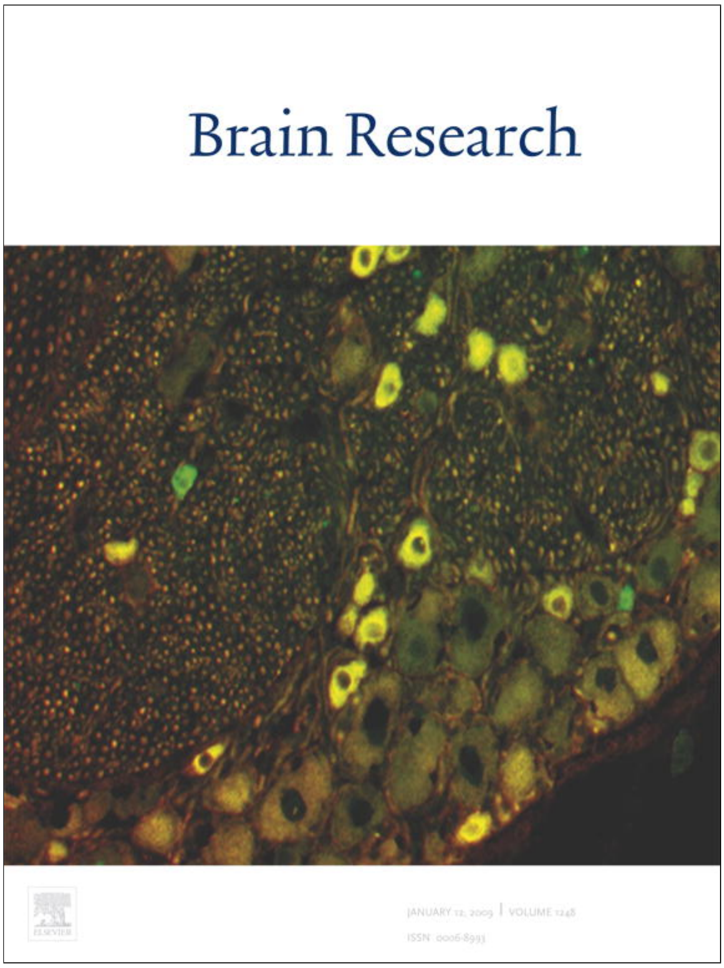
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Research Report

The time course of repetition effects for familiar faces and objects: An ERP study

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ABSTRACT

Face and object priming has been extensively studied, but less is known about the repetition processes which are specific to each material and those which are common to both types of material. In order to track the time course of these repetition processes, EEG was recorded while 12 healthy young subjects performed a long-term perceptual repetition priming task using faces and object drawings. Item repetition induced early (N170) and late (P300 and 400–600 ms time-window) event-related potential (ERP) modulations. The N170 component was reduced in response to primed stimuli even with several hundred intervening items and this repetition effect was larger for objects than for faces. This early repetition effect may reflect the implicit retrieval of perceptual features. The late repetition effects showed enhanced positivity for primed items at centro-parietal, central and frontal sites. During this later time-window (400 and 600 ms at central and frontal sites), ERP repetition effects were more obvious at the left side for objects and at the right side for faces. ERP repetition effects were also larger for famous faces during this time-window. These later repetition effects may reflect deeper semantic processing and/or greater involvement of involuntary explicit retrieval processes for the famous faces. Taken together, these results suggest that among the implicit and explicit memory processes elicited by a perceptual priming task, some of them are modulated by the type of item which is repeated.

1. Introduction

Repetition priming refers to the facilitated processing of a stimulus on repeated, relative to initial, presentation (Tulving and Schacter, 1990). Priming is a form of implicit memory which can be assessed by means of experimental tasks that do not require conscious recollection of previous experiences, unlike explicit memory.

Brain correlates of priming have been explored in haemodynamic studies (e.g. Squire et al., 1992; Lebreton et al., 2001; Gagnepain et al., 2008a; Henson, 2003 for review) and in electrophysiological studies. Event-related potentials (ERPs),

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Abbreviations: EEG, electroencephalography; EOG, electrooculography; ERP, event-related potentials; RT, reaction time; SD, standard deviation

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which consist of transient voltage changes time-locked to an event, are well-suited to the study of priming processes. They provide important insights of the underlying repetition processes. Two main effects of repetition have been consistently reported in ERP repetition studies. The first repetition effects modulate sensory components (e.g. the P100 and N170 components) and are measured on posterior regions (Itier and Taylor, 2002, 2004; Jemel et al., 2003; Henson et al., 2004; Trenner et al., 2004). These early effects are observed mostly with short-lag repetition studies (i.e. paradigms with at most 4 intervening items and a few seconds between both presentations). Later repetition effects have been consistently observed on centro-parietal and anterior regions and they are characterized by more positive waveforms for primed stimuli (for a review, see Rugg and Doyle, 1994; Paller, 2000). This second wave of repetition effects, which has been reported with short-lag as well as with long-lag repetition studies, arises generally from 300 to 600 ms and has been observed for a range of stimuli (Paller et al., 1992, 2003; Schweinberger et al., 2002a; Henson et al., 2004; Guo et al., 2007). However, when examining in a more detailed way, ERP repetition effects vary across different studies regarding their onset, their amplitude modulation, and their duration.

One of the variables which can account for this heterogeneity is the material. Indeed, processing of distinct types of stimuli involves partly specific cerebral network and cognitive processes. These specificities are particularly pronounced with faces and objects that engage distinct neural substrates (Kanwisher et al., 1997; Haxby et al., 2000) as well as distinct cognitive processes (Gauthier et al., 1999; Boutsen et al., 2006; Itier et al., 2007) during their processing. Among studies that compared several types of material, a lot of them found material modulations on repetition effects by comparing familiar vs. impossible or unfamiliar stimuli (Rugg and Nagy, 1987; Rugg et al., 1995; Schweinberger et al., 1995, 2002a; Van Petten and Senkfor, 1996; George et al., 1997; Eimer, 2000; Penney et al., 2000, 2001; Jemel et al., 2003). However, repetition of familiar and unfamiliar stimuli entails very different processes: repeated presentations of familiar items led to the reactivation of pre-existing representations in memory, whereas new representations in memory had to be created for unfamiliar stimuli.

Few studies have directly tested the ERP repetition effects elicited by different familiar stimuli (Pfütze et al., 2002; Martin-Loeches et al., 2005). Using short-lag repetition paradigms, they revealed the existence of variations between 200 and 350 ms: repetition effects were left-sided for verbal stimuli and right-sided for non verbal stimuli (Pfütze et al., 2002; Martin-Loeches et al., 2005). Moreover, within non verbal material (faces and object drawings), the right-sided repetition effects were more broadly distributed for faces (Martin-Loeches et al., 2005). The authors linked this repetition effect to the N250r, a component which typically arises in short-term repetition paradigms. This component may reflect increased activation of perceptual representations which, in turn, facilitates access to semantic information (Schweinberger et al., 1995, 2002a; Pickering and Schweinberger, 2003). Contrary to the N250r, earlier and later repetition effects were not investigated, nor were they modulated by the material in these studies (Pfütze et al., 2002; Martin-Loeches et al., 2005). The increased level of activation underpinning the repetition effects obtained by Pfütze et al. (2002) and Martin-Loeches et al. (2005) lasts no more than a few seconds. It has been suggested that priming resulting from immediate or long-lag repetition entails different mechanisms (see Bentin and Moscovitch, 1988; Schweinberger et al., 1995; Henson, 2003 for review). Only the long-lag repetition studies refer to the concepts of priming and implicit memory (Graf and Schacter, 1985; Tulving and Schacter, 1990). Thus, the two studies mentioned above suggest that some short-lag repetition processes are modulated by material. However, they offer an incomplete survey of the effect of material on repetition processes, since long-lag repetition processes have not yet been investigated. In the current study, we chose to follow the same classification as that employed by Henson et al. (2004) in their study investigating the effect of lag on repetition. For these authors, short-lag repetitions correspond to intervals of one to four intervening items, long lags refer to an interval beyond working memory but within the same experimental session (typically several minutes and several tens of intervening items), and lastly, very long lags correspond to intervals extending over several days. Immediate or short-lag repetitions may include contributions from a short-lived sensory store, whereas long-lag repetitions did not. Moreover, long and very long lag repetition may reflect strengthening of the representations activated (synaptic changes) rather than just a higher level of activation (transient neural activity) (Henson et al., 2004). The lag used in the current study corresponds to the long lag as it has been defined by Henson et al. (2004).

The goal of this study was to specify the effect of non verbal material on long-lag repetition effects. To this end, we used a design in two blocks separated by a 10-min time interval. We also used famous faces and object drawings, which have both pre-existing representations in memory. In order to specify the nature of these effects, we used event-related potentials (ERPs) which allowed us to explore early as well as late repetition processes. According to the repetition effects previously described in the literature, we focused our investigations on three main periods and four topographical regions. Repetition effects measured over parieto-occipital regions during an early period (N170) allowed us to catch perceptual processes. Those measured over centro-parietal, central and frontal regions during a later time-window (P300 and 400–600 time-window) allowed us to explore more elaborate processes such as the access to semantic representations, incidental explicit retrieval and/or encoding in episodic memory.

2. Results

2.1. *Behavioural analyses*

Only trials of the Test phase (retrieval phase) were analyzed. Mean reaction times (RTs) and hit rates are shown in Table 1. Mean hit rates and RTs were submitted to an analysis of variance (ANOVA), with Priming (primed vs. unprimed) and Material (drawings vs. faces) as within-subject factors. Only significant results are reported below.

The ANOVA on hit rates revealed a significant Priming effect ($F_{[1,11]}=26.94$, $P<0.001$): hit rates were higher for primed

Table 1 – Means and standard deviations of response times (RT) and hit rates during the face/object decision task

	RT (ms)	Hits (%)
Object drawings		
Mean	576.6+/−72.9	94.6+/−4.9
Primed	577.3+/−72.0	97.3+/−5.4
Unprimed	575.9+/−77.0	91.8+/−5.1
Familiar Faces		
Mean	503.6+/−69.0	98.2+/−2.7
Primed	504.3+/−67.9	99.0+/−3.5
Unprimed	502.9+/−73.1	97.3+/−2.5

than for unprimed stimuli. There was also a significant effect of Material, with lower hit rates in the object decision task than in the facial decision task ($F_{[1,11]}=7.34$, $P<0.05$). The Priming×Material interaction was significant ($F_{[1,11]}=8.52$, $P<0.05$). Post-hoc tests (Tukey) revealed a significant priming effect for object drawings ($P<0.001$) but not for faces ($P>0.3$).

The ANOVA on RTs revealed a significant effect of Material, revealing faster reactions (i.e. shorter RTs) for faces than for objects ($F_{[1,11]}=41.39$, $P<0.0001$). There was no other significant effect.

2.2. *ERP analyses*

ERP repetition effects were investigated at three time-windows: the first (140–180 ms) encompasses the N170 component and allowed us to investigate the early perceptual processes. The second (390–550 ms) encompasses the P300 component and the third (400–600 ms) enlarges the P300 repetition effects to central and frontal regions. Both the P300 and the 400–600 ms time-windows allowed us to investigate the late repetition effects. In order to further explore the time course of repetition processes during 400 and 600 ms, this time-window was subdivided in successive segments of 50 ms. The repeated-measures ANOVAs performed on latency and amplitude measures were the same as those used for the behavioural data, except for the inclusion of additional repeated factors: Electrode (PO9, PO10, O9, O10 for the N170; CPz, Pz and POz for the P300; AF3, AF7, F1, F3, F5, F7, AF4, AF8, F2, F4, F6, F8 for the frontal site; FC1, FC3, FC5, C1, C3, C5, FC2, FC4, FC6, C2, C4, C6 for the central site) and Laterality when appropriate (left vs. right). All ANOVAs used a Greenhouse–Geisser correction for violations of the assumption of sphericity. For sake of simplicity, noncorrected degrees of freedom are reported. As the Electrode factor was only of interest when it interacted with the Repetition factor, it is not reported as a main effect. Grand averages for correctly repeated and new famous faces and object drawings are depicted in Fig. 1.

2.2.1. *Grand average ERPs*

2.2.1.1. Latency measures. Concerning the N170 component, the ANOVA on latency measures revealed a Material effect ($F_{[1,11]}=56.97$, $P<0.0001$): the N170 peaked earlier for faces (148.1+/−6.5 ms) than for objects (160.8+/−8.3 ms). There was also a Material×Electrode interaction ($F_{[3,33]}=4.47$, $P=0.023$): post-hoc tests revealed that latencies were shorter for faces than for objects at all four electrode sites (for each, $P<0.0005$). There was no other significant effect on N170 latency measures. Concerning the P300 component, the ANOVA on peak latencies revealed a Material effect ($F_{[1,11]}=8.80$, $P=0.013$): P300 latency was shorter for faces (472.4+/−40.9 ms) than for objects (506.1+/−31.7 ms). Lastly, a Repetition×Electrode interaction was observed ($F_{[2,22]}=7.44$, $P<0.005$): P300 latency was longer for repeated (494.6+/−35.1 ms) than for new stimuli (484+/−36.6 ms) at CPz ($P=0.026$), Pz ($P=0.0001$) and POz ($P=0.0001$), with maximum repetition effects at POz.

2.2.1.2. Amplitude measures. Table 2 shows the results of the ANOVAs performed for each time-window.

A main effect of Repetition revealed that the ERP amplitude was more positive for repeated stimuli than for new for the N170 component (repeated: −6.5+/−4.7 μV; new: −7.2+/−4.8 μV), for the P300 component (repeated: 14.2+/−5.1 μV; new: 12.9+/−4.9 μV), during the 500–550 ms time-window at frontal site (repeated: 3.8+/−3.6 μV; new: 3.1+/−3.5 μV) and at central site (repeated: 6.6+/−4.1 μV; repeated: 5.5+/−3.7 μV) The effect of Materiel revealed that amplitude was greater for faces than for objects on the N170 component (faces: −8.4+/−4.4 μV; objects: −5.3+/−4.6 μV) and between 400–450 ms at both frontal (faces: 3.8+/−3.2 μV; objects: 2.3+/−3.2 μV) and central sites (faces: 6.7+/−4.0 μV; objects: 4.8+/−4.3 μV). The Lateralization effect observed at both frontal and central sites between 400 and 600 ms revealed that amplitude was greater at the right side for both faces and objects. Finally, the Repetition×Material×Lateralization interaction was significant at central region between 450 and 550 ms and at frontal region between 500 and 600 ms. All the interactions reported in this section reflect greater amplitude for repeated than for new items. At central site repetition effects were first (450–500 ms) left-sided for objects ($P<0.05$) and bilateral for faces (left: $P<0.01$; right: $P<0.001$). Afterwards (500–550 ms), they were bilateral for both objects (left: $P<0.001$; right: $P<0.001$) and faces (left: $P<0.001$; right: $P<0.001$), but more obvious on the right side for faces. At frontal site, repetition effects were first (500–550 ms) left-sided for objects ($P<0.05$) and right-sided for faces ($P<0.001$). Then (550–600 ms), they were left-sided for objects only ($P<0.05$). Repetition effects observed for the N170, the P300 and at central and frontal sites are depicted in Fig. 2.

2.2.2. *Difference waves*

To examine differences in the magnitude of repetition effects, we examined amplitude subtraction ERPs between repeated and new stimuli. Repeated-measure ANOVAs were performed on mean amplitude data for every time-window and for each topographical region.

Although the interactions between Material and Lateralization for the N170 as well as Material and Electrode for the P300 were not significant ($F<1$), post-hoc analyses revealed that the effect of repetition elicited by objects was greater for the N170 at the left ($P<0.001$) and at the right side ($P<0.01$) and for the P300 at Pz site ($P<0.05$) (Fig. 3). There was no other significant effect. On the contrary, difference waves revealed that repetition effect was larger for faces during the 400–600 ms time-window. At frontal site, between 400 and 450 ms, the Material×Lateralization interaction was not

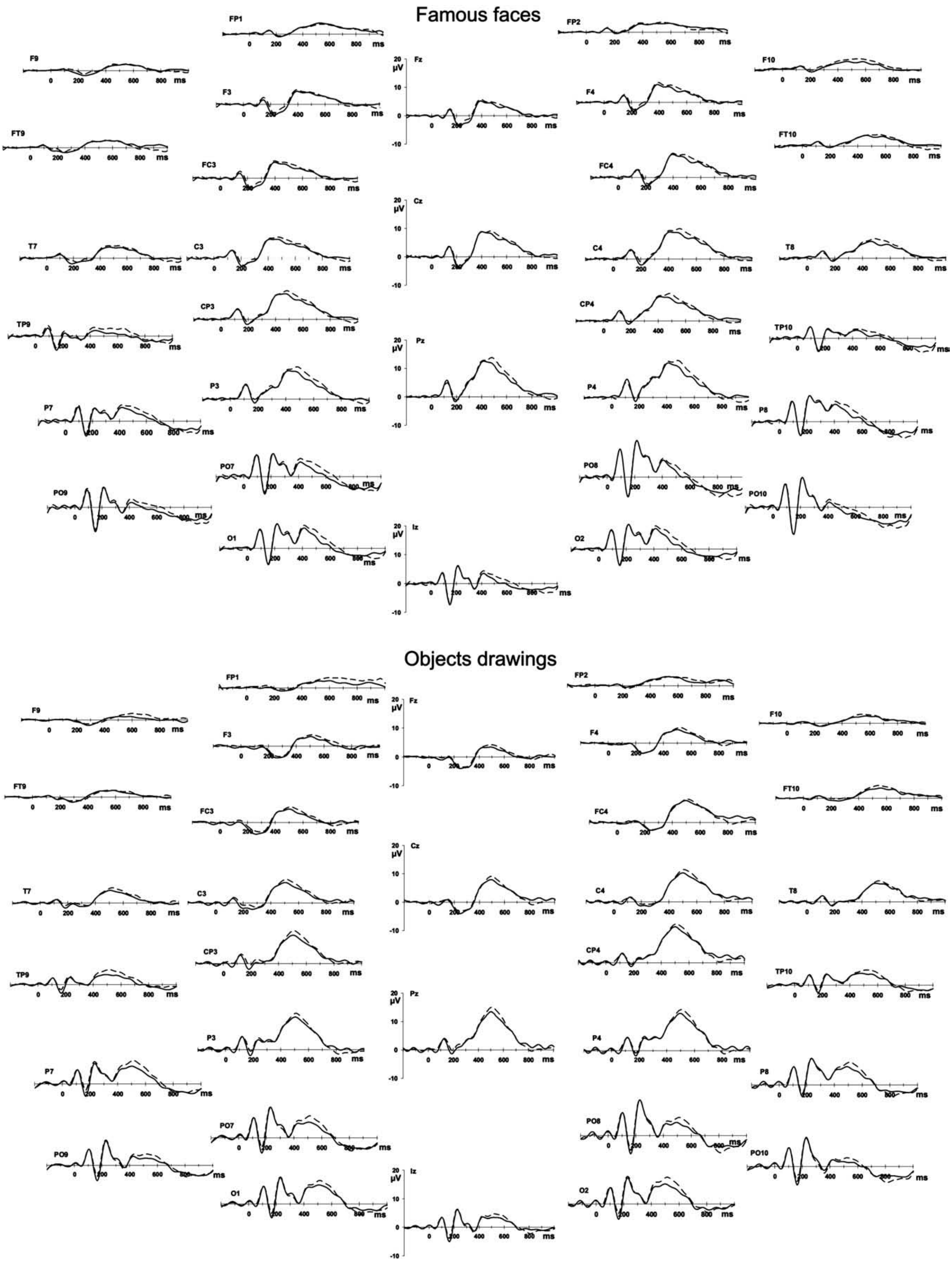

Fig. 1 – Grand-averaged ERPs evoked by primed (dotted line) and unprimed (thick line) famous faces and object drawings. For a better visualization, only 32 out of the 74 sites are shown.

Table 2 – Significant effects in ANOVAs on the mean ERP amplitude in time-windows of interest

Time-window	Site	Material	Lateraliz.	Priming	Material × priming × lateraliz.
		$F_{[1,11]}$	$F_{[1,11]}$	$F_{[1,11]}$	$F_{[1,11]}$
N170	PO9, PO10, O9, O10	24.73 ***		5.30 *	
P300	CPz, Pz, POz			6.59 *	
400–450	Frontal	11.10 **	6.40 *		
	Central	4.75 *	5.63 *		
450–500	Frontal		4.77 *		
	Central		7.61 *		4.75 *
500–550	Frontal			5.13 *	6.45 *
	Central		9.80 **	5.31 *	5.64 *
550–600	Frontal				5.43 *
	Central		14.62 **		

* $P<0.05$.
** $P<0.01$.
*** $P<0.001$.

significant ($F_{[1,11]}=1.06$, $P=0.3$) but post-hoc analyses revealed that repetition effect was larger for faces at the right side ($P<0.05$), whereas there was no difference at the left side. Although the interactions between Material and Lateralization were significant at frontal sites between 500–550 ms ($F_{[1,11]}=6.44$, $P<0.05$) and 550–600 ms ($F_{[1,11]}=5.43$, $P<0.05$), post-hoc analyses did not reveal any difference between the amount of repetition effects elicited by faces and objects (Fig. 4). Turning to central site, the interaction between Material and Lateralization during the 450–500 ms time-window ($F_{[1,11]}=4.75$, $P=0.05$) and during 500–550 ms time-window ($F_{[1,11]}=5.64$, $P<0.05$) revealed that repetition effects were significantly larger at the right side for faces ($P<0.05$ for both time-windows), whereas there was no difference at the left side (Fig. 4). There was no other significant effect.

3. Discussion

The aim of the present study was to investigate the effect of material on long-lag repetition processes, using famous faces and object drawings. In order to investigate the time course of early and late repetition processes, latency and amplitude of the N170 and P300 components were analyzed, as well as mean amplitude in the 400–600 time-window of ERPs elicited at central and frontal sites. By the use of a perceptual priming task, current results revealed the existence of long-term repetition processes. Some of them were common to both types of material, whereas others, belonging to both early and late repetition effects, were specifically modulated by material.

The first point to consider is the link between behavioural and electrophysiological effects, as we failed to find behavioural priming on RTs in the present study, whereas electrophysiological effects were observed in several time windows. The absence of behavioural result is probably explained by the lag and the high number of items intervening between both presentations: it has been indeed shown that the amount of priming decreases as lag increases, even with few intervening items (Henson et al., 2004). Moreover, the degree of overlap between processes performed in the study and the test phases was maybe not sufficient to allow priming effects. The absence of behavioural priming does not preclude however the absence of repetition effects on brain activity. One of the main advantages of ERPs is that they can reveal the different stages of processing, whereas RTs reflect the process as a whole without making any distinction between the duration and intensity of its different stages. Moreover, some authors have demonstrated that only certain neural repetition effects are specifically correlated with behavioural priming (see Schacter et al., 2007 for review). Several authors have argued that ERP measures are therefore more sensitive and have indeed observed ERP repetition effects using priming tasks without any behavioural priming (Begleiter et al., 1995; Rugg et al., 1995; Schweinberger et al., 1995, 2002a; George et al., 1997; Paller and Gross, 1998; Henson et al., 2003). However, it is most likely that ERP repetition effects obtained without behavioural priming are not comparable to those acquired together with priming effects.

3.1. *ERP repetition processes common to both famous faces and objects*

ERP repetition effects in the present study ranged over a large time-window and over posterior and anterior regions. Whatever the material, they are always expressed by a greater positivity for repeated stimuli. This leads to decreased amplitude for the N170 and to enhanced amplitude for the later time-windows. We will first discuss these effects which occurred for the both types of stimuli and then, we will turn to the specificities elicited by faces or objects.

Regarding the early repetition effect, it is now well-documented that ERP components occurring before 200 ms reflect perceptual processing: the first components to be elicited by the visual presentation of an object have been measured at around 100 ms and complex scenes are processed at under 150 ms (Thorpe et al., 1996). The N170 component, peaking at between 150 and 200 ms, reflects structural encoding and has been observed with faces (e.g. Bentin et al., 1996; George et al., 1996; Bentin and Deouell, 2000) and other visual objects (Rossion et al., 2000; Henson et al., 2004). Its enhanced amplitude and earlier latency for faces can be

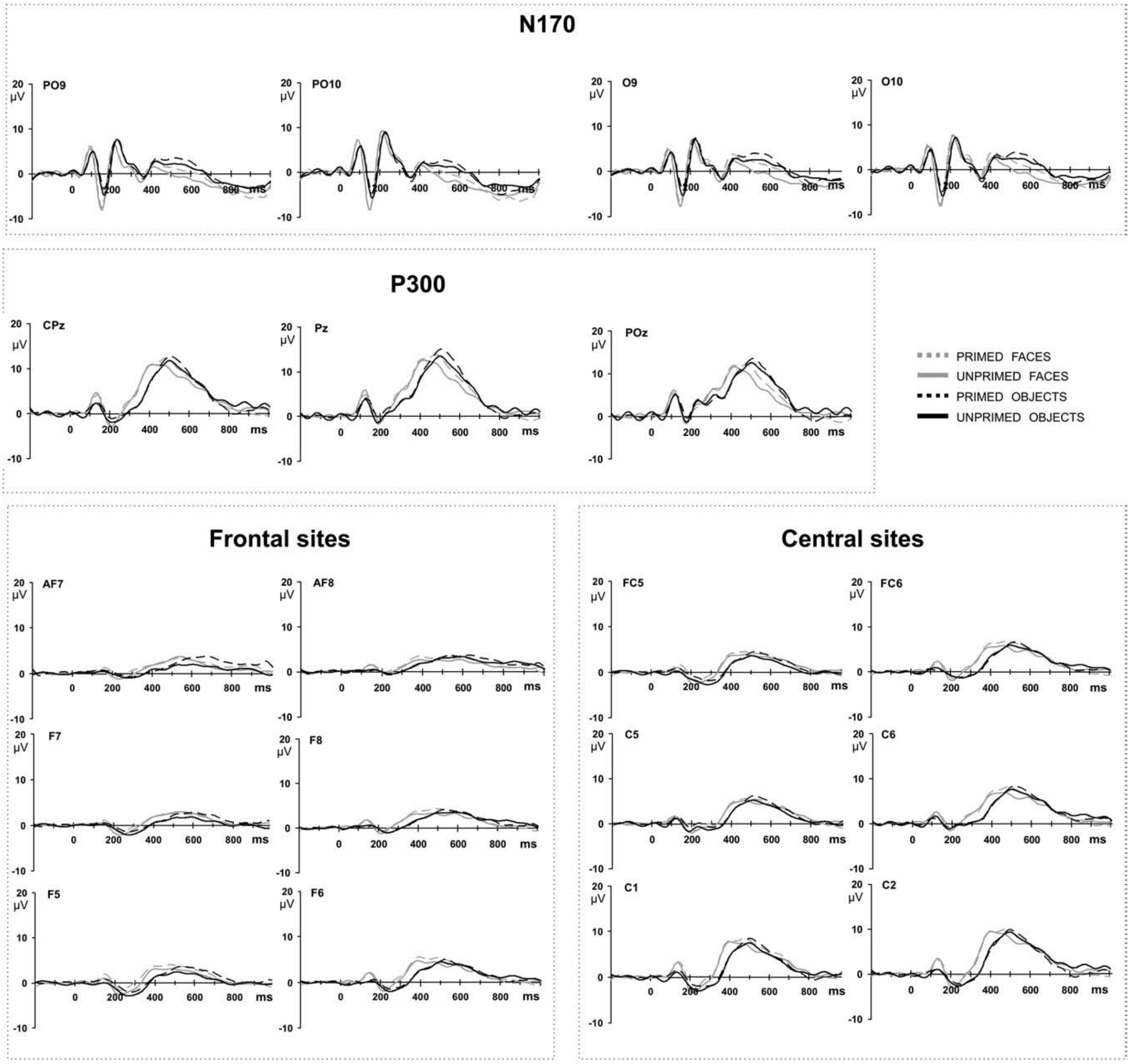

Fig. 2 – Grand-averaged ERPs evoked by repeated (dotted line) and new (thick line) famous faces (gray line) and object drawings (black line), showing the N170 component, the P300 component and the 400–600 ms time-window at frontal and central sites.

explained by expertise rather than by face specificity: N170 amplitude is enhanced when an object is processed at an individual representational level (a specific person, e.g. Bob) vs. a basic representational level (e.g. human) (Tanaka et al., 1999) and this has been demonstrated in bird and Greeble experts as well (Gauthier and Tarr, 1997; Rossion et al., 2002). Supporting its non face specificity, the N170 recorded in the present study was elicited by both faces and object drawings, but with a greater amplitude and earlier onset for faces. The reduction of amplitude observed for repeated items is consistent with previous studies (Itier and Taylor, 2002, 2004; Jemel et al., 2003; Henson et al., 2004) and may reflect reduced neural activity as well as facilitation of the perceptual processing when item recurs (Bagdaiyan and Posner, 1997; Wiggs and Martin, 1998). This early repetition effect may thus be a correlate of implicit memory of shapes and perceptual features.

In addition to the early repetition effects, a second wave of ERP repetition effects was recorded. The greater positivity currently observed for repeated stimuli from 390 to 600 ms reinforces previous findings obtained with faces (Schweinberger et al., 2002a,b; Henson et al., 2003), object drawings (Schendan and Kutas, 2003; Henson et al. 2004; Groh-Bordin et al., 2005) and words (Paller et al., 1992). The late latency of these ERP effects suggests the involvement of explicit and conscious processes rather than that of implicit processes. In fact, the constraints of our indirect task (perceptual processing in the study phase and fast presentation) do not prevent from the contamination of explicit processes. In the literature, several functional correlates have been attributed to this late increased potential, generally extending between 300 and 700 ms and widely distributed. As it has been observed during recognition tasks (for a review, see Rugg and Doyle, 1994; Friedman and Johnson, 2000), it has been linked to *explicit retrieval*. However, according to the debriefing questions, subjects noticed some item repetitions, but the rapid presentation rate and the focus on perceptual features prevented them from conducting intentional memory searches. Increased positivity may rather reflect conscious retrieval of repeated items but in an automatic and involuntary way (Van Petten and Senkfor, 1996). Another account is that it may also reflect the involvement of explicit processes such as *encoding* in episodic memory. A recent study has shown that the greater the perceptual priming, the greater the improvement in subsequent episodic performance (Gagnepain et al., 2008b). Finally, it has been suggested that this late positivity may reflect processes of association between the experimental stimulus, the linked personal knowledge, and memory owned by the subject who is viewing this stimulus (Van Petten et al., 1991; Guillem et al., 2001). The enhancement of positivity with repetition may thus reflect the larger amount of associative information extracted when item recurs.

3.2. *Repetition processes specific to famous faces and to objects*

These late ERP repetition effects occurred for both faces and object drawings but, this current study also revealed modulations specific to faces and other specific to objects.

First of all, it is worth noting that during the 400–600 ms time-window repetition, effects were preferentially left-sided for objects and right-sided for faces. This lateralization may suggest that the right hemisphere is preferentially involved in

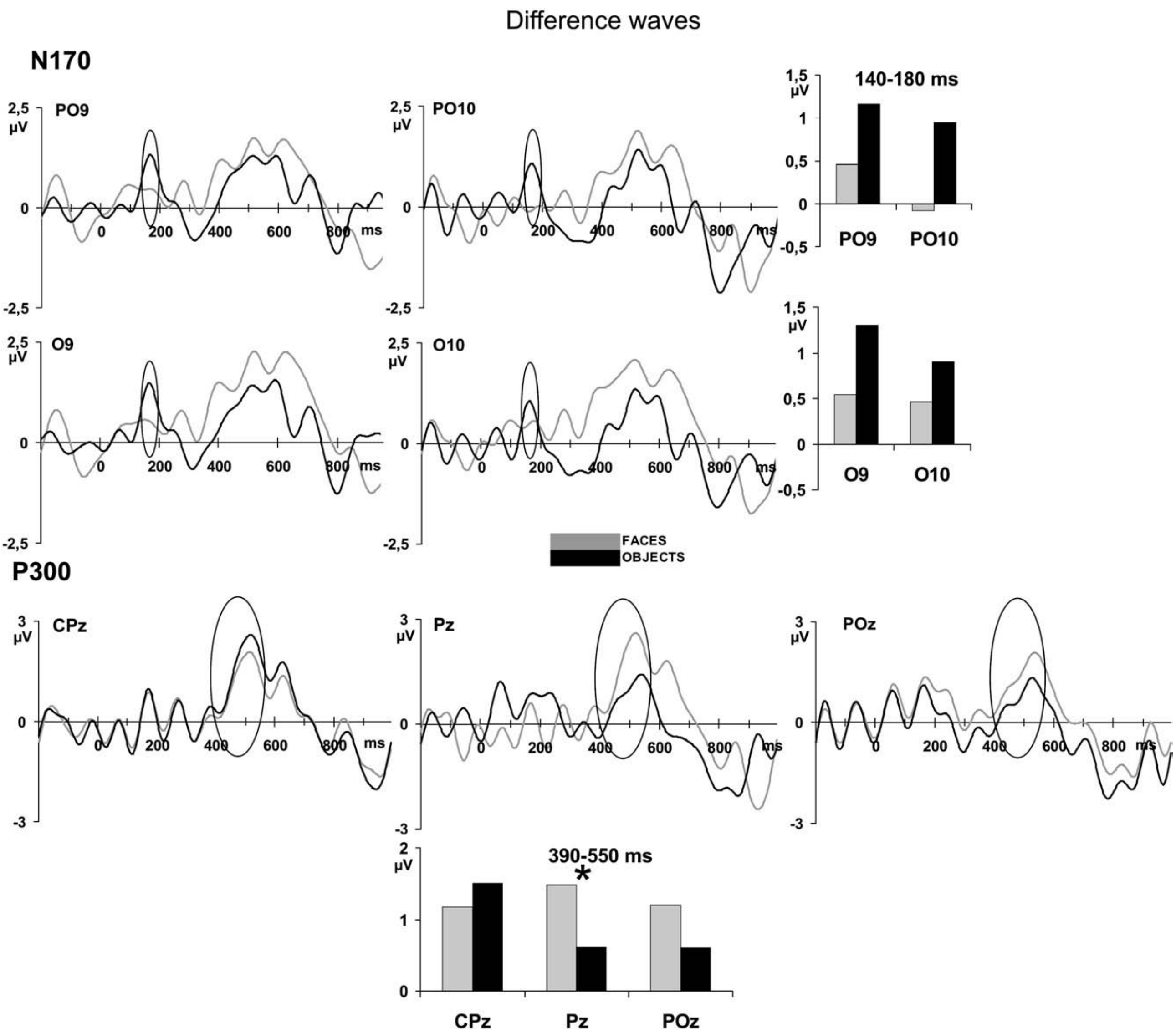

Fig. 3 – Difference waves (repeated – new) elicited by famous faces (gray line) and object drawings (black line) for the N170 and the P300 components. Histograms show the repetition effect elicited by famous faces (gray) and object drawings (black) during the time-windows of interest, indicated on the difference waves by an ellipse.

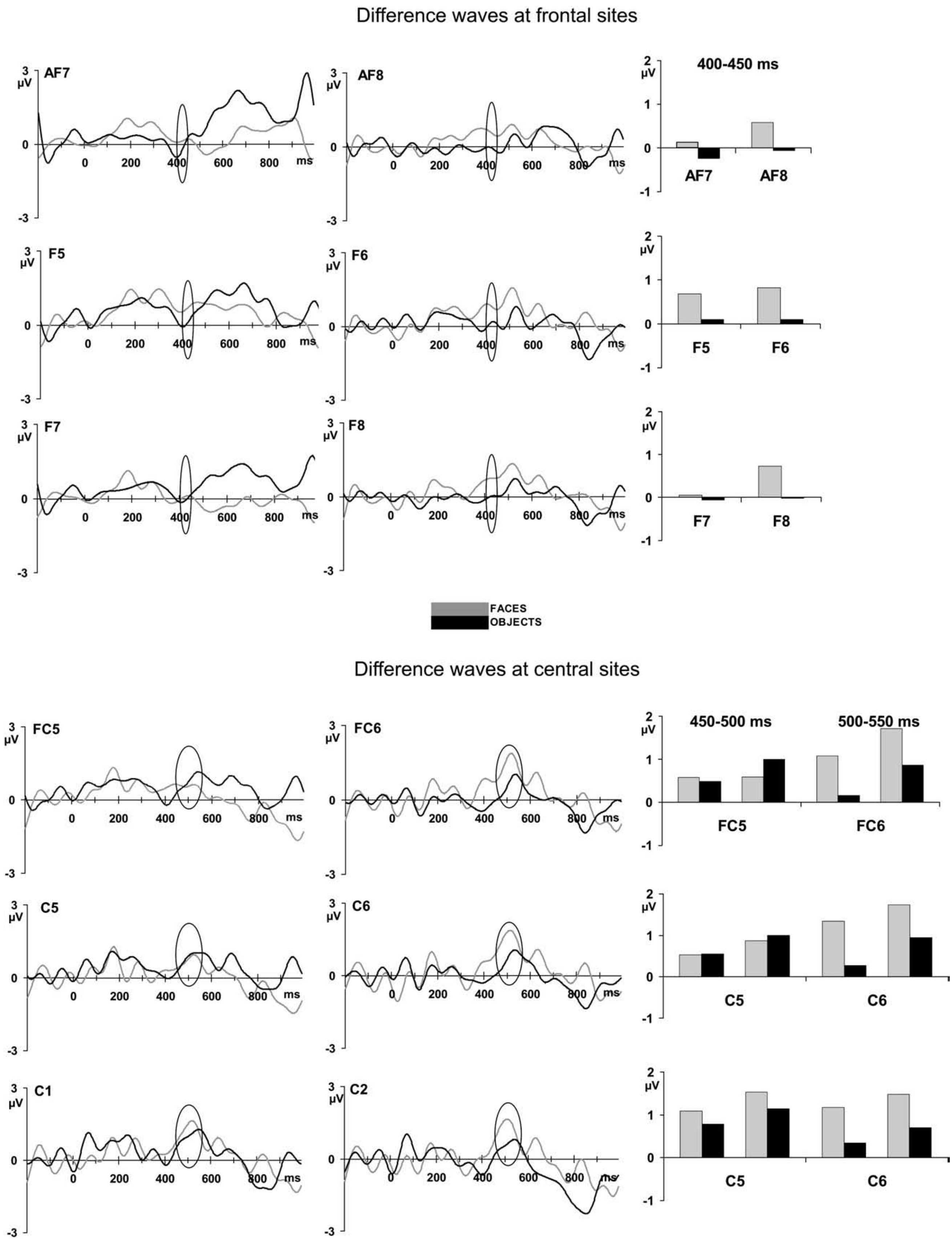

Fig. 4 – Difference waves (repeated – new) elicited by famous faces (gray line) and object drawings (black line) for the 400–600 time-window at frontal and central sites. At the right side, histograms show the repetition effect elicited by famous faces (gray) and object drawings (black) during the time-windows of interest, indicated on the difference waves by an ellipse.

face processing even for post-perceptual processes. This result may corroborate previous neuroimaging (Sergent et al., 1992; Henson et al., 2000; Leveroni et al., 2000) and neuropsychological data (Snowden et al., 2004; Gainotti, 2007), which have suggested the existence of a bilateral and multimodal semantic network rather than a left, unitary and amodal semantic network. According to these studies, the right temporal lobe would be involved in the storage of specific information retrieved from famous faces, whereas the left temporal lobe would be involved in the semantic storage of verbal knowledge. Although not required by our task, this ERP activity may sign an automatic semantic processing. Moreover, current results may reflect the differential involvement of the left and right localized semantic networks.

Variations of long-lag repetition processes according to the material were also revealed by the analysis of difference waves. Two main results were brought to light. First, the amount of repetition effect was larger for objects compared to faces during the N170 and the P300 time-windows. Second, the reverse pattern was found during the 400–600 time-window: famous faces were primed to a larger extent than objects. We will discuss alternately these two main results.

Most of the previous studies which have recorded decreased amplitude of the N170 used immediate or short-lag repetition only (Itier and Taylor, 2002, 2004; Jemel et al., 2003; Henson et al., 2004), this effect disappearing with long-lag repetition (Eimer, 2000; Schweinberger et al., 2002a; Henson et al., 2003, 2004). However, in almost all the long-lag studies where repetition effects disappeared, the material was constituted of faces. On the contrary, in all the long-lag studies where early repetition effects were found, authors did not use faces but words (Bagdaiyan and Posner, 1997) or pictures of objects (Tsivilis et al., 2001; Schendan and Kutas, 2003). The only exception is the study of Henson et al. (2004) which used objects and did not find early repetition effect with a long lag between both presentations. Thus, current results taken with previous ones (except for Henson et al., 2004) suggest that the reduced neuronal activity as well as the perceptual facilitation linked to repetition may not last as long for faces as for other visual objects. Faces constitute a material of greater importance than do other visual objects in terms of social relationships, social adaptation, etc. This is attested by the fact that their processing is faster and benefits from a larger neural activity, as revealed by the shorter latencies and the larger amplitude of the ERP components elicited by faces observed in the present experiment as well as in previous studies (e.g. George et al., 1996; Itier et al., 2006). Given their high significance, the absence of repetition effect as lag increases may prevent weakened processing for faces which may be potentially relevant to the subject. The greater amount of repetition effect elicited by objects was a consistent result for the N170, since it was confirmed for both left and right electrodes and this effect went in the same direction for each of the four electrodes (PO9, PO10, O9 and O10). This was not so consistent for the P300 however, since the larger ERP repetition effect for objects was significant for one electrode (Pz) only, and although not significant, the difference went in the opposite direction at CPz (larger ERP repetition for faces). Thus, this effect was not considered as a genuine effect and not further discussed.

During the later period, these were the famous faces which elicited more repetition effects at central and frontal sites. The greater positivity observed for repeated stimuli from 390 to 600 ms reinforces previous findings obtained with faces (Schweinberger et al., 2002a,b; Henson et al., 2003), object drawings (Schendan and Kutas, 2003; Henson et al. 2004; Groh-Bordin et al., 2005) and words (Paller et al., 1992). But in addition to this expected result, we also showed that this late repetition effect is modulated by material. As discussed previously, it is unlikely that it reflects unconscious perceptual memory processes required to perform the task given its late latency (around the behavioural response). We suggest rather that it may reflect semantic processing or involuntary explicit processing (encoding and/or retrieval). These explicit processes occur for both faces and objects but are enlarged for faces. Famous faces are indeed closely linked with biographical knowledge ("I know that after being married to Brooke Shields, Andre Agassi is now married to Steffi Graf") and with autobiographical memory ("I remember that Andre Agassi won the French Open when I was revising my high school diploma"). On the contrary, everyday objects refer to general concepts which have no personal relevance for the subjects: our semantic knowledge about a screwdriver is limited and we have no personal memory associated with this object for example. For both famous faces and objects, the second presentation leads to an easier access to the representations previously activated and to a deeper semantic processing. This deeper semantic processing is however more pronounced for famous faces since they are more richly connected in the semantic network than are objects. This fits well with prior repetition studies which showed that the late increased positivity reflects elaborative processes, linking associated knowledge and episodic information to the experimental stimuli (Van Petten et al., 1991; Guillem et al., 2001).

A final point to discuss is the repetitions effects which occur after 600 ms. Visual inspection of difference waves have suggested the presence of repetition effects in the last time-segments: additional analyses were conducted but revealed no significant effect. Whatever, this very late ERP activity occurred after the behavioural response and may sign updating processes and/or task-unrelated processes.

4. Conclusion

The repetition effects reported here emphasize the multiplicity of processes, implicit as well as explicit, involved during a perceptual long-lag priming task. Some of these processes were observed regardless of the perceptual features of the material memorized, whereas others were modulated according to the material. While objects evoked larger repetition effects during early stages of processing (implicit perceptual memory stage), faces evoked greater repetition effects during the later stages of processing (semantic retrieval and involuntary explicit memory). To sum up, the current study demonstrates that the repetition of the face of Andre Agassi elicits neural mechanisms which partly differ from those elicited by the repetition of a picture of screwdriver.

5. Experimental procedures

5.1. *Participants*

Twelve healthy native French-speaking subjects (six males; mean age=23.62 years, SD=3.33, range 20–30) were paid to take part in the experiment. All were right-handed, with an average handedness score of 1.5, ranging from 0 to 4 according to Dellatolas' Handedness Questionnaire (Dellatolas et al., 1988). Face processing was assessed by the Benton Facial Recognition Test (Benton et al., 1983) and all subjects performed normally (mean score=49.08, SD=3.09, range 45–54). None of the subjects was taking medication that could be expected to influence the EEG. All participants were fully informed of the recording technique, methods and proceedings before agreeing to participate.

5.2. *Stimuli*

Experimental stimuli comprised 100 famous faces from various fields (e.g. politicians, singers, actors, sports and TV personalities), 100 scrambled faces, 100 drawings of everyday objects and 100 scrambled drawings. The black-and-white photographs of the famous faces were recognized by at least 80% of a population of 45 students aged from 20 to 30 years. The scrambled faces were unfamiliar faces divided into four parts and randomly rearranged. The object drawings were adapted from Snodgrass and Vanderwart's set (Snodgrass et al., 1980) and were correctly named by at least 74% of the students questioned. The scrambled drawings were object drawings that had been randomly rearranged. Each face and drawing was converted to grayscale and homogenized with respect to average luminance and contrast. All backgrounds were removed and the pictures were given a resolution of 180×240 pixels.

The famous faces and object drawings were subdivided into two equivalent lists. The assignment of these lists to the two experimental conditions (unprimed and primed) was counterbalanced across participants.

5.3. *Procedure*

Participants were seated 80 cm away from a computer monitor in a dimly-lit room. The experiments consisted of Study and Test phases with famous faces and Study and Test phases with object drawings. The same procedure was used for both faces and object drawings, counterbalancing the order of presentation. During the Study phase, 50 experimental stimuli were presented, together with 5 fillers to avoid primacy and recency effects (2 at the beginning and 3 at the end). The subjects performed perceptual processing, deciding whether the photographs were full-face portraits or not and whether the object drawings were diagonally oriented or not. The Test phase started after a 1-min filler task (backward counting task) and a 4-min break: 50 stimuli that had been seen during the Study phase (primed stimuli), 50 new meaningful stimuli (unprimed) and 100 scrambled stimuli were presented in a pseudo-random order. Participants were instructed to detect meaningful faces or objects among the scrambled faces or objects.

Each stimulus was presented for 200 ms and the inter-stimulus interval varied randomly from 1800 to 2200 ms. Short resting periods (10 s) were provided every minute to minimize blinking during stimulus presentation. The design of this experiment is illustrated in Fig. 5.

There was no mention of stimulus repetition. The assignment of keys to press in order to indicate positive or negative responses was counterbalanced across subjects.

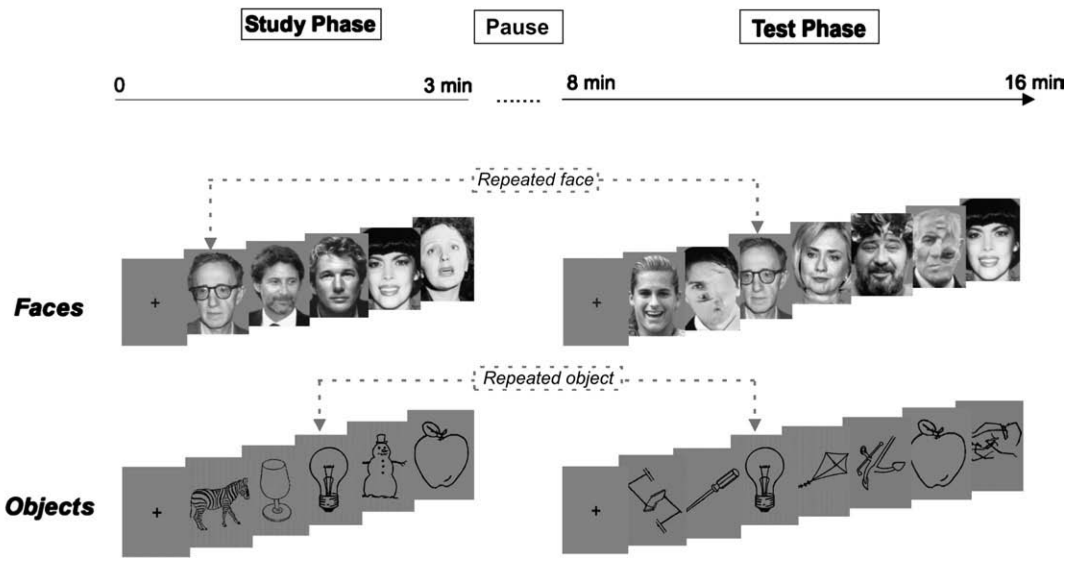

Fig. 5 – Experimental design. The order of passation of faces and objects priming tasks was counterbalanced across subjects. All the stimuli of the Study phase were repeated in the Test phase and mixed with unrepeated stimuli as well as with rearranged and impossible stimuli. The subjects were asked to perform a perceptual task during the study phase, and to discriminate possible from impossible faces or objects in the test phase.

Participants were given verbal instructions, and a short training session preceded each phase of the experiment.

5.4. EEG acquisition

Electroencephalograms (EEGs) were recorded continuously, using an EasyCap (http://www.easycap.de) with sintered Ag/AgCl electrodes covering 74 scalp locations of the extended 10–20 system (FP1, FPz, FP2, AF7, AF3, AFz, AF4, AF8, F9, F7, F5, F3, F1, Fz, F2, F4, F6, F8, F10, FT9, FT7, FC5, FC3, FC1, FCz, FC2, FC4, FC6, FT8, FT10, T7, C5, C3, C1, Cz,C2, C4, C6, T8, TP9, TP7, CP5, CP3, CP1, CPz, CP2, CP4, CP6, TP8, TP10, P9, P7, P5, P3, P1, Pz, P2, P4, P6, P8, P10, PO9, PO7, PO1, POz, PO2, PO8, PO10, O9, O1, Oz, O2, O10, Iz). The EEGs were measured relative to a reference electrode positioned on the tip of the nose. Blinks and eye movements were monitored via vertical and horizontal EOG electrodes placed supraorbitally and at the outer canthus of the right eye. Subjects were grounded with a shoulder electrode. The signals were amplified by a Micromed System-PLUS amplifier. Electrode impedance was always below 10 kΩ (cf Picton et al., 2000). The signals were continuously recorded with a bandpass ranging from 0.16 to 160 Hz and with a sampling rate of 512 Hz. Offline, data was digitally low-pass filtered at 10 Hz. The recording epochs began 200 ms prior to stimulus onset (baseline) and continued for 1000 ms after stimulus onset.

5.5. Data analysis

All statistical analyses were computed using repeated-measures analyses of variance (ANOVAs). Post-hoc analyses were performed using Tukey HSD tests.

For the behavioural data, mean reaction times (RTs) from stimulus onset were calculated for each subject, with separate calculations for drawings and faces (primed and unprimed taken together). Mistakes and outlier responses, more or less than 2 standard deviations (SD) from the individual means, were removed from the subsequent analysis.

For ERP data, trials that contained horizontal eye movements, drifts or excessive muscle artefacts were rejected on the basis of visual inspection. Vertical eye movements and blinks were then corrected using an automatic eye movement correction program (Gratton et al., 1983). Trials were averaged separately for each channel and each experimental condition (repeated vs. new in each material condition); after corrections, the mean number of averaged trials was 43+/−4 for primed faces, 41+/−4 for unprimed faces, 44+/−4 for primed objects and 39+/−5 for unprimed objects. Peak amplitude and latencies were analyzed for the N170 and P300 components and only amplitude was analyzed for the 400–600 time-window.

The same trials were taken into account for both behavioural and electrophysiological analyses: only trials associated with correct, artifact-free responses, within the ±2 SD window were included in each analysis.

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