a significant interaction between block and familiarity, $F_{2,22} = 1.01$.

3.1.3. Error rates

The numbers of errors are depicted in Table 2. The 2-way MANOVA with familiarity and block as factor

<table>
<thead>
<tr>
<th>Block</th>
<th>Known faces</th>
<th>Unknown faces</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>703 (61)</td>
<td>760 (64)</td>
</tr>
<tr>
<td>B</td>
<td>716 (74)</td>
<td>742 (84)</td>
</tr>
<tr>
<td>C</td>
<td>702 (87)</td>
<td>719 (73)</td>
</tr>
</tbody>
</table>

Table 1

Mean reaction time (ms) (and S.D. values) for known and unknown faces in the block A, rich in known faces (67% known and 33% unknown faces), in block B, neutral (50% known and 50% unknown faces) and in block C, poor in known faces (33% known and 67% unknown faces).

**Fig. 1.** Grand mean ERPs ($n = 12$) to known (left) and unknown faces (right). ERPs of the three upper lines are from electrodes of the midline longitudinal branch (FCz, CPz and POz) and ERPs of the two lower lines are from electrodes of the lateral branch (P3 and P4). Time is in s, and each tic mark representing 0.2 s, stimulus onset is at 0 s. Thin lines correspond to block A, rich in known faces, i.e. including 67% known and 33% unknown faces. Medium lines correspond to block B, neutral, i.e. including 50% known and 50% unknown faces. Thick lines correspond to block C, poor in known faces, i.e. including 33% known and 67% unknown faces.
Table 2
Number of errors (and S.D. values) for known and unknown faces in blocks A, B and C

<table>
<thead>
<tr>
<th>Block</th>
<th>Known faces</th>
<th>Unknown faces</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>3.96 (3.65)</td>
<td>2.25 (2.0)</td>
</tr>
<tr>
<td>B</td>
<td>6.00 (3.6)</td>
<td>0.59 (1.0)</td>
</tr>
<tr>
<td>C</td>
<td>4.75 (3.07)</td>
<td>1.08 (1.1)</td>
</tr>
</tbody>
</table>

revealed that subjects were more likely to fail to recognize the ‘known’ faces than to incorrectly ‘recognize’ the unknown faces. $F_{1,11} = 12.5$, $P < 0.005$. It also revealed a significant interaction between block and familiarity, $F_{2,22} = 6.21$, $P < 0.05$. Separate 1-way ANOVAs for known and unknown faces run to assess the source of this interaction showed that for known faces, the errors rate did not significantly varied across blocks. For unknown faces, the number of errors was significantly larger in the block A than in the block B, $F_{1,11} = 7.85$, $P < 0.025$, and than in the block C, $F_{1,11} = 4.82$, $P = 0.05$. Thus, unknown faces gave rise to more false recognitions when they occurred in the block rich in known faces than in the other blocks.

### 3.2. Electrophysiological results

The first deflection that can be identified on the ERP waveform (Fig. 1a,b) is a 5 μV negative peak or frontocentral N120, because it peaks around 120 ms on FCz, the most anterior lead. The second deflection is a large positive component, peaking at Cz around 180 ms. Its latency, its large amplitude, and its topography identify it as the vertex positive potential VPP obtained with faces [6,25–27,36,52]. The third wave is a large negative component, peaking at Cz at around 270 ms. This central N270 begins at about 200 ms or earlier and ends around 450 ms poststimulus but its ending overlaps with the following component. Its latency range and topography correspond to those of the N2b but its amplitude is rather large compared to that found in studies that did not use faces as stimuli (but used LEDs or pure tones instead). Large central N270s were also obtained in previous studies with faces [2,3,54]. Following N270 is a widely distributed wave that appears as a negative deflection on the downhill slope from the central N270 peak to the next positive component. This fourth wave peaks at approximately 450 ms and is clearly different from the central N270. Similar N450 waves have been reported in ERP face studies [3,54]. The fifth deflection is a positive wave with maximum amplitude at Pz peaking around 600 ms (P600). The beginning of this component is difficult to estimate due to overlapping with the N450. Because of its parietal maximum and latency, this P600 wave is assumed to be a component of the P3b family.

#### 3.2.1. Central N270 time window

For known faces (Fig. 1a), the amplitude of the central N270 did not vary across blocks. In contrast, for unknown faces, the amplitude of this component appeared larger in block A than in the two other blocks, primarily at the FCz and P3 locations. The 3-way MANOVA for the longitudinal montage did not however reveal any significant effects of block. But the same MANOVA on lateral electrodes revealed an interaction between percentage and familiarity, $F_{2,22} = 3.28$, $P < 0.05$. There was also an interaction of the three factors, percentage, familiarity and lateral leads, $F_{2,10} = 6.34$, $P < 0.05$, in accordance with the greater amplitude of the component at the left parietotemporal site (P3) for the block A. The separate 1-way ANOVAs which were then run for unknown faces and for each lead to assess the source of the interaction revealed that the effect of block was significant only at that lead, $F_{1,11} = 9.4$, $P < 0.02$.

#### 3.2.2. P600 (P3b) time window

For unknown faces (Fig. 1b), visual inspection revealed no effects of block, and thus of probability on P3 amplitude. For known faces, the ERPs were slightly more positive in the block C than in the other blocks. The two 3-way MANOVAs showed that the effect of block was neither significant on the lateral nor on the longitudinal branch. Despite this absence of significant results on the overall analysis, and to further check the absence of a probability effect in the P3b time window, 1-way ANOVAs for known faces with block (A and B, and A and C) as factor were run at each lead in the 560–700 ms time window which best captures the difference. No significant effects were found between blocks A and C. Table 3 which pictures the results of these ANOVAs for blocks A and B shows that the effect reached significance only at Cz, and that there was a trend on the two adjacent leads.

#### 3.2.3. N450 time window

Overall, visual inspection of Fig. 1a,b showed that ERPs to known and to unknown faces were more negative in the block A, rich in known faces than in the other

Table 3
Known faces: results of the site-by-site 1-way ANOVAs on mean ERP amplitude in a 560–700 ms latency region that best captures the difference in the P600 time region between blocks A and B

<table>
<thead>
<tr>
<th></th>
<th>FCz</th>
<th>Cz</th>
<th>CPz</th>
<th>Pz</th>
<th>POz</th>
<th>Oz</th>
<th>P4</th>
<th>PP4</th>
<th>PP3</th>
<th>P3</th>
</tr>
</thead>
<tbody>
<tr>
<td>$F_{1,11}$</td>
<td>4.66</td>
<td>6</td>
<td>4.80</td>
<td>2.6</td>
<td>1.7</td>
<td>0.3</td>
<td>0.3</td>
<td>2.9</td>
<td>2.8</td>
<td>2.0</td>
</tr>
</tbody>
</table>

Effect quotations: $P < 0.05$.
blocks, and that this difference appeared larger for unknown than for known faces.

The 3-way MANOVA performed on the longitudinal branch in the N450 latency region (350–500 ms) revealed that the ERPs to unknown faces were significantly more negative than the ERPs to known faces, $F_{11} = 21.3$, $P < 0.001$, that there was a significant interaction between block and familiarity, $F_{22} = 6.32$, $P < 0.025$, meaning that the effect of block was significantly greater for unknown than for known faces, and that there was an interaction between electrodes, block and familiarity, $F_{10,110} = 2.56$, $P < 0.025$. The same MANOVA run on the lateral electrodes revealed a significant interaction of block and familiarity, $F_{4,38} = 4.38$, $P = 0.025$, but no significant interaction with electrode sites.

Two 2-way MANOVA were run to assess the source of the interaction of familiarity, blocks and electrode sites on the longitudinal montage. For known faces, this analysis did not reveal any significant interaction between blocks and electrodes. In contrast, for unknown faces, this interaction was significant, $F_{10,110} = 2.88$, $P < 0.005$. Separate 1-way ANOVAs run to assess the source of this later interaction revealed that the differences between blocks A and B were significant at all leads, while the differences between blocks A and C were significant at all leads except POz and Oz, where there was only a trend.

Fig. 2 better illustrates the scalp distribution of the N450 difference between blocks A and B unknown faces for the longitudinal montage. It suggests that the interaction between the block effect and the electrodes comes from the existence of two different maxima, one at FCz and one at Pz. Indeed, large at FCz, the difference was smaller at Cz, reached a local minimum at CPz, then increased and exhibited a new maximum at Pz, after what it decreased again and was small at POz and even smaller at Oz (consistent with Table 4). Nevertheless, although CPz is less likely to be noisy than other electrodes since it is far from the eyes and from the muscles of the head (i.e. from temporal muscles and from muscles of the neck and of the jaw), it could argue that noise is responsible for the slightly smaller amplitude difference at Cz and CPz.

3.2.4. Effects of immediately preceding stimuli in N450 time window

In block A, rich in known faces, the two preceding stimuli were more often known than unknown faces, while in the blocks B and C, preceding stimuli were more often unknown faces. To assess whether the effect of block on the N450 was due to the immediately preceding stimuli, i.e. to a sequence effect, ERPs to known and unknown faces were reanalyzed segregating these stimuli according to the category of the two preceding faces. If the effect of block comes from an effect of sequence, then this effect should be at least as large as that of block. Thus, for both known and unknown faces, we examined the conditions in which they were preceded by two known faces (KK), by one unknown and one known face (UK), by one known and one unknown face (KU), and by two consecutive unknown faces (UU).

Fig. 3a,b shows these new averages. The amplitude of the N450 is largest for stimuli preceded by two consecutive known faces (KK condition), smaller for UK and KU conditions, and smallest for stimuli preceded by two consecutive unknown faces (UU). The shape, latencies and preferential locations (FCz and parietal) are iden-

### Table 4

Unknown faces: results of the site-by-site 1-way ANOVAs on mean ERP amplitude in the 350–500 ms latency region

<table>
<thead>
<tr>
<th></th>
<th>FCz</th>
<th>Cz</th>
<th>CPz</th>
<th>Pz</th>
<th>POz</th>
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$3.23 < F_{11} < 4.84$, $0.1 < P < 0.05$; $* P < 0.05$; $** P < 0.025$; $*** P < 0.01$; $**** P < 0.005$. 

Fig. 2. Scalp distribution of the ERP differences in the N400 time window for unknown faces between blocks A and B.
Fig. 3. Grand mean ERPs (n = 12) to known and unknown faces according to the sequence of preceding stimuli. Thick continuous lines correspond to faces that were preceded by two known faces (KK), horizontal dashed lines to faces that were preceded by a known and an unknown face (UK), vertical dashed lines by an unknown and an unknown face (KU) and thin continuous lines by two consecutive unknown faces (UU). All else is as in Fig. 1.

4. Discussion

In the time region of the P3 component (P600), block affected the ERPs only to a minimal extent. In contrast, in the time region of the N400, familiarity (known/unknown faces) and block significantly affected the ERPs. These latter effects were consistent with the predictions drawn from the N4KI hypothesis. Indeed, ERPs were more negative to unknown than to known faces, and in the block A, than in the other blocks, and this effect of block interacted with familiarity: it was large and significant for unknown faces only.

4.1. Disentangling P3b probability effects from effects on the N450

Only a few studies [39,44] suggest that when intertrial intervals (ITIs) are equal or longer than 4 s both frequent and rare stimuli elicit large P3s, and the classical effects of probability on P3 disappear. In the present study, ITIs varied at random between 3.5 and 4.5 s. Thus, before analyzing the variations of the ERPs within the N450 time window as genuine modulations of the amplitude of the N450 wave, one has first to see whether these variations were not due to a residual probability effect on the P3b (i.e. P600) component [28]. Indeed, both effects occur in approximately the same time regions and may overlap.

The P3 probability effect consists of an enhancement of the P3 amplitudes for infrequent stimuli. For known faces (Fig. 1a), probability could thus account for the differences in the P600 time window and for the (non-significant) differences in the N450 time window, since ERPs were slightly more positive when these stimuli were less frequent. However, these slight differences in the N450-P600 time region did not have much of the characteristics of a P3 effect (Fig. 1a). Indeed, they were only reliable at the central site (Cz), while the classical context effect on P3 is maximal at parietal site (Pz), and, instead of reaching their maximum at 600 ms poststimulus (i.e. the latency of the P3 peak in this study), they reached their maxima at, or more probably after, 1200 ms. Thus, these differences appear more likely to be due to two different causes, the first one being a small modulation of N450 in a direction consistent with the predictions drawn from the N4KI hy-
n hypothesis, and the second one, a modulation of a late component, occurring later than the P3b.

For unknown faces (Fig. 1b), ERPs were superimposable at the peak of the P600. However, this does not mean that there was no P3 probability effect. Indeed, this effect could be masked by an overlapping effect on N450 in the opposite direction. Such an overlapping would also diminish the size of the effect on N450, which may then be larger than it appears on Fig. 1b.

Thus, the effect of block on the N450 amplitude can be summarized as follows. For unknown faces, it is large, significant, and in the directions of the predictions drawn from the N4KI hypothesis. For known faces, it is either smaller (as predicted), non-significant, and in the directions of the predictions drawn from the N4KI hypothesis, or, less likely, totally absent since due to a P3 probability effect.

4.2. N450 wave and N400-like

These effects on the N450 wave are (at least partly) due to genuine N400-like effects. Indeed, three previous studies [3,12,54] already found that face stimuli elicit N450 waves whose amplitudes, just like that of the N400 component to words [22,30,48–50,58], are modulated by repetition and semantic priming. Moreover, the analysis of the ERPs to the slides of the first set, as a function of repetition (each slide of the first set was presented 3 times during the experiment), allowed us (in [13]) to see that the amplitude of this wave significantly decreases with repetition.

4.3. Could N400-like effects themselves be due to probability?

Before interpreting this N400-like effect as a consequence of the context richness in known faces, one has to assess the effect that probability could have on the amplitude of the N400 itself, and to determine whether the large N400 amplitudes to infrequent unknown faces in block A could be accounted for by such an effect.

Probability has been manipulated in several word studies [9,22,30] in order to modulate the extent to which subjects generate semantic expectancies. In these studies, subjects were presented with serial prime-target pairs and had to perform a lexical decision task (i.e. to decide whether the target was a real word or a pseudo-word). A proportion of the primes were words which were semantically associated with the target words, and probability was manipulated by varying this proportion. The idea was that greater proportions of associated pairs reinforce the generation of semantic expectancies, and therefore, N400 amplitudes. Consistently, in these three studies [9,22,30] N400 amplitudes to unprimed words were found larger in the blocks including high than in the blocks including low proportions of related pairs.

Given that the known faces belonged to the same semantic category, i.e. that of famous faces, they could have induced an N400 priming which could have been modulated by probability. However, such an N400 priming did not appear, and N400 amplitudes to known faces which were immediately preceded by other known faces were not smaller than that to known faces preceded by unknown faces. The re-averaging of the data according to the sequence of preceding stimuli showed not only the absence of such an N400 priming (because of the long ITIs?) but, moreover, it showed non-significantly larger N400 amplitudes to such known faces than to known faces preceded by unknown faces (Fig. 3a). Thus, a modulation of an effect of semantic priming by probability was unlikely to be responsible for the N400-like effects of the present study.

Alternatively, Deacon et al. [11] claimed that the N400 amplitude is, like the N2 amplitude, inversely proportional to probability even in conditions where ‘... all of the stimuli were unprimed’, and thus, independently from any semantic priming. They based their claim on the results of a prior study [47] that included a condition in which animal names occurred on 20% of the trials and non-animal names on 80% of the trials, and wherein subjects had to respond to the 20% category, and thus to the animal names. The substractions of the ERPs corresponding to the 80% category from those corresponding to the 20% category include a negativity peaking around 400 ms post-onset that was reinterpreted (in [11]), as an N400 component, and used to support the view that N400 amplitude is inversely proportional to the stimulus probability. However, infrequent stimuli, i.e. animal names, were more often preceded by frequent stimuli, and thus by stimuli of another category, than by stimuli of their own category. The additional N400 to infrequent stimuli in that condition can thus be accounted for by an effect of category mismatch on N400 as well as by an effect of probability.

As a matter of fact, if probability was able to modulate N400 amplitude independently, one would see such modulations in a word experiment where semantic relationships between words that were adjacent in the stimulus list were not at stake. This does not seem to be the case. Polich and Donchin [43] have run such an experiment where the probabilities of occurrence of both words and pseudo-words were manipulated while subjects were performing a lexical decision task. The inspection of the results in the N400 time region shows that neither the ERPs to words, nor those to pseudo-words were more negative when these items had a low (20%) than when they had a high (80%) probability of occurrence.

Finally, in the present experiment, such an independent effect of probability would have predicted larger N400 amplitudes to known faces when their probability of occurrence was lower than when that probability was high. This was not the case. As a matter of fact, in the N400 time region, the ERPs to known faces in the block C were less negative than those to known faces in the blocks A and B, although this difference was not significant. Therefore,
probability, as such, is unlikely to be responsible for N400 effects in the present experiment.

4.4. Functional significance of the N400 effects

4.4.1. Within the framework of the N4KI hypothesis

Within that framework, the larger amplitudes of the N400s to unknown than to known faces are due to the fact that the brain is less trained to process unknown than known faces. Accordingly, it more often errs, and the presentation of unknown faces more often activates, and/or activates to a greater extent, representations corresponding to resembling known faces and their corresponding knowledge. Hence, more incompatible knowledge would have to be inhibited than in the case of known faces.

Although pretty rare, false recognitions of unknown faces were significantly more frequent in the block A, rich in known faces, consistent with the idea that inaccurate representations corresponding to known faces which resemble the eliciting stimulus received an additional amount of activation in this block (since although inaccurate, these representations were consistent with the block’s context).

The greater N400-like amplitudes to unknown faces in the block A than in the other blocks would index the additional amount of knowledge inhibition required for accurate processing in that context.

For known faces, the N400-like differences between blocks were not significant, and, as expected, significantly smaller than for unknown faces. Within the N4KI hypothesis, this is due to the fact that for known faces, the additional amount of activation can also be allocated to the correct representations (since they are that of a known face), which does not increase the inhibition requirement. Moreover, since known faces activate less inaccurate representations than unknown faces, this additional amount of activation will be more focused on those correct representations.

4.4.2. Semantic activation

The present N400 results cannot be made consistent with the hypothesis that N400 indexes semantic activation [32]. Indeed, no faces were preceded by the face of a semantically associated person (in contrast to [8,3]). Thus, preceding stimuli were not able to carry on a part of the semantic activation and all this activation had to be done at the occurrence of each face. Accordingly, N400 amplitude should have always been large and there should have been no N400 amplitude differences. This was not the case.

Nevertheless, as above, it might be argued that even if known faces do not picture persons that have the same type of occupation (political, sport, etc.), they still share a common semantic property: that of being ‘famous media persons’ that appear in TV shows. In that sense, they might still semantically prime each other. But such a semantic priming effect implies that N400-like to known faces should have been of significantly smaller amplitudes in the priming context of the block A, rich in known faces. This was not the case since these amplitudes were either slightly and not significantly larger or exactly identical. It also implies that N400-like amplitude should have been smaller for known faces which were immediately preceded by other known faces than for known faces immediately preceded by unknown faces. This was also not the case, as mentioned above, the reaveraged data based on the sequence of preceding faces showed that there was a tendency in the opposite direction. Finally, the activation view would have predicted no N400 effects for unknown faces since these faces cannot be primed. This was not the case either.

4.4.3. Semantic mismatch

The view that N400 components index semantic mismatches [11,21,42,46] would have also predicted constant and large N400 amplitudes for each stimulus, since semantic mismatches occurred in every cases. Indeed, none of the faces were primed by the face of a semantically related person, and semantic mismatches were constant. In contrast, N400-like amplitudes varied across conditions. It could alternatively be proposed that the face of a famous known person does not produce a semantic mismatch when it occurs among other famous faces. The mismatch view then also predicts that the amplitudes of the N400-like to known faces would be significantly smaller in the block A, than in the other blocks. This was not the case. As discussed earlier these amplitudes were either slightly and not significantly larger or exactly identical. The semantic mismatch view would also have predicted that N400-like amplitude would be significantly smaller for known faces immediately preceded by other known faces than when preceded by unknown faces, which was neither the case.

4.4.4. Decision-making process

Koyama et al. [30] hypothesis that N400 amplitudes ‘are associated with a prolonged decision-making process for incongruous items’ could have accounted for a part of the result of the experiment. Indeed, faces were presented three times in the experiment. While on average, the level
of familiarity was greater for known than for unknown faces, unknown faces became a little familiar with repetition. Thus, by the 2nd and 3rd blocks, unknown faces could have induced a tendency to give the response corresponding to known faces, and the larger amplitudes of the N400-like to unknown than to known faces could be due to the prolonged decision-making process induced by that tendency. Similarly, the large amplitudes of the N400s elicited by unknown faces in the block A, dominated by known faces, could be related to the tendency to give the response corresponding to the known faces in that context.

But, the logic of this interpretation implies that infrequent known faces should have also activated the response corresponding to unknown faces in the context of the block C, rich in unknown faces, and thus elicited larger N400 amplitudes than known faces in the blocks A and B. This was not observed. These amplitudes were slightly and not significantly smaller or identical. Thus, Koyama et al. [30] idea does not account for the results, nor does it account for the large N400 amplitudes obtained in other studies wherein subjects were not required to make a decision (e.g. [58]).

5. Conclusion

The N4KI hypothesis thus accounts for the results in a more satisfying manner than the semantic activation, the mismatch, and the decision-making process views.

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References