



Prestimulus brain activity predicts primacy in list learning

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Brain activity immediately before an event can predict whether the event will later be remembered. This indicates that memory formation is influenced by anticipatory mechanisms engaged ahead of stimulus presentation. Here, we asked whether anticipatory processes affect the learning of short word lists, and whether such activity varies as a function of serial position. Participants memorized lists of intermixed visual and auditory words with either an elaborative or rote rehearsal strategy. At the end of each list, a distraction task was performed followed by free recall. Recall performance was better for words in initial list positions and following elaborative rehearsal. Electrical brain activity before auditory words predicted later recall in the elaborative rehearsal condition. Crucially, anticipatory activity only affected recall when words occurred in initial list positions. This indicates that anticipatory processes, possibly related to general semantic preparation, contribute to primacy effects.

Keywords: Memory encoding; Anticipation; List learning; Primacy; Electrical brain activity.

When learning short lists of words, people are more likely to recall words from the beginning than middle of the lists. This well-known phenomenon is termed the “primacy” effect, and it has been studied since the pioneering work of Ebbinghaus (1913). Despite the long history, however, the mechanisms underlying primacy effects are unknown. It has been convincingly demonstrated that the recall advantage for initial list items is dissociable from that for final items (the “recency” effect). For example, recency but not primacy effects are abolished when people engage in a distracting task prior to recall (Glanzer & Cunitz, 1966), and amnesics show recency but not primacy effects (Capitani, Della Sala, Logie, & Spinnler, 1992). Recency effects are thought to arise because final list items are maintained in working memory and therefore are more readily available for a short period of time (e.g., Shiffrin & Atkinson, 1969). Primacy effects, by contrast, occur because initial list items are more

likely to lead to enduring representations in long-term memory. Primacy effects thus provide a good opportunity to understand the processes that underlie effective memory formation.

Neuroimaging studies have begun to illuminate the neural bases of memory formation (for a review, see Paller & Wagner, 2002). Most studies have focused on the encoding of items in long study sequences, but a few have investigated the encoding of items in different positions in short lists. These studies have focused on an explanation of primacy effects in terms of brain activity elicited by initial list items (Azizan & Polich, 2007; Rushby, Barry, & Johnstone, 2002; Sederberg et al., 2006; Strange, Otten, Josephs, Rugg, & Dolan, 2002; Wiswede, Russeler, & Munte, 2007). Recently, however, it has been shown that successful encoding also depends on processes *before* an event. Brain activity elicited by a cue preceding an event can predict whether the event will later be remembered (e.g., Adcock, Thangavel, Whitfield-Gabrieli, Knutson, & Gabrieli,

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This work was supported by Wellcome Trust grant 084618/Z/08/Z to L.J.O. Stimulus presentation was programmed with the Cogent2000 software of the physics group of the Wellcome Trust Centre for Neuroimaging.

2006; Otten, Quayle, Akram, Ditewig, & Rugg, 2006). Encoding-related activity before an event is dissociable from activity thereafter, and the two thus reflect different processes.

It is unknown whether prestimulus activity contributes to primacy effects in list learning. Here, we address this issue, using the high temporal resolution of electrical brain activity. The first few items in a list are arguably more highly expected than the other items, raising the possibility that anticipatory processes may be especially prominent for initial items. An influence of prestimulus activity on the encoding of initial list items is also in line with functional accounts of primacy effects. Such accounts propose that initial list items are likely to be remembered because they receive more elaborative encoding (Rundus, 1971), are better attended (Azizan & Polich, 2007; Page & Norris, 1998; Sederberg et al., 2006), or are temporally more distinct and less sensitive to interference (Melton, 1963; Neath, 1993). Processes related to such mechanisms could take effect before or after an event.

In the present study, healthy adults memorized short lists of intermixed visual and auditory words. A cue before each word signaled the input modality of the upcoming word. Input modality was varied across trials to encourage the use of preparatory processes on each trial rather than processes sustained across trials (Otten, Henson, & Rugg, 2002; Otten, Quayle, & Puvaneswaran, 2010). Each list was followed by a distraction task and written free recall. The question of interest was whether activity elicited by the cues would predict later recall of a word, especially when the word occurred toward the beginning of the study list.

To understand the functional significance of any prestimulus activity that may be observed, we asked participants to memorize words in two ways. Half of the lists were memorized by associating the words into meaningful images or sentences (elaborative encoding) and half by silently repeating the words (rote rehearsal). Elaborative rehearsal engages semantic and associative processes to a greater degree (Craik & Lockhart, 1972; Fabiani, Karis, & Donchin, 1990; Karis, Fabiani, & Donchin, 1984). If encoding-related activity is primarily, or exclusively, observed during elaborative rehearsal, a word's semantic and associative attributes likely contribute to prestimulus activity. If prestimulus activity is sensitive to memorization strategy, this would also corroborate the idea that the deployment of such activity is under a person's control (cf. Gruber & Otten, 2010).

METHOD

Participants

The experimental procedures were approved by the joint University College London and University College London Hospital ethics committee. Twenty-six healthy adults (mean age 22.5 years, 13 men) gave written, informed consent before participating. All reported to be right-handed, native English speakers and to be without neurological and psychiatric history.

Materials

Stimuli consisted of 384 concrete nouns with a length of 3–12 letters and a written frequency of 0–500 occurrences per million (Kuçera & Francis, 1967). Each word was available in written (white Helvetica font, 500 ms duration, $\sim 0.7^\circ$ vertically and $1\text{--}4.5^\circ$ horizontally) and spoken (British adult male voice, 650 ms mean duration, range 310–1130 ms) form. Cues consisted of a red square (250 ms duration, 0.7° by 1°) or pure tone (250 ms duration, 500 Hz).

Stimuli were pseudorandomly split into four sets of 96 words each with the restriction that word lengths were equally distributed across sets. The sets were rotated across participants to create a new stimulus sequence of 384 words for each participant. All words appeared equally often in each relevant condition. The stimulus sequence was divided into 24 lists of 16 words (12 for each rehearsal condition). Each list contained eight randomly assigned visual and auditory words (input modalities were intermixed to encourage preparatory processes to be set up anew on each trial). An additional 32 words were selected to create a practice list for each memorization strategy.

Procedure

Participants were instructed to memorize series of words, half of which would be seen on the monitor and half heard through headphones. A cue presented 1.5 s before word onset indicated the upcoming input modality. A visual cue signaled a visual word and an auditory cue an auditory word. The time between successive word onsets varied randomly between 4 and 4.5 s. Participants memorized half of the lists with a rote rehearsal strategy (silently repeat the words) and half with an elaborative encoding strategy (connect the words in a meaningful way by creating associations,

stories, or images). At the end of each list, a distractor task was performed for 30 s. Participants counted backward in threes starting with a random number between 81 and 99 displayed on the screen. Then, participants were given 1 min to write down as many words as they could remember from the preceding list. Words could be recalled in any order. The 12 lists in each strategy were presented one after another. Half of the participants started with elaborative, and half with rote, rehearsal.

EEG acquisition and analysis

Electrical brain activity was recorded from 32 scalp sites and the two mastoids relative to a midfrontal site using silver/silver-chloride electrodes. Vertical eye movements were recorded bipolarly from electrodes above and below the right eye, and horizontal eye movements from electrodes at the outer canthi. Signals were band-pass filtered between 0.01 and 35 Hz (3 dB roll-off) and digitized at a rate of 500 Hz (12-bit resolution). Impedances were below 5 k Ω .

Off-line, the data were digitally filtered between 0.05 and 20 Hz (96 dB roll-off) and algebraically re-referenced to averaged mastoids (reinstating the online reference site). Epochs from 100 ms before cue onset until 1948 ms thereafter were extracted from the continuous record. Event-related potentials (ERPs) were generated for each participant and electrode site, separately for auditory and visual trials in each strategy condition. The 100 ms period before cue onset was used as a baseline. Blink artifacts were minimized with a linear regression procedure in which across-trial activity on the vertical eye movement channel was used to estimate the degree to which blinks propagate to each scalp site (Rugg, Mark, Gilchrist, & Roberts, 1997). Trials containing non-blink eye movements, drifts (± 50 μ V), amplifier saturation, or muscle artifacts were excluded from the averaging process. Activity elicited by words is not reported in light of space constraints.

The interest was in activity elicited by cues preceding words that were later recalled versus forgotten ("subsequent memory effects": Sanquist, Rohrbaugh, Syndulko, & Lindsley, 1980). Subsequent memory effects were quantified by measuring mean amplitudes in the 500 ms interval before word onset. This interval was based on previous work suggesting that anticipatory processes build up during the cue-word interval and can be captured by measuring activity shortly before word onset (Otten et al., 2006). An initial analysis on the final two 250 ms intervals before a word showed identical effects during these times, and we

therefore report activity collapsed across the 500 ms interval. Unless stated otherwise, the statistical significance of effects was evaluated with repeated-measures analyses of variance (ANOVAs) incorporating the Greenhouse–Geisser correction for violations of sphericity. The analyses were performed across 26 electrode sites to assess scalp distribution differences across anterior and posterior sites. The ANOVAs incorporated factors of scalp location (anterior/posterior) and electrode site (13 sites), in addition to the experimental factors of subsequent memory (recalled/forgotten), stimulus modality (visual/auditory), and memorization strategy (elaborative/rote).

Serial position effects in recall performance were assessed by partitioning lists into early (positions 1–5), middle (6–11), and late (12–16) sections. We used a scree test (Cattell, 1966) to identify the number of positions to use for primacy effects, because no standard procedure exists (Capitani et al., 1992). This test plots the events of interest in succession to see where a clear break exists in the rate of change. Recall performance showed a break after position 5, with performance leveling off from position 6 onward (Figure 1). We therefore aggregated recall across the first five positions to assess primacy effects. The same number of positions was used at the end of a list to assess recency effects.

RESULTS

Behavioral data

Figure 1 illustrates the percentage of recalled words as a function of serial position. Regardless of input modality and memorization strategy, recall was enhanced for words in initial list positions relative to words in the remainder of the list. A repeated-measures ANOVA on the data from the early, middle, and late sections showed main effects of strategy and serial position, $F(1, 25) = 331.60$, $MSE = 274.1$, and $F(1.6, 4.8) = 36.16$, $MSE = 243.6$, respectively, both $ps < .001$. Pairwise comparisons indicated that recall was better following elaborative than rote rehearsal, and for words in the early than middle and late sections of a list, $t(25) = 7.31$ and 7.33 , respectively, both $ps < .001$. The latter two did not differ significantly from each other, $t(25) = -0.34$, $p = .735$.

Electrical brain activity before word onset

Figure 2 depicts the group-averaged ERPs elicited by cues preceding visual and auditory words in the

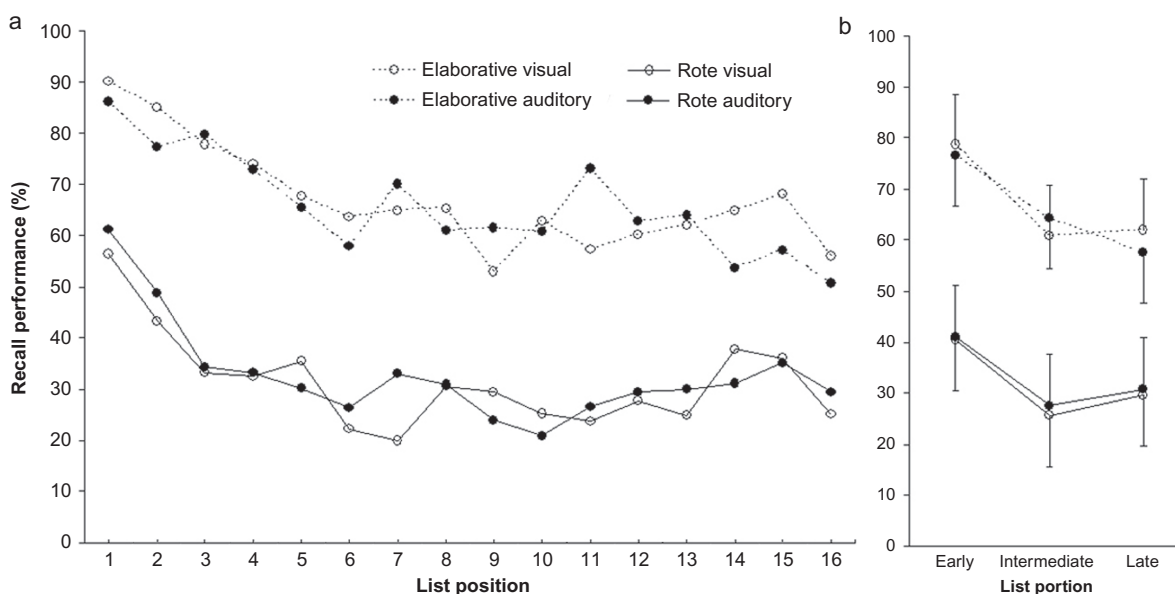


Figure 1. Recall performance. (a) Serial position curves displaying the percentages of recalled words from each of the 16 positions in the studied lists. Separate curves are shown for visual and auditory words, and for the elaborative and rote rehearsal conditions. (b) Representation of the data used for statistical analysis. Recall performance for words occurring in early (positions 1–5), intermediate (positions 6–11), and late (positions 12–16) portions of the lists. Error bars indicate *SEM*.

elaborative and rote rehearsal conditions. Activity just before word onset differed depending on subsequent memory performance to the word. As found previously (Otten et al., 2006, 2010; Padovani, Koenig, Brandeis, & Perrig, 2011), words that were later remembered were preceded by a negative deflection over frontal sites relative to words that were forgotten. However, this effect is only evident for auditory words in the elaborative encoding condition. The ANOVA showed a significant interaction between subsequent memory, strategy, modality, and scalp location, $F(1, 25) = 6.62$, $MSE = 7.7$, $p = .016$. Separate ANOVAs for each strategy did not reveal significant effects involving subsequent memory in the rote rehearsal condition ($ps > .263$). In contrast, in the elaborative rehearsal condition, a marginally significant interaction emerged between subsequent memory, modality, and scalp location, $F(1, 25) = 4.23$, $MSE = 11.4$, $p = .050$. Analyses on the activity over anterior sites revealed a significant subsequent memory effect for auditory words, $F(1, 25) = 5.81$, $MSE = 27.2$, $p = .024$, but not for visual words, $F(1, 25) = 0.13$, $MSE = 23.0$, $p = .717$. Subsequent memory effects were not significant over posterior scalp sites for auditory or visual words, $F(1, 25) = 0.73$ and 0.43 , $MSE = 12.4$ and 15.1 , $p = .402$ and $.520$, respectively.

Next, we assessed whether the effect preceding auditory words in the elaborative encoding condition depended on the word's list position. To that end,

activity preceding words in the initial five positions was contrasted with activity preceding the remaining words. The analyses were directed at the frontal negative-going effect observed earlier and therefore used activity in the 500 ms before word onset aggregated across sites where the effect was largest (all but the four most lateral anterior sites). One-tailed significance tests were used because of the expected negative polarity of the effect. Figure 3 shows the group-averaged ERPs elicited by cues preceding auditory words in initial versus later list positions. Pairwise comparisons between recalled and forgotten trials confirmed a frontal negative-going effect before initial list items, $t(25) = -2.16$, $p = .020$, but not before words in later positions, $t(25) = -0.74$, $p = .234$. A direct comparison of the effects across list positions only approached significance, however, $t(25) = -1.48$, $p = .152$.

A potential concern with the above analyses is that the primacy portion of a list contains relatively few forgotten items. The mean numbers of remembered and forgotten primacy items were 21 and 6, respectively, as opposed to 38 and 23 for the rest of the list. To address this concern, we used a bootstrap procedure to equate trial numbers. This procedure uses resampling to draw population-level conclusions and has been used successfully to supplement inferential statistics in similar situations (Gruber & Otten, 2010; Mathewson, Gratton, Fabiani, Beck, & Ro, 2009).

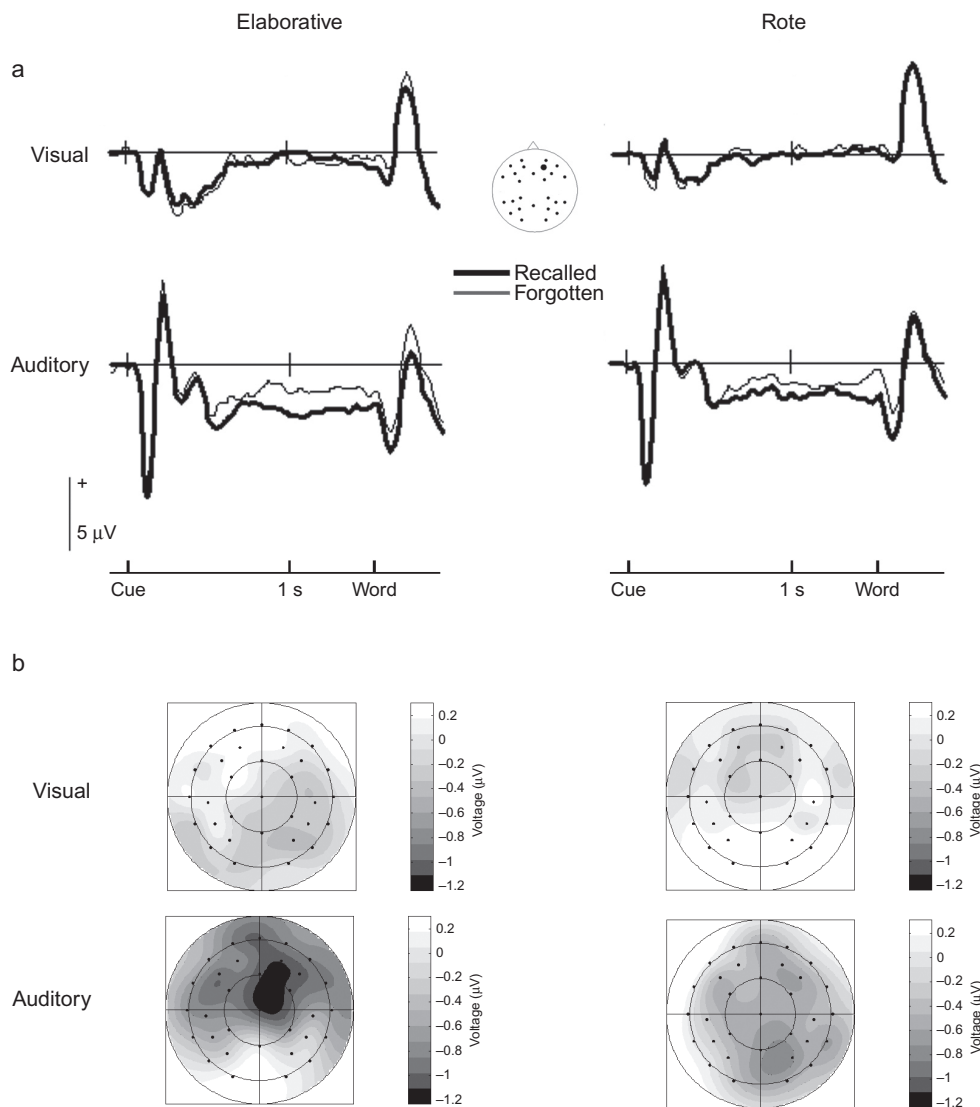


Figure 2. Prestimulus brain activity predicting later recall. (a) Group-averaged ERP waveforms elicited by cues preceding visual and auditory words in the elaborative and rote rehearsal conditions that were later recalled versus forgotten. Words could occur in any list position. Waveforms are shown for one of the frontal electrode sites where the prestimulus subsequent memory effect for auditory words was largest (site 21 from montage 10, www.easycap.de/easycap/e/electrodes/13_M10.htm). For graphical purposes, the waveforms in this and the following figure are low-pass filtered at 19.3 Hz. (b) Scalp distributions of the observed ERP differences. Voltage spline maps showing the ERP difference between recalled and forgotten words in each experimental condition in the 500 ms interval before word onset. The maps are scaled to the minimum and maximum difference across conditions to illustrate the distribution as well as size of the modulations.

For each subject, the minimum trial number for the subsequent memory comparisons was determined, and this number was drawn randomly with replacement from remembered and forgotten trials in each list portion. The group average was then computed, and the mean amplitude in the 500 ms interval before word onset measured across all but the four most lateral anterior sites. This process was repeated 10,000 times. Figure 4 shows the resulting distributions of sample means. A separation between remembered and forgotten words is only apparent for the primacy portion of

the list. Of the 10,000 samples, 9617 showed a negative-going subsequent memory effect for initial list items. The 90% confidence interval (corresponding with a one-tailed α level of 5%) indicated an effect that is less than $-0.15 \mu\text{V}$. For words in later list positions, 6515 samples showed a negative subsequent memory effect. The associated 90% confidence interval included zero and thus did not indicate a significant effect. These analyses corroborate the idea that prestimulus activity only influences the encoding of words in initial list positions.

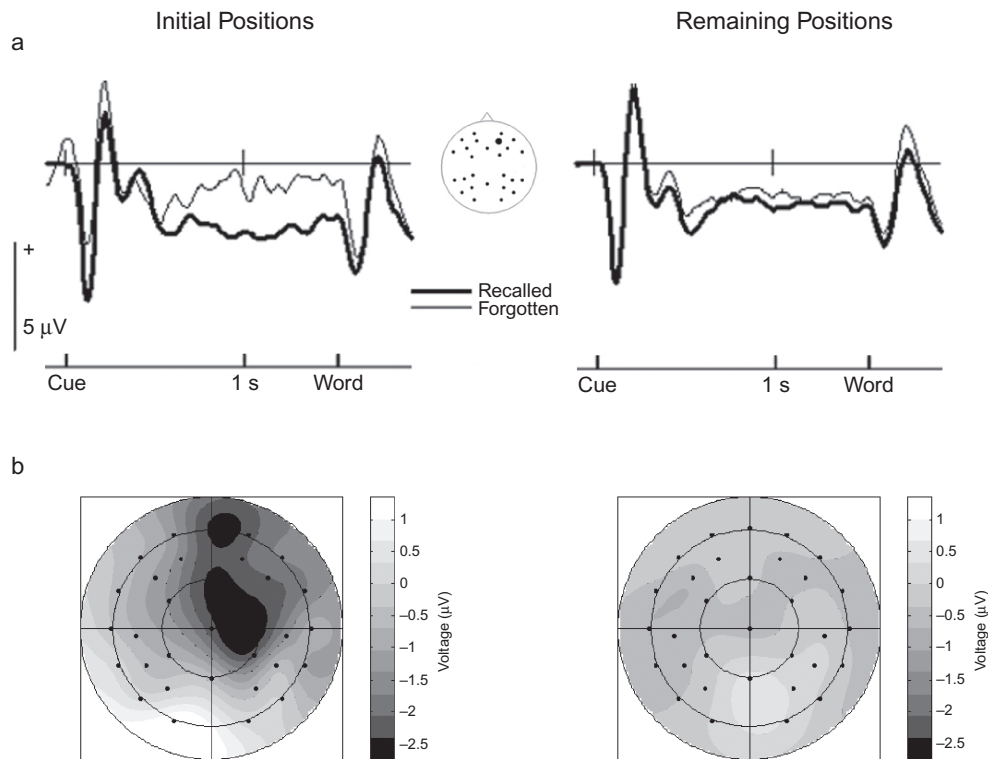


Figure 3. Prestimulus subsequent memory effect for auditory words in the elaborative rehearsal condition as a function of list position. (a) Group-averaged ERP waveforms for words in early (1–5) and later (6–16) list positions at the same frontal scalp site as shown in Figure 2. (b) Voltage spline maps for the effect preceding auditory words. The maps show the ERP difference between recalled and forgotten words in the 500 ms interval before word onset, scaled to the minimum and maximum difference across conditions.

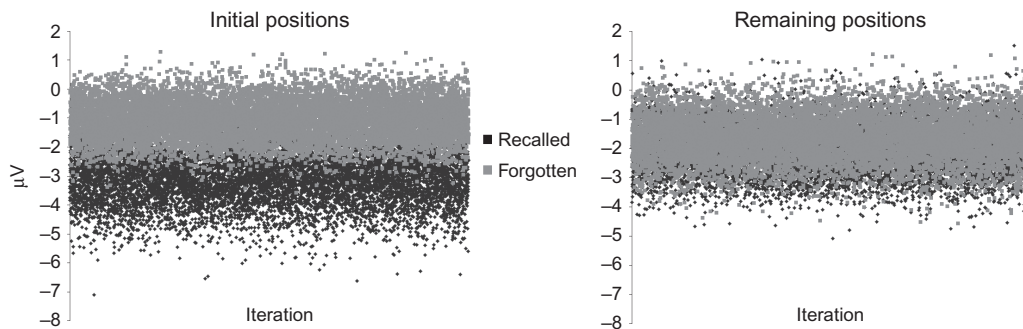


Figure 4. Results of a bootstrap analysis on encoding-related brain activity preceding auditory words in the elaborative rehearsal condition. Each gray dot represents a sample value for forgotten words, and each black dot a sample value for recalled words. Distributions are shown separately for words in early and later positions of the list. The distributions of recalled and forgotten words only differ for words in initial list positions.

DISCUSSION

As expected, words were more likely to be recalled when they occurred in initial list positions (Ebbinghaus, 1913) and when they were encoded with an elaborative memorization strategy (Craik & Lockhart, 1972). Crucially, electrical brain activity just before word onset predicted later recall of a word. Activity over frontal scalp sites was more

negative-going preceding words that were later remembered (cf. Otten et al., 2006, 2010). Prestimulus activity predicted encoding success during elaborative but not rote rehearsal, and this effect was specific to auditory items in initial list positions.

These findings indicate that neural, and therefore functional, processes before an event play a role in list learning. The specificity of prestimulus effects to the first few items in a list suggests that preparatory

processes are especially important for the encoding of initial list items. Prestimulus activity may thus in part explain the recall advantage seen for these items. Engaging encoding-related processes ahead of stimulus presentation may lead to stronger representations in memory, increasing the likelihood of later recall. Functional accounts of primacy effects propose that the recall advantage may be due to more elaborate encoding, increased attention, or reduced interference (Azizan & Polich, 2007; Melton, 1963; Neath, 1993; Page & Norris, 1998; Rundus, 1971; Sederberg et al., 2006). The present data do not adjudicate between these accounts, but do indicate that at least some of the processes that enhance recall already take effect before the presentation of initial list items.

The particular kind of prestimulus activity observed here strongly resembles the negative-going modulation over frontal scalp sites seen with incidental encoding tasks and recognition memory tests (Otten et al., 2006, 2010; Padovani et al., 2011). Because this effect has so far only been observed in semantic encoding tasks, it may reflect the degree to which semantic processes are mobilized in preparation for an upcoming semantic decision. The current findings support this interpretation. Prestimulus activity only affected encoding when participants memorized words by elaborative rehearsal, a strategy that relies particularly on a word's semantic and associative attributes (Craik & Lockhart, 1972). On this account, initial list items were especially likely to benefit from the preparation of semantic processes. It should be noted that any such preparation must be of a general rather than specific nature, given that the identity of the upcoming word was not yet known.

Interestingly, prestimulus effects were more prominent for auditory items. Although differences between visual and auditory modalities have been observed in an earlier study (Otten et al., 2006), this was in the context of a mismatch between cue and word modalities (Otten et al., 2010). In the present study, these modalities were held constant, and prestimulus activity could therefore have occurred for both. This is not what was observed. During debriefing, participants reported using mental imagery to associate items during elaborative encoding. A mental image of the item denoted by a word was created first and then incorporated into a scene. One could speculate that mental images are easier to create from visual words. On this account, auditory words required more extensive processing upon presentation, making them more prone to benefit from preparatory processes engaged beforehand. Alternatively, auditory words may in general require more extensive semantic or associative processing. Although we cannot offer a full functional interpretation on the basis of what is currently known, the

specificity of subsequent memory effects to auditory words at least indicates that prestimulus influences arise because of trial-by-trial fluctuations in brain activity rather than activity sustained across trials (Otten et al., 2002). Visual and auditory items were randomly intermixed, and differences between the two can therefore unlikely be attributed to processes that are engaged across trials.

Taken together, our findings suggest that prestimulus brain activity contributes to list learning and, in particular, primacy effects. Preparatory processes clearly do not *always* explain primacy effects. A recall advantage was observed for initial list items in all experimental conditions, but prestimulus activity only affected the encoding of auditory words during elaborative rehearsal. Other processes, such as those after word onset and those between encoding and retrieval, must therefore also influence likelihood of recall. Finally, the sensitivity of prestimulus effects to type of memorization strategy adds to existing evidence that people have some command over the deployment of such activity (cf. Gruber & Otten, 2010). An important question for future research is what determines that such activity be engaged.

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