

Immediate Repetition Priming: Measuring Synaptic Depression with ERPs

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We present two perceptual identification experiments that measure event-related potentials (ERPs) to a briefly flashed target word immediately following presentation of an identical or unrelated prime word. With increasing prime duration, behavioral bias switched from a preference to choose repeated words to a preference against choosing repeated words. Early posterior ERP components, corresponding to the P1 and N1, were more negative with repetition priming following a short prime presentation. However, following a long prime presentation, the later of the two components switched its response to a more positive deflection with repetition priming. Furthermore, the effects of the later component were primarily seen in the left hemisphere. The behavioral and ERP results are simultaneously explained by including the suppressing dynamics of synaptic depression in a neural network model of perceptual processing.

Using a forced-choice procedure similar to Figure 1, Huber, Shiffrin, Lyle, and Ruys (2001) observed that immediate short-term repetition priming resulted in a bias, causing accuracy to improve when the correct choice (i.e., the target) is primed but worsen when the incorrect choice (i.e., the foil) is primed. This pattern of costs and benefits reversed when prime words were presented for longer, suggesting that the bias in favor of primed words switched to a bias against primed words (see Figure 2). Traditionally, short-term priming paradigms have been used as tool for assessing linguistic structure and these findings highlight the need to consider the perceptual and decisional components of priming paradigms.

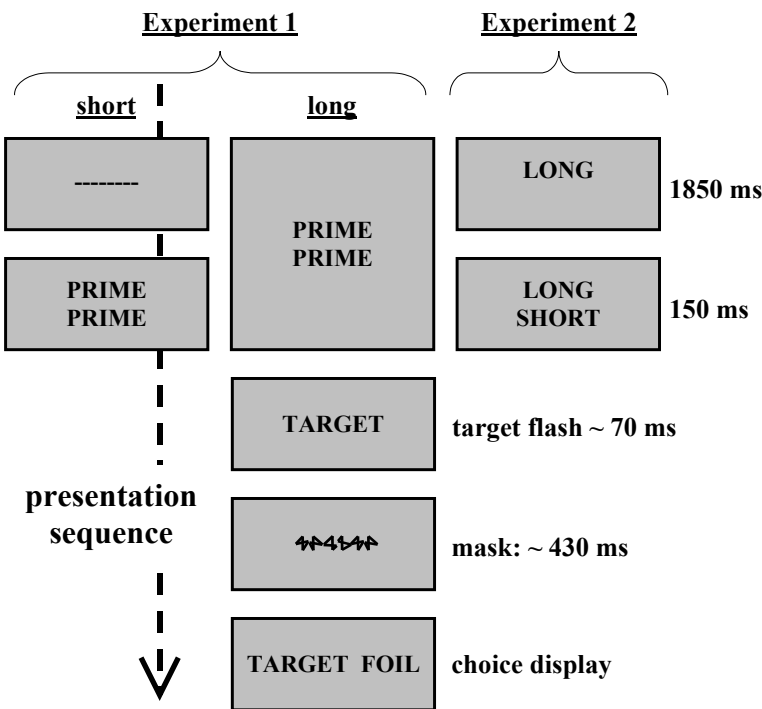


Figure 1. Presentation sequence for the two reported ERP experiments. Experiment 1 used a single prime word that was presented for 150 ms (short) or for 2000 ms (long). The same prime word appeared simultaneously both above and below fixation. Target flash times were set individually in order to place performance at 75%. Either the target or the foil repeated the prime word. Experiment 2 used two prime words with the upper prime word presented for 2000 ms (long) and the lower presented only for the final 150 ms (short) prior to the target flash. On every trial, one of these two prime words reappeared as the target or the foil.

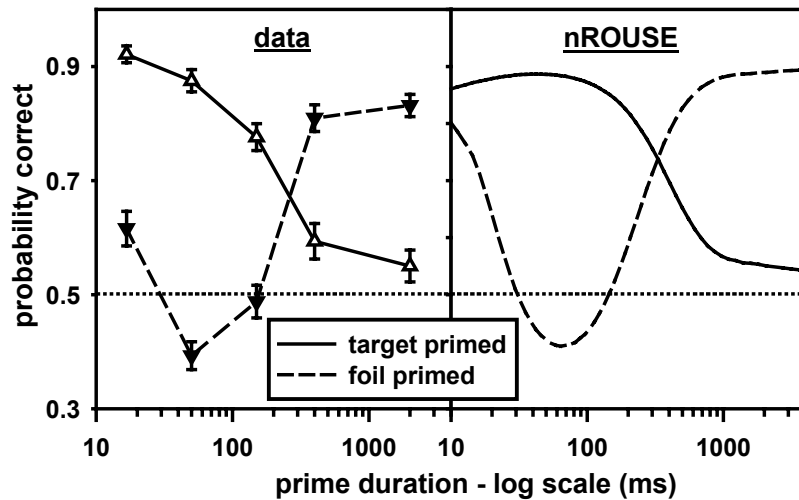


Figure 2. Repetition priming results of Huber (in preparation). This experiment was identical to Experiment 1 and additionally used prime durations of 17, 50, and 400 ms. In order to explain the effect of prime duration, Huber and O'Reilly (in press) proposed the nROUSE model (see Figures 3 and 4).

Huber et al. (2001) proposed a Bayesian decision model, termed Responding Optimally with Unknown Sources of Evidence (ROUSE), which accounted for the biasing effect of primes through the offsetting components of source confusion (i.e., prime features are mistaken for target features) and discounting (i.e., features that are known to have been primed are assigned a lower level of evidence). Source confusion results in a bias for primed words and excessive discounting can reverse this bias. However, in order to capture the dynamic pattern seen in Figure 2, different parameters are required at each prime duration. Borrowing much from the original ROUSE model, Huber and O'Reilly (in press) implemented synaptic depression within a neural network in order to explain bias as a function of prime duration, using a single set of parameters for all durations. Their model was termed a neural mechanism for responding optimally with unknown sources of evidence (nROUSE).

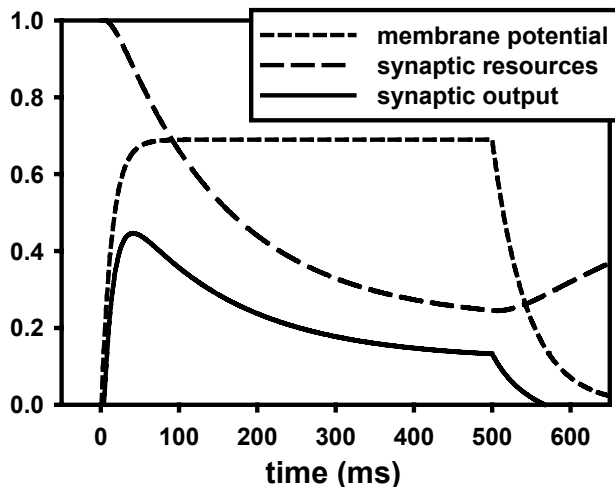


Figure 3. An example of rate-coded synaptic depression, as derived by Huber and O'Reilly (in press). Pre-synaptic activity (membrane potential) quickly rises with the presentation of an input at time 0. At a slower pace, this ongoing activity causes a depletion of synaptic resources, which results in a decrease in post-synaptic depolarization (synaptic output). At time 500, the input is removed causing the membrane potential to decay, allowing synaptic resources to slowly recover.

Synaptic depression refers to a process in which synaptic resources became depleted as a result of recent activity. This results in a lessening of the post-synaptic depolarization (i.e., synaptic output) that occurs in response to each pre-synaptic action potential. Tsodyks and Markram (1997) and Abbott et al. (1997) performed single-cell recording studies in order to mathematically specify the dynamics of synaptic depression in spiking neurons. Huber and O'Reilly (in press) derived a rate-coded version of synaptic depression from these equations in order to modify the dynamics of simulated neurons in the nROUSE model. Figure 3 presents Huber and O'Reilly's rate-coded version of synaptic depression. One difference equation specifies pre-synaptic activity (i.e., membrane potential), based upon excitatory

input, while a second difference equation specifies the depletion of synaptic resources as a function of ongoing pre-synaptic activity. Huber and O'Reilly also demonstrated that the Bayesian ROUSE model can mimic this depletion process when appropriate dynamics are added. They proposed that synaptic depression might have evolved as a mechanism to reduce unwanted persistent activation from previously presented perceptual input.

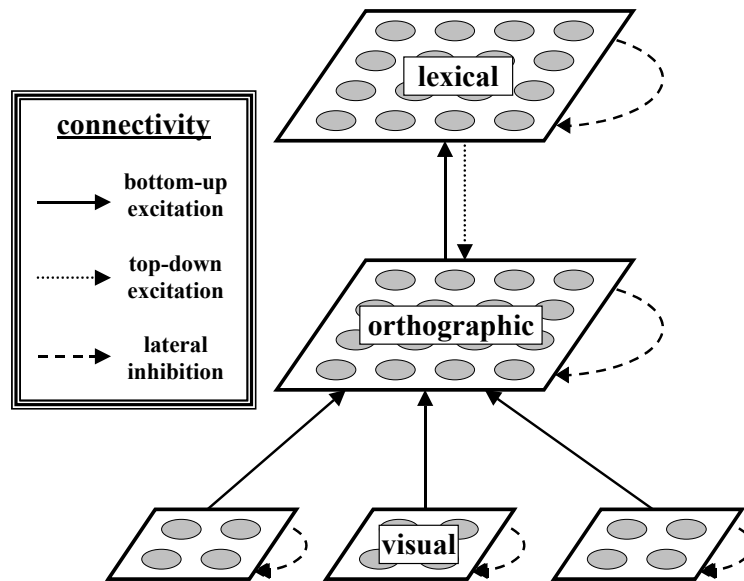


Figure 4. Perceptual hierarchy used in nROUSE. See Huber and O'Reilly (in press) for further details.

Using the perceptual hierarchy appearing in Figure 4 in combination with the dynamics of synaptic depression, the nROUSE model captured the results of Figure 2, both in terms of accuracy and reaction time. The decision rule in nROUSE is a horse race such that the choice word that reaches its peak activation first is chosen. Residual activation from an identical or related prime provides a head start in the race. Synaptic depression lessens this residual activation. Beyond this lessening, bias reversals are possible because synaptic depression also serves to slow down the rate of processing for words that have not fully recovered.

nROUSE specifies neural activation at the millisecond level and is ideally suited for testing with event-related potentials (ERPs). Using the experimental paradigms seen in Figure 1, participants performed forced-choice perceptual identification while a 128 electrode geodesic sensor net recorded scalp voltage potentials. ERP were time-locked to the onset of the target flash. If the results of Figure 2 are due to a decisional factor in response to the choice words, then there should be little or no change in the ERPs to the target flash. However, if the bias effects are due to changes in perceptual processing, such as assumed in nROUSE, it may be possible to observe the electrophysiological correlates of these bias effects prior to the presentation of the choice alternatives. The measure of interest is the difference in the ERPs when the target flash repeats a prime (the target condition) as compared to a target flash that presents a novel word (the foil condition).

Following Experiment 1 (see Figure 1), a potential confound was identified. In the short condition, a prime appears 150 ms prior to the target flash, and, therefore, ERP components in response to the prime overlap with the ERP components in response to the target flash. However, this is not true in the long condition and if components combine in some nonlinear fashion, this differential overlap could potentially explain the observed changes between the short and long conditions. In Experiment 2, everything is identical in all condition until the time when the target flash occurs (i.e., in Experiment 2 the shorter of the two primes always overlaps with the target flash).

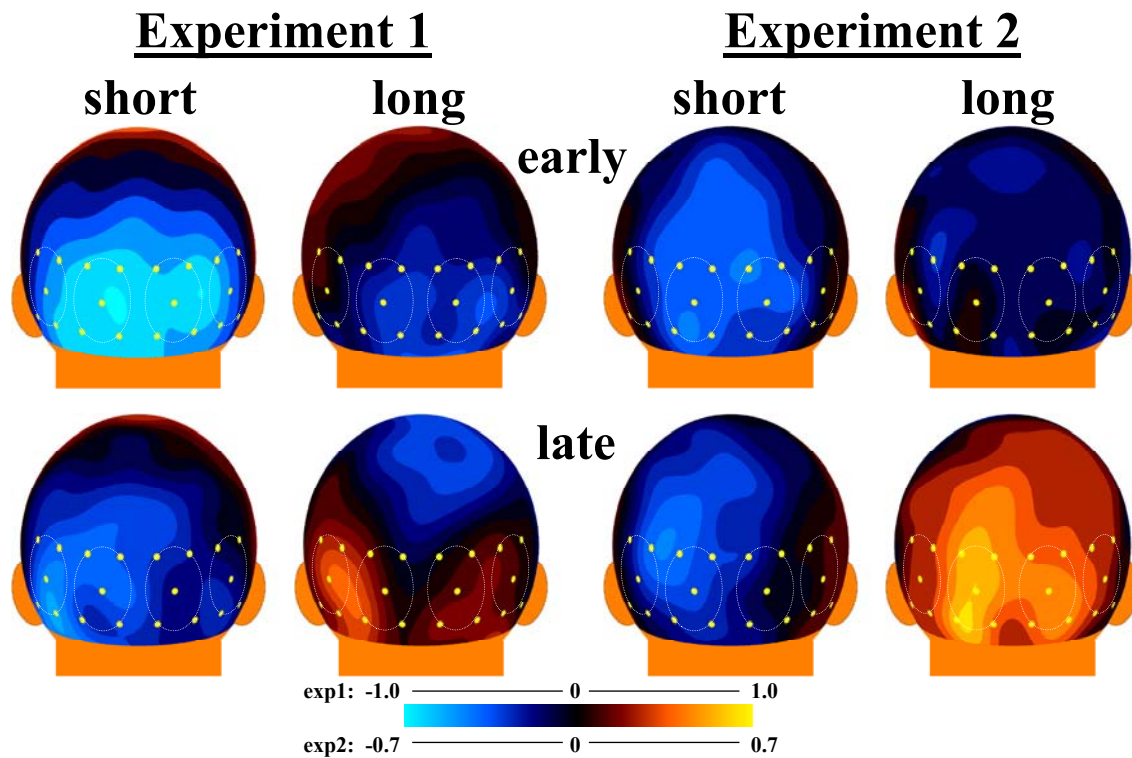


Figure 5. ERP difference between a repeated versus a novel target flash, shown from a posterior view. The early and late 40 ms averaged time periods roughly correspond to the P1 and N1 in response to the target flash. Statistics were run using the four different electrode groups shown by the four circles.

Figure 5 presents the ERP repetition effects computed as differences between the repeated (target) and novel (foil) conditions for short and long prime presentations, at two different time periods. The early time period occurred from 120-160 ms past the target flash in Experiment 1 and 100-140 ms past the target flash in Experiment 2, and roughly corresponds to the time at which the P1 to the target flash reached its peak. The late time period occurred from 160-200 ms past the target flash in Experiment 1 and 140-180 ms past the target flash in Experiment 2, and roughly corresponds to the time at which the N1 to the target flash reached its peak. The 20 ms difference in these time periods between the two experiments was also observed in the ERP components in response to the primes.

As seen in Figure 5 there was remarkable consistency across the two experiments. Early repetition effects were negative-going across both hemispheres, and this difference was greater in the short condition than the long condition. At the later time period, the difference switched directions, as a function of prime duration, and these effects were more pronounced in the left hemisphere. The results are further summarized in the bar graphs of Figure 6.

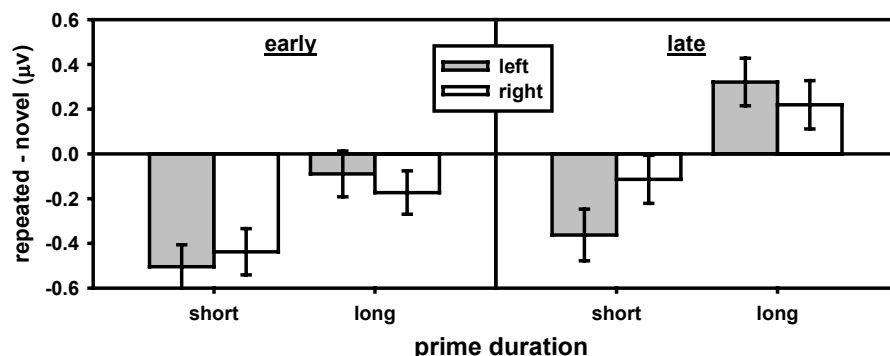


Figure 6. Summary of the ERP repetition effects (repeated minus novel), collapsed across the occipital and temporal electrode groups and collapsed across the two experiments. The error bars show two standard errors of the mean difference.

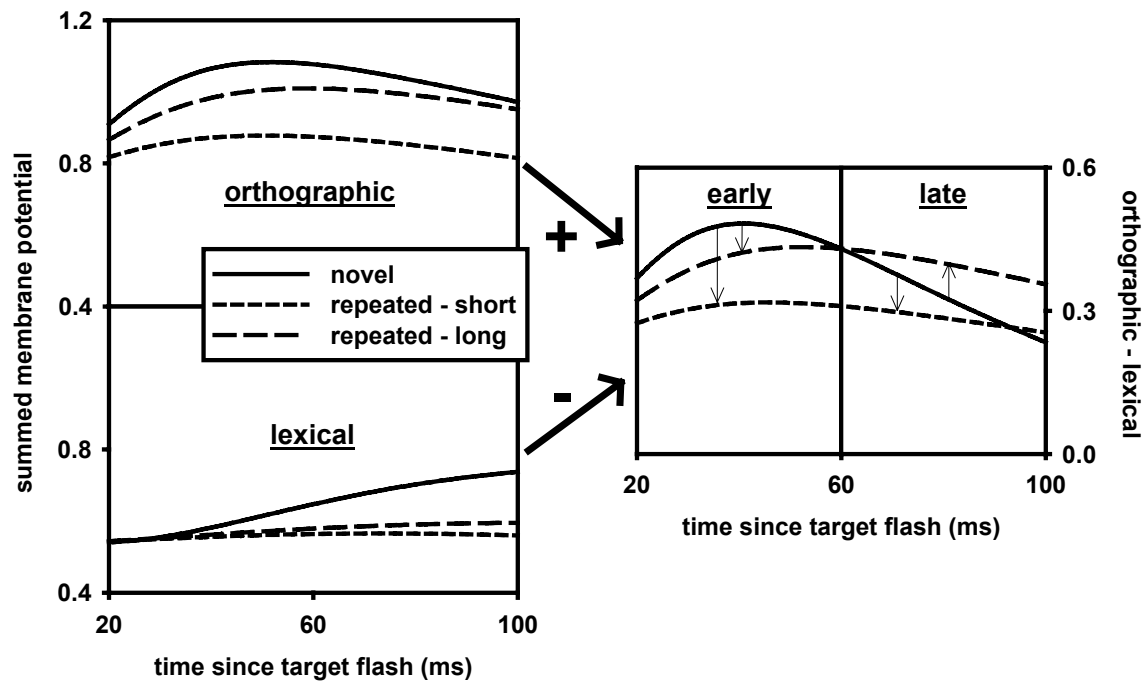


Figure 7. nROUSE activation curves using the same parameters as Figure 2 and the experimental paradigm of Experiment 2. Subtracting the lexical response from the orthographic response results in a negative repetition effect for the early time period but a change in the direction of the repetition effect, as a function of prime duration, for the late time period.

In modeling ERPs with nROUSE, we assumed that early ERP repetition effects primarily reflect activation differences within the orthographic level whereas later ERP repetition effects reflect the combined activity of the orthographic and lexical levels. The early effects are easily understood in terms of the lingering effects of prime activation. In the novel condition, something new is presented and this causes greater activity (more positive P1) as compared to the repeated condition. Because the ERP differences in Figures 5 and 6 subtract the novel condition from the repeated condition, the difference is negative.

According to the explanation provided by nROUSE, the late differences are more complex, resulting from the combined effect of different levels of processing. We assume that the orthographic level results in a positive potential (P1) whereas the lexical level results in a negative potential (N1) and that the two processing levels are close enough to summate at the scalp. The left-hand graphs of Figure 7 clearly show that presenting a novel word results in greater activation. However, due to synaptic depression in the visual level input, the amount of additional activation provided by a repeated word is greater following a long prime presentation. Because higher levels of the perceptual hierarchy process more slowly (and therefore depress more slowly), the effect of prime duration is more pronounced in the orthographic level compared to the lexical level.

Subtracting the lexical level from the orthographic level results in the right-hand graph that simulates the scalp summation of the P1 and N1. Similar to the ERP differences, the early differences are negative and larger for the short prime duration whereas the late differences (i.e., once lexical processing has more fully activated), switch from negative to positive between the short and long prime durations. These time periods are approximately 90 ms earlier than the ERP time periods, although this is

reasonable considering that the model does not include the delays needed in moving visual information from the retina to primary visual cortex.

Discussion

These experiments identify early perceptual ERP components that are affected by visual repetition priming of words, and, furthermore, are modulated by prime duration. This provides converging evidence that the biasing effects of prime presentations are due to changes in perceptual processing, rather than explicit decision strategies.

The nROUSE model explains behavioral bias in terms of persistent prime activation and the counteracting mechanism of synaptic depression, which serves to diminish the activation of items presented for prolonged durations. Assuming different levels of processing map onto P1 and N1 potentials, nROUSE accounts for the observed ERP effects. The late ERP repetition effect was primarily left lateralized. This is sensible in light of functional magnetic resonance imaging (fMRI) work identifying a visual word form area (i.e., an area sensitive to visual repetition, but not cross-modal repetitions) in the left fusiform gyrus that reduces in activation with immediate visual repetition (Dehaene et al., 2001). This result lends credibility to our claim that the change in the direction of the ERP repetition effect is due to the inclusion of lexical activation. Furthermore, this suggests that the term “lexical” may be inappropriate for the highest level of processing in nROUSE, and, perhaps, visual word form is more accurate.

In summary, the inclusion of synaptic depression in a neural network simultaneously accounts for behavioral bias as well as ERP differences in response to the target flash. This provides converging evidence that synaptic depression is an important component of perceptual processing.

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