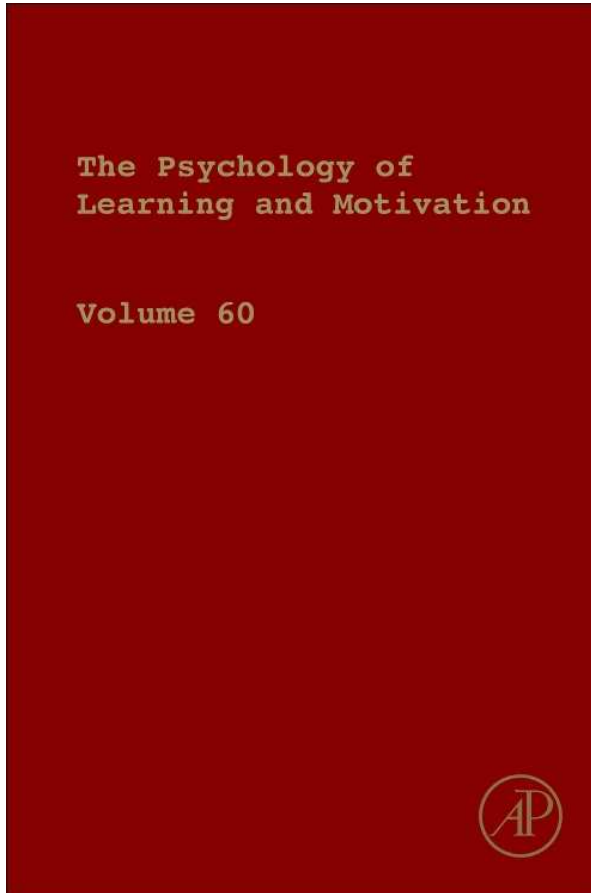


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The Rise and Fall of the Recent Past: A Unified Account of Immediate Repetition Paradigms

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Contents

1. Introduction: The Trade-off Between Integration and Separation	192
2. Marr's Levels of Explanation: From Bayes to Habituation	194
2.1 Responding Optimally with Unknown Sources of Evidence	194
2.2 Habituation Through Synaptic Depression	196
3. Results: Words, Faces, Places, and Semantics	198
3.1 Word Repetitions	198
3.2 Face, Place, and Semantic Repetitions	210
4. Conclusions	221
Acknowledgments	221
References	221

Abstract

Perception does not happen instantaneously. Instead, perceptual information is accumulated gradually (i.e., a rise in the perceptual response) to achieve accurate identification despite perceptual noise. This temporal integration of information predicts that previous presentations may become erroneously blended with subsequent presentations. An optimal decision process can reduce this source confusion by discounting perceptual evidence that may have come from previous presentations. Furthermore, habituation (i.e., a fall in the perceptual response) may be the brain's trick for approximating this optimal decision. Habituation reduces blending and enhances change detection: because previous perceptions are habituated, anything new stands out. However, this solution comes with a cost, making it difficult to detect immediate repetitions. Over the last 6 years, my coauthors and I have tested this theory, examining its application to a range of different behavioral tasks that involve immediate repetitions. Here, I review these findings, demonstrating the broad implications of this theory.



1. INTRODUCTION: THE TRADE-OFF BETWEEN INTEGRATION AND SEPARATION

Our eyes receive a wealth of constantly changing perceptual information due to constant changes in the environment, eye/body movements, and various forms of perceptual noise. To average out these fluctuations, perceptual processes integrate information on a relatively slow timescale (Ratcliff & Rouder, 1998; Smith, 1998). As predicted from slow temporal integration, perceptual responses linger for hundreds of milliseconds in the absence of a mask (Sperling, 1960). Because there is no external signal that resets the integration process when a new object appears, the ongoing temporal integration of perceptual information may erroneously bridge across different objects presented in sequence and cause perceptual blending and source confusion. Thus, there is a need to reduce source confusion by temporally separating the perceptual response to each object.

The trade-off between temporal integration and separation is made clear with a simple example from low-level vision. The top row of Fig. 5.1 shows

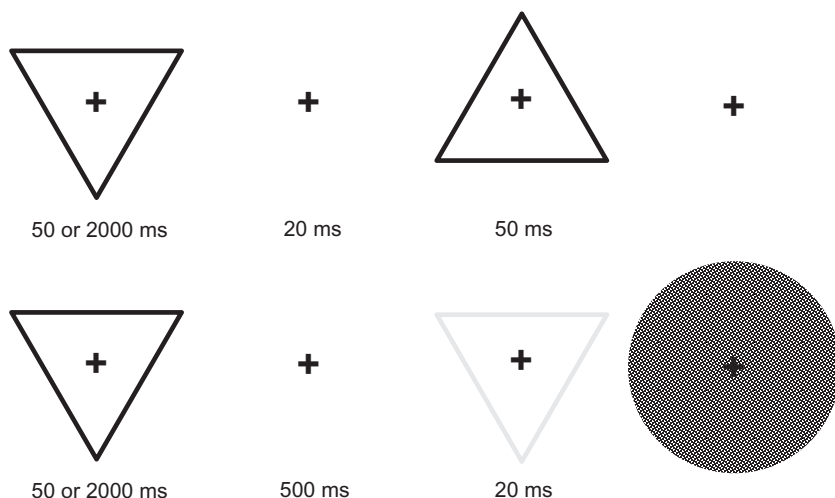


Figure 5.1 Example of temporal integration versus separation with two sequences (top vs. bottom) of four displays, with display durations shown below each display. Top row: Depending on the duration of the first triangle, the percept is either a six-pointed star or two different triangles in sequence. Bottom row: Following a short-duration first triangle, it is possible to detect the faint repetition before the final mask. However, the repetition becomes impossible to detect following a long-duration first triangle.

a sequence of four displays, from left to right, and associated display durations. This sequence is easily created in PowerPoint using the animation pane (alternatively, a PowerPoint file of this sequence is available on my webpage). With these durations and a typical LCD monitor, there are two different percepts depending on the duration of the first display (50 or 2000 ms). If the first triangle is only viewed for 50 ms, the perceptual response to that triangle is still active when the second triangle appears, resulting in the percept of a six-pointed “Star of David.” This situation demonstrates blending due to the integration of information across subsequent objects.

Next, consider the sequence of the top row when the first triangle appears for 2000 ms rather than 50 ms. In this case, the percept accurately reflects the sequence, with the upward-pointing triangle appearing after the downward-pointing triangle. This occurs because the visual response to the first triangle becomes habituated, shortening the amount of visible persistence (Duyssens, Orban, Cremieux, & Maes, 1985), such that the first triangle is no longer apparent when the second triangle appears. Termed the ‘inverse-duration effect,’ experiments have demonstrated that increases in duration beyond 200 ms reduce rather than increase visible persistence and reduce the ability to integrate previous displays with subsequent displays (Coltheart, 1980; Hogben & Di Lollo, 1974).

The bottom row of Fig. 5.1 begins with exactly the same short- or long-duration downward-pointing triangle, but this is followed by a longer-duration interstimulus interval to place the second triangle outside the window of temporal integration regardless of the duration of the first triangle. Unlike the top row, the second triangle is identical to the first triangle, and the question of interest is whether the faint repetition can be detected. To make this repetition detection difficult, the second triangle is shown at lower contrast for a shorter duration and it is followed by a pattern mask. When the first triangle appears for 50 ms, it is just possible to detect that a repetition has occurred. However, when the first triangle appears for 2000 ms, it is all but impossible to detect the repetition, provided that your eyes remain fixated on the plus sign throughout the sequence. This repetition blindness is an example of a visual aftereffect (Gibson, 1933)—the neurons that prefer the black lines of the triangle have been habituated and fail to respond sufficiently to the repetition. To convince yourself that there is a repetition, instead, focus on a vertex of the long-duration first triangle and then move your eyes to the plus sign when the first triangle disappears. If you move your

eyes, it is possible to detect the repetition because this particular example of habituation occurs in retinotopic representations.

These two examples highlight the important predictions of the theory that guided the work reviewed in the succeeding text: (1) Up until a point, increasing stimulus duration increases perceptual responses, causing increased blending between one stimulus and the next (i.e., temporal integration); (2) beyond that point, additional increases in the duration of the first stimulus reduce this blending (i.e., temporal separation); and (3) although temporal separation reduces erroneous blending, it comes with a cost, making it difficult to detect immediate repetitions. As explained next, these predictions arise from a model that assumes neural habituation at all stages of perceptual processing. Given the generality of this mechanism, similar results are predicted for any task that involves rapid serial visual presentations (RSVPs).



2. MARR'S LEVELS OF EXPLANATION: FROM BAYES TO HABITUATION

Marr (1982) famously proposed that phenomena can be explained at one of the three levels, depending on whether the explanation describes the core *computations*, the processing *algorithms*, or the neural hardware that *implements* a solution. These levels of explanation offer different advantages and disadvantages, and it may prove fruitful to provide different Marr-level explanations of the same phenomenon. The current theory proposes that recently viewed features should be discounted to reduce source confusion between previously viewed objects and subsequently viewed objects. As explained next, this theory has been formalized at the computational level through the mathematics of Bayesian decision making and at the implementation level through the dynamics of neural habituation.

2.1. Responding Optimally with Unknown Sources of Evidence

The theory is termed 'ROUSE,' which stands for responding optimally with unknown sources of evidence. The Bayesian ROUSE model assumes a feature activation process and then uses Bayes rule to determine how much evidence should be assigned to each feature in the percept (Huber, 2006; Huber, Shiffrin, Lyle, & Ruys, 2001). In brief, the left-hand panel of Fig. 5.2 shows the Bayesian ROUSE model. In the generative activation process, a pattern of activated features is determined by the different sources included in the experiment, such as the previous input (the prime) or the

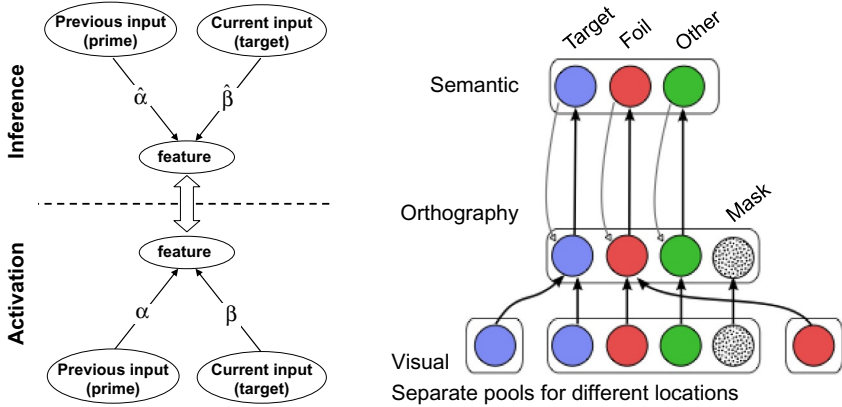


Figure 5.2 Illustrations of two different ROUSE models that explain the discounting of features that belong to previously viewed objects. Left-hand panel: The Bayesian ROUSE model assumes that previous and current inputs are separate sources of feature activation, and Bayes rule is used to determine how much evidence a feature provides towards the currently viewed object considering that a previously viewed object might have been the cause of feature activation. The neural ROUSE model assumes that features exist in a cascaded hierarchy, and neural habituation through synaptic depression dictates that nodes (i.e., features) gradually lose their ability to excite other nodes as synaptic resources deplete owing to recent activation. The neural ROUSE model was designed to capture perceptual dynamics rather than distributed patterns of representation, and simulations with this model use only the nodes shown in the figure. The visual level of the model captures visual representations at different locations in the visual field (see Fig. 5.4 for display sequence), with the four nodes in the center corresponding to any word or mask shown in the center, whereas the target node on the left (in blue) and the foil node on the right (in red) correspond to the presentation of the target and foil on the left versus right side of the screen during the test display. Adapted from *Huber and O'Reilly (2003)*, with permission.

current input (the target). The extent to which these sources activate their associated features is determined by the parameters alpha and beta. When attempting to identify the currently viewed object, the observer must infer which sources gave rise to these activated features. If the object that gave rise to the previous input has been identified, then any features that are consistent with that previous object are 'explained away' (i.e., assigned a discounted level of evidence than they would have been if they were not part of the previous object). This reduces source confusion between subsequently presented objects provided that the objects do not share any features (e.g., each triangle is perceived separately, rather than as a blended percept). However,

if the objects share features, there is a cost when identifying the second object, with the magnitude of this cost determined by the system's estimate of source confusion (the estimated value of α used in Bayesian inference).

The Bayesian ROUSE explains the core computational need for feature discounting and it is a remarkably successful model, providing counterintuitive a priori predictions, which were subsequently confirmed (Huber, Shiffrin, Lyle, & Quach, 2002; Huber, Shiffrin, Quach, & Lyle, 2002; Weidemann, Huber, & Shiffrin, 2005, 2008). However, this model is static in nature (although see Huber, 2008a), and different stimulus durations (e.g., duration of the previous object) required different free parameters for the probability of source confusion (α) and discounting (estimate of α). Furthermore, it was not clear how the brain might implement feature discounting. To address these limitations, a different ROUSE model was formalized with neural dynamics.

2.2. Habituation Through Synaptic Depression

The neural habituation ROUSE model (Huber & O'Reilly, 2003) assumes that features exist in a cascaded hierarchy, similar to McClelland and Rumelhart's (1981) interactive-activation model of word superiority effects. As applied to reading (see the right-hand panel of Fig. 5.2), the first level captures the dynamic activation of simple visual features, such as the line segments that are identified in primary visual cortex (Hubel & Wiesel, 1959). These representations in turn activate orthographic representations. Finally, orthographic representations activate lexical-semantic representations. Critically, lexical-semantic activation also provides feedback onto orthographic representations, which gives the model attractor dynamics. Each node in the model describes the average neural response of many neurons that have similar input and output connections. The activation equation specifies a rate-coded (rather than spiking) value at every millisecond after presentation of visual input (O'Reilly & Munakata, 2000).

Because the activation equation in the neural ROUSE model updates activation gradually, the model naturally integrates information over time and will blend previous and current inputs (i.e., source confusion). However, unlike most neural networks, this model also includes neural habituation for all of its nodes. The specific form of habituation used in the neural ROUSE model is termed 'synaptic depression' (Abbott, Varela, Sen, &

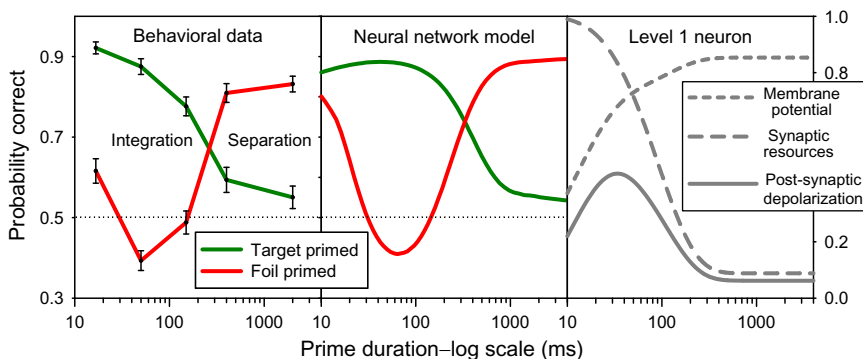


Figure 5.3 Illustration of the neural ROUSE model applied to immediate repetition priming in a masked priming paradigm with forced-choice testing. The left-hand panel shows the accuracy results of Huber's (2008b) experiment 1, which used the display sequence shown in Fig. 5.4. The middle panel demonstrates that the neural ROUSE model can adequately explain these results. The right-hand panel demonstrates the behavior of the level 1 visual nodes of the model with best-fitting parameters, demonstrating the manner in which the output (postsynaptic depolarization) of the simulated neurons habituates owing to the loss of synaptic resources as a function of stimulus duration. Adapted from Huber, Tian, Curran, O'Reilly, and Woroch (2008), with permission.

Nelson, 1997; Grossberg, 1969; Nelson, Varela, Sen, & Abbott, 1997; Tsodyks & Markram, 1997), which is the dynamic loss and recovery of synaptic resources (e.g., neurotransmitter) that enable a neuron to effectively communicate with other neurons. As seen in the right-hand panel of Fig. 5.3, the connection between any pair of nodes is captured by presynaptic activity (i.e., membrane potential), the currently available synaptic resources, and the output to the receiving node (i.e., postsynaptic depolarization), which is the product of the first two variables. Roughly speaking, this can be thought of as the average spike rate, the effect of each spike, and the product of these, which describes synaptic output. When an object is shown to the model, the synaptic resources of the representations associated with that object gradually become depleted over the span of a few hundred milliseconds. However, the timing of this habituation process will depend on the specific properties of the visual sequence, the strength of the learned representation, and attention. Applications of the model also assume that higher levels integrate and deplete at a slower rate; for instance, words are more likely to change from one moment to the next as compared to the semantic topic (Landauer & Dumais, 1997).



3. RESULTS: WORDS, FACES, PLACES, AND SEMANTICS

Both the Bayesian and the neural ROUSE models assume that previously viewed features are discounted, which reduces source confusion between a previously viewed object and a subsequent object. Both models also produce repetition deficits as a result of feature discounting. However, the neural ROUSE model additionally describes the dynamic processes that give rise to these effects—because synaptic resources are depleted for a period of time after the prolonged presentation of an object, the perceptual response to an immediate repetition is less than it otherwise might have been. As applied to the example found in [Fig. 5.1](#), this makes it difficult to detect the low-contrast masked repetition when the first triangle is presented for 2000 ms. Because the neural ROUSE model assumes that habituation occurs at all levels of processing, the notion of perceptual aftereffects is expanded to ‘cognitive aftereffects.’ Thus, aftereffects are predicted to exist not only for low-level perceptual properties like visual line segments but also for abstract high-level properties like the meaning of a word. Because temporal integration and the need to reduce source confusion exist for all forms of feature detection, similar effects are predicted for a wide variety of stimuli and tasks that involve immediate repetitions. We have tested these predictions in separate studies as reviewed later.

3.1. Word Repetitions

Many different tasks involve RSVP sequences although a large proportion of these studies use words. Among RSVP word studies, many simplify the situation by using a single ‘prime’ word that is followed by a ‘target’ word. A variety of tasks are used depending on target duration: experiments that use clearly visible targets examine reaction times (RTs) to name the target or verify that the target is a properly spelled word (i.e., lexical decision), whereas experiments that use short-duration masked targets (i.e., threshold identification) examine accuracy. In addition to these tasks that examine reading performance, other tasks present sequences of two words and test recognition memory or change detection. In this section, I summarize the results of four different studies that examined different tasks and different measures in tasks that contained immediate word repetitions. Each of these studies tested key predictions of the neural ROUSE model.

3.1.1 Threshold Identification

When primes are brief, nearly any type of similarity between prime and target will enhance performance as compared to control conditions that present an unrelated prime (Lukatela, Eaton, Lee, Carello, & Turvey, 2002; Lukatela, Frost, & Turvey, 1998; McKoon & Ratcliff, 1992; McNamara, 2005; Meyer & Schvaneveldt, 1971; Meyer, Schvaneveldt, & Ruddy, 1974; Neely, 1991; Pecher & Raaijmakers, 1999; Perea & Gotor, 1997; Peressotti & Grainger, 1999). That this also occurs with repetition priming (Evelt & Humphreys, 1981) supports the hypothesis that briefly presented words become blended with subsequent words, producing a facilitation when the two words are identical. However, there are two limitations to this result. First, the task in these experiments does not explicitly test whether observers are capable of differentiating between prime and target (i.e., it is not clear whether the facilitation reflects a blend of prime and target vs. enhanced perception for the target). Second, longer-duration primes are problematic with these tasks because observers will adopt a strategy of preparing a response based on the prime's identity (Hutchison, 2007). In the study reported next, both of these limitations were addressed by using a forced-choice variant of threshold identification. More specifically, by having an equal number of trials that prime the incorrect choice (foil-primed) versus the correct choice (target-primed), there is no effective strategy based on the prime (see Fig. 5.4). Observers were explicitly told this and trial-by-trial accuracy feedback reinforced this assertion. The foil-primed condition can be viewed as a test of whether observers can differentiate between prime and target because the choice in this condition is between the prime and the target (i.e., which choice word appeared second).

Figure 5.4 shows two of the four conditions examined in experiment 1 of Huber (2008b). The prime was shown as a doubled-up version so that there was some visual difference between the prime and a repeated target (alternatively, this can be achieved by switching from lower to upper case or by inserting a brief blank screen between prime and target). Five different prime durations were used and conditions occurred in random order during the experiment. The target flash duration was set separately for each observer to place accuracy at 75%. The duration of the mask that followed the target was set so the time between the onset of the target and the onset of the test display was 500 ms.

The left-hand panel of Fig. 5.3 shows the choice accuracy results from this experiment. As predicted, short prime durations revealed a pattern

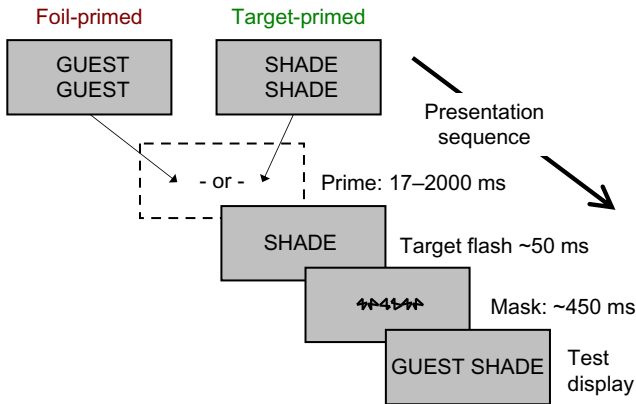


Figure 5.4 The display sequence used in the Huber's (2008b) experiment 1. The experiment tested five different prime durations from the range of values shown in the figure. There was also a baseline neither-primed condition and a condition that presented a mask instead of a prime (not shown). The test display remained onscreen until the observer chose the word judged to be the briefly flashed target. Adapted from Huber (2008b), with permission.

indicative of integration, or blending, resulting in increased accuracy in the target-primed condition but equivalently decreased accuracy in the foil-primed condition (a baseline neither-primed condition was approximately halfway between these conditions). In particular, the foil-primed condition suggests that observers were confused as to which word was first versus second and frequently mistook the prime for the target, resulting in significantly below chance performance in the case of a 50 ms prime. However, this pattern of costs and benefits completely reversed when the prime duration was 400 ms or longer. As predicted, long prime durations revealed a pattern indicative of separation, or discounting, resulting in repetition deficits in the target-primed condition but increased accuracy in the foil-primed-condition. The finding of better performance in the foil-primed condition than the baseline condition suggests that observers knew that the target was something other than the prime (i.e., enhanced change detection)—in this condition, observers did not necessarily have to identify the target but merely appreciate that target was something different than the prime, causing them to avoid choosing the foil that repeated the prime.

The middle panel of Fig. 5.3 demonstrates that the neural ROUSE model can adequately explain these results. The right-hand panel shows the behavior of the first-level visual nodes of the model with best-fitting parameters. The rise and fall of output from these nodes mirror the accuracy

pattern for the foil-primed condition. In other words, the prime duration that produced the strongest visual response to the prime at the time when the target appeared was also the prime duration that produced the greatest amount of source confusion between prime and target. The model also provided an accurate explanation of the baseline neither-primed condition as well as a condition that presented a mask of different durations instead of a prime word (not shown).

3.1.2 Episodic Recognition

The immediate repetition priming paradigm in threshold identification has many similarities to a classic memory illusion of [Jacoby and Whitehouse \(1989\)](#). Similar to the paradigm used by [Huber \(2008b\)](#), their paradigm compared a brief subliminal prime to an easily seen long-duration prime, and in both cases, the prime word was followed by a test word that might or might not be identical to the prime. However, the task in their experiments was not the identification of the test word but rather episodic recognition (i.e., did the test word appear on a previous study list). Nevertheless, the results were strikingly similar to the threshold identification results—for both paradigms, brief primes caused a bias to endorse a primed test word, whereas long-duration primes caused a bias against endorsing a primed test word. For subliminal prime words in the episodic recognition paradigm, enhanced perceptual fluency is thought to cause the observed bias ([Jacoby & Whitehouse, 1989](#); [Joordens & Merikle, 1992](#); [Lindsay & Kelley, 1996](#); [Lloyd, Westerman, & Miller, 2003](#); [Rajaram, 1993](#); [Whittlesea & Jacoby, 1990](#)). More specifically, when the test word is a repetition of the prime word, it is easier to perceive the test word and this enhanced perceptual fluency increases the sense of familiarity for the word. The cause of the reverse bias with easily seen primes is thought to reflect an overcorrection for this misattribution of perceptual fluency ([Jacoby & Whitehouse, 1989](#); [Whittlesea & Williams, 2000](#)). However, it is not clear whether there is any perceptual fluency following a long-duration prime, whereas my threshold identification results suggest that there might even be a perceptual disfluency. As explained next, my coauthors and I undertook a series of experiments designed to determine whether the negative priming effect with easily seen primes in episodic recognition is due to a process designed to correct for the effect of perceptual fluency or whether it might instead reflect perceptual disfluency ([Huber, Clark, Curran, & Winkielman, 2008](#)).

Rather than use subliminal primes, we used 100 ms short-duration primes, which pilot work found to be above the identification threshold. To discourage any strategic responding, all experiments used forced-choice testing and all experiments explicitly informed participants that there was no effective strategy based on the prime, with trial-by-trial accuracy feedback reinforcing this assertion. Despite these changes, the same Jacoby/Whitehouse memory illusion was observed, with short prime durations causing a bias to remember the primed-choice word, whereas long prime durations caused a bias against remembering the primed-choice word. However, just because participants could be aware of the 100 ms primes does not mean that they were aware of the primes. To encourage attention to the primes, some experiments used a secondary task in relation to the primes (can this word be a verb?), with it unknown at the start of the display sequence whether the prime would be a brief flash or whether it would remain on the screen for this verb task prior to the recognition test. Furthermore, one experiment tested awareness of the brief primes, finding that forced-choice accuracy for prime identification was 100% for 100 ms primes even though it was not known at the start of the trial which task (prime identification or target identification) would be performed. Finally, two of the experiments broke the results down into familiarity-based recognition versus explicit recall of the study episode (Mandler, 1980; Tulving, 1985). In these experiments, participants studied word pairs but recognition was for single items. After each recognition choice, participants were asked if they could recall the word that had been studied with the target word, regardless of whether they did or did not recognize the target word. As expected, for recognition trials that were followed by correct recall, there were no priming effects.

The last experiment of this study examined a range of prime durations and the results are shown in Fig. 5.5. The longest prime duration of 2430 was not a fixed duration. Instead, this duration is the average time that participants took to decide that the prime was a verb. The neural network behavior shown in Fig. 5.5 comes from the same neural ROUSE habituation model as described earlier, with the same parameters used in Fig. 5.3. However, because this was an episodic recognition task, it was assumed that the lexical-semantic level of the model provides input to a familiarity response. For the model behavior shown in Fig. 5.5, there was one free parameter reflecting the strength of the episodic connection between the lexical-semantic level and the familiarity level for a previously studied word and a second free parameter reflecting the magnitude of noise in the decision

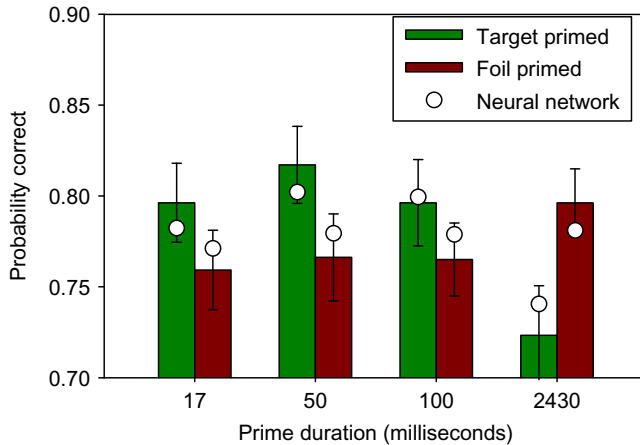


Figure 5.5 Forced-choice recognition accuracy as a function of prime duration for experiment 5 of Huber, Clark, et al. (2008). Similar to threshold identification, each trial presented a prime word followed by a choice between two words. However, there was no briefly flashed target word and the task was to choose the previously studied word. The neural network was the same neural habituation model used for threshold identification with the addition of a familiarity level with learned connections for targets. Adapted from Huber, Clark, et al. (2008), with permission.

process—with these two free parameters, the model provided an accurate description of the eight conditions.

3.1.3 Change Detection

The studies reviewed so far examined the disadvantages of neural habituation, highlighting situations in which perception or memory was impaired for a repeated word after prolonged exposure to the first instance of that word. However, ROUSE assumes that habituation exists to reduce source confusion, making it easier to separate previous objects from subsequent objects. By habituating to the previous object, new attributes of the visual environment are made salient—habituation enhances novelty detection. To test this prediction, my collaborators and I again used the visual presentation of words (Davelaar, Tian, Weidemann, & Huber, 2011), but unlike the previous studies, the task was change detection rather word identification or episodic recognition.

Studies of visual change detection often use displays with many objects presented simultaneously, identifying situations in which observers fail to detect change if they are not focusing their attention on the correct location

or changed attribute (Rensink, 2000, 2002; Simons, 1996; Simons & Levin, 1997). In contrast, our study measured the efficiency of change detection rather than the limitations that attention places on change detection. Therefore, we used a simple stripped-down procedure with a single fixated cue word followed by a single fixated target word that was either identical or different from the cue word (cue words were always in lower case and target words were always upper case). This paradigm is most similar to the study of Johnston and Hale (1984), which is considered an early example of repetition blindness (Kanwisher, 1987; Kanwisher, Kim, & Wickens, 1996). The only difference between our paradigm and that of Johnston and Hale was cue duration—in their study, the cue duration was at the identification threshold and performance was measured with signal detection theory (Macmillan & Creelman, 1991), whereas the cue words in our study were easily seen, with the efficiency of change detection measured with RT.

Our experiments used both 200 and 1000 ms cue due durations although in both cases, the cues were easily seen and observers were nearly perfect in their responses. The results did not differ as a function of cue duration and the reported results collapsed across cue duration. In experiment 1, we collected magnetoencephalography (MEG) measurements to test whether the pattern of neural responses was similar when the target and cue differed as compared to the pattern of neural response when target and cue were the same word. These patterns were not significantly different, implicating the same neural processes for both conditions. Furthermore, neural response magnitude was greater for different trials as compared to same trials, supporting the hypothesis that the underlying variable used to determine the appropriate behavioral response was change detection rather than repetition detection.

Given that observers appeared to detect changes rather than repetitions, key predictions of the neural ROUSE model were tested in experiment 2. The left-hand column of Fig. 5.6 shows the summed lexical-semantic level response of the neural ROUSE model for three different priming conditions when the target and cue differed. First, consider the unprimed condition in which both cue and target are seen for the first time in the experiment. Because the two words are different, the summed activity across the whole of the lexical-semantic level receives a second boost when the target appears (in this example simulation, the target word was presented 400 ms after the cue word). We hypothesized that this boost of new lexical-semantic activation is the measure used to determine the behavioral response—because there is new boost of lexical-semantic activation, the observer quickly

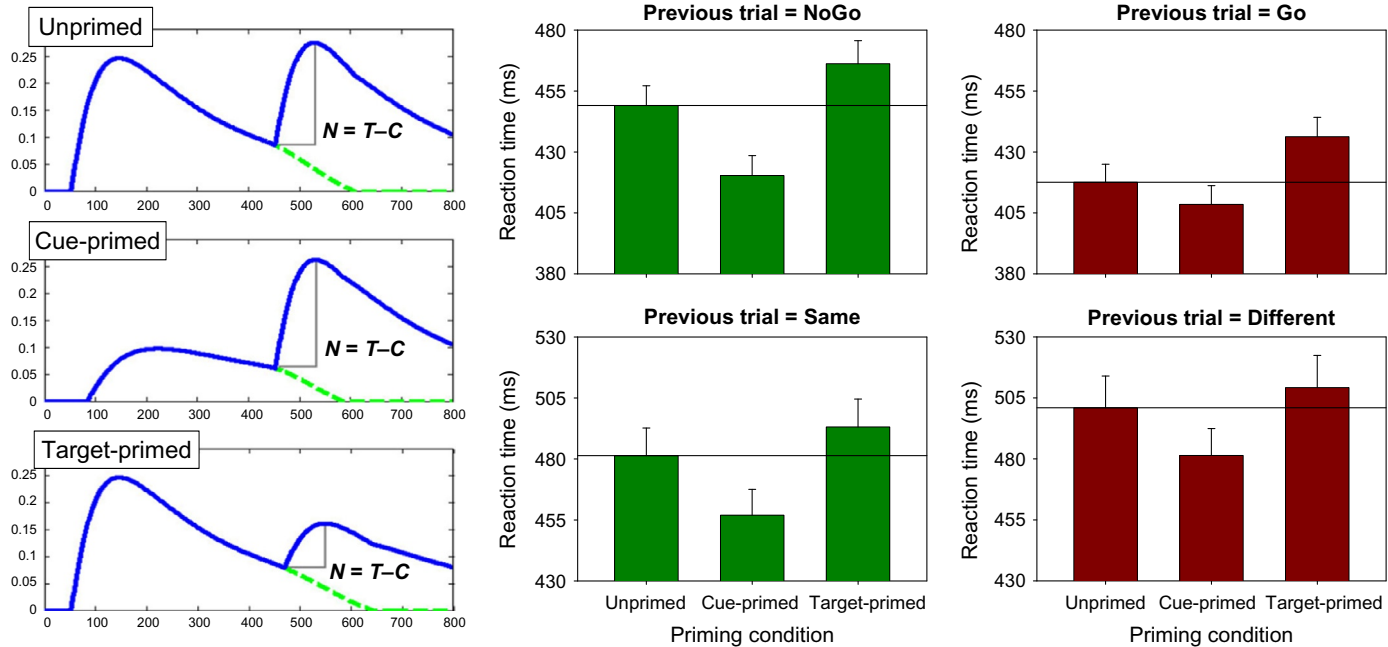


Figure 5.6 Model predictions and reaction time results for experiment 2 of [Davelaar et al. \(2011\)](#). The left-hand column shows predictions of the neural ROUSE model. The blue line shows the summed lexical-semantic activation, which has a second peak to the target word, presented 400 ms after the cue word in this example simulation. Because the target word is different than the cue, there is a second boost in the blue line, and the magnitude of this change (Novelty = Target – Cue) is the measure used to rapidly detect changes. The green dashed line in the figure shows the magnitude of the lexical-semantic activation to the cue word, with the difference between the blue line (summed activation) and the green dashed line showing target word activation. The target-primed condition stipulates that the target of the current trial be the same as the target of the previous trial, whereas the cue-primed condition stipulates that the cue of the current trial be the same as the target of the previous trial. Because of lingering neural habituation for the repeated word, this enhances change detection in the cue-primed condition but impairs change detection in the target-primed condition. These predictions were confirmed with the reaction time (RT) to correctly detect change in both a go/no-go task (i.e., respond only when the target differed from the cue) and a same/different task. The middle column shows RT when cue and target were the same on the previous trial, whereas the right-hand column shows RT when cue and target were different on the previous trial. Adapted from [Davelaar et al. \(2011\)](#), with permission.

detects that the target word is different than the cue word. Formally, this measure is the magnitude of lexical-semantic activation increase when the target appears, as shown in Fig. 5.6 by the equation: $\text{Novelty} = \text{Target} - \text{Cue}$ ($N = T - C$).

In the neural ROUSE model, the rate at which synaptic resources are recovered is substantially slower than the rate at which they become depleted. Thus, even with several seconds between repetitions, there is a repetition deficit. This allowed us to examine whether habituation enhances change detection. The target-primed and cue-primed predictions shown in the second and third graphs are for simulations in which the cue or target of the current trial was a repetition of the target word from the preceding trial, with a 2.5 s break between the end of the previous trial and the start of the current trial. Because of lingering habituation for the primed word, the lexical-semantic response to the primed word is substantially less as compared to the unprimed situation, and this was predicted to affect performance in different ways for each condition. More specifically, in the cue-primed condition, there is less of a response to the cue word and thus a larger boost in summed activation when the target is presented, resulting in enhanced change detection and faster RTs. In contrast, in the target-primed condition, this is less of a response to the target word and thus a smaller boost in summer activation when the target is presented, resulting in change detection difficulty and slower RTs. These predictions were confirmed regardless of the same/different status of the previous trial (middle column vs. right-hand column) and regardless of whether the task involved responding only on different trials (go/no go; top row) or same/different judgments on every trial (bottom row).

3.1.4 Neural Habituation

A key advantage of using a neural model is that it can address both behavioral and neural data. However, the studies reviewed earlier did not rigorously test neural predictions of the neural ROUSE model. The model does not make predictions for specific cortical locations but it does make predictions for the time course of neural activation for different representations. These predictions are best tested with event-related voltage potential (ERPs) or magnetic field strength (MEG). Therefore, my coauthors and I replicated experiment 1 of Huber (2008b) while recording ERPs and event-related MEG (Huber, Tian, et al., 2008).

The left-hand panel of Fig. 5.7 shows the a priori predictions of the neural ROUSE model using the parameters that best described the behavioral

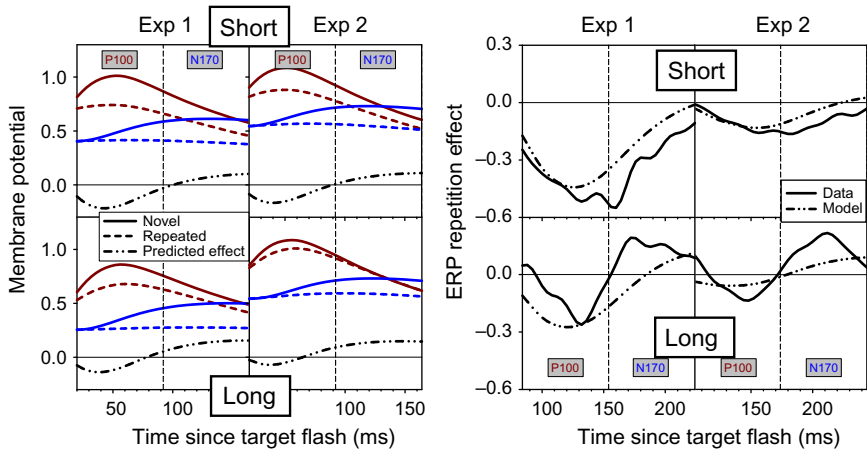


Figure 5.7 A priori predictions of the neural ROUSE model for ERPs, observed ERPs, and best-fitting model results (Huber, Tian, et al., 2008). Experiment 1 used the 150 and 2000 ms prime durations of experiment 1 of Huber (2008b), and the a priori predicted repetition effect is shown in the left-hand panel based on the parameters that fit the behavioral data of Huber's (2008b) experiment 1. The yellow lines show predicted activation for the orthographic level of the model, and the blue lines show predicted activation for the lexical-semantic level of the model. Because the target word is different than the prime for the foil-primed condition (labeled 'novel'), two words are simultaneously active at the time of the target flash, resulting in greater activation (i.e., temporal integration) as compared to the target-primed condition (labeled 'repeated'). Assuming that the lexical-semantic level underlies the N170, the activation levels of the lexical-semantic level are subtracted from the orthographic level to produce the 'predicted effect' of repetition priming. These predictions were confirmed, as seen in the graphs of the right-hand panel. The model was applied to all electrodes and each observer separately and the average of these is shown in the 'data' and 'model' curves in the right-hand panel (see text for additional details). Experiment 2 used two different prime words on every trial, with the first appearing 2000 ms prior to the target, while the second appeared 150 ms prior to the target, such that all conditions were visually identical up until the time when the target flash occurred. Adapted from Huber, Tian, Curran, O'Reilly, and Woroch (2008), with permission.

data of Huber's (2008b) experiment 1. These predictions were made in terms of electrodes placed over the posterior scalp. In the priming paradigm, there are no retinotopic repetitions (i.e., even though words and letters repeat, they do not appear in exactly the same place) and so it is only the orthographic and lexical-semantic levels of the model that vary as a function of repetitions. There is a large literature examining late ERP responses to visually presented words, which are thought to reflect higher-level processes such as sentence integration. However, the neural ROUSE model was

designed to capture early perceptual responses. Studies examining these early ERP waveforms in response to visually presented words find that priming and other manipulations affect an early positive potential around 100 (P100) and a negative potential around 170 (N170), and we hypothesized that the orthographic level is the principle source of the P100, whereas the lexical-semantic level is the principle source of the N170 (Holcomb & Grainger, 2006; Petit, Midgley, Holcomb, & Grainger, 2006; Sereno, Brewer, & O'Donnell, 2003; Sereno, Rayner, & Posner, 1998). The left-hand panel of Fig. 5.7 shows the simulated activation of these two levels for the target-primed condition, which is relabeled 'repeated,' and the foil-primed condition, which is relabeled 'novel,' with this relabeling designed to reflect the relationship of the prime to the target flash (rather than the prime to the choice words). As seen in the figure, the peak responses of the model mimic the timing of the P100 and N170 if 40 ms is added to the x -axis, reflecting the delay between the time when light first hits the eyes and the time when primary visual cortex responds (Inui & Kakigi, 2006). Because the same posterior electrodes measure both P100s and N170s, we subtracted the activity of the lexical-semantic level (the N170) from the activity of the orthographic level (the P100), giving rise to the black dashed/dotted 'predicted effect' lines at the bottom of each graph.

To avoid differences between short- and long-duration priming that might result from conscious awareness of the prime in only one condition, the short prime duration in this study was 150 ms (i.e., long enough to be easily seen) and the long prime duration was 2000 ms. Otherwise, experiment 1 of this study was identical to experiment 1 of Huber (2008b). For this design, the prime and target ERP waveforms were overlapping in the short prime condition but not in the long prime condition, which complicates the analyses. Experiment 2 addressed this concern by presenting two different prime words on every trial, with the first occurring 2000 ms before the target flash, whereas the second appeared 150 ms before the target flash. Thus, all conditions were visually identical at the moment when the target word first appeared. Nonetheless, as seen in the a priori predictions of Fig. 5.7, the predictions for both experiments were similar—during the time period of the P100, the model predicted smaller voltage potential for repetitions, and during the time period of the N170, the model predicted larger voltage potential for receptions. These predictions reflect temporal integration between prime and target—in the novel condition, two different words are presented in sequence and so there is more total activation owing to the

simultaneous activation of two different words. Habituation serves to modulate this integration effect as seen by comparing the short- versus long-prime-duration predictions. More specifically, there is a substantial habituation effect for the orthographic level (the difference between the repeated and the novel conditions is diminished for the orthographic level), resulting in much less of an integration effect for the source of the P100. In contrast, the lexical-semantic level is relatively unaffected by the prime duration manipulation because the time constant of the lexical-semantic level is smaller (i.e., lexical-semantic habituation is slower to accrue). In summary, increasing prime duration was predicted to shift the repetition effect predictions upward during both the P100 and the N170 time periods because the orthographic representation contributes to the ERP response during both time periods.

The repetition effect data from these experiments were modeled in full, providing an explanation of all electrodes during these two time periods, separately for each observer, by assuming that these two levels of the model, with dynamics fixed a priori, specify the magnitude of activation for equivalent source dipoles (Berg & Scherg, 1994; Stok, 1986). This is a radically different solution to the ‘inverse problem’ of electrophysiology because it is based on a particular assumed model for the number of active brain regions and the dynamic time course of those regions. In applying the model, the only free parameters were a temporal offset to capture the delay between retinal input and early cortical responses and the cortical locations and orientations of the dipoles, with different values of these parameters for each observer. As a result of these factors, the model behavior, averaged across observers as shown in the right-hand panel of Fig. 5.7, was changed slightly from the a priori predictions. Although the model was applied to all electrodes, the right-hand panel of Fig. 5.7 is an average of the data that treated the electrodes as if they were posterior electrodes. More specifically, if an electrode revealed a positive rather than a negative repetition effect during the P100 time window, the mathematical sign of that electrode was flipped before averaging. This was done for both the real data and the model data, separately for each observer, with the results shown in the graphs of the right-hand panel of Fig. 5.7. In line with the a priori predictions, both experiments produced negative repetition effects during the P100 and positive repetition effects during the N170, and these effects shifted in the positive direction for the long-prime-duration condition.

This modeling revealed substantial individual differences in terms of the placement of the best-fitting equivalent dipoles for the orthographic and

lexical-semantic levels. To assess these differences, and to test the generality of the findings, experiment 3 used the same design as experiment 2 while recording event-related MEG. Indeed, the same pattern of results was obtained in terms of repetition priming and the effect of increasing prime duration. Furthermore, the topographic patterns for the M100 and M170 were substantially different for each individual, as predicted from the ERP modeling results.

3.2. Face, Place, and Semantic Repetitions

The studies mentioned earlier used immediate repetition of words in situations where the letters of one word might be confused with then next word. However, the ROUSE theory not only is a theory of word priming but also concerns temporal integration and separation more generally. Thus, a crucial test of the theory is whether similar effects exist for other types of stimuli and representations.

3.2.1 Face Repetitions

Similar to expertise with reading, most people have a high degree of expertise when it comes to processing the identity and attributes of faces. However, there is evidence that face expertise is fundamentally different in important ways (Kanwisher, McDermott, & Chun, 1997). In the neural ROUSE model of reading, expertise is implemented through connection strength in a perceptual hierarchy and through attractor dynamics via feedback connections. To test the generality of this model, Rieth and Huber (2010) examined whether the same model could be applied to threshold face identification and the immediate repetitions of faces. Of particular interest, we contrasted upright and inverted faces considering that face inversion effects are one way that faces differ from other visual objects (Yin, 1969).

The paradigm used by Rieth and Huber (2010) was identical to experiment 1 of Huber (2008b), except for the stimuli—the sequence of displays was as seen in Fig. 5.4 except that faces were shown instead of words. The faces were previously unknown to the observers and each face only appeared on one trial (i.e., there was no opportunity to learn these particular faces). Besides replicating the transition from positive to negative priming, the initial experiments found an intriguing individual difference effect that did not occur with words. Using a post hoc median split of observers based on the target flash duration needed to place performance at the 75% threshold, we found that the ‘fast’ observers (i.e., individuals who needed shorter target durations for threshold performance) also had a faster/stronger transition

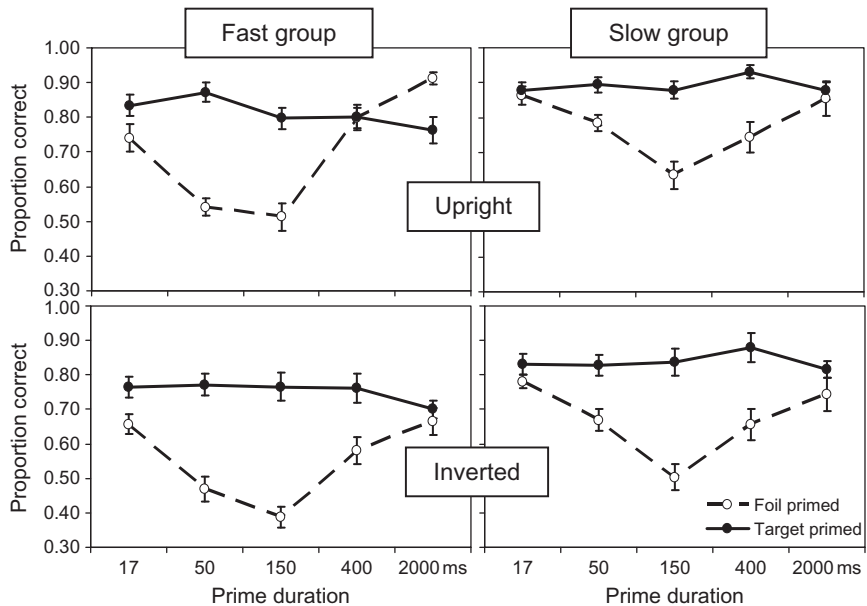


Figure 5.8 Immediate face repetition priming for upright and inverted faces (Rieth & Huber, 2010), using the same paradigm as the word priming experiment 1 of Huber (2008b). On each trial, all of the face images were upright or inverted throughout the display sequence. The first part of the experiment determined the target duration needed to place accuracy at the 75% threshold, and a median split of these threshold durations was used to create a post hoc ‘fast group’ (i.e., shorter target durations) and a ‘slow group’ (i.e., longer target durations). Adapted from Rieth and Huber (2010), with permission.

from positive to negative priming as a function of increasing prime duration. Additional experiments replicated this effect and ruled out uninteresting alternative explanations. Experiment 4 compared performance for upright and inverted faces—on each trial, either all of the face images were upright or all of the face images were inverted. Figure 5.8 shows the results broken down by face inversion and by the duration needed for threshold performance (fast group vs. slow group). As seen in the figure, the fast group produced a different priming pattern for upright versus inverted faces, whereas the priming pattern for the slow group was essentially the same regardless of face inversion, except for a main effect (i.e., worse performance with inverted faces). Furthermore, the only situation that produced negative priming (i.e., target-primed < foil-primed) was the fast group with upright faces.

We did not initiate this study expecting to find individual differences. However, these differences are naturally explained by the neural ROUSE model. We hypothesized that expertise with upright faces stems from stronger feedforward connections between the second level (i.e., the identification of face parts) and the third level (i.e., the identification of specific configurations of face parts that uniquely specify a particular face) of processing. Besides modulating the speed of face identification, this connection strength affects habituation because synaptic depression is caused by recent activation. Thus, a stronger connection between the second and third level of the model causes faster identification of the face (i.e., a shorter target duration is needed for threshold performance) as well as earlier/stronger habituation (i.e., more rapid depletion of the synaptic resources for the connections between the second and third level). In applying the model to these data, the only parameter allowed to vary between the upright and the inverted face conditions was this connection strength. The fits of the model were remarkably accurate with the values: (1) fast group upright, 2.05; (2) fast group inverted, 0.73; (3) slow group upright, 0.83; and (4) slow group inverted, 0.50. In other words, upright faces were processed 2.81 times as strongly as inverted faces for the group of participants that was better at threshold face identification, whereas this ratio was only 1.66 for the group that was worse at threshold face identification.

3.2.2 Place Repetitions

The studies mentioned earlier described the rise and fall activation dynamic of visual features. In the case of upright versus inverted faces, this dynamic differed in the predicted manner, with well-learned representations (i.e., upright faces) activating and habituating more quickly. However, upright and inverted faces may differ in ways besides amount of experience. A fully controlled test of this prediction requires a training study in which observers receive more experience with some features than others. Nevertheless, because it is difficult to identify the psychologically relevant features, it is challenging to design such a study.

Instead of using visual features, the location where an object is placed can be considered a feature (Cohen, Servanschreiber, & McClelland, 1992). Furthermore, sequences of locations need to be temporally separated to avoid positional source confusion. Indeed, a similar rise and fall dynamic is observed in spatial cuing studies—a short stimulus onset asynchrony (SOA) between a spatial cue and a subsequent target (e.g., 100 ms) facilitates detection of the targets at the cued location (Posner, Snyder, & Davidson, 1980), whereas

a slightly longer SOA (e.g., 350 ms) makes it difficult to detect targets (Posner & Cohen, 1984). The latter effect is termed ‘inhibition of return’ (IOR), although the mechanism that produces IOR is debated and likely differs with different kinds of IOR effects (Berlucchi, 2006; Taylor & Klein, 2000). Following the suggestion of Dukewich (2009), it may be that IOR effects reflect habituation, although the specific nature of that habituation will depend on task/stimulus details.

Some training studies of spatial cuing have manipulated how frequently targets appear in different locations (Farrell, Ludwig, Ellis, & Gilchrist, 2010) and others have manipulated the frequency of different SOAs (Gabay & Henik, 2008). However, the combination of these factors has not been examined, and it is this combination that tests key predictions of the neural ROUSE model as applied to spatial features. Consider a simple speeded target detection task with two possible left/right locations where cues (e.g., a brightened square) and targets (e.g., an asterisk) can appear. One form of training presents targets at the cued location (i.e., a valid cue) with a short SOA or at an uncued location (i.e., an invalid cue) with a longer SOA. An optimal adaptation to this training would involve a rapid shift of attention to the cued location followed by a shift to the uncued location. Such behavior corresponds to the typical cuing pattern, with facilitation following short SOAs but deficits following long SOAs (because a valid cue with a long SOA is in contradiction to training). Next, consider training with targets appearing opposite the cue with a short SOA or at the cued location with a long SOA. This training contradicts the standard pattern of results and optimal adaptation would involve a rapid shift of attention away from the cue followed by a shift to the cue. However, if exogenous cues automatically activate spatial attention features, an initial shift away from the cue would be difficult to learn.

To address this issue, we performed a spatial cuing training study and the results of our first experiment are shown in Fig. 5.9 (Rieth & Huber, 2013). In the figure, the red circles highlight the combinations of SOA and cuing that observers experienced during the first phase of the single-session experiment. Remarkably, observers remained completely unaware of these manipulations, presumably because targets appeared equally on either side (i.e., observers did not explicitly detect these cue/SOA contingencies). After training, observers experienced all 10 conditions shown in the figure in equal proportions. Throughout each trial, observers kept their eyes fixated on a central cross, and target-absent catch trials were used to make sure that observers only responded to the appearance of targets.

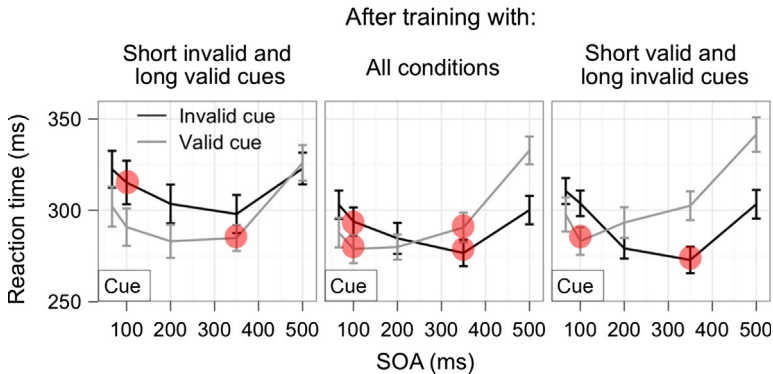


Figure 5.9 Spatial cuing as a function of stimulus onset asynchrony (SOA) between the onset of a square (the cue) and a subsequent asterisk (the target) as reported in experiment 1 of [Rieth and Huber \(2013\)](#). Each graph shows average reaction time to detect the target for separate groups of observers that were first trained with the conditions highlighted by the red circles. After training, all 10 of the conditions were tested. Valid cues appeared at the target location and invalid cues appeared at the left/right opposite location. *Adapted from Rieth and Huber (2013), with permission.*

As seen in [Fig. 5.9](#), target detection RTs were strongly affected by training for SOAs greater than 200 ms. Indeed, the typical IOR effect was fully reversed for the group shown in the left-hand graph, suggesting that attention to the cued location was maintained for these individuals. In contrast, there was no reliable effect of training for SOAs that were less than 200 ms. This suggests that exogenous cues automatically grab spatial attention (i.e., automatic spatial feature attention). However, the cue always appeared for 150 ms (as indicated by the box in the lower left-hand corner of each graph), and it is possible that the increased visual contrast for short SOA targets made these contingencies difficult to learn. Experiment 2 replicated these effects and ruled out this explanation by using shorter duration cues that always disappeared before the target. Another explanation of these results supposes that attention is lazy or cannot shift quickly enough to fully adapt to a contingency that requires a rapid shift to/from the cue followed by a shift to the opposite side—instead, perhaps, the system only learns the second contingency because 100 ms after the cue, there is certainty as to where the target will appear if it has not already appeared. Experiment 3 addressed this alternative by using only a single short SOA contingency. However, to avoid having the target always appear on the cued or uncued side, probabilistic

training was used (e.g., 87.5% of targets appeared at the cued side 100 ms after the cue, whereas the remaining targets appeared at the uncued location after 100 ms). Finding some support for this alternative explanation, there were modest training effects for the short SOAs in this experiment, although cuing facilitation was merely reduced, rather than eliminated or reversed.

These experiments demonstrated that the rise and fall of spatial attention can flexibly adapt to the spatial–temporal regularities. However, these experiments also found important limitations for this adaptation. These results and limitations are consistent with these hypotheses that (1) an exogenous cue automatically activates spatial attention features at the cued location; (2) spatial attention features habituate, resulting in a shift of attention away from the cue and also difficulty reactivating the same spatial attention feature when a subsequent target appears at the cued location; and (3) with training, the system can learn to maintain spatial attention feature activation. A full implementation of this model awaits additional experiments to determine whether this maintenance of attention is a top–down influence (i.e., maintained activation of spatial attention features despite habituation) or whether it reflects an adaptation of the habituation mechanism (e.g., an adjustment to the dynamics of synaptic depression).

3.2.3 *Semantic Repetitions*

To test whether habituation is a general mechanism for temporal separation, Xing Tian and I performed a series of experiments examining temporal separation of semantic features (Tian & Huber, 2010). These experiments relate to the classic phenomenon of ‘semantic satiation,’ in which a word repeated 20–30 times appears to lose its meaning (Severance & Washburn, 1907). However, rather than asking observers to speak the word aloud, we used the paradigm of Smith and Klein (1990) that visually presents a category name repeatedly followed by a match/mismatch judgment to visually presented category member. In our version of the task, observers experienced a series of 20 cue–target trials of which 10 trials presented a repeated category name, whereas the other 10 trials presented a new category name (see the left-hand panel of Fig. 5.10 for an example sequence of trials). After one such block, a new repeated category name was chosen for the next block of 20 trials. On each trial, the category name appeared for 1 s followed by a category member just below the cue. The 10 trials of the repeated (R) and novel (N) conditions were further divided into 5 match (S for same category) and 5 mismatch (D for different categories) trials, and the order of the 20 trials was random. There are two advantages of this design. First, because each

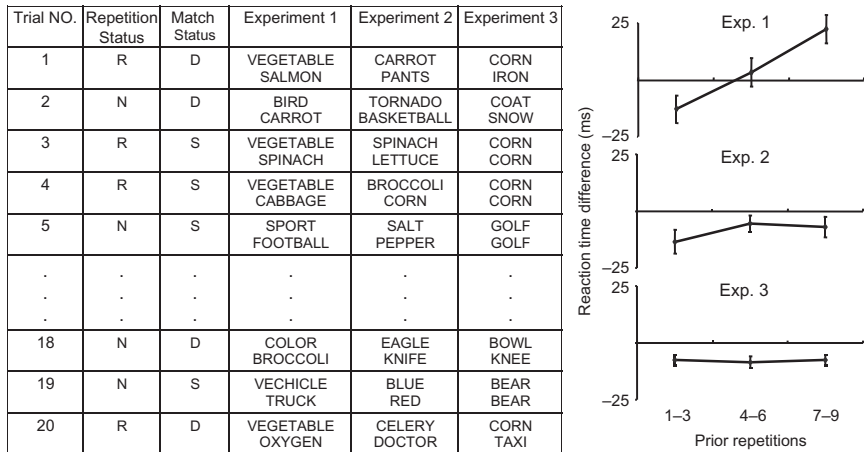


Figure 5.10 The effect of repeating a word, or the meaning of a word, within a block of 20 trials (Tian & Huber, 2010). The left-hand panel shows an example block of 20 trials for the design of each experiment. Every trial presented a category cue for 1 s as indicated by the upper word in each cell, followed by a target word as indicated by the lower word in each cell. 10 of the 20 trials repeated (R) the same category for the cue and the other 10 trials presented new categories (N), with the order of trials randomly determined. Observers gave speeded 'match' (S for same) or 'mismatch' (D for different) judgments. As seen in the right-hand panel, only the design of experiment 1 produced a satiation effect, revealing increasingly slower responses for the repeated category as the number of repetitions increased. Adapted from Tian and Huber (2010), with permission.

block provides data for both the repeated and novel conditions, the results are not confounded with a general sense of fatigue that might arise from repeating the same word. Second, because all trials provide data, the time course of semantic satiation is fully mapped out.

Semantic repetitions provide a unique opportunity for testing whether the connections between representations habituate (i.e., synaptic depression) by examining what happens for words that have similar meaning but different orthography. For semantic satiation to a visually repeated word, we predicted that the loss of meaning occurs because the orthography (or phonology) of the repeated word can no longer activate the associated meaning. If this account is correct, that meaning should be accessible by presenting a similar-meaning word that has a different orthography. In terms of this experimental design, we predicted that the repeated category name (e.g., *vegetable*) can no longer activate the meaning of the vegetable category but a novel vegetable member (e.g., *broccoli*) would activate the meaning of vegetable by using a nondepleted connection.

Based on the change detection study reported in [Section 3.1.3](#), we assumed that ‘mismatch’ judgments are made when the observer detects a sufficiently large boost in activated meaning. For instance, after seeing the category cue *sport*, the presentation of *football* does not result in much new meaning beyond the meaning implied by *sport* and so the observer responds ‘match.’ However, a repeated category name will fail to activate its associated meaning and so a matching category member will activate a great deal of new meaning despite matching the category. In other words, after reading *vegetable* ten times, the observer will no longer think about vegetables and so a presentation of *broccoli* will appear to mismatch the category. As a result, the observer must slow down to avoid errors. In summary, the observer is led astray by experiencing greater contrast (i.e., enhanced change detection) between the repeated category name and a matching category member.

The right-hand panel of [Fig. 5.10](#) shows our results across three experiments, using the designs shown in the left-hand panel of the figure. The results were analyzed in terms of the number of prior repetitions of the repeated or novel condition within each block of 20 trials (match status did not interact with this factor). There are up to nine prior repetitions and these are broken into thirds in the graphs. Median RT for the repeated condition was subtracted from median RT for the novel condition for each observer and the average of these median RT differences is plotted.

As seen in the experiment 1 graph, the first third revealed better performance for the repeated category, the middle third found no difference, and the last third revealed worse performance for the repeated category—over a time period of tens of seconds, there was a repetition benefit (a rise) followed by a repetition deficit (a fall). However, this semantic satiation effect is also consistent with explanations that assume satiation of the orthographic/phonemic representation ([Esposito & Pelton, 1971](#)) or satiation of the semantic representation ([Jakobovits & Lambert, 1962](#)). Experiments 2 and 3 ruled out these alternatives, supporting the claim that these results reflect satiation of the connection between orthography and semantics.

Experiment 2 used a new category member on every trial such that the inferred category repeated but no specific orthography repeated. Unlike experiment 1, this experiment produced facilitation for the repeated category, regardless of the number of prior repetitions. Experiment 3 used repeated words but changed the task to simple word change detection (i.e., directly analogous to the cue-primed conditions of [Section 3.1.3](#)). Similar to experiment 2, this experiment produced facilitation for the repeated

condition, regardless of the number of prior repetitions. Thus, the semantic satiation effect requires repetitions of the same word in a task that requires access to the meaning of that word.

3.2.4 Neural Connectivity with Semantic Repetitions

The study in [Section 3.2.3](#) used behavioral data to test whether the connections between representations habituate. However, a direct test of synaptic depression requires neural data rather than behavioral data. Therefore, we replicated experiment 1 of [Tian and Huber \(2010\)](#) while measuring neural responses with MEG ([Tian & Huber, 2013](#)). In this study, we used two different analyses, providing converging evidence that repeated presentation of the same category cue word causes a progressive weakening of neural connection strength. The first analysis used the nROUSE model as applied to change detection, similar to [Section 3.1.3](#), to make predictions regarding different waveforms as a function of the number of prior repetitions. The second analysis directly tested connectivity change by using dynamic causal modeling (DCM; [Friston, Harrison, & Penny, 2003](#)), which is a technique that describes patterns of activity and connectivity using all of the raw data.

The first step for both analyses is the identification of brain regions and associated waveforms thought to be most relevant to this paradigm. For the visual presentation of words, there are three distinct waveforms ([Bentin, Mouchetant-Rostaing, Giard, Echallier, & Pernier, 1999](#); [Tarkiainen, Helenius, Hansen, Cornelissen, & Salmelin, 1999](#)), which have been labeled the M100, M170, and M400 in the literature. As in the study reported in [Section 3.1.4](#), we assumed that the M100 reflects a combination of primary visual cortex (the first level of the nROUSE model) and orthographic representations, such as found in the visual word form area (VWFA; [Dehaene, Le Clec, Poline, Le Bihan, & Cohen, 2002](#)). However, unlike the study in [Section 3.1.4](#), the semantic satiation paradigm presents other words between each repetition, which supplants any lingering activation, and we did not expect (and did not observe) any M100 repetition effects. Although there is no carryover of orthographic activation, synaptic resources do not fully recover between repetitions, increasing depletion with additional repetitions. Critically, this effect is not evident in the activation of the orthographic representations. Instead, this depletion is apparent in the output of the orthographic representations, which affect activity in the lexical-semantic representations, such as found in the left middle temporal gyrus (MTG) thought to underlie the M170 ([Lau, Phillips, & Poeppel, 2008](#)).

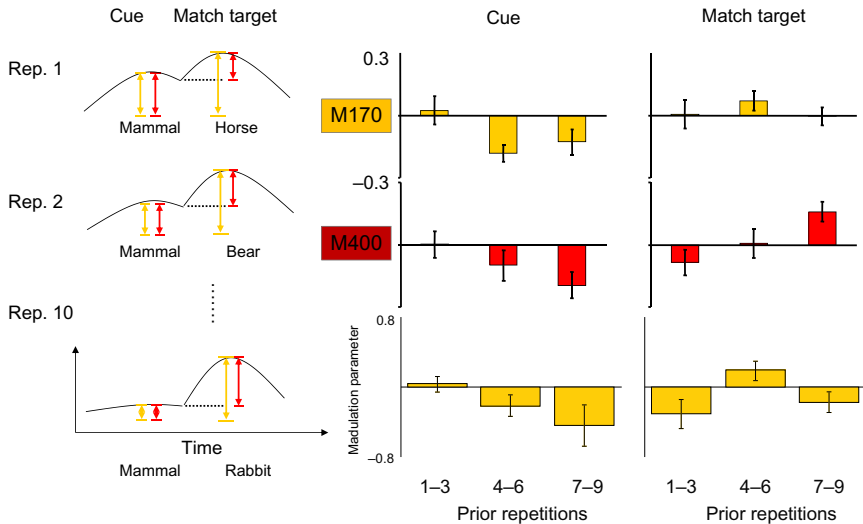


Figure 5.11 A replication of [Tian and Huber's \(2010\)](#) experiment 1 while collecting MEG responses ([Tian & Huber, 2013](#)). Predictions (left-hand panel) and results (right-hand panel) are shown for the M100 and M400 waveforms. The predicted graphs show the lexical-semantic level of the nROUSE model and the yellow and red double-headed arrows are predictions for the M170 and M400, respectively. As predicted, the M400 (a measure of semantic mismatch) in response to a matching target increased as function of prior repetitions, corresponding to worse performance. The bottom two graphs of the right-hand panel show the modulation parameter between the left visual word form area (a brain region related to orthography) and the left inferior frontal gyrus (a brain region related to semantics). The modulation parameter was determined with dynamic causal modeling and describes the connectivity between brain regions, revealing a progressive reduction between orthographic and semantic processing with increasing repetitions. Adapted from [Tian and Huber \(2013\)](#), with permission.

The predicted effect of increasing synaptic depression with repetitions is shown in the left-hand panel of [Fig. 5.11](#), which graphs the lexical-semantic response (i.e., the M170, as shown by the double-headed yellow arrows in the figure) over the course of each trial. The M170 was predicted to progressively decrease across the 10 repetitions of the category name within a block. As in the study of [Section 3.1.3](#), we assumed that match/mismatch judgments were based on the amount of new semantic activity in response to the category member. This difference, shown by the double-headed red

arrows in the left-hand panel of Fig. 5.11, needs to be calculated somewhere, and we hypothesized that this arises from an interplay between the left MTG and context-dependent integration in the left inferior frontal gyrus (IFG; Brown & Hagoort, 1993; Kutas & Federmeier, 2000). The left IFG is thought to underlie the M400 (the analog of the ERP N400) and is sensitive to unexpected lexical-semantic events (Halgren et al., 2002; Kutas & Hillyard, 1980). Thus, in response to a matching category member that follows the repeated category name, we predicted that the M400 would increase as a function of increasing prior repetitions. As discussed earlier, we hypothesized that people slow down with increasing repetitions because habituation gives the false impression that a matching category member is a mismatch—thus, the M400, which reflects semantic mismatch, should increase.

The top four graphs of the right-hand panel of Fig. 5.11 confirmed these predictions. The MEG waveforms were analyzed in the same way as the behavioral data by breaking the number of prior repetitions into thirds and by taking the difference between the repeated and the novel category conditions. As seen in the figure, the M170 and the M400 to the repeated category name (cue) progressively decreased as a function of the number of prior repetitions. Also as predicted, the M400 to the matching category member (match target) increased as a function of the number of prior repetitions, corresponding to faster RT responses in the repetition condition for the first third but slower RT responses in the repetition condition for the final third.

These predictions were generated assuming that connectivity between orthographic and lexical-semantic representations decreased with increasing repetitions. Next, DCM was used to directly test for reduced connectivity (David et al., 2006). Using the cortical regions discussed earlier, the first step in applying DCM was the identification of the connectivity pattern between regions. With the most likely connectivity determined by Bayesian model selection, we then examined the connectivity modulation parameters as a function of prior repetitions. Only the connectivity between the left VWFA and the left MTG varied as a function of prior repetitions, revealing a decrease in connectivity in response to the repeated category name, as shown in the bottom two graphs of the right-hand panel of Fig. 5.11. Thus, the observed semantic satiation effect reflects a decrease in connectivity between a brain region related to orthographic processing and a brain region related to lexical-semantic processing.



4. CONCLUSIONS

In psychological research, there is a tendency to focus on different experimental effects in isolation, developing separate theories of effect X or effect Y, rather than general theories of cognitive processing that might explain both X and Y. In this chapter, I have attempted to demonstrate how a general theory that addresses the need to reduce source confusion between sequentially presented visual objects can explain a wide variety of different effects in different areas of research. What these effects have in common is that they involve repetitions with relatively short delays between each occurrence. That these repetitions occur in radically different tasks (e.g., threshold identification, recognition memory, and semantic matching) and that they reflect radically different representations (e.g., repetitions of orthography, faces, meaning) are immaterial because in all situations, there is a need to integrate perceptual information over time with minimal blending between subsequent objects. In all of these situations, we see signatures of temporal integration and activity-dependent habituation, producing repetition advantages with minimal processing of the prior object but repetition deficits with longer durations or more repetitions of the prior object. However, these repetition deficits are essentially a side effect of habituation and the advantage of habituation is revealed by an increased ability to detect change.

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