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Contextual modulation of hippocampal activity during picture naming

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ABSTRACT

Picture naming is a standard task used to probe language processes in healthy and impaired speakers. It recruits a broad neural network of language related areas, among which the hippocampus is rarely included. However, the hippocampus could play a role during picture naming, subtending, for example, implicit learning of the links between pictured objects and their names. To test this hypothesis, we recorded hippocampal activity during plain picture naming, without memorization requirement; we further assessed whether this activity was modulated by contextual factors such as repetition priming and semantic interference. Local field potentials recorded from intracerebral electrodes implanted in the healthy hippocampi of epileptic patients revealed a specific and reliable pattern of activity, markedly modulated by repetition priming and semantic context. These results indicate that the hippocampus is recruited during picture naming, presumably in relation to implicit learning, with contextual factors promoting differential hippocampal processes, possibly subtended by different sub-circuitries.

1. Introduction

Picture naming is a standard task used to probe language processes in healthy (e.g. Cattell, 1886; Glaser, 1992) and impaired speakers (e.g. DeLeon et al., 2007; Goodglass & Blumstein, 1973). This task is associated with a broad neural network, including visual areas, bilateral temporal lobes for semantic processing, the left mid- and infero-temporal areas for word retrieval, left inferior frontal areas for conflict resolution and response programming, and pre-motor and motor areas for articulation (for reviews see: Indefrey, 2011; Llorens, Trébuchon, Liégeois-Chauvel, & Alario, 2011; Munding, Dubarry, & Alario, 2015).

Picture naming can be said to engage both language and memory processes, for example during semantic processing and during word retrieval. Still, much research based on picture naming is construed in the context of language processing hypothesis (see references above), without explicit consideration of memory research (for discussion, see Introduction in Hamamé, Alario, Llorens, Liégeois-Chauvel, & Trébuchon-Da Fonseca (2014)). Recently, however, a processing model has highlighted the connections between language and memory, and has implemented them to account for picture naming performance. Oppenheim, Dell, and Schwartz (2010) propose that a memory process, namely incremental learning between semantic and lexical representations, occurs during word/lexical retrieval. It is not unreasonable to assume that incremental learning can occur incidentally during picture naming, as the task requires the implicit association between picture, concept and word. A critical aspect of Oppenheim et al. (2010) model is that learning drives a process that is central to many psycholinguistic models, namely lexical retrieval.

Oppenheim et al. (2010) speculated that the Left Inferior Frontal Gyrus (LIFG) might play a role in the modulations of learning and selection efficiency induced by semantic context; they did not intend to discuss possible neural loci beyond that point. Incremental or associative learning is well studied in memory research, and has been consistently linked to hippocampus (Gluck, Meeter, & Myers, 2003; Meeter, Myers, & Gluck, 2005; Yang et al., 2003). Hippocampal activity has been repeatedly investigated in memory tasks involving picture processing (e.g. Squire, Stark, & Clark, 2004; Stern et al., 1996), but this structure is not commonly included in the picture naming network. The considerations above suggest that the hippocampus could be active during picture naming, driving incidental learning and/or the processes of retrieval, and that its activity is sensitive to repeated naming.

The available literature does not provide a clear view of the recruitment of the hippocampus during picture naming. In fMRI studies, the hippocampus was not among the regions showing

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repetition suppression due to repeated naming (Van Turennout, Bielamowicz, & Martin, 2003; Van Turennout, Ellmore, & Martin, 2000), although hippocampal repetition suppression (i.e. a decrease of bold signal driven by repetition) has been reported during the retrieval of learned face-name pairs (Kremers et al., 2014; Rand-Giovannetti et al., 2006; Vannini, Hedden, Sullivan, & Sperling, 2013; Zeineh, Engel, Thompson, & Bookheimer, 2003). Patients with hippocampal lesions showed intact priming during repeated naming of pictures (Cave & Squire, 1992). HM, the most famous hippocampal patient whose medial temporal lobe resection included both hippocampi, is typically described as having no language deficit (although see MacKay, James, Hadley, & Fogler, 2011; and footnote 1 in Hamamé et al. (2014)). These and other observations have prompted the conclusion that repetition in picture naming involves "an implicit, nonhippocampal form of memory" (Francis, 2014). In short, efficient naming or intact priming without hippocampal involvement has suggested that the task does not depend on the structure.

More recently, however, a number of reports highlighted the possible role of the hippocampus in picture naming. Hippocampal sclerosis has been associated with degraded performance in naming tasks (Bonelli et al., 2011; Hamberger, Seidel, Goodman, & McKhann, 2010; Hamberger, Seidel, McKhann, & Goodman, 2010). Some of these deficits are thought to reflect degraded word retrieval *per se*, with preservation of meaning (Miozzo & Hamberger, 2015; Trebuchon-Da Fonseca et al., 2009). Intra-cerebral recordings performed during pre-surgical investigations revealed sustained hippocampal activity that was closely tied to naming behavior (i.e. to naming latencies and, in one patient, to word finding difficulties; Hamamé et al., 2014). Finally, two fMRI studies exploring picture naming in a protocol combining repetition with a semantic context manipulation reported a modulation of left hippocampal activity that was related to lexical processing (De Zubicaray, Johnson, Howard, & McMahon, 2014; Hocking, McMahon, & de Zubicaray, 2008).

In this context, we hypothesized that hippocampal activity should be detected during plain picture naming, and that it could be modulated by contextual factors thought to promote learning, such as repetition and semantic context. Such a learning mechanism has been proposed as a unitary cause for two robust contextual effects observed in picture naming behavior (Oppenheim et al., 2010): generic priming from repeated use (Bartram, 1973; Bartram, 1974), and specific interference from semantically related material (Howard, Nickels, Coltheart, & Cole-Virtue, 2006). We report a test of the hypothesis based on intra-cerebral electrophysiological data (Bancaud et al., 1969; Talairach et al., 1974) recorded directly from structurally healthy hippocampi that had been anatomically and functionally identified. Native French speakers overtly named pictures they had never seen before, and then named them again in a block-design protocol previously used to elicit the contextual effects of repetition priming and semantic interference (Damian, Vigliocco, & Levelt, 2001). There was no memorization or encoding requirement. The analysis sought to detect hippocampal activity during the task and its possible modulation by the two contextual factors.

2. Materials and methods

2.1. Subjects

We analyzed data from nine patients with epilepsy undergoing pre-surgical stereotactical electro-encephalographic investigations (SEEG) in La Timone Hospital, Marseille. These patients had been stereotactically implanted with intra-cerebral electrodes to define the epileptogenic zone by recording local field potentials (LFP) with millimetric spatial resolution (Talairach et al., 1974). The implantation consists of 5–11 multi-lead linear-array depth-electrodes comprising 10–15 contact sites (3 mm spaced, 0.8 mm diameter; Alcis, Besançon, France). The electrode implantation was based strictly on clinical requirements and was decided independently of the present study.

The nine patients were right-handed (Oldfield Questionnaire) native French speakers with a left dominant hemisphere for language. All patients had left hemispheric dominance as revealed by different criteria including: (1) the recording of auditory evoked potential in auditory cortex in response to French voiced and voiceless stop consonants (*/ba/, /pa/;* detailed methods in Trébuchon-Da Fonseca, Giraud, Badier, Chauvel, and Liégeois-Chauvel (2005); (2) functional mapping of language using direct electrical stimulation, whereby left hemisphere stimulation induced language deficit in all patients; (3) fMRI or WADA test; (4) pattern of ictal aphasia when seizures involved left hemisphere. Anticonvulsant therapy was reduced or withdrawn during the clinical exploration in order to facilitate seizure occurrence. However, no subject had presented any seizure in the 12 h before testing. Participants or their parents (required for the two minor patients) provided written informed consents. As described below, the data analysis procedure led to exclude data from three patients, leaving a total of six.

2.2. Recording sites

The imaging analyses of the nine patients showed no hippocampal sclerosis or other structural abnormality. The functional integrity of the recorded hippocampi was tested using a visual odd-ball task. The patients had to count the number of times a rare stimulus (previously shown to the subjects) appeared on the screen while ignoring the frequent stimulus. It is well established that, within a healthy hippocampus, rare stimuli elicit a large negativity peaking around 300–600 ms (Halgren, Marinkovic, & Chauvel, 1998; Halgren et al., 1995; Knight, 1996; Ludowig, Bien, Elger, & Rosburg, 2010; Soltani & Knight, 2000). The recordings from one of these patients during this task did not reveal the expected negativity. This was interpreted as a dysfunctional hippocampus, and the patient was removed from the study. Moreover, two other patients were also excluded because the physiological activity recorded from the electrodes corresponded to far-field potentials (i.e. field potentials remotely generated, recognizable by a similar pattern of electrophysiological activity all along the electrode) and not to hippocampal local field potentials.

Among the six remaining patients, two had electrodes in the right hippocampus, three in the left and one patient bilaterally. These patients also had electrodes in perirhinal cortex (PRC), involved in object recognition processing (Buckley & Gaffan, 2006). The location and the number of contacts are listed in Table 1.

2.3. Experimental procedure

All procedures were performed in accordance with the INSERM Institutional Review Board (N 0000388).

The experiment started with a "familiarization phase" during which the patients sequentially named 108 black and white object images (Alario & Ferrand, 1999) that were novel to them. The pictures were presented in a pseudo-random order (Van Casteren & Davis, 2006) with the constraints that consecutive trials did not involve items from the same semantic category nor items beginning with the same phoneme (see Fig. S1a). This familiarization phase was followed by a "repetition phase" in which 36 items among those 108 were used in a design directly inspired by that of

Table 1
Localizations of the implanted contacts of interest across the six patients included in the analysis.

	Hippocampus						Perirhinal			
	Left			Right			Left		Right	
	Electrodes	Contacts	Location	Electrodes	Contacts	Location	Electrodes	Contacts	Electrodes	Contacts
Patient 1	1	2	Rostral				2	4		
Patient 2	2	5	Rostral				1	3	1	
Patient 3	1	1	Caudal				1	2		
Patient 4	1	1	Rostral	1	2	Rostral	1	1	1	2
Patient 5				1	3	Rostral	1	3	1	3
Patient 6				1	2	Rostral			1	2

Damian et al. (2001).[1] The 36 items were common to all patients; they were chosen from six different semantic categories (Accessories, Buildings, Kitchen Utensils, Fruits, Furniture, and Musical Instruments). The pictures were presented in blocks comprising six items repeated five times each within a block, yielding 30 trials for each of the 12 blocks, and a total of 360 trials. The items within a block could either be from a single semantic category (semantically homogeneous blocks) or from six different semantic categories (semantically heterogeneous blocks). Four different block lists were created; a pseudo-random order was used to vary the alternation between homogeneous and heterogeneous context blocks (see Fig. S1b).

The experiment was performed using the software E-Prime v2.0.1 (Psychology Software Tools, Pittsburgh, USA). The pictures were presented on the center of the screen within an angular size of $6° \times 6°$. Naming latencies were recorded with a microphone (audio Technica ATR20) placed 13 cm in front of the participant. Response times (in ms) were automatically recorded by the software voice-key. A trial consisted of a fixation point (variable duration across trials, between 1400 and 2100 ms), followed by the black and white target picture (presented for fixed duration of 1000 ms).

Patients were seated in a sound- and light-attenuated room that was electrically shielded, in the epilepsy unit at the hospital. This room is specifically equipped for this type of experiments and provides a safe and identical environment for each patient. The clinical monitoring recordings continued to be acquired during this session and overseen by an epileptologist who was physically present during the experiments. Patients were seated comfortably in front of a display monitor located 70 cm away. An experimenter was sitting behind the participant to monitor the performance and writing down erroneous responses (error types are described below in Section 3). Participants were instructed to name the pictures as fast and accurate as possible; they were asked to remain silent if they did not recognize the depicted object. The duration of the protocol was approximately thirty minutes (further details about the experimental procedure can be found in Llorens et al. (2014)).

2.4. SEEG recordings

The Stereo-Electroencephalographic (SEEG) signal was recorded with a 256 channel BrainAmp amplifier system (Brain Products GmbH, Munich, Germany). The sampling frequency was 1000 Hz with an acquisition filter band-passed of 0.16–200 Hz. the recordings were referenced to a scalp-electrode located in Fz.

Off-line processing of SEEG recordings was performed with the BrainVision Analyzer® software (Brain Products GmbH, Munich, Germany). The anatomical location of the electrode was identified on the CT-MRI image-fusion using MedINRIA Software.

2.5. Electrophysiological analysis

For each participant, the continuous monopolar SEEG recording was filtered digitally (0.15–40 Hz, 24 dB/oct and 48 dB/oct respectively). Epochs starting 1000 ms before stimulus onset and lasting 2000 ms post-stimulus were created, for a total of 3000 ms per trial. Only the epochs corresponding to correct behavioral responses were kept for the analysis. Epochs containing epileptic activity (spikes) were removed manually. A baseline correction was applied between −800 ms and −100 ms. An average per participant and a grand-average containing all the participants were created for each condition. These conditions allowed contrasting the effect of the two naming phases, novel vs. familiar items, as well as testing, within familiar items, for the effect of item repetition and the effect of semantic context (homogeneous vs. heterogeneous).

2.6. Statistical analysis

2.6.1. Behavioral data

The analysis of naming latencies was conducted on correct responses only. First, a one-way repeated-measure analysis of variance (ANOVA) was performed to test for the familiarity effect (novel vs. familiar pictures). Then, within familiar trials (second experimental phase), the effects of item repetition, semantic context (heterogeneous versus homogeneous) and their possible interaction were tested with two-way repeated-measure ANOVAs. The error rates were analyzed with logistic regression models (Jaeger, 2008) involving the same factors. The analysis of error rates did not distinguish among different error types (semantic paraphasias, hesitations, anomia, etc.). Trials with responses faster than 300 ms were not analyzed.

2.6.2. Electrophysiological data

A simple procedure of epoch averaging revealed various clear electrophysiological components occurring after picture presentation. These components were similarly apparent for the hippocampal contacts of any given patient and also across patients, allowing a systematic identification in every individual as well as a group-level statistical analysis. Because these evoked components were so clearly visible (see Fig. S2 for the main effect of difference between familiarization and blocked naming protocol but also see Fig. S3 for the more fine-grained difference between homogenous and heterogeneous context within the blocked naming protocol at the individual level), we decided to focus our analysis on the components' amplitudes and latencies (on a trial by trial basis), rather than running time-resolved running tests. Within each hippocampus, the contact with the highest amplitude was identified, and the analysis was performed on measures derived from it. The choice of the contact with the highest amplitude was guided by the fact that the

[1] The repetition phase only included 36 items, from the 108 that were familiarized, in order to replicate the original design structure used by Damian et al. (2001). We have previously used such design and procedure in a surface EEG experiment (see (Llorens, Trébuchon, Riès, Liégeois-Chauvel, & Alario, 2014) for details).

gradient of amplitude reflects the distance to the underlying source (Nunez & Srinivasan, 2006), that is, the contact with the highest amplitude is located the closest to the source. Inversely, less ample activity in neighboring contacts reflects gradually weakening signal because of increased distance to the underlying source. Another argument for the representativity of the contact with the highest amplitude comes from the fact that the hippocampus is a closed-field structure. That is, the activity recorded within it is generated locally (Benito et al., 2014; Halgren et al., 1980; Lopes da Silva, 1991; McCarthy, Wood, Williamson, & Spencer, 1989). After defining the electrophysiological component visible within each participant average, we identified the peak timing and smoothed amplitude of the equivalent of this average component within every single trial (see Fig. S4 for details). A statistical assessment of the electrophysiological measures of peak timing and amplitude was then performed at the group level, with participant and items (pictures) as random factors.

For novel items (during the familiarization phase), a single positive peak was clearly observable; no other component was apparent. For every patient, the amplitude maximum was identified on the average of all trials within a time-window of interest from 0 to 500 ms after stimulus onset. When a patient had several contacts within hippocampus, the contact with the maximum absolute amplitude was retained. Then, a [−200; 200 ms] time-window of interest was defined around the peak timing of the amplitude peak identified in the average; within this window, three electrophysiological measures were extracted from each single-trial signal values: (i) the absolute amplitude maximum, (ii) the peak timing of this amplitude maximum, and (iii) a smoothed version of the amplitude maximum, defined as the signed area under curve calculated over a 200 ms time-window (50 ms before and 150 ms after the peak) divided by the number of time samples (2 0 0).

For familiar items (in the repetition phase), two components were readily apparent: a negative peak followed by a positive peak. A similar procedure as described earlier was applied using the maximum and minimum within the time-window of interest from 0 to 500 ms after stimulus onset; thus, two windows of interest were defined and two series of single-trial measures were extracted.

The series of single-trial peak latencies and smoothed maximum amplitudes (i.e. areas under the curve) were analyzed using linear regression models including fixed effects (e.g. repetition, semantic context) and random effects (participants, pictures). First, trials with artefactual physiological activity or behaviorally inappropriate responses were removed (see error analysis below). Then, extreme outlier values were removed on a per-patient basis by examining the different data distributions (22 trials removed from 2662, 0.8%). Finally, a sequential procedure for the construction of regression models was used to determine which factors showed significant effects. Where appropriate, the models included behavioral or electrophysiological parameters such as the vocal response time (to ascertain that the reported effects were not due to response time jitters across conditions) or the amplitude of an earlier component (to distinguish intrinsic from carry-over effects). An alpha level of 0.01 was used to establish significance. For every analysis, we report the statistical results observed in the final model resulting from this procedure, where any non-significant predictors were excluded.

For consistency with the hippocampal analysis, the perirhinal contacts were tested in the same way.

3. Results

3.1. Behavioral results

Mean naming latencies were significantly slower for novel than for familiarized items (Fig. 1a; $F[1,5] = 204.41$ $p < 0.001$). There were 23% errors for novel items (215 errors out of 936 trials; 15.7% omissions, 7.3% production errors), and 9.6% in the repetition phase involving familiar items (195 errors out of 2040 trials; 3.7% omissions, 5.9% production errors). The difference of accuracy between the familiarization and the blocked naming phases was significant ($z = 6.85$, $p < 0.01$).

The ANOVA analysis revealed that naming latencies were significantly modulated by the semantic context of naming (Heterogeneous = 700 ms vs. Homogeneous = 743 ms; $F[1,5] = 15.13$, $p = 0.012$, Fig. 1a) and the repetition $F[4,20] = 19.85$, $p < 0.001$, Fig. 1b). The interaction semantic context X repetition was significant ($F[4,20] = 3.72$, $p = 0.02$). Patients were slower in the homogeneous than in the heterogeneous blocks only after the second repetition (Fig. 1b).

The error analysis revealed that the number of naming errors was not significantly different between naming contexts (homogeneous vs. heterogeneous: $z = 1.04$, $p = 0.3$). The probability of errors decreased with repetition ($z = 3.21$, $p < 0.01$), with essentially more errors in repetition one than in repetitions 2–5 (14%, 9.3%, 8.1%, 8.3%, 8.1%). There was no significant interaction between the two contexts ($z = 1.25$, $p = 0.2$).

3.1.1. Electrophysiological results

The local field potentials (LFP) recorded from the hippocampus revealed stable and specific patterns that were different for novel and for familiarized items. These patterns were observable in right and/ or left hippocampi in each patient (Fig. 2a and b) and in the grand average (Fig. 2c). A biphasic response (N2/P4) was observed in response to picture presentation for novel items. In contrast, a triphasic response N2/P4/N6 was observed for familiarized items presented during the repetition phase (see contacts 1 and 2 on Fig. 2b). This hippocampal activity was strictly local since the activity dropped at the adjacent contact located outside the hippocampus indicated that the evoked response was generated within the hippocampus (see contacts 3, 4 on Fig. 2b).

The statistical analysis focused on the components observed beyond the N2 response, which is known to be insensitive to repetition (Grill-Spector, Henson, & Martin, 2006; Schweinberger, Huddy, & Burton, 2004).

Novel pictures in the familiarization phase elicited a positivity (labeled P4) whose amplitude was significantly different from baseline (mean smoothed maximum amplitude ~160 mV, $t = 3.52$, $p < 0.001$). This positivity was present both in left hippocampus ($p < 0.01$) and in right contacts ($p < 0.01$). Most importantly, when both phases were compared (i.e. novel vs. familiarized pictures), the positivity for novel pictures occurred later (effect on peak timing: ~200 ms; $t = 26.9$, $p < 0.001$) and had a substantially higher amplitude (effect on smoothed maximum amplitudes: ~50 mV; $t = 7.90$, $p < 0.001$) than for familiarized pictures presented in the repetition phase protocol (Fig. 2c).[2]

During the repetition phase of the protocol, this positivity was modulated by the repetition factor (Fig. 3a). This amplitude decrease was present both in right (significant effect magnitude: ~28 mV per repetition, $p < 0.001$) and in left (significant effect magnitude: ~16 mV per repetition, $p < 0.001$) hippocampi, and was accompanied by a decrease in peak timing (on average, ~15 ms per repetition; $t = 8.25$, $p < 0.001$). Finally, this component was essentially not affected by the semantic composition (homogeneous vs. heterogeneous) of the naming blocks (Fig. 4, P4 component; amplitude: $t = 1.28$, $p = 0.1$; peak timing: $t = 1.69$ $p = 0.04$).

[2] The contrasts between novel and repeated items (i.e. familiarization vs. blocked naming phases) were conducted on approximately similar number of trials across conditions (the N's were 667 vs. 773) by including only the first two repetitions of the repetition phase.

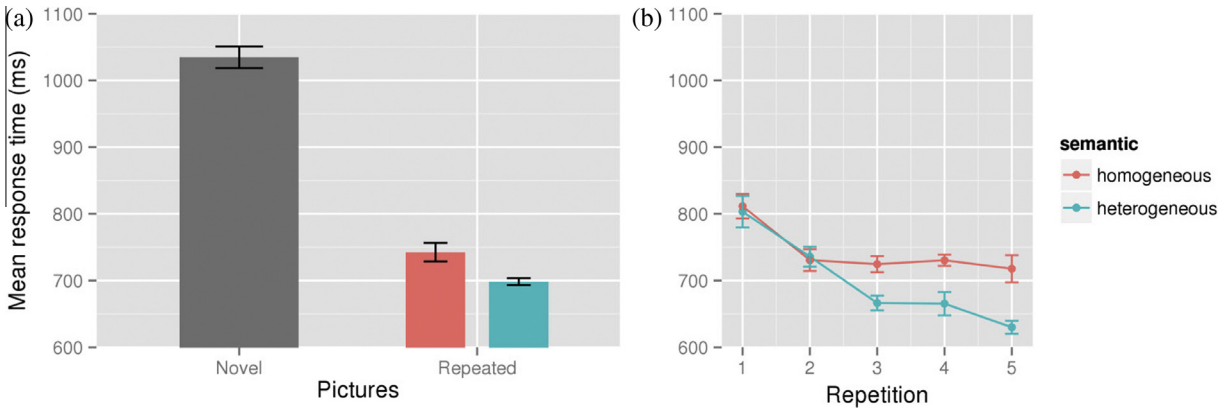

Fig. 1. Average naming latencies in milliseconds across the different experimental conditions. (a) Contrast between novel and repeated pictures, the latter being in homogeneous or heterogeneous contexts. (b) For repeated pictures, effects of semantic context and repetition. Error bars represent 95% confidence intervals of differences between conditions (because the contrasts are within-participants: (Morey, 2008)).

The negativity peaking around 600 ms (N6) behaved quite differently (Fig. 3, late component). The amplitude of the component increased with repetition (average effect on measured areas: measured areas: ~6 mV per repetition; $t = 3.26$, $p < 0.01$), a modulation that was significantly detected in left ($t = 3.04$, $p < 0.01$) but not right hippocampi ($t < 1$). As the amplitude of the component increased, its peak timing decreased (on average, ~13 ms per repetition; $t = 7.50$, $p < 0.001$). Finally, this component was affected by the semantic composition of the naming blocks, it was smaller within homogeneous than within heterogeneous blocks (Fig. 4, N6 component; amplitude effect: 12 mV, $t = 2.73$, $p < 0.01$; no effect on latencies: $t < 1$; see also Fig. S3 to observe this difference of amplitude at the individual level). Note that all the effects reported for the N6 component were estimated with the amplitude (resp. peak timing) of the earlier P4 component included as covariate in the model. Thus they reflected modulations occurring over and above statistical carry over effects from variations driven by the previous component.

3.1.1.1. Perirhinal activity analysis. The repetition of pictures modulated the LFP recorded from perirhinal cortex (PRC). The negativity, peaking around 300 ms (N3), observed in this structure displayed a significant decrease in amplitude as a function of the number of repetitions ($p = 0.0053$; Fig. 5). This bilateral effect was essentially driven by the first repetition.

4. Discussion

The hippocampus is not commonly included in descriptions of the language production network. However, the hippocampus can be reasonably expected to be recruited during word production tasks such as picture naming by driving incremental or associative learning (Gluck et al., 2003; Meeter et al., 2005; Yang et al., 2003) between a stimulus (the picture) and a response (the word). Such a mechanism is at the heart of the lexical selection process in the psycholinguistic model proposed by Oppenheim et al. (2010). Previous research on the involvement of the hippocampus in picture naming is relatively scarce, and inconclusive. This led us to test the hypothesis that the hippocampus is activated by picture naming, and that its activity is modulated by contextual learning factors (repetition and semantics). For this purpose, SEEG data were recorded directly from the hippocampus while French native speakers performed a plain picture naming task, without any memorization or encoding instruction.

4.1. Summary of findings

Hippocampus recordings performed during picture naming revealed a significant and intricate activity that appeared to be specific to this brain structure (e.g. this pattern is not observed in the perirhinal cortex). Hippocampal activity was reliably modulated by two contextual factors: *repetition of the items* and *semantic context*. The first presentation of a picture elicited a large positivity peaking around 400 ms (labeled P4) whose peak timing and amplitude diminished as a function of the number of presentations of the pictures. In contrast, repetitions promoted the progressive emergence of a negative component peaking around 600 ms (labeled N6). This N6 was the only component sensitive to semantic context, with a smaller peak amplitude during semantically homogeneous contexts.

Of note, the component we observed at 400 ms should not be mistaken for a N400 component since it was not sensitive to the semantic manipulation; besides the N400 does not originate from the hippocampus but from a left fronto-temporal network involving the anterior temporal cortex as well as the middle temporal gyrus and angular gyrus (for review see Lau, Phillips, & Poeppel, 2008).

Repetition and semantic context also affected behavioral performance. Response latencies decreased significantly with repetition and were shorter in semantically heterogeneous contexts (compared to homogeneous). Importantly, the physiological effects described above are not a mere consequence of responses being significantly faster or slower across conditions (e.g. larger amplitude in a condition that is faster and less variable). While the peak timing and amplitude of the components were indeed significantly tied to response latency (see also Hamamé et al., 2014), the contextual effects (repetition and semantic context) remained significant when this variable was included as a co-variate.

4.2. Cognitive mechanisms

The consistent and intricate patterns of activation demonstrate that the hippocampus is indeed active during picture naming. Contextual modulations of performance (e.g. repetition improvement and semantic interference) are directly reflected by hippocampal activity. This alone argues against the view that picture naming repetition involves a "non-hippocampal form of memory" (Francis, 2014), and suggests a possible role for the hippocampus during naming.

In terms of implicit learning, the hippocampus might keep track of the repetitions of the materials, providing a neural locus for the

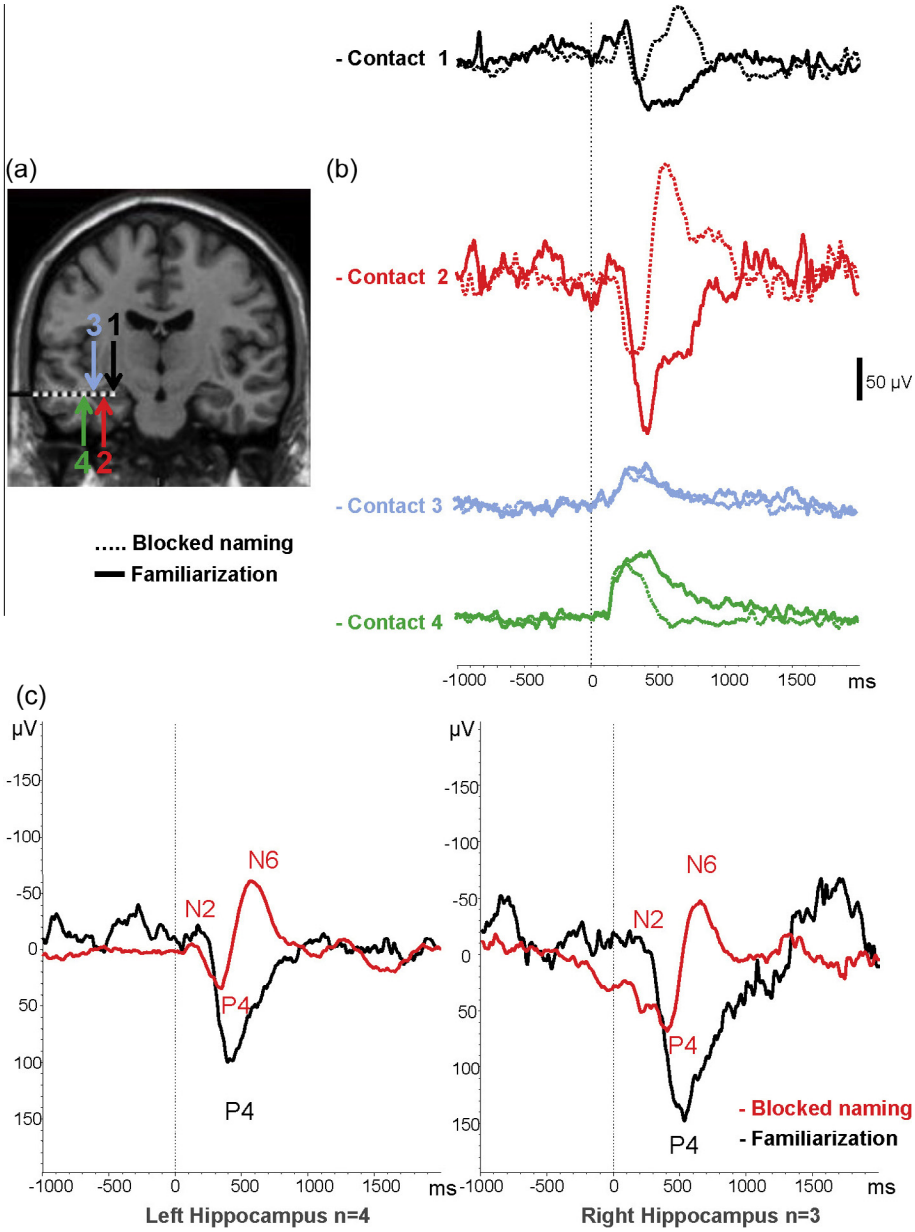

Fig. 2. Specificity of hippocampal responses in a single patient and in the group. (a) Location of the electrode implanted in the left hippocampus of patient 04 (only contacts 1 and 2 are located in the left hippocampal structure). (b) Comparison of average local field potentials (LFP) between the familiarization phase (novel pictures) and the blocked naming phase (repeated pictures) for patient 04 in hippocampal as well as neighboring contacts. (c) Grand average of all the contacts located in left or right hippocampus across the 6 patients.

mechanism postulated in Oppenheim et al. (2010) model. Our observation that both repetition and semantic context affect the N6 component argues in favor this hypothesis. Repetition promotes learning, and is accompanied by an increase in the peak amplitude of the N6. Such learning might be less efficient in (the notoriously more difficult) semantically homogeneous contexts. The N6 increase is indeed smaller in homogeneous than in heterogeneous contexts: the semantic context effect. Previous reports of a similar semantic context manipulation on hippocampal activity were inconsistent (homogenous contexts yielded a bilateral increase of perfusion in the two hippocampi, Hocking et al. (2008), vs. a decrease of perfusion in the left hippocampus only, De Zubicaray et al. (2014)). The complex sub-second modulation of hippocampal activity revealed here might have been integrated and smoothed in the slower fMRI signal modulation, and that could provide some reason for the discrepancies. In addition, a similar semantic context manipulation, used in studies involving surface recordings, yielded earlier effects (i.e. around 250 ms; Aristei, Melinger, & Abdel Rahman, 2011; Janssen, Carreiras, & Barber, 2011; Maess, Friederici, Damian, Meyer, & Levelt, 2002; but see Llorens et al., 2014). Such effects might be different from those we report, and reflect lexical retrieval (only) as was proposed in previous behavioral research (Damian et al., 2001). The role of the hippocampus might not primarily be in the retrieval of long-term links between objects and their names (lexical access in its stricter sense) but rather reflect incremental learning of such semantico-lexical links that bind the stimulus with the response in the task at hand. We note however that the Oppenheim et al. (2010) model closely combines both lexical retrieval and incremental learning into a single mechanism (see also (Quiroga, Reddy, Kreiman, Koch, & Fried, 2005), for MTL activity linking persons names and their faces). Interestingly, Oppenheim et al. (2010) considered the possible links between incremental learning

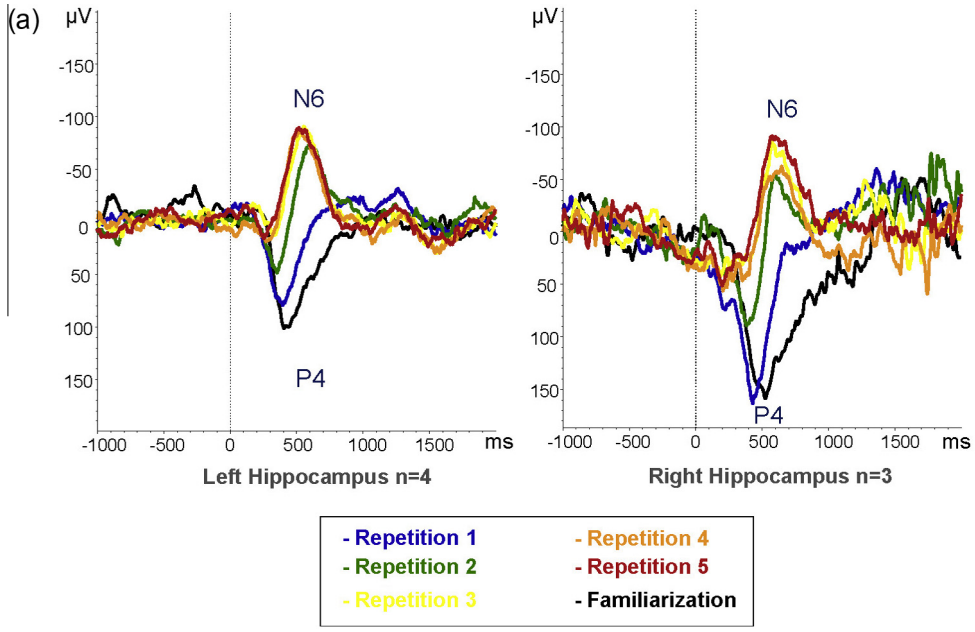

Fig. 3. Modulation of hippocampal activity induced by repeated picture naming. (a) Grand average local field potential (LFP) for novel pictures in the familiarization phase, and for their subsequent repetition (1–5) in the block naming phase, in left and right hippocampi.

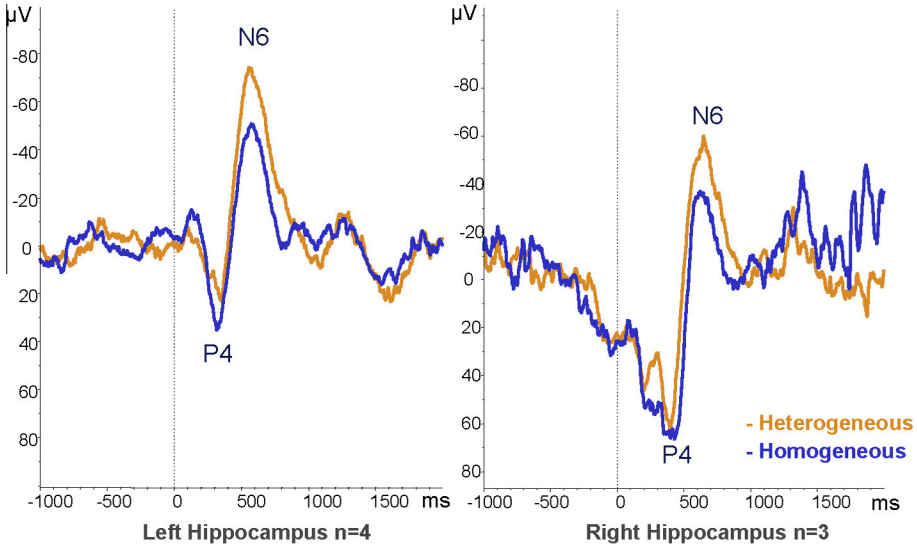

Fig. 4. Modulation of hippocampal activity induced by the semantic context (semantically homogeneous vs. heterogeneous blocks) during the block naming phase of the experiment. Grand averaged local field potential (LFP) for all contacts located in left or right hippocampus across the 6 patients.

in language and the retrieval induced forgetting phenomenon (Anderson, Bjork, & Bjork, 2000; Norman, Newman, & Detre, 2007), a phenomenon that has in turn be linked to hippocampus (Norman et al., 2007; see also Gluck et al., 2003; Meeter et al., 2005).

Our data do not implicate the hippocampus as a necessary structure for word retrieval. Impairment data from patients provide a stronger case (e.g. Miozzo & Hamberger, 2015, as well as previous work; see also Patient 1 described in Hamamé et al. (2014)). Poorer visual naming in patients with left hippocampal sclerosis compared with those with structurally normal hippocampi has been observed (Davies, Bell, Bush, & Wyler, 1998). A decline of naming is only observed in left temporal lobe epilepsy patients with a left or bilateral dominance for language (Kovac et al., 2010). More generally, the most commonly cited predictor of naming decline after an anterior temporal lobectomy in a dominant hemisphere is the absence of structural hippocampal pathology (Dulay & Busch, 2012; for a review, see Ives-Deliperi & Butler, 2012).

4.3. Neurophysiological considerations

Our results revealed a striking difference in the electrophysiological pattern evoked in hippocampus by novel and repeated items (Fig. 2C), specifically pointing to a complex and dynamic differential circuitry for learning and retrieval. The pattern is not suggestive of unidirectional repetition-suppression effect across repetitions (Kremers et al., 2014; Rand-Giovannetti et al., 2006; Van Turennout et al., 2000; Van Turennout et al., 2003; Vannini et al., 2013; Zeineh et al., 2003) but rather point to a more complex modulation subserved by different physiological mechanisms reflected

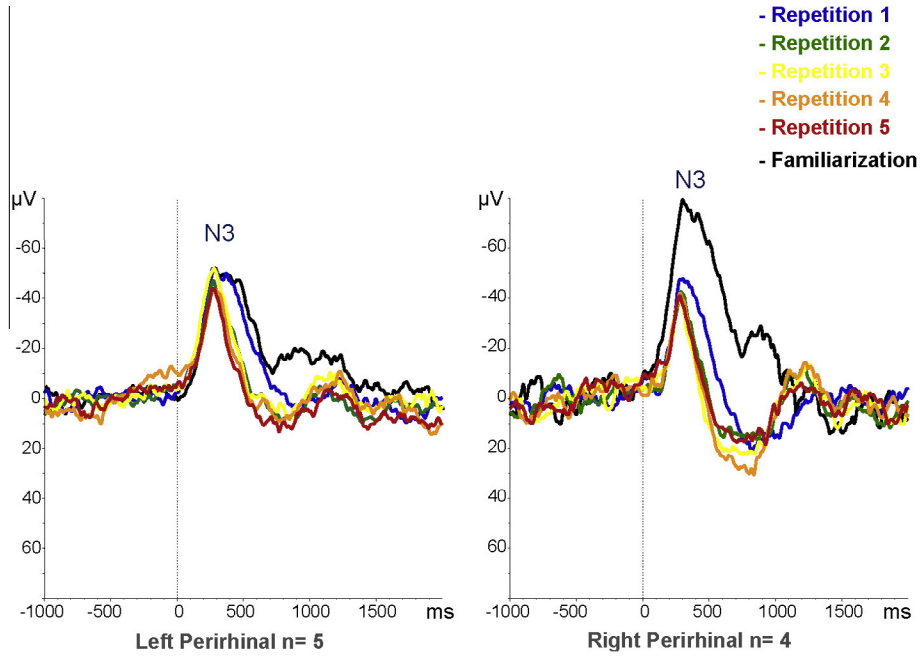

Fig. 5. Modulation of perirhinal activity, bilaterally, induced by repeated picture naming. Grand averaged local field potential (LFP) for novel pictures in the familiarization phase, and for their subsequent repetition (1–5) in the block naming phase for all the contacts.

in the recording of opposite polarity components. That is, the repetition suppression effect of the P4 and the enhancement of the N6 could result from distinct and general mechanisms: neural tuning and long term potentiation (LTP) (Gotts, Chow, & Martin, 2012; Grill-Spector et al., 2006).

Neural tuning is a process through which a set of neurons becomes more selective and narrows the range of stimuli or inputs to which it reacts, such that the number of neurons that respond to a given input decreases with repetition. This has been previously reported for perirhinal cortex with a decrease of the P3 observed bilaterally, which is in line with our own observation (Fernández et al., 1999; Halgren, Baudena, Heit, Clarke, & Marinkovic, 1994; Halgren et al., 2006). In contrast, long-term potentiation (LTP) is a process by which an increase in synaptic efficacy leads to specific set of neurons becoming more efficiently activated. This process is thought to correspond to a long lasting enhancement in signal transmission after repeated stimulation, with cellular and molecular underpinnings (Lynch, 2004). Assuming that processing a stimulus results in a specific pattern of electrophysiological responses, the induction of an LTP-like phenomenon strengthened by repeated exposure to the learning event would magnify that pattern, which could account for the increasing amplitude modulation of the P6 with repetition. Besides this repetition effect, this same component is the one that is sensitive to the semantic manipulation; it is reduced in homogeneous vs. heterogeneous contexts. Thus we relate the semantic effect with the potentiation mechanism. Such potentiation would be partly attenuated in homogeneous blocks because repetition is less efficient there (see also previous section). Overall, this interpretation suggests that the two phenomena of neural tuning and long term potentiation may be at play in hippocampus during repeated picture naming.

Alternatively, the different electrophysiological pattern we recorded for familiarization and repetition could be due to modifications in the synaptic connections between subfields of the hippocampus. The hippocampus consists of different subfields (CA3, CA2, and CA1), the dentate gyrus (DG) and the subiculum. The inputs and outputs of the hippocampus are linked to Entorhinal cortex (EC) through well characterized circuits: an indirect, trisynaptic pathway from EC to DG and CA3, and from there to CA1; and a direct, monosynaptic pathway, where EC directly projects to CA1 (Kajiwara et al., 2008; Van Strien, Cappaert, & Witter, 2009). Both pathways converge to CA1 pyramidal cells, but at different levels of the dendritic tree: either on the apical dendrites for the indirect pathway or basal dendrites for the direct one (Doller & Weight, 1982). Accordingly, activation of one or the other pathways generates synaptic current sinks at different levels of CA1 pyramidal dendritic tree. These different sites of excitation at the pyramidal level lead to two electrophysiological patterns of opposite polarity (Holsheimer, Boer, Da Silva, & Van Rotterdam, 1982). A given electrode contact, in a fixed position, will record potentials of opposite polarity depending on the pathway activated. This would be consistent with the pattern (P4 and N6) we observed in familiarization and repetition phases respectively.

The trisynaptic afferent pathway to hippocampus connects entorhinal cortex with DG, CA3 and CA1. The recruitment of CA3 is required during (i) learning, based on its self-association properties, (ii) storing information, based on its recursive loop, and finally during (iii) the recall of stored information (Rolls, 2010). In a second time, when these links are already established, the passage through DG and CA3 is no longer necessary, and the monosynaptic way (Kumaran & Maguire, 2007; McNaughton, Barnes, Meltzer, & Sutherland, 1989) will be activated to maintain a mnemonic trace and to facilitate stimulus (i.e. picture) processing.

A third and final hypothesis is that the activity of two distinct neuronal populations, one responding to novel pictures and the other to old ones, was recorded in our data. This has been previously shown in (Rutishauser, Mamelak, & Schuman, 2006). By using microwires electrodes implanted within the human anterior hippocampus, these authors identified two groups of neurons that signal novelty or familiarity. In our data, naming novel pictures (during the familiarization phase and the first repetition) elicited a P4; subsequent repetitions lead to a decrease of this component and the emergence of a large N6 (see also Puce, Allison, and McCarthy (1999).

The considerations above suggest that it is critical to take into account the fine local organization of hippocampal neurons, including whether they are excitatory or inhibitory, before drawing any firm conclusion about the neurophysiological mechanisms underlying the patterns we report. In this respect, it is clear that the size of the depth electrodes used in this study prevents further disambiguation of these hypotheses. Such endeavor would call for further work using appropriate electrode size and state of the art MRI reconstruction (Yushkevich et al., 2010) to view distinguished hippocampal subfields.

5. Conclusion

The reported data reveal a specific, intricate and reliable sequence of hippocampal activity during plain picture naming, in the absence of memorization or encoding instructions. Such involvement of hippocampus presumably reveals incremental learning, as predicted from models of hippocampal function (Gluck et al., 2003; Meeter et al., 2005) and psycholinguistic processes (Oppenheim et al., 2010). An early negativity is observed essentially when pictures are first presented, whereas subsequent repetitions dissipate this negativity and promote a later positivity. This opposing pattern does not solely reflect repetition-suppression or increased efficiency. Rather, it could reflect differential processes subtended by different sub-circuits in the hippocampus, namely a switch from tri- to mono-synaptic pathways induced by the contextual factors (repetition and semantic context).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.bandl.2016.05.011.

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