Published in final edited form as:

Neuropsychologia. 2016 January 8; 80: 201–211. doi:10.1016/j.neuropsychologia.2015.11.025.

Trans-Saccadic Repetition Priming: ERPs Reveal On-line Integration of Information across Words

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Abstract

We used a trans-saccadic priming paradigm combined with ERP recordings to track the time-course of integration of information across a prime word briefly presented at fixation and a subsequent target word presented 4 degrees to the right of fixation. Trans-saccadic repetition priming effects (Experiments 1 & 2) were compared with priming effects obtained with centrally located targets (Experiment 3). In Experiment 2, target stimuli were preceded by a 100 ms forward mask at the target location, hence allowing an attention shift to the target location prior to target onset. Compared with centrally located targets, repetition priming effects were found to onset later in Experiment 2 and even later in Experiment 1, and the growth of priming effects was slower in both Experiments 1 and 2 compared with Experiment 3. The results demonstrate integration of information across spatially distinct primes and targets, with the time-course of trans-saccadic priming being determined by the speed with which attention can be allocated to peripheral targets plus the quality of information available in peripheral vision prior to fixation of target stimuli.

Keywords

reading; repetition priming; ERPs; eye-movements; trans-saccadic priming

1. Introduction

In recent research combining ERP recordings with fast priming techniques (e.g., Forster & Davis, 1984), we have begun to link specific ERP components that are modulated by a particular priming manipulation to the underlying processing thought to be driving the ERP effect. Most of this work has used the masked priming paradigm which involves rapidly presenting a sequence of stimuli that typically include a pattern mask, a brief prime

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stimulus, and a clearly visible target word. Changes in the amplitude of two ERP components, the N250 and N400, have been found to be sensitive to masked priming. Both of these components are more negative-going for unrelated than repeated words (e.g., Holcomb & Grainger, 2006; 2007; Kiyonaga et al., 2007; see Grainger & Holcomb, 2009, and Laszlo & Federmeier, 2014, for reviews). We have proposed that the N250 component reflects the bulk of activity in sublexical representations as they receive information from lower levels and send forward information to whole-word (lexical) form representations. The N400, on the other hand, is thought to reflect activity related to the mapping of whole-word form representations onto semantic representations, at least in experiments using single words rather than sentences. However, in all these studies the prime and target stimuli occupied the same spatial location, and given the brief prime exposures typically used, it is thought that priming effects are driven by the temporal integration of information across primes and targets treated as a unique object (Grainger & Jacobs, 1999; Grainger, Lopez, Eddy, Dufau, & Holcomb, 2012). In the present work we ask what might happen when primes and targets are spatially distinct objects and an eye movement is required in order to identify target words? Under normal reading conditions, the word on fixation and the to-be-fixated word need to be distinguished for the purposes of successful sentence-level integration of distinct word meanings. One might therefore expect to find reduced priming, or no priming at all, in conditions where primes and targets are presented at different spatial locations. That is, when prime and target stimuli should be taken as distinct linguistic entities, then one might expect little or no integration of information that is extracted from prime and target prior to the work of sentence-level integration mechanisms. It is important to note here the distinction between integration of information across a saccadic eye movement with stimuli at the same spatiotopic location,¹ as demonstrated in parafoveal preview effects (see Rayner, 1998, and Schotter, Angele, & Rayner, 2012, for reviews), and integration of information across stimuli at different spatiotopic locations. That is, the priming conditions to be tested in the present study are to be distinguished from the conditions used to demonstrate parafoveal preview effects, where the prime stimulus is shown in the parafovea at the same location as the upcoming target, which is then fixated.

There is, however, growing evidence that some amount of integration occurs across words at different spatiotopic locations. For example, it has been shown that orthographic information extracted from the to-be-fixated parafoveal word influences on-going processing of the currently fixated word (Angele, Tran, & Rayner, 2013; Dare & Shillcock, 2013; Dimigen, Kliegl, & Sommer, 2012). In order to account for these and related findings, it has been proposed that there is some form of spatial integration of orthographic information that is extracted in parallel from several words (Angele et al., 2013; Grainger, Mathôt, & Vitu, 2014). Grainger et al. (2014) described such spatial integration processes using the framework for orthographic processing developed by Grainger and van Heuven (2003). Retinotopically coded letter-level information is processed in parallel across several words, within the limits imposed by visual acuity and crowding, and fed-forward into a single

¹Spatiotopic coordinates define object location in terms of where the object is located in a scene, independently of where the eyes are fixating the scene.

channel for processing word-centered sublexical orthographic information and subsequent word recognition processes.

More directly relevant for the present study is the work of Marzouki, Meeter, and Grainger (2013), who found repetition priming with centrally located masked primes and targets located in the periphery ($\pm 4^\circ$ along the horizontal meridian for the word stimuli of their Experiment 2). Most important is that these priming effects did not depend on target location, with repetition effects even being numerically larger with peripheral targets than centrally located targets, and primes always on fixation. This is therefore clear evidence that information can be integrated across spatially distinct word stimuli. However, we do not know whether it is shared form (i.e., orthography and phonology) and/or shared meaning that is driving the behavioral facilitation found by Marzouki et al. (2013). That is, given that the priming manipulation involved a comparison of primes that were the same word as the target e.g., ape-ape) and completely unrelated primes (e.g., bin-ape), the priming effects could reflect overlap at the level of sublexical form, lexical form, or semantic representations, or any combination of these. In the present study, the same repetition priming manipulation was tested, and we use ERPs to distinguish between effects of form and meaning as revealed in our prior research using standard masked priming (e.g., Holcomb & Grainger, 2006; see Grainger & Holcomb, 2009, for a review). That is, we will infer what processing is influenced by the priming manipulation as a function of the timing of the effect relative to our proposed mapping of the timing of ERP priming effects and the timing of component processes in visual word recognition (Grainger & Holcomb, 2009).

Rather than simply record ERPs using the same paradigm as Marzouki et al. (2013), here we use a variant of the trans-saccadic priming paradigm in which primes are always presented on fixation and participants then make a rightward saccade to process targets that are initially located to the right of fixation. In this way, the spatiotopic locations of prime and target stimuli do not vary, just as in standard priming, and the rightward location of targets mimics left-to-right eye movements in sentence reading. Indeed, our trans-saccadic priming paradigm is similar to the paradigm used in two prior studies combining eye-movements and ERP recordings in order to examine parafoveal-on-foveal influences in fluent reading (Baccino & Manunta, 2005; Simola, Holmqvist, & Lindgren, 2009). The main difference with respect to the present work is that prime and target stimuli were presented simultaneously in these earlier studies, precisely in order to study parafoveal-on-foveal effects (see also Reichle, Tokowicz, Liu, & Perfetti, 2011, for an experiment with simultaneous presentation of central and peripheral stimuli with an aim to use ERPs to evaluate the nature of the processing of the fixated word that triggers a saccade to the peripheral word). Here we focus on how information extracted from a foveal prime stimulus can influence the processing of a peripherally located target word as the eyes prepare to move toward that target and when the eyes land on the target. A more relevant study in this respect, is the one by Dimigen et al. (2012), where participants had to read mini word lists from left-to-right, and at the end of each list to indicate if an animal word was present or not. Final and penultimate words could be the same word (e.g., Paint Excuse Chair Blade Blade), semantically related words (Paint Excuse Chair Knife Blade), or unrelated words (Paint Excuse Chair Sugar Blade). Of particular interest for the present study is that Dimigen et al. found very early repetition priming effects in ERPs time-locked to fixation of the final word,

with effects emerging around 100 ms and remaining until about 500 ms after the onset of the final word. Semantic priming effects, on the other hand, emerged about 100 ms later. These results again point to integration of information (both orthographic and semantic) across spatially distinct words, and suggest that trans-saccadic priming effects begin before the eyes fixate the target word.

In line with this possibility, several studies have shown that preparing to move the eyes to a peripheral target location leads to improvement in visual discrimination tasks for targets at the to-be-fixated location (Deubel & Schneider, 1996; Kowler, Anderson, Doshier, & Blaser, 1995), and that this advantage can occur within 150–200 ms following saccade cue onset (Castet, Jeanjean, Montagnini, Laugier, & Masson, 2006; Montagnini & Castet, 2007). More recent research suggests that such saccade-linked preparation can act even more rapidly, with processing benefits at the target location being observed as early as 60 ms following the cue to move the eyes (Rolfs & Carrasco, 2012).

The trans-saccadic priming paradigm to be used in the present study involves the prior brief presentation of a prime word on fixation, followed by a target stimulus located 4° to the right of fixation and shown for 300 ms (see Figure 1). Participants were asked to press a button whenever they detected an animal name (16% of trials), and all other stimuli were not to be responded to. By randomly placing animal name probe stimuli in both the prime and target positions it was necessary for participants to attend to the semantic properties of all words in both positions. For this reason, prime stimuli were presented for longer than in a typical masked priming experiment, but within the range of prime durations known to generate early priming effects (Holcomb & Grainger, 2007). We will use this paradigm to investigate the on-line integration of information from spatially distinct words, and to estimate the timing and the nature of the processing of peripheral targets prior to fixation of these targets.

2. Experiment 1

2.1 Methods

2.1.1 Participants—Fifteen right-handed, native English speaking Tufts University students (7 male, mean age = 20.0 years) received compensation for their participation. All were right handed, and reported normal or corrected-to-normal visual acuity with no history of neurological insult or language disability. All participants reported that they had learned no other language before the age of five.

2.1.2 Stimuli—The critical stimuli for this study were 120 five letter words ranging from 4.14 to 13.7 log HAL word frequency (mean = 8.45 – English Lexicon Project; Balota et al., 2007). Items were arranged in pairs, with the first member of each pair being referred to as the prime and the second member as the target. There were two critical conditions: repeated and unrelated. Repeated refers to trials where the target word was a full repetition of the prior prime word (e.g., table - TABLE), and unrelated refers to trials where the prime and target were different unrelated words (e.g., space - TABLE). All 120 critical words were paired with both an unrelated prime word and a repetition of the same word, together forming the 240 critical trials presented to each participant. These 240 trials were subdivided

into 3 blocks of 80 trials each. Across blocks each target word appeared once in each of the repeated (prime and target), unrelated prime and unrelated target conditions, but no item was presented on more than one trial within a block as either a target or a prime. For example, if the word TABLE appeared in the repetition condition of block 1, it would not appear again until the second block where it would be presented as an unrelated prime and then once more as an unrelated target in block 3. For another item like SPACE it would appear first as an unrelated target in block 1, as an unrelated prime in block 2, and as a related target in block 3. In this way, across the experiment, each participant saw each target word in the repeated and the unrelated conditions, and unrelated primes were re-pairings of repetition primes, which assures that average ERPs in the repetition and unrelated conditions are formed from exactly the same items (for both primes and targets) within participants. The order of the three blocks was counterbalanced across participants.

Each block also contained 16 trials where an animal probe name appeared either in the target (8) or prime (8) position (non-animal filler words were paired with probes). Animal probes were used as go items in a go/no-go semantic categorization task in which participants were instructed to rapidly press a single button (response hand counterbalanced) with their thumb whenever they detected an animal name in either the prime or target position. Participants were told to read all other words passively without responding (i.e., the critical prime and target stimuli did not require an overt response). By placing probes in both the prime and target position we equally emphasized processing of all words at the two locations. In total there were 288 trials of which 240 contained critical words (120 repetition trials and 120 were unrelated trials) and 48 contained probe words.

2.1.3 Procedure—All stimuli were presented on a 19 inch monitor set to a refresh rate of 100Hz and located 145 cm directly in front of the participant. Stimuli were displayed as white letters on a black background in a fixed width font (New Courier) with each character occupying a 20×40 pixel matrix. Using this procedure all stimuli subtended < 2 degrees of visual angle with central prime words extending slightly less than one degree to the right (and left) of central fixation whereas the first letter of target words begins just beyond three degrees to the right of the center of the screen and extended just short of five degrees to the right of the center (i.e., prime center to target center distance was 4 degrees). Each trial began with a fixation mark (“+”) presented centered at the midpoint of the monitor for 750 ms and was followed by a 250 ms blank screen. The fixation was followed at the same location by a centered prime word in lower case letters (e.g., table) displayed for 100 ms. The prime was then immediately replaced by a 300 ms duration target word centered on a point four degrees to the right of the midpoint of the screen. Targets were followed by a 1500 ms asterisk centered at the location of the third letter of the target. This stimulus was used to indicate that the participant should hold their eyes steady at this location. A final blink stimulus centered at the midpoint of the screen indicated that the trial was complete and that the participant should return their gaze to this central location. Participants were instructed to blink only during the time when the blink stimulus was present. A participant button press was required to begin the next trial, and 500 ms later the next fixation stimulus appeared. The same button was used to give a go response whenever participants detected the presence of an animal name.

Prior to the experimental run, two familiarization tasks were used. In the first, we practiced participants in making accurate rightward 4 degree saccades by having them repeatedly move their eyes from the center of the screen to a location 4 degrees to the right. We used a cross (“+”) presented at the center of the screen for two seconds followed by an asterisk (“*”) presented for two more seconds 4 degrees to the right. This sequence was repeated 25 times. A second practice block of 25 trials with word stimuli of the same type used in the actual experiment immediately preceded the main experiment. This gave additional practice with making lateral saccades.

2.1.4 EEG Recording Procedure—Participants were seated in a comfortable chair in a sound attenuated darkened room. An electro-cap fitted with tin electrodes was used to record continuous EEG from scalp 29 sites (see Figure 2). Five additional electrodes were used: one over the left mastoid which served as the reference site for all scalp electrodes, one over the right mastoid (recorded actively to monitor for differential mastoid activity), one below the left eye (referenced to the left mastoid -- to monitor for vertical eye movement/blinks), and a pair of electrodes with one to the right of the right eye and a second to the left of the left eye were used in a bipolar montage to monitor horizontal eye movements. All electrode impedances were maintained below 5 k Ω . The 32 channels of EEG and eye activity (EOG) were amplified by an SA Bioamplifier with a bandpass of 0.01 and 40 Hz and were continuously sampled at a rate of 250 Hz.

2.1.5 Data Analysis—Separate ERPs from the two critical prime-target conditions (repeated vs. unrelated) were calculated time-locked to the onset of target words. We averaged 1024 ms of electrical activity starting 100 ms pre-target onset at each of the 32 recording sites. The resulting data were baselined to the mean voltage in a period from –100 to 0 ms pre-target onset. Averaged data were then filtered with a low-pass digital filter at 15 Hz. Only trials without muscle artifact or vertical eye movement/blink activity (less than 10% of trials were rejected) were included in the averages. We inspected the average activity at the right mastoid across the two conditions of interest to determine if differential mastoid activity necessitated re-referencing to the average of the two mastoids. No such activity was noted so the data from the left mastoid reference were used for subsequent analysis.

To track the time-course of priming effects we quantified the ERPs in both priming conditions using mean amplitude in four consecutive time windows corresponding to the epochs most frequently used in our prior masked priming studies: 100–200 ms (N/P150), 200–300 ms (N250), 300–500 ms (N400) and 500–700 ms (late positivity). Repeated measures analyses of variance (ANOVAs) were used to analyze the ERP data. These analyses included within-participant factors of Priming (repeated vs. unrepeated), and two electrode position factors, Laterality (left vs. midline vs. right) and Ant-post (anterior-posterior, FP vs. F vs. C vs. P vs. O -- see Figure 2 for a diagram of the sites used). For all statistical analyses Geisser-Greenhouse correction was used for all repeated measures factors with greater than 1 degree of freedom in the numerator (Geisser & Greenhouse, 1959).

Finally, we also used the horizontal eye channel to determine the mean onset and offset latencies of saccades. These values were determined by measuring the latency (relative to target onset) of the beginning of the saccade and the end of the saccade in the single trial raw data. This calculation was made by searching the horizontal eye channel on each trial between 100 and 350 ms post target onset for the large voltage transient associated with the target saccade. The latency of the point in the transient that was 10% of the eventual peak amplitude of the saccade was taken as the onset latency of the saccade. Saccade offset was calculated as the latency that was 100% of peak amplitude of the saccade.

2.2 Results

2.2.1 Behavioral results—Participants detected an average of 82% of the animal probe words in the prime position and 81% in the target position. Mean saccade onset was on average 161 ms (SD = 30) for repeated target words and 162 ms (SD = 32 ms) for unrelated target words. Mean saccade offset latency was 212 ms (SD = 20) for repeated targets and 211 ms (SD = 20) for unrelated targets. Neither onset nor offset latency differed significantly as a function of priming (both p s > .22 -- see HE site in Figure 3).

2.2.2 Event-related potentials—Grand average ERPs to repeated and unrelated targets from the 15 scalp sites used for analyses are plotted in Figure 3 along with the corresponding difference waves (priming effects). Figure 4 shows priming effects plotted as voltage maps for the four consecutive analysis windows. As can be seen in Figure 3 there are clear effects of priming with unrelated targets producing more negative-going ERPs than repeated targets across a wide temporal span. It is also clear from Figure 3 that the rightward eye movement had a substantial impact (> 30 microvolts) on the bi-polar montage of electrodes used to monitor for these movements, as well as smaller but still notable influence on the scalp electrode sites, especially those closer to the eyes (i.e., the more frontal sites). Importantly, because all these movements were in one direction, the distribution of eye movement activity across the lateral scalp is opposite in polarity (e.g., compare FP1 and FP2 in Figure 3). This demonstrates why ERP researchers typically monitor and reject trials in their experiments where such eye movements occur. This is especially important in cases where treatment effects might differentially influence the timing or frequency of such movements and thus leave one condition with a higher proportion of contamination. Here the possibility of differential contamination has been reduced because the size and frequency of movements was carefully controlled such that both experimental conditions had equivalent influences (in both size and frequency). So, while the left and right hemisphere raw ERPs plotted in Figure 3 clearly show the impact of eye movements, there is no indication that these movements differentially impacted the two priming conditions. This can be seen by examining the difference waves in Figure 3.

2.2.3 Epoch Analysis

100–200 ms: In the average ERPs time-locked to the onset of target words there was a robust effect of electrode laterality (main effect of laterality: $F(2,28) = 19.11$, $p = .0001$) with an almost 2 microvolt average difference between right and left hemisphere electrode sites. There were however, no significant effects of priming or interactions involving the priming variable in this epoch (all p s > .1).

200–300 ms: A similar pattern of effects continued into the next measurement epoch. There was again a large main effect of laterality ($F(2,28) = 94.59$, $p < .0001$, but no significant priming effects ($p > .28$).

300–500 ms: In this epoch, which spans the latency range of the N400, the first signs of priming are apparent in the target-locked averages (main effect of Priming: $F(1,14) = 24.77$, $p = .0002$), and this effect tended to be larger at central-midline sites (see Figures 3 & 4; Priming x Ant-post interaction: $F(4,56) = 10.26$, $p = .0013$). There was again a large laterality effect which was due to the residual influence of the rightward eye movement ($F(2,28) = 65.15$, $p < .0001$).

500–700 ms: In the final measurement window there was a main effect of priming ($F(1,14) = 15.86$, $p = .0014$) as well as interactions between priming and the scalp distribution factors (Priming x Ant-post: $F(4,56) = 9.98$, $p = .0003$; Priming x Laterality: $F(2,28) = 10.09$, $p = .0011$). As can be seen in Figures 3 and 4, these interactions were due to somewhat larger priming effects in this epoch at central-posterior sites over the midline and right hemisphere. The main effect of Laterality continued into this epoch ($F(2,28) = 38.86$, $p < .0001$).

2.3 Discussion

Experiment 1 revealed robust trans-saccadic repetition priming effects that were first evident in the time-window of the N400 (300–500 ms). There was no evidence for priming in any earlier components, which is in line with our prior research showing a gradual drop in the size of N250 repetition priming effects as the prime-target stimulus-onset-asynchrony (SOA) is increased (Holcomb & Grainger, 2007). Most important, however, is that the very presence of priming effects in Experiment 1 provides further evidence for spatial integration of orthographic information when primes and targets are spatially distinct objects. Furthermore, the timing of the priming effects seen in Experiment 1, points to whole-word orthographic representations, and the mapping of these representations onto semantics, as their likely locus.

Compared with prior research investigating repetition priming with primes and targets presented on fixation (see Grainger & Holcomb, 2009, for a review), the trans-saccadic priming effects seen in Experiment 1 emerged distinctly later. In the studies summarized in Grainger and Holcomb (2009), N400 peak latency was always around 400 ms post-target onset, independently of prime duration or prime-target SOA. The delayed N400 priming effect of Experiment 1 (see Figure 3) therefore points to a limited amount of target preprocessing (i.e., prior to fixation of the target). However, if we examine the evolution of priming effects from the time the eyes fixate the target, on average 211 ms post-target onset, then it is clear that some pre-processing of the target has occurred prior to fixation of the target, since priming effects emerge much earlier than would be expected if no preprocessing had occurred. The likely scenario here is that attention has shifted to the target location before an eye-movement is triggered, thus enabling processing of target stimuli in peripheral vision. Priming effects would begin to develop prior to fixation of the target, but the diminished processing associated with peripheral vision would greatly reduce the growth of priming effects prior to target fixation. This combination of events would lead to a delay

in the onset of priming effects, compared with priming obtained with centrally located targets, and a slower build-up in the size of priming effects. We return to more closely examine these timing issues after measuring priming effects with centrally located targets in Experiment 3. Before that, Experiment 2 provides a further examination of trans-saccadic priming in conditions where attention is directed to the target location prior to target onset.

3. Experiment 2

In Experiment 2 we replace the first 100 ms of target presentation with the presentation of a five-letter random consonant string at the same location where the target would eventually be displayed. After 100 ms the target itself replaced the consonant string and was displayed for 200 ms. This manipulation serves two purposes. First, by introducing a mask prior to target presentation at the same location as the target, we mimic the kind of forward-masking caused by prime stimuli that might occur when primes and targets occupy the same location. Any such forward-masking should delay the onset of target processing, hence delaying target-locked priming effects. Second, since it is the masking stimulus that triggers an eye movement in Experiment 2, attention can be shifted to the up-coming target location as soon as the peripheral mask stimulus is presented, hence improving target pre-processing and generating earlier priming effects time-locked to target onset.

3.1 Methods

3.1.1 Participants—Fifteen right-handed, native English speaking Tufts University students (6 male, mean age 20.1 years) were recruited and received compensation for their participation. All were right handed, and had normal or corrected-to-normal visual acuity with no history of neurological insult or language disability. All participants reported that they learned no other language before the age of five. None of these participants had taken part in Experiment 1.

3.1.2 Procedure—The stimuli and procedure were identical to Experiment 1 except for the insertion of an additional stimulus between the presentation of the prime and target words (see Figure 1 bottom). Immediately following the presentation of the central prime word (100 ms) a five letter upper case consonant string (e.g., CFQBM) centered on a point four degrees to the right of the midpoint of the screen was displayed. After 100 ms the consonant string was replaced, at the same screen coordinates, by a 200 ms upper case five letter target word (e.g., TABLE -- note that together the consonant string and target equal the duration of targets in Experiment 1). As in Experiment 1 targets were followed by a 1500 ms asterisk centered at the same lateral screen coordinates (indicating that the participant should hold their eyes steady at this location). A final blink stimulus back at the center of the screen indicated that the trial was complete and that the participant should return their gaze to central location. Participants were instructed to blink only during this time period. Participants pressed a button when they were ready to begin the next trial, 500 ms later the next fixation stimulus appeared. As in Experiment 1, participants were encouraged to quickly read each prime word and then make a rightward saccade to the stimulus that followed the prime.

3.2 Results

3.2.1 Behavioral results—Participants detected an average of 79% of the animal probe words in the target position and 76% in the prime position within a window from 200 to 1500 ms. As in Experiment 1 we also measured saccade onset and offset latencies (see Experiment 1 methods). Mean saccade onset latency relative to target onset was 86 ms (SD = 21) for repeated and 88 ms (SD = 23) for unrelated targets. Mean saccade offset latency relative to target onset was 123 ms (SD = 25) for repeated and 122 ms (SD = 25) for unrelated targets. Neither onset nor offset latency differed significantly as a function of priming (both p s > .1 -- see HE site in Figure 5).

3.2.2 Event-related potentials—Grand average ERPs to target words time-locked to target stimulus onset as well as difference waves calculated by subtracting the repeated from the unrelated target ERPs are over-plotted in Figure 5. Plotted in Figure 6 are the voltage maps calculated from the priming effect in each of the four consecutive analysis windows. As can be seen by comparing the data in these figures to the data depicted in Figures 3 and 4, a similar pattern of ERPs was obtained in both experiments. Most obvious is the presence of a similarly large horizontal eye movement that differentially influences scalp electrodes over the two hemispheres for the point of movement onset to hundreds of ms later (in fact past the end of the ERP recording epoch). However, as in Experiment 1 it is clear that the impact of these movements did not differentially impact the two priming conditions (see Figure 5).

3.2.3 Epoch Analysis

100–200 ms: In the average ERPs time-locked to the onset of target words there was a significant effect of electrode laterality (main effect of laterality: $F(2,28) = 33.93$, $p < .0001$) with a three microvolt average difference between right and left hemisphere electrode sites. As in Experiment 1 there were no significant effects of priming or interactions involving the priming variable in this epoch (all p s > .8 – see Figures 5 and 6).

200–300 ms: In the next measurement epoch there were large main effects of laterality ($F(2,28) = 26.00$, $p < .0001$) and still no significant priming ($p > .31$ – see Figure 5 & 6).

300–500 ms: As in Experiment 1, in the epoch spanning the N400, the first signs of priming became apparent in the target-locked averages (main effect of Priming: $F(1,14) = 21.28$, $p = .0004$). And this effect tended to be larger at central-midline sites (see Figure 5 & 6; Priming x Ant-post interaction: $F(4,56) = 5.60$, $p = .0062$). Laterality continued to generate a large main effect ($F(2,28) = 22.30$, $p < .0001$).

500–700 ms: In the final measurement window in the target-locked ERPs there was a significant effect of priming, but only at more posterior sites (Priming x Ant-post interaction: $F(4,56) = 3.32$, $p = .0016$ - see Figures 5 & 6). The main effect of Laterality continued into this epoch ($F(2,28) = 9.31$, $p < .0033$).

3.3 Discussion

The results of Experiment 2 once again revealed robust trans-saccadic repetition priming effects. Like Experiment 1, these priming effects took the form of a delayed N400 priming effect, but the delay was greatly reduced in Experiment 2 compared with Experiment 1 (compare Figures 3 and 5). This suggests that rather than hindering target processing in Experiment 2, the forward mask enabled an earlier onset of target pre-processing via a shift in attention to the target location prior to target onset. Given that on average saccades were initiated 86 ms after target onset, we suspect that attention was already directed at the target location upon target onset, thus permitting a brief period of target pre-processing prior to the saccadic eye-movement. This brief period would be enough to initiate priming effects, and therefore reduce the delay in priming as reflected in the time to shift attention to the target location in the conditions tested in Experiment 1. Priming remains delayed compared with priming obtained with centrally located targets due to the lower quality of information in peripheral vision as well as the disruption of sensory processing caused by a saccadic eye movement.

4. Experiment 3

In order to provide a more precise comparison of priming effects obtained in the trans-saccadic priming paradigm and those obtained in a more standard priming situation, Experiment 3 used the same stimuli as Experiments 1 and 2, but now targets were presented on fixation at the same location as prime stimuli.

4.1 Methods

4.1.1 Participants—Fifteen right-handed, native English speaking Tufts University students (6 male, mean age 20 years) were recruited and received compensation for their participation. All were right handed, and had normal or corrected-to-normal visual acuity with no history of neurological insult or language disability. All participants reported that they learned no other language before the age of five. None of these participants had taken part in Experiments 1 or 2.

4.1.2 Stimuli and Procedure—Stimuli were the same as tested in Experiments 1 and 2, and the procedure for stimulus presentation was identical to that of Experiments 1 and 2 with two exceptions: first, targets, like primes were presented at fixation, and second, the 100 ms consonant string which followed the prime in Experiment 2 was replaced with 100 ms blank interval (in order to prevent backward masking of the prime which did not occur in Experiment 1 because the consonant string was presented laterally). All else was the same for all three experiments.

4.2 Results

4.2.1 Behavioral Results—Participants detected on average 79% of the animal probe words in the target position and 79% in the prime position.

4.2.2 Event-related potentials—Grand average ERP's in Experiment 3 time-locked to repeated and unrelated trials are plotted in Figure 7. Plotted in Figure 8 are the voltage maps

corresponding to the four analysis epochs. While the overall ERPs look quite similar to those in Experiments 1 and 2 (compare Figures 3, 5 and 7) one notable difference is the absence of the large eye-induced transient potential in the HE electrode site that was clearly visible in Experiments 1 and 2.

4.2.3 Epoch Analysis

100–200 ms: In the average ERPs time-locked to target onset there was a significant effect of electrode laterality (main effect of laterality: $F(2,28) = 5.18$, $p < .015$). However, unlike Experiments 1 and 2 this effect would seem to be more likely due to an asymmetry of electrical brain activity as opposed to an eye movement. This is because the data from the right hemisphere were actually more negative-going than either the midline or left hemisphere sites in this experiment (the reverse was true in Experiments 1 and 2). There were no significant priming effects in this epoch (all $ps > .13$).

200–300 ms: Previous masked priming studies using primes and targets presented at fixation have reported an early priming effect, the N250, in this window (e.g., Holcomb & Grainger, 2006). Unlike Experiments 1 and 2 there were significant priming effects during this epoch (main effect of priming: $F(1,14) = 11.16$, $p = .0049$ – see Figures 7 & 8) with unrelated targets showing more negative-going ERPs than repeated targets. Priming did not significantly interact with either scalp distribution factor ($ps > .06$).

300–500 ms: In the epoch spanning the N400, there was a very robust priming effect (main effect of Priming: $F(1,14) = 67.96$, $p < .0001$). And this effect tended to be larger at central-midline sites (see Figure 7 & 8; Priming x Ant-post interaction: $F(4,56) = 30.84$, $p < .0001$) and were larger at midline and right hemisphere sites than left hemisphere sites (Priming x Laterality interaction; $F(2,28) = 4.18$, $p = .042$).

500–700 ms: In the final measurement window there were no significant effects of Priming (all $ps > .25$).

4.3 Discussion

The time-course of priming effects seen in Experiment 3 is largely consistent with prior masked priming ERP effects previously reported (see Grainger & Holcomb, 2009, for a review), showing an early effect of priming between 200 and 300 ms (the N250) and a later effect between 300 and 500 ms (the N400). By moving the target to fixation in Experiment 3, the time-course of priming effects time-locked to target onset were indeed shifted earlier than comparable target-locked averages in Experiments 1 and 2. This is likely due to the diminished efficiency in extracting information from target stimuli in peripheral vision (Experiments 1 & 2) compared with centrally located targets (Experiment 3). In other words, although the results of Experiments 1 and 2 suggest that processing of peripherally located targets begins prior to fixation of the target stimulus, this pre-processing is clearly less efficient than the processing of centrally located targets.

5. Cross-Experiment time-course analyses

In order to provide a more precise estimate of the timing of priming effects seen in each experiment, we ran a series of time-point-by-time-point t-tests contrasting the repeated target ERPs with the unrelated target ERPs starting at target onset and running through 700 ms. Because of the increased risk of chance findings when running this many statistical tests, we applied a false discovery rate (FDR) correction (as recommended by Groppe, Urbach, & Kutas, 2011a as recommended by Groppe, Urbach, & Kutas, 2011b from the procedure developed by Benjamini & Yekutieli, 2001) to the p-values from these analyses. Given the centro-posterior distribution of priming effects, as can be seen in Figures 4, 6, and 8, we chose electrode site Cz as the most representative site for the time-course analyses.

Plotted in Figure 9 are the difference waves (priming effects) from the three experiments along with a scale that indicates the time-course of priming (including onset and offset latencies). The onset of priming effects was earlier in Experiment 3 compared with Experiment 2, by an average 40 ms, and the onset of priming effects was on average 35 ms earlier in Experiment 2 compared with Experiment 1. It is also interesting to note that priming effects were slower to develop in Experiments 1 and 2 compared with Experiment 3, with a distinct shift in the peak of the effects by about 100 ms (see Figure 9). Finally, the offset of priming was also later in Experiments 1 and 2 compared with Experiment 3 (70 ms later in Experiment 2 and 110 ms later in Experiment 1). The results of this time-course analysis are in line with the overall pattern of priming effects seen in the epoch analyses performed for each experiment.

Finally, it is interesting to note that although there were relatively large differences in the estimated onset of priming effects across experiments, the peak amplitude of the N400 priming effect is quite similar in the three experiments (see Figure 9). This is likely due to the fact that prime duration remained constant across experiments, and that it is prime duration that is the key factor in determining the amplitude of priming effects (Holcomb & Grainger, 2007). Furthermore, since it is known that allocation of attention can modulate the size of N400 effects (see Van Petten, 2014, for a review), this points to equal allocation of attentional resources for target word processing across experiments, with differences across experiments being driven mainly by the timing of attention shifts to the target location.

6. General Discussion

In the present study we used a variant of the trans-saccadic priming paradigm combined with ERP recordings in order to investigate the timing of integration of information across spatially distinct words. By presenting prime stimuli on fixation followed by target stimuli in peripheral vision to the right of fixation in Experiments 1 and 2, we could estimate the amount of pre-processing of peripherally located targets prior to fixation of these target words. The results showed robust trans-saccadic repetition priming effects in the ERP waveforms that mostly took the form of a delayed N400 priming effect as seen in prior research with centrally located targets (see Grainger & Holcomb, 2009, for a review) and replicated in Experiment 3 of the present study.

The mere presence of trans-saccadic priming effects in Experiments 1 and 2 is evidence that information is integrated across spatially distinct stimuli. This finding is in line with prior behavioral evidence using masked priming (Marzouki et al., 2013), and experiments showing parafoveal influences on foveal word recognition (Angele et al., 2013; Dare & Shillcock, 2013; Grainger et al., 2014; Vitu, Brysbaert, & Lancelin, 2004). Like the Marzouki et al. (2013) study, primes and targets did not temporally overlap in the present study, and the integration mechanisms are therefore likely to differ from the kind of spatial integration that might operate with temporally overlapping stimuli (see Grainger et al., 2014, for a specific proposal). Semantic representations are one likely source of priming effects with both spatially and temporally distinct primes and targets, given that form-level information (orthographic, phonological) needs to be reset from one word to the next in order to minimize interference during sequential word reading. The assumption here is that, while we can only identify one word form at a time, the semantic representations of several words must remain co-active as they contribute to sentence-level meaning. In line with this reasoning, the centro-posterior distribution of priming effects in Experiments 1 and 2 suggests that these are delayed N400 priming effects, driven by differences in the ease with which whole-word orthographic representations are mapped onto semantics. In other words, the pre-activation of semantic representations by the prime stimulus would influence this mapping process during processing of the target word.

Over and above issues of across-word integration, the complete pattern of results of the present study can be captured by the combined influence of two factors. First, the onset of priming effects would be determined by the moment that attention is directed to the target, enabling initiation of processing of the target stimulus. Second, the growth in priming effects would be determined by the quality of the information extracted from the target, which is greatly diminished in peripheral vision, and even more so during a saccadic eye-movement during which information up-take is disrupted. Thus, priming effects onset most rapidly in Experiment 3 (central targets), and with the greatest delay in onset occurring in Experiment 1 where it was the appearance of the target that triggered an attention shift to the target location. By attracting attention to the target location prior to target onset, Experiment 2 produced an earlier onset of priming effects than Experiment 1, but there was still a delayed onset compared with Experiment 3 (see Figure 9). The delay in the onset in priming effects between Experiments 1 and 3 suggests that it took about 70 ms to direct attention to the target location in Experiment 1. This timing estimate is in line with one study showing enhanced processing at the target location as early as 60 ms following a cue to move the eyes to that location (Rolfs & Carrasco, 2012).

These timing estimates would suggest that attention was already directed at the target location upon target onset in Experiment 2, where a 100 ms pre-mask was used to attract attention to that location. There was nevertheless a delay in the onset of priming effects in Experiment 2 compared with Experiment 3, suggesting that the onset of priming effects is not only determined by allocation of attention, but also by the quality of information extracted at the attended location. This in turn suggests that attention may have shifted even earlier to the target location in Experiment 1, with the total delay in the onset of priming effects compared with Experiment 3 (75 ms) being driven by a combination of attention shift time and slower information uptake in peripheral vision.

The other notable difference in the time-course of priming effects across the three experiments concerns the rate at which these effects develop once they have onset. This is clear when comparing the grand average waveforms and scalp topographies of priming effects observed in each experiment. The overall pattern is conveniently summarized in the difference waves shown in Figure 9, where we can see that priming effects peak at around 400 ms post-target onset in Experiment 3 (a typical pattern for central targets), and around 500 ms or later in Experiments 1 and 2. This delay is greater than the estimated delays in the onset of priming effects, thus pointing to a slower rise in the size of priming effects following their onset. This would most likely be due to the lower quality of information available from target stimuli in peripheral vision prior to fixation of the targets.

An alternative interpretation of the pattern of effects in this study is that the timing and eccentricity of targets used in Experiments 1 and 2 did not enable pre-processing of target stimuli prior to fixation, or at least enough pre-processing to account for all of the observed priming effects. If this were indeed the case, then it would make more sense to evaluate priming effects from the moment in time that the eyes fixate the target, using so-called fixation-related potentials (e.g., Hutzler, Braun, Vo, Engl, Hofmann, Dambacher, Leder, & Jacobs, 2007). Given the estimated target fixation times in Experiments 1 and 2 (approximately 212 ms post-target onset in Experiment 1, and 122 ms in Experiment 2, see Figures 3 & 5) this provides a very different picture of the time-course of priming effects compared with the target-locked analyses that we have presented. Subtracting these values from the estimated onset of priming effects shown in Figure 9 provides an estimated onset of fixated-locked priming effects at 103 ms in Experiment 1 and 158 ms in Experiment 2. These fixation-related priming effects therefore clearly onset much earlier than the priming effects seen with central target presentation in Experiment 3. In the hypothesized absence of target pre-processing in peripheral vision, such early priming effects could be driven by different kinds of preparatory mechanisms linked to saccadic eye movements during reading, such as predicting the identity of the upcoming word from prior context. An experiment that completely excludes any role for target pre-processing prior to target fixation in our trans-saccadic priming paradigm would help determine the relative role of target pre-processing and other saccade-linked preparatory mechanisms.

In sum, the results obtained with the trans-saccadic ERP priming paradigm suggest that this technique can be usefully applied to study the on-line integration of information across spatially distinct prime and target stimuli. Future research using this paradigm while varying parameters such as prime-target temporal overlap and prime-target orthographic overlap, should help further specify the nature of such spatial integration processes as well the timing of information uptake from peripheral stimuli.

Acknowledgments

This research was supported by NIH grant HD25889 and ERC grant 230313.

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Highlights

- Priming across spatially distinct prime and target word stimuli is investigated.
- Event-related potentials reveal the timing of spatial integration processes.
- Rapid attention shifts to peripheral targets enables early onset of priming effects.
- Delayed N400 priming arises for peripheral compared with central targets.

Figure 1.

The trans-saccadic priming paradigm. Schematic of the sequence of events on a typical trial in Experiment 1. The prime is presented centered on fixation for 100 ms followed immediately by the target stimulus located 4° to the right of fixation for 300 ms. The small figure at the right is an average of the horizontal EOG time locked to the onset of the target showing the regularity of the rightward saccade with respect to the onset of target words.

Figure 2.

Electrode montage and the 15 analysis sites used for ANOVAs. Note that the Ant-post factor is defined by the five sites (FP, F, C, P, O) in each of the three Laterality columns, which are indicated with connecting lines.

Figure 3.

ERPs time locked to target onset in Experiment 1 from 15 scalp sites and the bipolar horizontal EOG channel (HE). Note that the HE channel is plotted on a larger amplitude scale (calibration bar is 10 μ volts vs. 2 μ volts for the other scalp sites). The solid black line is from the repeated target word condition, the red dashed line is from the unrelated target condition and the solid blue line is the difference wave (Unrelated – Repeated). Note that the HE channel is very flat in the Difference plot suggesting little differential lateral eye movement contamination of priming effects. Also plotted are two vertical lines indicating the point of mean onset and offset of saccadic eye movements across participants.

Figure 4.
Voltage maps calculated from the mean difference (in microvolts) between Unrelated and Repeated target ERPs at 29 scalp sites in each of the four measurement epochs in Experiment 1.

Figure 5.

ERPs time locked to target onset in Experiment 2 from 15 scalp sites and the bipolar horizontal EOG channel. The solid black line is from the repeated target word condition, the dashed red line is from the unrelated target condition and the difference (unrelated – repeated) is the solid blue line. Mean saccade onset and offset latencies are marked on the HE channel.

Figure 6.
Voltage maps calculated from the mean difference (in microvolts) between Unrelated and Repeated target ERPs from 29 scalp sites in each of four latency windows in Experiment 2.

Figure 7.

ERPs time locked to target onset in Experiment 3 from 15 scalp sites and the horizontal EOG channel. The solid black line is from the repeated target word condition, the dashed red line is from the unrelated target condition and the solid blue line is the difference (Unrelated – Repeated).

Figure 8.

Voltage maps calculated from the mean difference (in microvolts) between Unrelated and Repeated target ERPs from 29 scalp sites in each of four latency windows from Experiment 3 (Target-locked averages).

Figure 9.

ERP difference waves (i.e., priming effects) computed by subtracting repeated target word ERPs from unrelated target word ERPs time-locked to target onset in Experiments 1, 2 and 3 at electrode Cz. The bar below the x-axis indicate regions where the ERPs were significantly different as well as the latency of the first and last points that were significant at .05 (false discovery rate corrected – see main text for explanation).