

Electrophysiological correlates of perceptual auditory priming without explicit recognition memory

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Abstract

The aim of this study was to identify an event-related potential (ERP correlate) of perceptual auditory priming using a method that can dissociate it from explicit memory similar to Rugg et al., (1998). EEG was recorded during performance of an auditory word recognition test, where 17 participants discriminated 'old' from 'new' aural words, encoded using either a 'deep' or 'shallow' levels-of-processing (LOP) study task. A right-lateralised P200 effect was modulated by words' old/new status but not by accuracy of recognition or LOP manipulation. Because this effect was driven by simple repetition rather than factors known to influence episodic recognition memory, a 'bottom-up' perceptual priming function was inferred which was substantiated by its early temporal appearance. A similar ERP amplitude modulation was evident across a broader topographical region during the subsequent N400 time interval. Conversely the late posterior component (LPC; 500 to 800 ms) for deeply-encoded, correctly-recognised words was of higher amplitude than LPCs for shallowly encoded and new words, consistent with proposals that this ERP component indexes episodic memory. To our knowledge this is the first report of an ERP correlate of auditory perceptual priming dissociated from explicit episodic memory.

Keywords: Auditory Perceptual Priming, P200, N400, ERP, Event-Related Potential

1. Introduction

Priming refers to facilitated processing (e.g., more rapid or accurate processing) of repeated stimuli compared to stimuli experienced for the first time. Perceptual priming, the focus of the current research, is enhanced when the form or structure of the ‘prime’ (i.e., the initial presentation of the stimulus) and the ‘target’ (i.e., the subsequent presentation of the stimulus) are matched; for example, when font type, shape, or acoustic properties remain constant across stimulus presentations. On this basis, perceptual priming is also labelled ‘repetition priming’. In contrast, conceptual priming is elicited when semantically-related primes and targets are paired.

Both forms of priming are categorised as implicit memory because unlike explicit memory, the effects of previous experience are apparent in the absence of any conscious or deliberate attempts to retrieve prior information (Wiggs & Martin, 1998). This is evidenced in studies showing that priming, of visual and aural stimuli, is frequently preserved in people with explicit memory deficits such as those with anterograde amnesia. Corroborating demonstrations in non-clinical groups are that perceptual priming is generally not modulated by cognitive effort, such as ‘deeper’ levels of processing at encoding (i.e., levels-of-processing manipulation, LOP, Craik & Lockhart, 1972) and that it is commonly attenuated by changes in the surface features or mode of presentation across study-to-test periods. Together these outcomes suggest perceptual priming is driven by perceptually-based, ‘bottom-up’ neural mechanism(s) that are largely distinct from those subserving episodic memory (Schacter, Wig & Stevens, 2007; Wiggs & Martin, 1998).

Tulving and Schacter (1990) and Schacter (1994) proposed the perceptual representation system (PRS) model wherein perceptual priming is mediated via facilitated processing in cortical area(s) separate from other brain regions (i.e., in the medial temporal lobe) known to be critical to explicit memory and compromised in people with anterograde

amnesia. The PRS comprises three domain-specific subsystems: the visual word form subsystem, the auditory word form subsystem, and the structural description subsystem, that process stimuli (from the various modes) in a similar way, albeit to some degree at modality-specific cortical locations (Schacter, 1994).

Importantly, Rugg et al. (1998) identified an electrophysiological dissociation between explicit memory and visual priming, employing a design that prevented participants from using explicit memory retrieval strategies to enhance their priming performance (Henson, 2003). Dissociations revealed under these conditions provide convincing evidence to support the independence of explicit and implicit memory systems. Rugg et al. (1998) employed a LOP manipulation at encoding which for the shallow encoding condition ensured sufficient numbers of ‘miss’ trials for reliable comparison to recognition-trial ERPs. Comparisons between ‘shallow miss’ versus other conditions’ ERPs indicated that the N400 (but not late positive component [LPC]) effects index perceptual word priming in the absence of explicit recognition memory. We subsequently extended their design and were the first to report data indicating that the preceding P150 and P200 effects, at midline and parietal sites, respectively, index perceptual object priming processes that are indeed distinct from explicit recognition memory (Harris et al., 2009). In the current study we employed an analogous approach to investigate the ERP correlates of auditory perceptual priming.

To our knowledge, an electrophysiological dissociation between auditory perceptual priming and explicit memory has not yet been reported. Instead, evidence for such a distinction in the auditory system has been garnered from neuropsychological and behavioural studies, which have corroborated the pre-semantic properties of perceptual priming identified using visual stimuli. For example, performance is attenuated in auditory priming tasks relative to auditory explicit memory tasks, with study-to-test changes in speaking rate (Sommers, 1999); fundamental frequency (Church & Schacter, 1994; Sommers,

1999); sentence intonation (Church & Schacter, 1994); and voice (Schacter & Church, 1992 [Experiments 3,4]; Schacter, Church, & Bolton, 1995 [in people with amnesia]; Sheffert, 1998; Sommers, 1999). Also, semantic encoding (i.e., LOP manipulation) does not enhance auditory priming, with performance equivalent following deep and shallow encoding tasks (Schacter & Church, 1992; Schacter, Church, & Treadwell, 1994).

In the field of linguistics, ERPs acquired during phonological priming demonstrated faster and more accurate responses to target words when they were immediately preceded by similar sounding (i.e., phonologically-related) priming words (see Dufour, 2008 for a review). These results support the view that pre-lexical processes contribute to the automatic identification of auditory words, in addition to the well-documented facilitating effects of semantic priming (Bentin, Kutas & Hillyard, 1993; Holcomb & Neville, 1990). From these studies, a reliable ERP effect is attenuation of N400 amplitudes (more positive) to phonologically-related versus –unrelated prime/target combinations (Dumay et al., 2001; Praamstra & Stegeman, 1993; Radeau et al., 1998). These studies indicate that the temporal window encompassing the N400 component is sensitive to changes in lower-order (non-semantic) features of repeated auditory phonemes.

The results from mnemonic and linguistic studies indicate that auditory perceptual priming is driven by similar mechanisms as visual (word and object) perceptual priming, but further evidence is required to determine whether this mode of perceptual priming can act independently of auditory explicit memory. In the current study we addressed this issue by employing a design very similar to our past visual study (Harris et al., 2009) and that of Rugg et al. (1998) but now using aurally-presented words as stimuli. We hypothesised that primed words' ERPs would show an enhanced P200 and/or N400 effect relative to novel words' ERPs, and that this would be independent of explicit recognition memory. Recognition is thought to consist of the dual retrieval processes of familiarity and recollection (Rugg &

Curran, 2007). Although recollection is well-defined and robustly evidenced by old/new effects overlapping the LPC component, conceptualisations of familiarity vary (e.g., cf. Curran, 1999; Finnigan et al., 2002; Rugg & Curran, 2007) and debate remains as to whether or not familiarity is totally distinct from implicit memory (e.g., see Rugg & Curran, 2007 for summary and review). Finding that primed but unrecognised items activate one brain region more than another whilst recognized items do not show this pattern would provide further support for such a distinction and motivated the present research. Further, the degree of overlap or relationship between parietal and frontal (“FN400”; e.g., Curran, 1999) N400 old/new effects, that may reflect perceptual priming and familiarity, respectively, is not fully clear (e.g., Rugg et al., 1998). Notwithstanding these unresolved issues, our study focuses on experimentally manipulating ERP old/new effects for auditory perceptual priming and recollection.

This approach has the potential to provide new insights into perceptual auditory priming in the absence of explicit recognition memory, and particularly the ERP correlates of the same; including in relation to the PRS model of Schacter and Tulving.

2. Methods

2.1. Participants

Nineteen participants were recruited from Griffith University, School of Psychology first-year subject pool and received course credit for their participation. The ERP data of two participants were discarded due to excessive artifacts. The remaining subset of participants (13 females & 4 males) were aged between 18 and 47 years ($M = 22.12$ years, $SD = 7.66$) and all but one participant was aged between 18 and 35 years. All participants were right handed, had English as their first language, reported having normal hearing and not having a brain injury. Institutional ethics approval was obtained prior to conducting the study and each participant gave written informed consent prior to their participation.

2.2. Auditory recognition test

2.2.1. Stimuli and task

154 names of objects were derived from Snodgrass and Vanderwart's (1980) standardised set of pictures of objects¹. The mean frequency count for words (Kucera & Francis, 1967) was 31.64 per million ($SD = 57.23$), the mean number of syllables was 1.62 ($SD = .83$), and the mean word length was 5.38 letters ($SD = 1.92$). This group was divided into three sets of 48 words matched for frequency, number of syllables, and word length. These word sets appeared as either words in the deep or shallow encoding task or new words in the test phase. The order of the word sets were rotated across participants such that words appeared equally often in each study/test condition. Shallow and deep trials were randomly interspersed during the study phase, as were shallow, deep and new trials in the test phase; and not presented as separate blocks. Six words were used in filler trials at the beginning and end of the study and test lists to reduce primacy and recency effects. One hundred words were presented at study and 150 words at test.

Auditory words were presented as stimuli throughout the experiment. These were recorded in a quiet room by a single female speaker using the Goldwave_{TM} (v5.10) wave file editor on a PC computer. Stimuli were digitised at a sampling rate of 11 kHz using an analogue-to-digital sound card. Each sound file was edited to ensure that the acoustic onset of the word was aligned to the beginning of the file. The duration of the spoken words had an average length of 563 ms ($SD = 126$ ms). Words were presented binaurally through closed dynamic stereo headphones (Sennheiser_{TM} hd25 SP) at a comfortable level of loudness as nominated by the participant. Visual icons presented on a computer monitor during the study and test tasks (i.e., **X**, **O**, **?**, *, ,) were shown centrally in black font on a white background. The maximum visual angle subtended was 3° horizontally and 0.5° vertically.

¹ These stimuli were the same as those used in our previous experiment (Harris et al., 2009) with the difference being that the current study presented the names of objects aurally while our previous study presented them as visual objects.

An auditory recognition test was employed where participants attempted to discriminate old words, included in a preceding study phase, from new words. An LOP manipulation was used in the study phase so half of the trials comprised a perceptual or ‘shallow’ task, and half a conceptual or ‘deep’ task. The perceptual task (termed here the X task) was to determine if the auditory word contained the long vowel sounds /ay/ or /ee/ and respond by saying either “yes” or “no”. The conceptual task (termed here the O task) was to incorporate the auditory word into a meaningful sentence and say it aloud.

Each study trial commenced with an ‘X’ or ‘O’ cue for 1000 ms specifying which study task (i.e., shallow or deep) to use. The auditory word followed, the onset of which coincided with a white screen for 900 ms, then a “?” cue appeared for 3500 ms during which the participant responded verbally to the task. The total time of each study trial was 5400 ms. Each trial in the test phase began with a fixation asterisk for 2100 ms, followed by a blank screen for 100 ms, and then an auditory word which coincided with a white screen presented for 900 ms. A “?” cue then appeared for 2300 ms during which the participant gave a yes/no recognition response by pressing either a ‘yes’ or ‘no’ marked key on a response pad using the index and middle fingers of their right hand. The positions of these keys were counterbalanced across participants. The total time of each test trial was 5400 ms. Figure 1 is a schematic illustration of a study and test trial.

2.2.2. Procedure

Participants completed consent and medical history pro formas then entered an electrically shielded and darkened room where headphones were fitted, sound levels tested and the study phase of the experiment completed. Participants were told prior to the study phase that a recognition phase would follow. To ensure participants were completing the study tasks correctly, the researcher listened to responses via an intercom and manually recorded responses. Participants were then taken to an adjoining preparatory room where the

electrode cap was fitted. The participant then re-entered the shielded room and completed the test phase of the experiment during which EEG was recorded. To reduce ERP artifacts, participants were instructed to be still and relaxed, maintain fixation at the centre of the monitor and blink only when the asterisk was on the screen. These procedures were rehearsed through the practice trials that preceded the test phase.

An interval of approximately 30 min separated the study and test phases. Participants read study and test instruction manuals prior to each phase. They were instructed to attend to words presented by headphones and to press a response key when a “?” appeared on the screen. They were told: “Press ‘yes’ if you think the word was in the study activity. Press ‘no’ if you do not think it was in the study activity. Respond as accurately and quickly as you can” A block of five practice trials preceded the study phase and six practice trials preceded the test.

2.3. Recording

Scalp EEG was acquired continuously from an array of 32 electrodes (Ag/AgCl sintered electrode cap) using a Neuroscan SynAmps²™ amplifier, digitized at a sampling rate of 1000 Hz, and online filtered (bandwidth: 0.15 to 40 Hz). Electrode locations corresponded to the following sites of the International 10-20 electrode positioning system (Jasper, 1958; Sharbrough et al., 1991): F_p1, F_p2, F3, F4, F7, F8, Fz, FT7, FT8, FC3, FC4, C3, C4, Cz, CP3, CP4, T7, T8, TP7, TP8, P3, P4, P7, P8, Pz, O1, O2, Oz. Electrode impedance was reduced to below 10kOhms. Recordings were made with respect to the left mastoid process and were re-referenced offline to the computerised average of both mastoid processes. Bipolar vertical and horizontal EOG was recorded from electrodes placed above the supra-orbital ridge of the left eye and below the left eye, and adjacent to the outer canthi of both eyes. Eye blink artifacts were corrected by means of the Semlitsch et al. (1986) algorithm a function incorporated into the Neuroscan Edit 4.3 program. EEG data were

divided into epochs beginning 100 ms pre-stimulus and ending 1000ms post-stimulus. These epochs were baseline corrected using the pre-stimulus period and offline filtered (bandwidth of 0.15 to 30 Hz). Trials on which baseline to peak EOG amplitude exceeded 100 μ V, baseline-to-peak drift exceeded 60 μ V, or saturation of the A/D converters occurred, were excluded from averaging. Data were discarded if there were fewer than 10 artifact free trials in any of the conditions (Finnigan et al., 2002).

2.4. Analysis strategy

ERPs were investigated across four time intervals incorporating the putative N100 (80 to 150 ms), P200 (150 to 250 ms), N400 (350 to 550 ms) and LPC (600 to 900 ms) old/new effects. Epochs were typical of those previously used to identify ERP priming and explicit memory effects and maximally captured distinct old/new word type differences apparent in the current data. The peak amplitude and latency of the N100 and P200 and the mean amplitude of the N400 and LPC effects were analysed. The peak amplitude was defined as the largest negative (N100) or positive (P200) deflection occurring within the stated intervals and peak latency as the time instant of the largest deflection within these intervals. The peak amplitude and latency of the N100 and P200 was used to best capture the short (or narrow) latencies of these early ERP effects. Using wider intervals, as is typically the case for the analysis of mean amplitude, would have caused the contamination of one mean amplitude measure (e.g. N100) with data more relevant to an overlapping/following component (e.g. P200).

Widely distributed old/new effects allowed ERPs to be averaged across specific scalp regions. Obligatory auditory ERP effects (i.e., N100 and P200) were tested at regions representative of the primary auditory cortex (temporal, central and fronto-central regions); that is, the left lateral (FT7, T7, TP7), the left medial (FC3, C3, CP3), the right medial (FC4, C4, CP4), and the right lateral (FT8, T8, TP8) regions. These effects were also investigated at

the vertex (CZ). In contrast, ERPs more likely to represent endogenous explicit memory effects (i.e., N400 and LPC effects) were measured at left anterior (F7, F3, FT7, FC3), left posterior (TP7, CP3, P7, P3), right anterior (F8, F4, FT8, FC4), and right posterior (P8, P4, TP8, CP4) regions. This regional selection is consistent with prior ERP studies of recognition memory that have identified frontal and posterior N400 old/new effects and left posterior LPC old/new effects (Curran & Dien, 2003; Rugg et al., 1998).

N100 and P200 old/new effects were analysed using 2 (laterality: medial, lateral) x 2 (hemisphere: left, right) x 3 (word type: shallow recognised, shallow unrecognised, correctly classified new) within-subjects ANOVAs and the N400 and LPC old/new effects using 2 (location: anterior, posterior) x 2 (hemisphere: left, right) x 3 (word type) within-subjects ANOVAs. A difference existed in the levels of the word type factor between the N400 and LPC analyses such that the N400 analyses included the same levels as the N100 and P200 analyses, while the LPC analysis included the deep recognised, shallow recognised and correctly classified new word types. Consistent with the method of Rugg et al. (1998) the shallow recognised, shallow unrecognised, and new word types were used to detect putative priming effect/s (i.e., N100, P200, N400). Using these three levels (instead of four were the deep recognised condition included) reduced the number of planned comparisons undertaken and provided suitable evidence that amplitudes differed as a function of old/new status rather than recognition, which substantiates a priming effect. In contrast, the LPC old/new effect included the deep recognised, shallow recognised, and new word levels which allowed the LOP study manipulation to be tested. A demonstration that ERP amplitudes differed according to a word's study status, wherein deep recognised words were more accurately recognised and elicited more positive amplitudes than shallow recognised words corroborates an episodic function (Gonsalves & Paller, 2000; Rugg & Curran, 2007). In summary, the differing levels of the word type factor used to test the putative priming and recognition ERP

effects provided a means to detect a dissociation between these functions while containing familywise error due to multiple comparisons.

A subsequent analysis was conducted using ERPs for the old-minus-new word difference amounts at time intervals where significant omnibus ANOVA word type effects had been shown (i.e., P200, N400 and LPC time intervals). Reliable deviations from zero were identified using the one sample *t*-test. Paired *t*-tests were also conducted between the deep(recognised)-minus-new and shallow(recognised)-minus-new amplitudes at the P200 and N400 intervals to test whether depth of encoding modulated these early putative priming effects.

The Geisser-Greenhouse correction was used to correct for violations of the assumption of the homogeneity of covariance in within-subjects ANOVAs. Alpha was set at .05. A restricted number of planned comparisons were used, thus alphas were not adjusted to compensate for familywise Type 1 error (Keppel, 1991). For each ANOVA result, the uncorrected *df* value, *F* value, the epsilon-corrected *P* value and the corresponding epsilon value was reported. The partial eta squared (η_p^2) statistic was used to determine the magnitude of effects for all significant single-*df* a priori tests because these outcomes were central to the study aims.

The mean, range and sum of ERP trials per condition were: deep recognised: 32.53, 22-45, 553; shallow recognised: 19.94, 10-30, 339; shallow unrecognised: 17.76, 10-33, 302; and new: 31.76, 24-44, 540. Apparent in these descriptives is signal-to-noise inequalities between conditions. Therefore, to preclude this disparity as a potential contributor to word type differences, we created a second dataset with equal trial numbers per word type (termed here the matched-trial data). This was achieved by randomly removing trials from the deep recognised, shallow recognised and new conditions so that each participant's dataset had about the same number of trials as that participant's shallow unrecognised condition.

Consequently, the mean, range and sum of ERP trials per condition for the matched-trial data were: deep recognised: 17.76, 10-32, 302; shallow recognised: 17.76, 10-30, 302; and new: 17.76, 10-32, 302). Analyses were then conducted to compare the outcomes of the original and the matched-trial data and no word type differences were found between these datasets. We include the analyses undertaken using the matched-trial data in the current report.

3. Results

3.1. ERP waveforms

The grand average ERP waveforms are presented in Figure 2. Evident in these was a broadly occurring negative deflection commencing at about 50 ms post-stimulus and peaking at about 90 ms, termed the N100. Neither the peak amplitude nor the latency of the peak amplitude of the N100 appeared to be modulated by the experimental factor word type.

A P200 component was prominent at midline, medial, and right lateral (or temporal) regions, with the peak positive amplitude for all word types recorded at the vertex (CZ) at about 200 ms. At these regions, amplitudes appeared to differ according to words' old/new status, with those for old words appearing of a similar magnitude – irrespective of LOP or recognition accuracy - yet all more positive than those for new words. Likewise, N400 ERPs appeared to be influenced primarily by repetition. Apparent at the LPC time interval was a typical LOP effect because from about 600 ms onwards there was a positive going wave for recognised words previously encoded using the deep study task compared to recognised and unrecognised words encoded using the shallow study task and new words.

3.2. Behavioural data

Significantly more words in the deep encoding condition were recognised ($M = 89\%$, $SD = 8.33\%$) than those encoded in the shallow condition ($M = 52\%$, $SD = 17.60\%$), $t(16) = 9.98$, $p < .001$. This reflects a LOP effect (Craik & Lockhart, 1972). Eighty-five percent of the new words were correctly classified.

An unbiased estimate of memory performance for the deep and shallow word conditions was tested by comparing the memory discrimination indices, Pr (Pr = hit rate minus false alarm rate, Snodgrass & Corwin, 1988), of both with zero. This analyses showed that both conditions' Pr index reliably differed from zero (deep recognised: $M=.74$, $t(16) = 24.04$, $p < .001$; shallow recognised: $M=.37$, $t(16) = 8.95$, $p < .001$) and provides evidence of a memory effect for both word type conditions.

3.3. *Electrophysiological data*

3.3.1. *N100 old/new effect (80 to 150 ms)*

A 2 (laterality: medial, lateral) x 2 (hemisphere: left, right) x 3 (word type: shallow recognised, shallow unrecognised, new) within-subjects ANOVA revealed no ERP peak amplitude or latency differences associated with the various word types. Further, there were no ERP differences for word types at the vertex (Cz).

3.3.2. *P200 old/new effect (150 to 250 ms)*

A 2 (laterality: medial, lateral) x 2 (hemisphere: left, right) x 3 (word type: shallow recognised, shallow unrecognised, new) within-subjects ANOVA using peak ERP amplitudes resulted in a significant main effect for Word Type, $F(2,32) = 3.89$; $p < .05$ and a significant Hemisphere x Word Type interaction, $F(2,32) = 3.65$; $p < .05$. The Hemisphere x Word Type interaction was explained by single df contrasts conducted first between word types at the right hemisphere (collapsed across right medial & lateral regions: FC4+C4+ CP4+ FT8+T8+TP8) and then for word types at the left hemisphere (collapsed across left medial & lateral regions: FC3+C3+ CP3+ FT7+T7+TP7). These left and right hemisphere averaged ERP waveforms are shown in Figure 3. At the right hemisphere, peak amplitudes did not differ between ERPs for the shallow recognised and unrecognised words, however, both were significantly more positive than those obtained for new words (shallow recognised: $F(1,16)$

= 6.45, $p < .05$, $\eta_p^2 = .29$, shallow unrecognised: $F(1,16) = 6.67$, $p < .05$, $\eta_p^2 = .29$). No differences existed between peak amplitudes for word types at the left hemisphere.

Peak amplitudes at the vertex (Cz) were not modulated by word type.

There were no peak latency differences to word type at medial or lateral regions or at Cz.

3.3.3. *N400 old/new effect (350 to 550 ms)*

A 2 (location: anterior, posterior) x 2 (hemisphere: left, right) x 3 (word type: shallow recognised, shallow unrecognised, new) within-subjects ANOVA conducted on mean ERP amplitudes between 350 and 550 ms yielded a significant main effect for Word Type, $F(2,32) = 5.97$, $p < .01$. Single *df* comparisons of ERPs for word types collapsed over the levels of location and hemisphere showed no difference between amplitudes for the shallow recognised and unrecognised words but ERPs for both word types were significantly more positive than those obtained for new words (shallow recognised: $F(1,16) = 13.48$, $p < .01$, $\eta_p^2 = .46$; shallow unrecognised: $F(1,16) = 5.89$, $p < .05$, $\eta_p^2 = .27$). These shallow and new word ERPs, collapsed across left and right anterior and posterior regions, are displayed in Figure 4.

3.3.4. *LPC old/new effect (600 to 900 ms)*

A 2 (location: anterior, posterior) x 2 (hemisphere: left, right) x 3 (word type: deep recognised, shallow recognised, new) within-subjects ANOVA conducted on mean ERP amplitudes between 600 and 900 ms revealed a significant main effect for Word Type, $F(1,16) = 24.32$, $p < .0001$. Comparisons undertaken on ERP amplitudes for word types collapsed across location and hemisphere showed that ERPs for the deep recognised words were significantly more positive than those obtained for shallow recognised words, $F(1,16) = 11.38$, $p < .01$, $\eta_p^2 = .42$ and new, $F(1,16) = 52.31$, $p < .0001$, $\eta_p^2 = .77$. These LPC-related ERPs, averaged across all electrode regions (left/right; anterior/posterior) are shown in Figure 4.

3.3.5. Old/new difference effects

The old-minus-new difference amounts for the old word types at the P200, N400 and LPC time intervals are displayed in Figure 5. These figures illustrate the impact of varying the depth of encoding at study and as such can be used to elucidate whether outcomes were likely subserved by perceptual or conceptual processes. For example, a well-documented finding is that conceptually-oriented processes are sensitive to the LOP manipulation such that parameters associated with deeply encoded words differ relative to those of shallowly-encoded and new words (Craik & Lockhart, 1972).

Consistent with the previously reported P200 ANOVA which revealed a significant Word Type x Hemisphere interaction, P200s (Figure 5A) for shallow word types at the right hemisphere (particularly at the right lateral region) deviated from zero by a similar amplitude. Importantly, this diagram also shows that ERPs for deeply recognised words at this hemisphere differed from zero at a similar magnitude to shallowly encoded words. Furthermore, a 3-way ANOVA on the means shown in Figure 5A for Word Type (all 4) by Region by Hemisphere resulted in a significant interaction between Word Type and Hemisphere $F(2,32) = 4.59, p = 0.018$. Follow-up paired comparisons between hemispheres for each word type showed no difference for either the deep or shallowly recognised conditions but did show that right shallowly unrecognised condition had a greater amplitude than the left shallowly unrecognised condition, $t(16) = 2.48, p = 0.025$. Further confirmation that depth of encoding did not drive P200 peak amplitude differences between the deep and shallow recognised conditions was garnered from the finding that paired t -tests failed to identify reliable differences between deep-minus-new and shallow(recognised)-minus-new word conditions at the left and right hemispheres (collapsed across medial & lateral regions) (Left: $t(16) = 1.41, p = .18$; Right: $t(16) = 1.56, p = .14$). That this is not a result of loss of sensitivity due to hemispheric averaging was confirmed by performing old-minus-new

compared to shallow(recognised)-minus-new t -tests at the four individual regions for P200 in Figure 5A. None of these showed a significant difference.

At the subsequent 350 to 550 (N400) time interval (Figure 5B) a 3-way ANOVA on the means shown in Figure 5B for Word Type (all 4) by Region by Hemisphere was performed but showed no significant effects. However, old-minus-new differences for all of the old word types show similar deviations from zero at each of the regions. Further, paired t -tests showed there were no significant differences between the deep-minus-new and shallow(recognised)-minus-new mean amplitudes at the left and right anterior and posterior sites (LA: $t(16) = .67, p = .51$; LP: $t(16) = -.73, p = .48$; RA: $t(16) = .90, p = .38$; RP: $t(16) = .48, p = .64$). Conversely, old-minus-new deviations from zero at the LPC interval reflect a typical LOP effect with those for the deep recognised condition being relatively more positive than those for the shallowly recognised and unrecognised words. This pattern was evident across all regions.

4. Discussion

The aim of this study was to identify an electrophysiological correlate of auditory perceptual priming dissociable from explicit memory. The amplitude of a P200 component (Figure 3, 150 to 250 ms) at right hemisphere frontal, central and temporal electrodes was found to differ between old versus new word ERPs, irrespective of the LOP study condition or recognition accuracy for old words. A subsequent N400 effect (350 to 550 ms) showed similar between-condition ERP modulations across a broader scalp region, and the 3-way ANOVA failed to show significant effects between the word types. In contrast, a qualitatively different pattern was evident for the LPC (600 to 900 ms), with amplitudes for deeply-recognised words larger than those for shallowly-recognised and new words.

4.1. P200 and N400 old/new effects

P200 amplitude was significantly larger for repeated words, irrespective of whether they were recognised or missed, than new words at right hemisphere frontal, temporal and central electrode sites. Further, at the same hemisphere old-minus-new, P200 amplitude differences were not modulated according to whether words were encoded using the conceptual (meaning-based) task (see Figure 5A). Taken together, these observations that amplitude was driven by simple repetition and not semantic encoding infers a P200 perceptual priming function that excludes episodic recognition memory processes (Boehm, Sommer, & Lueschow, 2005; Fay et al., 2005; Graf & Mandler, 1984; Jacoby & Dallas, 1981; Rugg et al., 1998). If the P200 reflected explicit memory, then it would be expected to vary as a function of recognition accuracy and semantic encoding (Craik & Lockhart, 1972).

A few studies using visual stimuli have shown right P200 perceptual priming effects that were disrupted by changes in surface features across presentations (Schendan & Kutas, 2007), were independent of explicit memory and persisted across intervals of at least 30 minutes (Harris et al., 2009). Our current outcomes add to the P200 priming literature demonstrating an aural form that is also unaffected by episodic memory and that persists over extended periods.

The observed right P200 asymmetry, found using an averaged left/right mastoid reference (to reduce bias of voltage distribution) may imply involvement of the right hemisphere in perceptual auditory priming. Recent behavioural outcomes have shown that the right, compared to the left, hemisphere is more sensitive to alterations in the form or surface features of repeated visual (words and objects; for a review see Marsolek & Burgund, 2008) and more recently, aural stimuli (Gonzalez, Cervera-Crespo & McLennan, 2010; Gonzalez & McLennan, 2009). Further, Kayser and colleagues (Kayser & Tenke, 2006; Kayser, Tenke & Bruder, 1998) have consistently shown that tones versus phonetic stimuli in oddball tasks

elicit enhanced N200 ERPs at right frontotemporal sites compared to left sites. In contrast, phonetic stimuli elicit an enhanced N200 at left parietotemporal sites. Studies using positron emission tomography (PET) also support a role for the right hemisphere in processing auditory pitch patterns (Wong et al., 2004) and spectral qualities of sounds (Zatorre & Belin, 2001). Together these outcomes indicate a differential hemispheric priming effect may be observed in processing auditory words that require consonant discrimination as opposed to vowel discrimination.

The same pattern of between-condition ERP differences observed during the P200 interval was obtained for amplitude analyses from the subsequent N400 time interval; wherein the amplitudes for all old word types were similarly enhanced (more positive) compared to those of new words (see Figure 4 and 5B). As such, this outcome represents a replication of the Rugg et al.'s. (1998) and Harris et al.'s. (2009) N400 effects obtained using visual words and pictures of objects, respectively. However, our auditory and object priming results have demonstrated a broader topography than Rugg et al.'s effect which was localised to the parietal electrodes.

Figure 5B also shows the N400 to be right lateralized which may be indicative of subsequent processing of the pitch trace indexed by the right-hemisphere P200 described above. It should be noted that priming duration (on the order of 30 min or more) as manipulated in the present experiment (as compared to seconds or milliseconds in most other studies) shows that the facilitatory trace can be quite long-lived. It is also pointed out that compared to words and visual objects, relatively few studies (Church & Schacter, 1994; Schacter, Church & Bolton, 1995; Schacter & Church, 1992; Sheffert, 1998; Sommers, 1999) have used auditory words to study priming or implicit memory and it would be of interest to determine if the P200 and N400 priming effects extend to other types of non-verbal auditory stimuli such as natural sounds or musical phrases.

4.2. LPC old/new effect

An LPC old/new effect peaked between 600 and 900 ms post-stimulus across anterior/posterior and left/right regions with ERPs for deeply-recognised words significantly more positive than those for both shallowly-recognised and new words. The functional significance of this ERP modulation to ‘old’ recognised words can be elucidated with reference to our behavioural recognition results; wherein accuracy was significantly enhanced for deeply-encoded (89% recognised) compared to shallowly-encoded (52% recognised) words. To the extent that the LOP effect taps episodic memory processes (Craik & Lockhart, 1978), the current LPC old/new effect likely does as well. Similarly, Gonsalves and Paller (2000) termed a late positive ERP effect (P820, 600 – 900 ms) garnered by spoken words in a study/test memory paradigm, a recollection effect because it was driven by depth of encoding. That is, it was enhanced at test for semantically compared to perceptually encoded words or new words. Kayser, Fong, Tenke and Bruder (2003) further demonstrated that the episodic processes underpinning the auditory old/new effect were likely analogous to those of the more commonly described visual old/new effect. Using a continuous recognition task where auditory and visual words were included as a within subject condition they isolated old/new ERP effects for both modes of stimuli at a similar latency (560 ms) that overlapped ERP components unique to each mode (i.e., latency, topography). This similar time course of old/new effects was indicative of a common function across modes.

In view of Kayser et al’s (2003; see also Kayser, Tenke, Gates & Bruder, 2007) outcomes it is important to consider the extent to which our old/new results reflect one mnemonic effect that extends across multiple ERP components (i.e., P200, N400, LPC). However, according to the modulation of between-condition (i.e. word type) ERPs it is more likely that our data demonstrate two independent old/new effects: an early perceptual priming effect overlapping P200 and N400 components and a subsequent effect at the LPC interval

representing episodic memory. While the LPC effect was characterised by the deeply-recognised words being significantly more positive than shallowly-encoded (recognised and unrecognised) and new words, another qualitative pattern was present for both earlier effects. No significant differences were found between the ERPs of deeply- and shallowly-encoded word types at the P200 and N400 epochs, the only difference found to exist at these epochs was between old and new words.

An alternative explanation of our LPC results, unable to be tested here, is that decisional factor(s) such as accuracy (Finnigan et al., 2002; cf. Curran, Tepe, & Piatt, 2006) influence LPC outcomes. It must be noted, however, that LPC old/new effects obtained in recognition tests are predominantly interpreted as being reflective of episodic memory (Rugg et al., 2007).

In summary, this study has identified a right hemisphere P200 effect which is evidently an ERP correlate of auditory perceptual priming as distinct from episodic memory, given that it was unaffected by recognition accuracy or depth of processing. This extends our prior finding from the visual object domain (Harris et al., 2009). Together these outcomes provide converging electrophysiological evidence that perceptual priming (in auditory and visual domains) occurs in a manner distinct from explicit memory.

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Captions for Figures:

Figure 1. Schematic of one trial from each of the study and test phases

Figure 2: Overall grand average ERPs.

Grand average ERP amplitudes elicited by the deep recognised (Deep Rec), shallow recognised (Shall Rec), shallow unrecognised (Shall Unrec), and new auditory word conditions at scalp electrode sites. Data are depicted at 26 scalp electrodes that are representative of the full 32-channel array.

Note. Shaded areas represent the P200 (150 to 250 ms), N400 (350 to 550 ms) and LPC (600 to 900 ms) time intervals across which the ERP amplitudes were analysed.

Figure 3: Grand average P200 ERP amplitudes.

These were elicited by the shallow recognised (Shall Rec), shallow unrecognised (Shall Unrec), and new auditory word conditions averaged across left (FT7, T7, TP7, FC3, C3, CP3), and right (FC4, C4, CP4, FT8, T8, TP8) medial and lateral regional scalp electrodes.

Note. The shaded area represents the P200 (150 to 250 ms) time intervals across which the mean peak amplitude ERPs were analysed.

Figure 4: N400 and LPC grand average ERP amplitudes

These were elicited by the deep recognised (Deep Rec), shallow recognised (Shall Rec), shallow unrecognised (Shall Unrec), and new auditory word conditions averaged across all left and right frontal and posterior regional scalp electrodes (F7, F3, FT7, FC3, F8, F4, FT8, FC4, TP7, CP3, P7, P3, P8, P4, TP8, CP4).

Note. Shaded areas represent the N400 (350 to 550 ms) and LPC (600 to 900 ms) time intervals across which the mean amplitude ERPs were analysed.

Figure 5: Old minus new ERP means

A. Mean (and *SEM*) old-minus-new ERPs for the peak amplitude between 150-250 ms (P200) for the deep recognised- (Deep Rec - New), shallow recognised- (Shall Rec - New), and shallow unrecognised- (Shall Unrec - New) minus-new word conditions at the left and right lateral and medial regions.

B. Mean (and *SEM*) old-minus-new ERPs for the mean amplitude between the 350-550 ms (N400) and 600-900 ms (LPC) intervals for the deep recognised- (Deep Rec-New), shallow recognised- (Shall Rec-New), and shallow unrecognised- (Shall Unrec-New) minus-new word conditions at the left and right anterior (LA, RA) and posterior (LP, RP) regions.

Note. * differs from zero with $p < .05$; ** differs from zero with $p < .01$; ^ differs from zero with $p < .0001$

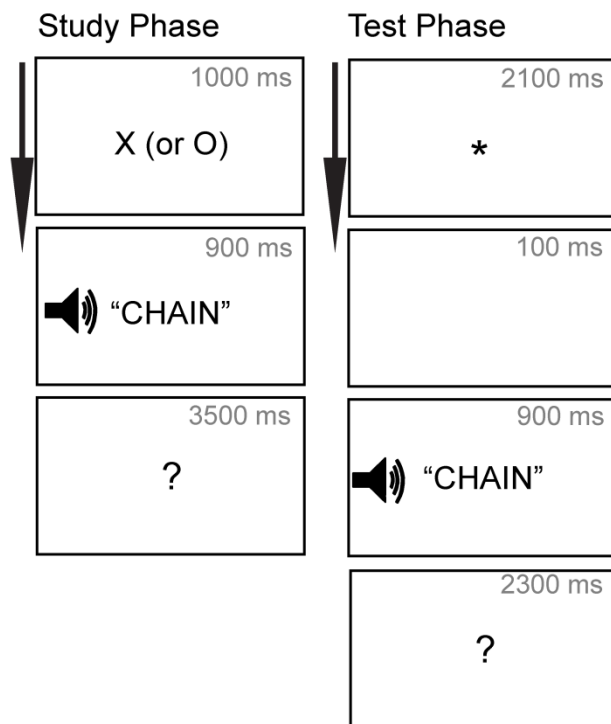


Figure 1

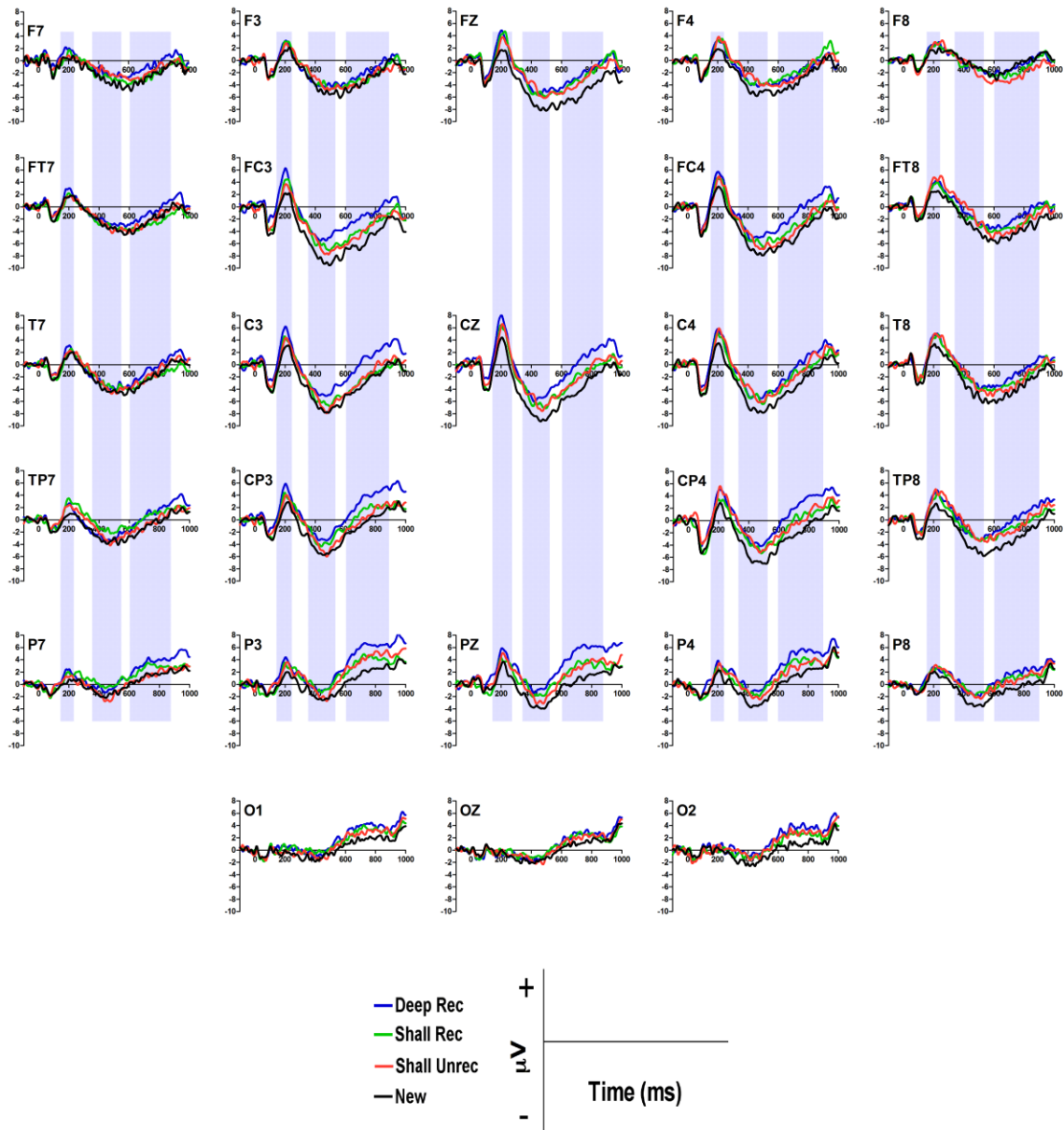


Figure 2

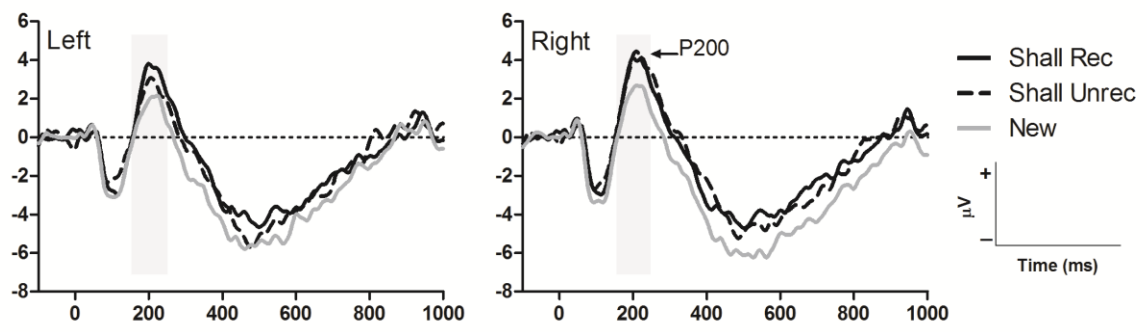


Figure 3

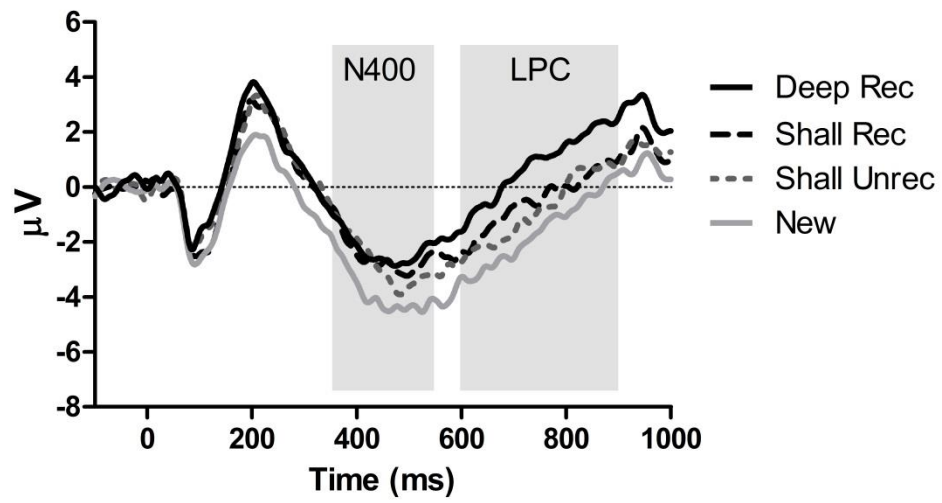


Figure 4

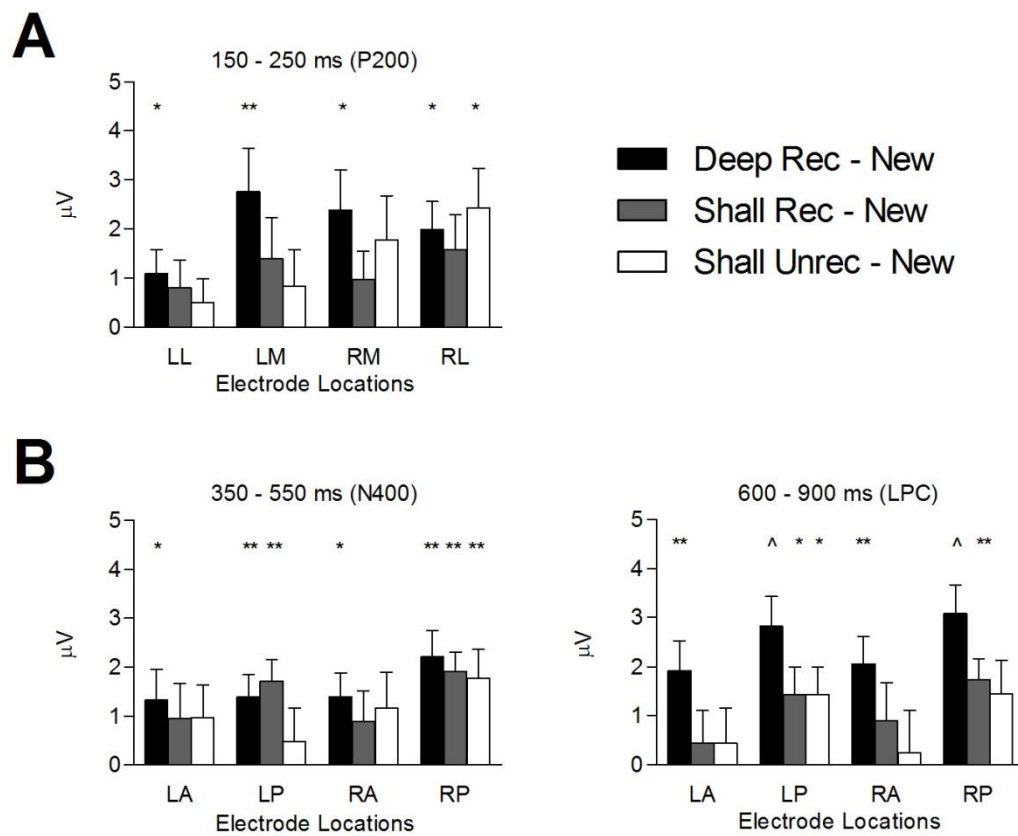


Figure 5