ABSTRACT

Title of Document: TESTING A DYNAMIC ACCOUNT OF NEURAL PROCESSING: BEHAVIORAL AND ELECTROPHYSIOLOGICAL STUDIES OF SEMANTIC SATIATION

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In everyday perception, we easily and automatically identify objects. However, there is evidence that this ability results from complicated interactions between levels of perception. An example of hierarchical perception is accessing the meaning of visually presented words through the identification of line segments, letters, lexical entries, and meaning. Studies of word reading demonstrate a dynamic course to identification, producing benefits following brief presentations (excitation) but deficits following longer presentations (habituation). This dissertation investigates hierarchical perception and the role of transient excitatory and habituation dynamics through behavioral and neural studies of word reading. More specifically, the effect of interest is ‘semantic satiation’, which refers to the gradual loss of meaning when repeating a word.

The reported studies test the hypothesis that habituation occurs in the associations between levels. As applied to semantic satiation, this theory supposes that there is not a loss of meaning, but, rather, an inability to access meaning from a repeated word. This application was tested in three behavioral experiments using a speeded matching task, demonstrating that meaning is lost when accessing the meaning of a repeated category label, but is not lost when accessing the category through new exemplars, or when the matching task is changed to simple word matching.

To model these results, it is assumed that speeded matching results from detection of novel meaning to the target word after presentation of the cue word. This model was tested by examining neural dynamics with MEG recordings. As predicted by semantic satiation through loss of association, repeated cue words produced smaller M170 responses. M400 responses to the cue also diminished, as expected by a hierarchy in which lower levels drive higher levels. If the M400 corresponds to the post-lexical detection of new meaning, this model predicted that the M400 to targets following repeated cues would increase. This unique prediction was confirmed. These results were tested using a new method of analyzing MEG data that can differentiate between response magnitude versus differences in activity patterns. By considering hierarchical perception and processing dynamics, this work presents a new understanding of transient habituation and a new interpretation of electrophysiological data.

TESTING A DYNAMIC ACCOUNT OF NEURAL PROCESSING: BEHAVIORAL AND ELECTROPHYSIOLOGICAL STUDIES OF SEMANTIC SATIATION

By

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I dedicate this dissertation with all my love
to my grandfather Tian Baoheng and my grandmother Zhang Shuqin

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Chapter 1: General introduction

Object identification is one of the important skills that we acquire over a lifetime of experience and the complexity of this process is commonly underestimated. The neural system achieves these complex cognitive functions in a specific and efficient way both automatically and with remarkable accuracy. In this dissertation we examine the dynamic processes that underlie such behavior with the representative task of word identification. Recognizing a single written word is not a trivial task. First, the visual features are extracted from the background to shape a consistent perception for each letter. Second, different letters are grouped together to form a ‘word-like’ orthographic figure. This orthographic figure triggers the corresponding meaning and finally one can report the intrinsic properties that associate with the different ink patterns. The whole procedure of identifying words represents a typical hierarchical cognitive process that involves constant information processing at each level and transfer of information between distinct stages of process.

In real life, words are usually presented in a serial manner such as in the tasks of reading and listening. Hence, the information processing and transferring in single word identification can be affected by the same proceeding process. The effect of recent experience can be beneficial in terms of faster and more accurately identification. For instance, people respond to a word faster when they encounter the same word at the second time, such as ‘table-table’, or when the following word is semantically related to the previous word, such as ‘table – chair’. More interestingly, the different quantity of experience may induce a transition from beneficial to detrimental effects on the identification of current words. For instance, a word loses its meaning after prolonged exposure of that word. Hence, studying effects of recent experience may shed light on the dynamics of information processing and transfer.

All cognitive behaviors, including the word identification process, are realized by the brain and the ultimate goal of cognitive neuroscience is to understand how our behavior arises from the computation in the enormous number of neurons in the brain. More specifically, the questions in this study are how the hierarchical structure in the neural system work and cooperate to process the information from the external world and produce accurate identification, and how recent experience affects this computation.

Different approaches and tools employed in cognitive neuroscience can lead to different interpretations of results. Carefully designed behavioral studies can reveal the basic input/output relationship, but leave neural processing unexplained. Thus, to explore the neural computational functions that produce the cognitive outputs from the external inputs, methods must record the intermediate steps of neural activity and link the physical stimuli to the behavioral response. The available methods include single neuron recording, electrophysiological recording such as Electroencephalography (EEG) and Magnetoencephalography (MEG), and hemodynamic neuroimaging such as Positron emission tomography (PET) and functional Magnetic resonance imaging (fMRI). Different advantages of these methods should be considered before using them to link human behavior and neural activity in a specific experimental design. Moreover, different mechanisms, assumptions, and limitations of each method should be carefully considered before drawing any conclusions.

There are two goals of this dissertation. The primary goal is to explore information processing and flow in word identification, which is representative of well-learned complex cognitive skills. We demonstrate the importance of considering associations between different stages of processing by examining the transition from benefit to deficit effects of recent experience in a speeded category matching task. This semantic satiation effect can be explained by neural habituation in associations and this account is tested both through behavioral experiments (Chapter 2) and with MEG recordings (Chapter 3).

Since electrophysiological recording is used as a tool to test our theory (part II of Chapter 3), a secondary goal is to develop a method to separate the changes in response magnitude versus activity pattern and overcome individual differences in data analysis (part I of Chapter 3).

Chapter 2: Behavioral study of semantic satiation: Speeded category matching

Recent experience can facilitate word identification, in terms of faster and more accurate responses. One example is priming effects (see reviews by Brown & Mitchell, 1994; Farah, 1989; Ochsner, Chiu, & Schacter, 1994). Two stimuli are presented successively and the response to the second presentation (target) is faster when the first presentation (prime) is related.

Interpretation of this facilitation is that the prime helps construct the perceptual representation and orthography of the target (Wiggs & Martin, 1998). When the prime is identical to the target, such as repeating the word “chair” two times in a row, people make correct responses to the second occurrence much faster (Humphreys, Besner, & Quinlan, 1988; Norris, 1984). Besides repetition priming, orthographic similarities (Evett & Humphreys, 1981), such as “beach – peach” between prime and target also make the responses to the target easier.

Besides facilitation for the construction of perceptual and orthographic representations, priming also facilitates lexical and semantic processing. For instance, the semantic priming effects demonstrated by Neely (1977), in which a semantically associated word pair, such as “table - chair”, help people make lexical decisions on the second word. These semantic priming effects have been demonstrated in many tasks that involve lexical and semantic processing, including word naming, lexical decision, and word categorization (Neely, 1991). It has been concluded that semantic priming effects are either due to the retrieval context induced by the semantically related prime (Morton, 1969, 1979) or directly caused by the residual semantic representation of the prime (Jacoby, 1983; Logan, 1990).

Depending on the presentation duration of the first stimulus, priming effects show an interesting transition from benefits to deficits (Huber, Shiffrin, Quach, & Lyle, 2002). In semantic process, depending on the presentation duration or the number of repetitions of the prime, the response benefit in semantic priming effects changes into a response deficit effect, which is termed as semantic satiation, such that people tend to lose the meaning of a word after long duration exposure of that word (Jakobovits & Lambert, 1962; Smith & Klein, 1990). We focus on semantic satiation because it is a high level of identification, thus allowing study of the lower level dynamics that give rise to accurate identification.

2.1 Introduction

Say the word 'science' to yourself. Now say it again, and again, at least 20 times. Most people experience the sensation that a repeated word loses its meaning under such repetitive conditions. In this chapter, we investigate this interesting phenomenon termed ‘semantic satiation’ by 1) developing a well controlled paradigm with a quantitative measure of semantic satiation that is relatively free of task demands and other influences such as general fatigue and 2) comparing different kinds of repetitions (i.e., word and meaning, meaning alone, or word alone) to ascertain the underlying mechanism behind the apparent loss of meaning.

In seeming contradiction to the phenomenon of semantic satiation, traditional priming experiments (see the review by Farah, 1989) typically reveal facilitation for speeded lexical decisions (Neely, 1977) or perceptual identification accuracy (Wiggs & Martin, 1998). However, in a two-alternative force choice perceptual identification task, Huber et al. (2002) found that the responses on the target word depended on the duration of the prime word. Namely, participants were biased to judge that the target was the same as the prime with short prime durations, but judge that the target was different from the prime with long prime durations. Providing a mechanistic interpretation of these effects, Huber and O'Reilly (2003) explained priming reversals through the build up of habituation with increasing prime duration. More recently, this habituation model was tested not only with repetition priming, but also with semantic priming (Huber, 2008), suggesting that habituation plays a role even with higher level representations. Critically, this habituation model was based on the mechanisms of synaptic depression (Tsodyks & Markram, 1997), in which the available resources between sending and receiving neurons are depleted due to recent activity. As such, this account suggests the possibility that semantic satiation is not due to repeated access of a lexical entry, nor is it due to repeated access of the same meaning, but rather it arises when the same lexical entry is used to repeatedly retrieve the associated semantics. We refer to this theoretical possibility as *Associative Satiation* (Figure 2-1c) Next we review the literature on semantic satiation, and compare our *Associative Satiation* theory with other theoretical perspectives.

Providing one of the earliest measures of semantic satiation, Severance and Washburn (1907) found that participants reported lapses of meaning after a prolonged visual fixation on written words. Rather than merely fixating, Bassett et al. (1919) instructed participants to repeat the same word aloud until it lost its meaning. These early studies relied upon self-report and introspection as dependent measures and so they may be subject to report bias. Later experiments used more objective measures to quantify semantic satiation through ratings of lexical validity (Lambert & Jakobovits, 1960), exemplar commonality (Smith & Raygor, 1956), or the number of produced associates (Kanungo & Lambert, 1963).

None of these early studies measured speeded reaction times, and so they still might include report bias or other control processes. Therefore, Smith and Klein (1990) used a speeded category membership task in which participants judged whether two words were from the same category, with this judgment occurring after a category label was repeated for 3 or 30 times. Although they still found positive priming following both 3 and 30 repetitions, the effect size following 30 times was greatly diminished. However, there is concern in directly comparing performance following 3 versus 30 repetitions because these two conditions are not equivalent in terms of general fatigue and other factors. Therefore, Black (2001) used a more complicated design that repeated a word, which was then followed by word pairs that were either related or unrelated to the repeated word. Thus, unrelated trials served as a baseline control. Critically, the first word of the word pairs was always a homograph (e.g. “ORGAN”), with one of the two meanings related to the repeated word in the related condition. The basic task was to quickly indicate whether the homograph matched the other word of the word pair (e.g., “ORGAN-HEART”). They found that reaction time increased as a function of the number of repetitions for a related repeated word (e.g., “KIDNEY”) as compared to an unrelated repeated word (e.g., “CEILING”).

This discussion highlights that the measurement of semantic satiation is complicated, and that there are a variety of potentially confounding factors (see review, Esposito & Pelton, 1971). One concern is use of two separate tasks to measure semantic satiation that may produce report bias and task switching. In previous studies, participants were usually asked to repeat one word several times. This method does not control attention as a function of number of repetitions, because of passive nature of this task (e.g. Smith & Klein, 1990). This method also involves task switching and other factors that may contribute to the measure of semantic satiation (e.g. Black, 2001). Finally, this two-task method failed to capture the dynamics of semantic retrieval, because it typically compares just two or three points as semantic satiation accrues (e.g. Balota & Black, 1997; Black, 2001).

Besides the methodological issues involved in studies of semantic satiation, the causes of semantic satiation is still in debate. Two theories have been proposed to account for semantic satiation. Jakobovits and Lambert (1962) first proposed that repeated stimuli reduce in the semantic intensity with each repetition. Smith and Klein (1990) also concluded that semantic satiation is mediated by fatigue or adaptation in the neural process that underlie meaning. We refer to this mental fatigue of semantics as the theory of *meaning satiation* (Figure 2-1b). Esposito and Pelton (1971) proposed an alternative theory implicates the effect of perceptual process in semantic satiation. This theory states that semantic satiation arises from the changes in perceptual processing of a stimulus after prolonged exposure. The perceptual input becomes meaningless after extensive repetitions, resulting in the inability to access meaning through perception. This change of perceptual process is referred as the theory of *perceptual satiation* (Figure 2-1a), although we note that the nature of perception depends on what is repeated—in the above cases with visually presented words, this corresponds to *orthographic satiation*. Another example of perceptual satiation would be *phonological satiation* with repeated aural presentations of the same word. Beside the repetitive processes in different levels, our theory of *associative satiation* (Figure 2-1c) states that the repeated orthography of a word followed by the repeated access to the same meaning leads to less efficient information transfer in the associations between orthography and meaning.

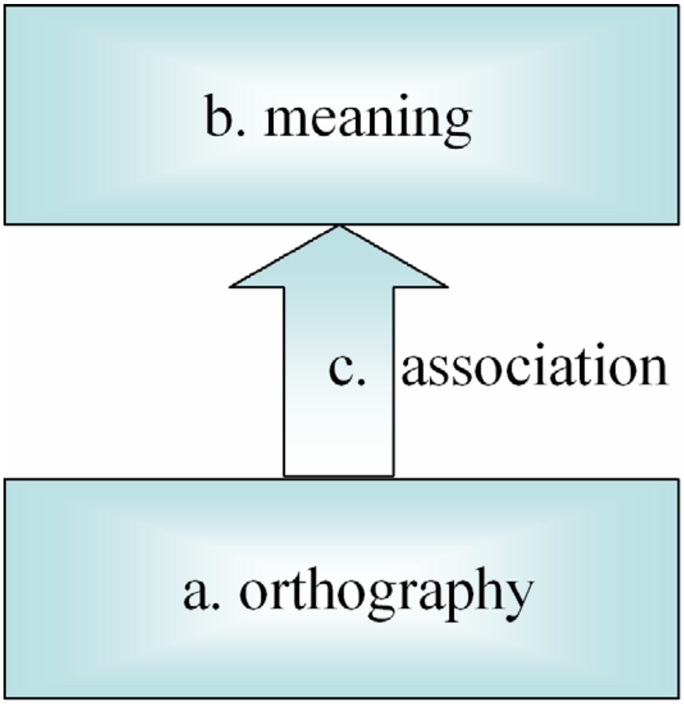


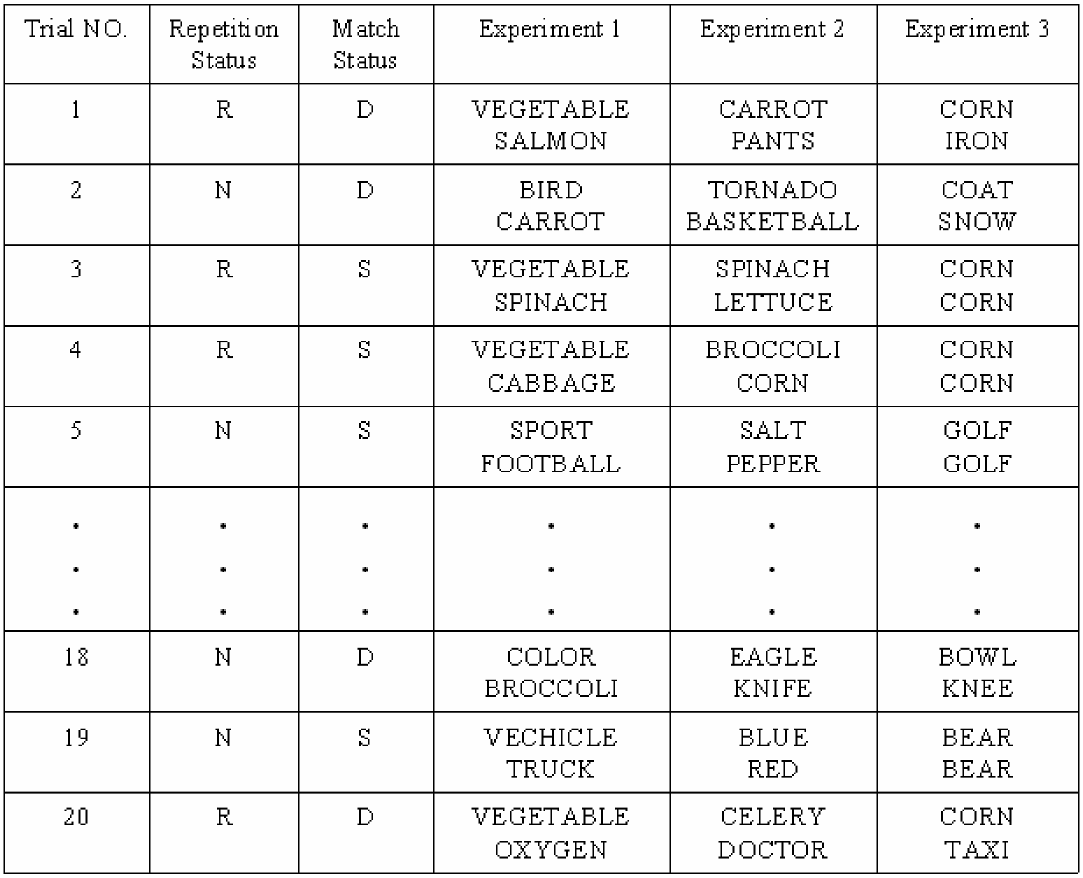
Figure 2-1Illustration of three theoretical accounts of semantic satiation: a. *perceptual satiation*: repetitions produce satiation in the orthographic representation, causing reading difficulty for that word; b. *meaning satiation*: repetitions produce satiation in the semantic representation, causing an inability to access that meaning regardless of the manner in which access is attempted; and c. *associative satiation*: repetitions produce satiation in the association between the repeated orthography and its meaning, causing an inability to access that meaning through presentation of that particular repeated word.

Previous experimental designs cannot distinguish between these theoretical accounts of semantic satiation. Because previous semantic satiation experiments used repetitions of the same word, they involved repetitions for both the orthography and meaning of a word. Therefore, to distinguish among the theory of *associative satiation*, the theory of *meaning satiation* and the theory of *perceptual satiation,* we used a speeded category matching task, which was similar to the experimental designs of Smith and Klein (1990), but we tested both category and exemplar repetitions as well as word repetitions across trials in the same paradigm. Furthermore, because the same task was used both to induce and to test semantic satiation, this paradigm allowed parametric variation for the number of repetitions in one block to map the dynamic time course of transition from benefits to deficits.

2.2Overview of experiments

In Experiment 1, the task required participants to fully process orthographic and semantic information with each repetition of the category label. In Experiment 2, only semantic repetitions occurred by using multiple exemplar from the same category. In Experiment 3, only orthographic repetitions occurred by changing the task to word matching. All experiments used the speeded matching in mix lists paradigm, which eliminated expectation and task switching while controlling attention. The continuous nature of this paradigm made it possible to measure the dynamic time course of repetition effects in semantic memory retrieval. The experimental procedures of the three experiments are demonstrated in Figure 2-2 (see method section for details).

The three aforementioned theories can be tested by using this series of three experiments because each makes different predictions. The theory of *meaning satiation* predicts that whenever the same meaning is accessed, that meaning is fatigued. Therefore, in both Experiment 1 (meaning and orthographic repetitions) and Experiment 2 (meaning repetitions), the theory of *meaning satiation* predicts semantic satiation, but there should be no satiation in Experiment 3 (orthographic repetitions only). Similarly, the theory of *perceptual satiation* predicts that whenever the same orthography is accessed, that orthography is fatigued. Therefore, in both Experiment 1 and Experiment 3, theory of *perceptual satiation* predicts the responses slow down but not in Experiment 2. On the contrary, the theory of *associative satiation* we proposed requires the co-occurrence of orthographic and meaning repetitions to satiate the associations. Therefore, the theory of *associative satiation* predicts semantic satiation only in Experiment 1 but not in Experiment 2 or 3.



Trial NO.	Repetition Status	Match Status	Experiment 1	Experiment 2	Experiment 3
1	R	D	VEGETABLE SALMON	CARROT PANTS	CORN IRON
2	N	D	BIRD CARROT	TORNADO BASKETBALL	COAT SNOW
3	R	S	VEGETABLE SPINACH	SPINACH LETTUCE	CORN CORN
4	R	S	VEGETABLE CABBAGE	BROCCOLI CORN	CORN CORN
5	N	S	SPORT FOOTBALL	SALT PEPPER	GOLF GOLF
· · ·	· · ·	· · ·	· · ·	· · ·	· · ·
18	N	D	COLOR BROCCOLI	EAGLE KNIFE	BOWL KNEE
19	N	S	VECHICLE TRUCK	BLUE RED	BEAR BEAR
20	R	D	VEGETABLE OXYGEN	CELERY DOCTOR	CORN TAXI

Figure 2-2 Experimental designs of Experiments 1-3. This table provides examples of a single block of 20 trials, although only 8 trials are shown. The second column is the repetition status of

each trial, where R and N stand for the repeated condition and the non-repeated condition respectively. The third column is the match status for cue and target on that trial, where S stands for ‘yes’ responses (Same = match), while D stand for ‘no’ responses (Different = mismatch). Two words are presented in each trial as shown in the last three columns. First, the cue word appeared in the center of the screen above the middle line for 1000ms (the cue is the upper of the two words shown) followed by the target word below the middle line. At that point, both words remained on the screen until participants responded. In Experiment 1, the cue word was always the category label and the second word was always a new exemplar. In Experiment 2, both words were always new exemplars (category repetition but no repeated words). In Experiment 3, exemplars were selected and used for cues and targets, with the cue and target presenting the same word twice for match trials (repeated cue words, but no need to access category). The matching task in each experiment is therefore slightly different: in Experiment 1 the cue provides the name of the category, in Experiment 2, the category must be inferred by the cue, and in Experiment 3 the matching is of the word rather than the category.

2.3 Experiment 1: Repeated Category, Same Label

2.3.1 Experiment 1a

In the first experiment, participants were required to process both orthography and meaning of word. However, compared with the passive nature of repetitions in previous studies, this current design demanded participants to process both level of information during each repetition in an active way to fulfill the task. Moreover, the continuous measures in one block, instead of switching from the task of repetitions to a lexical task enabled us to obtain reaction time as a continuous function of the number of repetitions.

Method

Participants. A total of 43 students in University of California, San Diego voluntarily participated in this experiment in return for extra credit in an introductory psychology course.

Materials. Eleven single-word category labels were selected (see Appendix 1a). Twenty single-word exemplars were included in each category (McEvoy & Nelson, 1982; Van Overschelde, Rawson, & Dunlosky, 2004). All stimuli were presented in white on the center of a computer screen with black background. Reaction time was collected using 2 buttons of a 5-button serial response box.

Design and procedure. A 2 (repetition status) X 2 (matching status) X 3 (positions) factorial design was implemented in this experiment (In order to increase power, every position was obtained by averaging every 3rd trials starting from the second in each repetition status, see outline of analysis for detail.).

On each trial, a category label was presented above the midline for 1000ms. Next, an exemplar was presented below the midline while the category label remained on the screen until participants responded. Participants were asked to give a category matching judgment between category label and exemplar. Following their responses, the screen went black for 100ms and feedback (a green check or a red cross) was presented before the next trial began.

One block consisted of 20 trials. One of the 11 category labels was randomly chosen without replacement to repeat on 10 trials (repeated condition) with the other 10 trials using 10 different category labels presented one time each (nonrepeated condition). The sequence of these 20 trials was randomized. Half of the trials were matched and the other half trials were mismatched between category labels and exemplars and this was true for both the repeated and nonrepeated conditions. The mismatch trials in both conditions were created by switching the exemplars. Namely, in each block, 5 exemplars from the repeated category were paired with 5 other category labels to form nonrepeated mismatched trials and 5 exemplars from 5 different categories were paired with the repeated category label to form 5 repeated mismatch trials (table 2.1). Eleven blocks in which different category labels served as the repeated category formed one set. All 220 exemplars were only used once in one set. There were 4 sets with 44 blocks and 20 trials in each block. The presentation sequence of blocks in each set was randomized. The pairing of category labels and exemplars of each trial in each set was also randomized. There were two practice blocks before the real experiment, which used different stimuli. Participants were encouraged to respond as fast and accurately as possible. The reaction time and accuracy of each trial were recorded for data analysis.

Repeated match	A-a
Repeated mismatch	A-b
Nonrepeated match	C-c
Nonrepeated mismatch	B-a

Table 2-1 Different types of trials in Experiment 1a. Four different types of trials were included in one block by paring one categorical label (the upper case letter) and one exemplar (the lower case letter). The lower case letter represented an exemplar that was from the category of the same letter in upper case. Match trials were constructed by pairing the exemplars from the same category (the same letters regardless the case difference) while the mismatch trials were constructed by pairing the exemplars from different category (different letters). The mismatch trials in both conditions were constructed by switching the exemplars from corresponding categories. That was, pairing an exemplar from category B with category label A formed a repeated mismatch trial, while pairing an exemplar from category A with category label B formed a nonrepeated mismatch trial. These 4 different trials were presented 5 times each in one block. The repeated category (A) was presented 10 times in 10 repeated trials in one block while in other 10 nonrepeated trials, each of the remaining 10 category labels were only presented once. The task in this experiment was to judge whether the exemplar belonged to the proceeded category cue.

Outline of analysis. Because all 3 experiments reported in this study used the same paradigm (i.e. a series of 20 trials in a block), a common analysis procedure was applied to all experiments. Participants whose overall accuracy was under 90%[1] were excluded from further analysis. The correct reaction time data were truncated between

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[1] The same criterion was used for all experiments as determined from performance in Experiment 2, which was the most difficult experiment. We obtained the same trial number and condition interactions in all three experiments when all participants were included.

300ms and 1500ms. Because there is no difference at the beginning of repeated and unrepeated condition, the first trials in each condition were excluded. The median reaction times of every third trials were averaged and 3 positions were created out of the remaining 9 trials in each condition. A repeated measures three-way ANOVA with factors of position (3), repetition status (2), and match status (2) was run. If the match status did not interact with other 2 factors, the power of this analysis can be increased by averaging across different match status and a repeated measures two-way ANOVA with the factors of position (3) and repetition status (2) was implemented to assess the interaction between repetition status and number of repetitions. The results are reported as differences between repeated and nonrepeated condition (baseline) from repeated condition across the 3 positions. Because of the concern of speed-accuracy tradeoff, the same repeated measures two-way ANOVA was applied after analyzing reaction time data.

All ANOVAs with a level of significance of 0.05 were further investigated with pairwise comparisons. Greenhouse-Geisser corrections were reported with all effects having ≥2 *df* in the numerator.

Results

Ten participants were excluded based on the 90% accuracy criterion, leaving 33 participants to run further analyses. A repeated measures three-way ANOVA on correct median RT was applied on the factors of position (3), repetition status (2), and match status (2). The match status did not interact with the other factors, $F(2,64) = 1.51$, $p = .23$. Therefore, the results were collapsed over match status to increase power in the following analyses.

Figure 2-3A illustrates the median reaction time difference between repeated and nonrepeated as a function of number of repetitions. A repeated measures two-way ANOVA revealed a significant main effect of position due to a slowing across the number of repetitions, *F*(2,64) = 3.86, p < .05. More importantly, the position X condition interaction was significant, *F*(2,64) = 7.58, *p* < .005. Further paired t-tests comparing repeated with nonrepeated conditions at a given position confirmed a during trials 2 to 4, *t*(32) = -2.093, *p* < .05. However, as the number of repetitions increased, this facilitation was eliminated during trials 5 to 7, *t*(32) = .59, *p* = .56. Finally, by the end of the block, the effect was reversed, with slower response in the repeated condition during trials 8 to 10, *t*(32) = 3.69, *p* =.001.

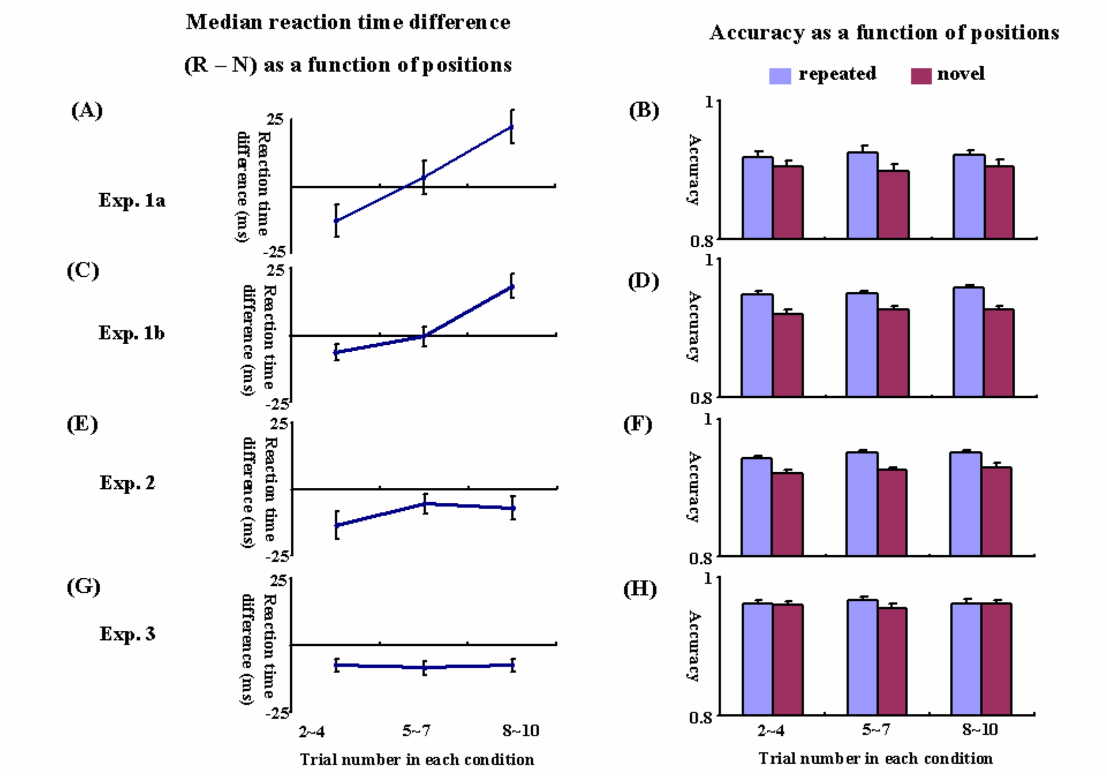

Figure 2-3 Speed and accuracy results as a function of trial number in Experiment 1-3. All results are collapsed over match and mismatch trials, which did not interact with other variables. Trial number is not list position. Instead, trial number is the nth occurrence of the repeated or non-repeated condition within the list of 20 total trials, where n can take on values 1-10. Trial number 1 is not shown because it is not yet known which category is repeating at that point

within the list (thus, there is no difference between the conditions). The remaining 9 trial numbers are broken into thirds. The left columns shows reaction time differences between correct median RT to repeated conditions minus correct median RT to non-repeated conditions. Experiments 1a and 1b both show a transition from benefits to deficits for the repeated condition as a function of increasing trial number. In contrast, Experiments 2 and 3 only show benefits for the repeated condition regardless of trial number. The accuracy data (the right column) did not reveal any interactions between condition and trial number and so the interaction with trial number is not due to a speed accuracy tradeoff.

A similar repeated measures two-way ANOVA on accuracy found a main effect of condition, with participants responding more accurately in the repeated condition, $F(1,32) = 20.08$, $p < .001$. However, the condition X position interaction was not significant, $F(2, 64) = 2.38$, $p = .11$. Therefore, a speed-accuracy tradeoff cannot explain the interaction found with reaction times (Figure 2-3B).

In Experiment 1a, there was a potential confound that might have produced these results. The mismatch trials in the repeated condition and nonrepeated condition were constructed by switching the exemplars in one block (refer to table 2.1, row 2 and 4). Hence, if certain mismatch trials in the repeated condition occurred before the mismatch trials in the nonrepeated condition between which the exemplars were switched, the participants could have known in advance to give an answer of mismatch when viewing the category label. The speedup in the mismatch nonrepeated condition might have produced the apparent slow down in the repeated condition. However, this should have been seen in the 3-way interaction. In any case, a modified experiment was needed to test this potential confounding problem.

2.3.2 Experiment 1b

In Experiment 1b, the repeated mismatched trials were constructed by using exemplars from additional categories. Therefore, the potential confounding problem in previous experiment was solved. This change necessitated the use of 16 categories rather than 11.

Method

Participants. A total of 40 students in University of California, San Diego voluntarily participated in this experiment in return for extra credit in an introductory psychology. These participants were different from those participated in Experiment 1a.

Materials. All the materials used in this experiment were the same as Experiment 1b, except for the inclusion of 5 additional categories (McEvoy & Nelson, 1982; Van Overschelde, Rawson, & Dunlosky, 2004). The categories are listed in Appedix Ib.

Design and procedure. All experimental design and procedures were the same as in the Experiment 1a, except as noted. There were 16 blocks in one set and each set was repeated 3 times, for a total of 48 blocks in the experiment. The 5 mismatch trials in repeated condition were created by pairing the repeated category label with 5 exemplars from categories that otherwise did not appear in the block. However, the 5 mismatch trials in nonrepeated condition were still created by 5 exemplars from repeated category (table 2.2). Thus maintaining the non-diagnostic status of exemplars from the repeated category.

Repeated match	A-a
Repeated mismatch	A-b
Nonrepeated match	C-c
Nonrepeated mismatch	D-a

Table 2-2 Different types of trials in Experiment 1b. Similar to Experiment 1a, 4 different types of trials were included in one block by paring one categorical label (the upper case letter) and one exemplar (the lower case letter). The lower case letter represented an exemplar that was from the category of the same letter in upper case. However, instead of switching exemplars to form mismatch trials in Experiment 1a, the category label in nonrepeated mismatch trials used a new category in Experiment 1b (D, instead B as in Experiment 1a).

Results

Six participants were excluded based on the 90% accuracy criterion, leaving 34 participants to run further analyses. A repeated measures three-way ANOVA on correct median RT was applied on the factors of position, repetition status, and match status. The match status did not interact with the other factors ($F < 1$). Therefore, match status was collapsed to increase power in the following analyses.

Figure 2-3C illustrates the median reaction time difference between repeated and nonrepeated as a function of number of repetitions. A repeated measures two-way ANOVA revealed a significant main effect of position due to a slowing across trials in one block, $F(2, 66) = 9.99$, $p < .001$. More importantly, the position X condition interaction was significant, $F(2, 66) = 15.59$, $p < .001$. Further paired t-tests comparing repeated with nonrepeated conditions at a given position confirmed a facilitation during trials 2 to 4, with $t(33) = -2.11$, $p < .05$. However, as the number of repetition increased, this facilitation was eliminated during trials 5 to 7, $t(33) = -.14$, p

= .89. Finally, by the end of the block, the effect was reversed and there were slower responses in the repeated condition during trials 8 to 10, with $t(33) = 4.29$, p <001.

A similar repeated measures two-way ANOVA on accuracy revealed a main effect of condition, with participants responding more accurately in the repeated condition, $F(1,33) = 52.31$, $p < .001$. However, the condition X position interaction was not significant ($F < 1$). Therefore, speed-accuracy trade-off cannot explain the interaction found with reaction times (Figure 2-3D).

In summary, a transition from response benefits to response deficits of recent experience was observed across repetitions when the same orthography and meaning of a word were repeated. This experimental paradigm controlled more factors than previous work, such as response bias, attention level. Because the repetitions were implemented in a consistent categorical matching task, this is the first study to map out the full time course of semantic satiation. This experiment revealed response facilitation for the 2nd to 4th repetition of the category, followed by the elimination of the facilitation from the 5th through 7th repetition. Finally, the 8th through the 10th repetition was sufficient to produce semantic satiation and a slow down in responding.

2.4 Experiment 2: Repeated Category, Different Exemplars

In Experiment 1, when the repetition of orthography and meaning of a word co-occurred, participants' responses slowed down across repetitions. Namely, the semantic satiation effect was observed when participants were required to repeatedly access the same categorical information through the same lexical form. However, all 3 theories predicted the outcome of Experiment 1. Therefore, Experiment 2 used repetitions of the same categorical information, but these occurred in response to newly presented lexical forms (new exemplars). This allows us to potentially falsify the theory of meaning satiation. The theories of associative satiation and perceptual satiation predict that there will be no satiation in this new design because it is just the meaning that repeats but there is no single word that repeats. In contrast, the theory of meaning satiation predicts that there will still be a satiation effect due to repetitions of the category.

Method

Participants. A total of 40 students in University of California, San Diego voluntarily participated in this experiment in return for extra credit in introductory psychology course. These students were different from who participated in Experiment 1.

Materials. Sixteen different category were selected with 20 exemplars in each list (McEvoy & Nelson, 1982; Van Overschelde, Rawson, & Dunlosky, 2004). The categories are listed in Appendix II.

Design and procedure. The procedure was identical to that in Experiment 1b, except that the material used as the first stimulus in each trial were also exemplars instead of category labels. That is, in each trial, two exemplars appeared with one appearing above the midline, and then a second appearing below the midline 1000ms later. They remained on screen until participants responded. The task was to judge whether the two exemplars belonged to the same category.

As before, one of the16 category was randomly selected without replacement as the repeated category in that block, so that 10 trials in the block used an exemplar from that category (repeated condition) while the other 10 trials used 10 different exemplars for the first exemplar, with each from a different category (nonrepeated condition). The presentation sequence of these 20 trials in one block was randomized. Similar to experiment 1b, in the repeated condition and nonrepeated condition, half of trials were matched and the other half were mismatched. The match trials in both conditions were created by pairing another exemplar from the same category as the first exemplar. Out of the remaining 10 categories, the mismatched trials in repeated condition were created by pairing 5 exemplars from repeated category with 5 exemplars from 5 different categories, while the mismatched trials in nonrepeated condition were created by pairing 5 exemplars from the rest of 5 different categories with another 5 exemplars in repeated category (table 2.3). Each of sixteen blocks used a different category for the repeated category and this formed one set. All 320 exemplars were used twice in one set. Three sets were included in this experiment. The presentation sequence of blocks and pairing of exemplars in each set were randomized. There were two practice blocks before the experiment, which used different stimuli. Participants were encouraged to respond as fast and as accurately as possible. The reaction time and accuracy of each trial was recorded for data analysis.

Repeated match	a1-a2
Repeated mismatch	a3-b1
Nonrepeated match	c1-c2
Nonrepeated mismatch	d1-a4

Table 2-3 Different types of trials in Experiment 2. Similar to Experiment 1b, 4 different types of trials were included in one block. However, the category cue was replaced by an exemplar from that category in Experiment 2. The same letters represented exemplars that were from one category. The number after the lower letter indicated different exemplars. Match trials were constructed by pairing the exemplars from the same category (same letters) while the mismatch

trials were constructed by pairing the exemplars from different category (different letters). The task in this experiment was to judge whether these two exemplars belonged to one category.

Results

Six participants were excluded based on the 90% accuracy criterion, leaving 34 participants to run further analyses. A repeated measures three-way ANOVA on correct median RT was applied on the factors of position, repetition status, and match status. The match status did not interact with the other factors (F < 1). Therefore, the results were collapsed over match status to increase power in the following analyses.

Figure 2-3E illustrates the median reaction time difference between repeated and nonrepeated as a function of number of repetitions. A repeated measures two-way ANOVA revealed a main effect of repetition status due to faster responses in repeated than in nonrepeated condition, $F(1,33) = 9.98$, $p < .005$, and a main effect of position due to a slowing across the number of repetitions, $F(2, 66) = 15.50$, $p <.001$. However, the position X condition interaction was not significant ($F < 1$).

The accuracy results were depicted in Figure 2-3F. A similar repeated measures two-way ANOVA found a main effect of condition, with participants making fewer errors in repeated condition, $F(1,33) = 41.73$, $p < .001$. However, the condition X position interaction was not significant ($F < 1$).

In summary, neither the reaction time nor the accuracy changed as the number of repetitions increased in Experiment 2. Therefore, these results contradict with the prediction of *meaning satiation*. Although the same categorical meaning was repeated several times, no response deficit was observed in Experiment 2. Instead, a response benefit was observed regardless of the number of repetitions.

2.5 Experiment 3: Repeated exemplar, Orthographic Matching

The theory of *perceptual satiation* and the theory of *associative satiation* both predicted the results of Experiment 2 and hence, were not distinguished. In Experiment 3, participants were asked to respond to exemplars at the perceptual level to test whether perception changes after a number of repetitions. According to the theory of *perceptual satiation*, perception is changed due to the repetitions. Therefore, the theory of *perceptual satiation* predicts just as in Experiment 1, a perceptual word matching task will also produce slower RTs with increasing repetitions. However, the theory of *associative satiation* predicts that the behavioral response pattern will not be changed across repetitions in this experiment.

Method

Participants. A total of 40 students in University of California, San Diego voluntarily participated in this experiment in return for extra credit in introductory psychology course. These students were different from who participated in Experiment 1 and 2.

Materials. Sixteen four-letter exemplars were selected from 16 different categories used in Experiment 2 with each from one category, by best matching written frequency (*M* = 37.4, *SD* = 17.1). The words are listed in Appendix III.

Design and procedure. The procedure was identical to Experiment 2, except that the task switched to perceptual word matching in Experiment 3. As before, one of the 16 exemplar words was randomly selected without replacement as the repeated word in that block, so that 10 trials in the block used that exemplar word (repeated condition) while the other 10 trials used 10 different words for the first stimulus (nonrepeated condition). In each condition, half of trials were match trials in which the following exemplar word was identical to the first stimulus; while half of trials were mismatch trials created by pairing two different exemplars (table 2.4). The task was to judge whether the two exemplars were the same only based on their orthography. The reaction time and accuracy of each trial was recorded for data analysis.

Repeated match	a-a
Repeated mismatch	a-b
Nonrepeated match	c-c
Nonrepeated mismatch	d-a

Table 2-4 Different types of trials in Experiment 3. Similar to Experiment 2, 4 different types of trials were included in one block. However, only 16 selected exemplars were presented. The lower case letter represented a word that was an exemplar selected from a category in Experiment 2. Match trials were constructed by repeating the same exemplar, while the mismatch trials were constructed by pairing different exemplars. The task in this experiment was to judge whether these two exemplars that were presented successively in one trial were the same only based on orthography.

Results

One participant was excluded based on the 90% accuracy criterion, leaving 39 participants to run further analyses. A repeated measures three-way ANOVA on correct median RT was applied on the factors of position, repetition status, and match status. The match status did not interact with the other factors ($F < 1$). Therefore, the results were collapsed over match status increase power in the following analyses.

Figure 2-3G illustrates the median reaction time difference between repeated and nonrepeated as a function of number of repetitions. A repeated measure two-way ANOVA revealed a main effect of repetition status due to faster responses in repeated than in nonrepeated condition, *F*(1,38) =21.11, *p* < .001 and a main effect of position due to a slowing across the number of repetitions, *F*(2, 76) = 13.89, *p* <.001. However, the position X condition interaction was not significant (F < 1).

The accuracy results were presented in Figure 2-3H. A similar repeated measure two-way ANOVA revealed a main effect of condition, with participants made fewer errors in repeated condition, *F*(1,38) = 4.35, *p* < .05. However, the condition X position interaction was not significant, with *F*(2,76) = 2.73, *p* > .05.

Therefore, neither the reaction time slowed down nor the accuracy became worse across the repetition in Experiment 3. That is, the results did not support the hypothesis that the perceptual inputs were changed after the same amount of repetitions that only provided in perceptual process as in Experiment 1. These results contradicted the prediction of *perceptual satiation*. Repetitions only in orthography did not induce the same transition in response as presented in Experiment 1. Perceptual response was slightly facilitated for the repeated exemplar across repetitions. Hence, the results of semantic satiation in Experiment 1 were not due to the change of perceptual inputs. Only the theory of associative satiation can simultaneously explain the results in 3 experiments.

2.6 Discussion

A series of 3 speeded matching in mixed lists experiments were carried out, in which repetitions in different levels of processing were presented. Experiment 1 required the access to the meaning of one category at every time the category label repeated and a slow down in reaction time was observed across repetitions. However, Experiment 2 and Experiment 3 produced only benefits for the repeated condition when the same amount of repetitions were presented alone in semantic process by repeating categorical meaning or in perceptual process by repeating orthographic features, respectively.

The results of these 3 experiments did not support the theory of *meaning satiation* and the theory of *perceptual satiation*. According to the theory of *meaning satiation*, the repetition in meaning level alone should be sufficient to induce semantic satiation (Lambert & Jakobovits, 1960; Smith & Klein, 1990). However, when the repetitions were presented in meaning process alone in Experiment 2, the semantic satiation was not observed. Hence, this result contradicted the prediction of *meaning satiation*. On the other hand, according to the theory of *perceptual satiation*, repetitions of the same perceptual form produce satiation in the perceptual representation (Esposito & Pelton, 1971). Therefore, the lack of perceptuion for the repeated word should block identification. However, this theoretical possible explanation was ruled out by the results in Experiment 3. The reaction time did not slow down after excessive orthographic repetitions and the semantic satiation observed in Experiment 1 cannot be accounted by perceptual input changes. Therefore, neither the presentation of meaning repetition alone as in Experiment 2 nor the presentation of perceptual repetition alone as in Experiment 3 was the cause of semantic satiation.

Only the theory of associative satiation can explain the results in all 3 experiments. Compared with the results in Experiment 2 and 3 in which reaction times did not slow down across repetitions in either perceptual or meaning level alone, only in Experiment 1 did the reaction time slow down. Furthermore, all three experiments used similar numbers of participants and identical numbers of trials per participant, resulting in equivalent power to observe interactions between trial number and condition. Nevertheless, there was no interaction in Experiment 2 and 3 despite significant main effects of condition. Unlike the other experiments, only in Experiment 1 used the category labels repeatedly in a task that required accessing the categorical meaning at every time the specific category label repeated. Therefore, the associative repetitions caused reaction time increased across a number of repetitions, but separate contribution from either level was insufficient to obtain the same results. Because the associative repetition requires the information to transfer from orthographic process to lexical/semantic process at every time a word repeated, the connections between these two processes become inefficient to transfer information. Hence, the associative repetition in the connections is the primary cause of semantic satiation.

The time scales of habituation effects in association and in individual process may be different. We do not exclude that the repetitions in each level alone cannot affect on orthographic or lexical/semantic process. In fact, the same level of facilitation in every trial in Experiment 2 and 3 was observed. However, the dynamic changes across trials were only observed in Experiment 1 but not in Experiment 2 or 3. It indicates that the repetition effects in perceptual or semantic process have been recovered by beginning of the next trial but the repetition effects in the associations accumulated across trials. Therefore, the satiation in associations was the primary cause for the observation of slower response across trials in semantic satiation as demonstrated in Experiment 1.

The stroop effect (Stroop, 1935) demonstrates that people automatically process the meaning when encountering words. Thus, the information flow from perceptual to semantic process is relative automatic. One would expect semantic satiation in Experiment 3 according to the theory of *associative satiation* if the semantic response served as the measure for responding. However, in Experiment 3, participants were instructed to compare the orthography of two words and the decision can be made directly based on the outputs of perceptual process. Unlike in Experiment 1, there was no response change across repetitions. In fact, reaction times in Experiment 3 were faster than in Experiment 1. Therefore, participants were not using meaning to perform the task in Experiment 3.

The same performance deficit across repetitions has been found in other semantic memory tasks. In a study conducted by Brown, Zoccoli and Leahy (2005), participants needed to recall 12 exemplars from the same category based on their first letters which served as cues. They found that retrieval success declined across 12 successive items. This is similar to what we found in Experiment 1 as the reaction time slowed down across the 10 trials of repetitions. They concluded that accessing exemplars from a category inhibit the access of subsequent exemplars from the same category. However, in their studies, they also repeated the categorical label on each trial. According to the theory of *associative satiation*, it is possible that the repetitions of category label was the cause of the semantic satiation in their experiment

The lexical/semantic response transition from benefits to deficits has also been found in subliminal priming. A subliminal repetition study conducted by Wentura and Frings (2005) used design that alternately repeated a prime category word and a mask for 20 times, such that participants were unaware of the primes and total presentation duration of repeated masked prime was equal to the duration of the primes in nonmasked primed condition or in single masked primed condition. Negative priming effects were found and lexical decision responses were slower in repeated masked primed condition but not in nonmasked primed condition or single masked primed condition. The difference between repetition masked condition and single masked condition was the number of repetitions with the former repeated 20 times while the latter only repeated once. One assumption would be that associative satiation just requires use of the association, but not fully activation of the meaning. Every time the prime was repeated, the same perceptual information transferred to higher level process and the association between them became less efficient. Because the information in perception and meaning never accumulated to the threshold due to subliminal design, no awareness of the primes was report. However, the satiation in associations gradually accumulated and was slow to recover. When the lexical decision of the exemplar from the repeated category was required, the response slowed down due to the inefficient association. Therefore, interpreted with caution, the observation of subliminal inhibition of semantic retrieval (Wentura & Frings, 2005) can be explained by our theory of *associative satiation* and subliminal repetitions are enough to induce the habituation in associations.

In summary, the *associative satiation* caused by the number of repetitions was proposed to account for the semantic satiation. Results in 3 speeded category matching task supported the theory of *associative satiation*. Thus, the meaning loss after repeating “science” 20 times is caused by the less efficient information transfer in the associations from the repeated orthography of “science” to the meaning process of “science”. This study of semantic satiation highlights the dynamics of information flow and advance the understanding of hierarchical process at the system level.

Chapter 3: Electrophysiological study of semantic satiation: Methods and application of MEG

In Chapter 2, 3 behavioral experiments were carried out to assess semantic satiation. All experiments used speed matching task with 20 trials in one block, with repetitions in different levels of process in 10 of these trials and the other 10 trials did not involve any repetitions in different experiments. A response pattern transition from RT facilitation at the beginning to response deficit towards the end of block was found when category labels were repeated in Experiment 1. Assuming that this slow down measures semantic satiation, Experiments 2 and 3 tested whether semantic satiation results from repeated category semantics by using different exemplars as cues on every trial (Experiment 2) or whether semantic satiation results from repeated words by changing the task to simple word matching (Experiment 3). Because these two experiments only produced response facilitation, we conclude that semantic satiation requires repeating a word while continuing to access the meaning of that word (i.e., a repeated association).

The behavioral results suggest that semantic satiation occurs through a loss of association. However, these results do not identify whether this loss of association is an automatic aspect of lexical processing or whether it might arise from task demands or other forms of strategic and post-lexical responding. For instance, if participants elected to stop attending to the meaning of repeated words (i.e., a decision enacted after lexical access), this would also produce the observed behavioral results.

Moreover, the observed behavioral results only indirectly reflect the effects of repetitions on the responses to targets. There is no direct way to assess the same effects on the process of the repeated cues in behavioral experiments. In fact, the response to the cue is more informative and direct to assess the associative satiation. Therefore, in this chapter, we use a neural measure to monitor the time course of lexical-semantic processing with the procedures of Experiment 1b, which produced semantic satiation. Our assumption is that a strategic account of these effects would correspond to a later neural response (post-lexical) whereas an explanation that is intrinsic to lexical processing would be apparent early in the response to a repeated word (i.e., prior to the point where it could be known that a stimulus was a repeated word).

In part I of Chapter 3, we considered the methodological issue in directly measuring neural activity. First, various neural measures in cognitive neuroscience are discussed and the most feasible one in measuring neural processing correlated with semantic satiation is chosen. Furthermore, the limitation of this neural measure is demonstrated and a method to overcome this limitation is proposed and used in part II of Chapter 3 to facilitate the investigation of semantic satiation.

Part I: Projection method in electrophysiological recording

A method to separate changes in response magnitude and changes in activity patterns in electrophysiological recording is introduced in part I of this chapter. Section 3.13 to section 3.4 was an original paper about this method that first appeared in Brain Topography (Tian & Huber, 2008) and it is included here for the completeness of this dissertation.

3.1 Introduction

Carefully designed behavioral studies can reveal the cognitive functions performed by the neural system. However, behavioral studies can only provide the basic input/output function; the underlying neural mechanisms and computation are still mysteries that are needed to be assessed. To advance the understanding of neural underpinnings of cognitive functions, we need to use tools that can directly measure neural activity.

3.1.1 Available tools

The major tools that are available for investigating neural mechanisms underlying cognitive functions include, but are not limited to, single neuron recording, hemodynamic neuroimaging and electrophysiological recording. Each of these tools has unique advantages as well as limitations.

The method that most directly measures neural activity is single neuron recording. The action potential generated by the neuron is detected by an electrode inserted into the brain of living animals. Because of the extremely small tip of the electrode, the activity of a single neuron can be recorded. The electric activity can be recorded directly in neurons or the voltage changes outside neurons that are associated with the action potential can be measured. Single neuron recording has been used widely in the studies of animal behavior and has provided crucial insights into neural processing. The seminal work of Hubel and Wiesel (1959) demonstrated the receptive fields of simple cells by recording the single neurons in the primary visual cortex of the anesthetized cat that showed how single neurons in striate cortex selectively respond to different orientation of bars.

More recently, many neurons can be recorded simultaneously by a multiple-electrode array. This technique can reveal how information is processed in the neural population and how behavior relates to the activity of the neural population. For example, Georgopoulos et al (1986) found that the direction of movement of an arm is similar to the summation of the activity across a population of motor neurons. Two hundred and twenty-four neurons from the arm area of motor cortex that are broadly tuned to a particular direction in three-dimensional space were recorded simultaneously. The population vector that summed the preferred directional vectors of these 224 neurons consistently agreed with the movement direction. These results demonstrated that the information of movement direction is encoded in a population of motor neurons.

Although single neuron recording has been proven to be one of the most powerful methods to link neural activity and behavior, it is not suitable for investigating the semantic satiation. Reading is only performed by humans and there is no comparable animal behavior task that is a well learned and involves multiple levels of process. It is hard, if not impossible to research this complex cognitive function using animal model. Moreover, because of ethical issues, it is not possible to use this invasive method to record single neuron activity in living human beings. Furthermore, we seek to investigate the cognitive functions at the system level, which requires recording the summed response of cell assemblies.

A widely used non-invasive method to explore neural mechanisms in human is hemodynamic neuroimaging, including Positron emission tomography (PET) and functional Magnetic resonance imaging (fMRI). Both techniques measure neural responses by measuring changes in blood flow. PET measures hemodynamic changes by detecting radioactive tracer (a positron-emitting radioisotope) that is injected before experiments, whereas fMRI measures blood flow changes through the levels of blood oxygenation. A cortical region engaged in a cognitive task with necessitate that more oxyhemoglobin be brought to that region as oxygen consumption takes place to drive neural activity. This contrast called Blood Oxygenation Level Dependent (BOLD) is the signal detected with MRI. The areas underlying a specific cognitive function can be identified by comparing a task to an appropriate control condition. Both PET and fMRI can provide three-dimensional image results by reconstruction the received signals.

Because of the excellent spatial resolution, the hemodynamic neuroimaging techniques can precisely identify regions associated with a certain cognitive task. Hence, they can investigate the neural architecture that underlies specific cognitive functions. For instance, distributed neural networks that involve single word comprehension and retrieval have been demonstrated by using PET (e.g. Petersen, Fox, Posner, Mintun, & Raichle, 1989; Wise et al., 1991). These networks include primary auditory/visual cortex (depending on the input modalities), anterior and superior temporal cortex, and prefrontal cortex. Using fMRI, Kanwisher et al (1997) found an area in the fusiform gyrus was significantly more active when participants processed faces than when they viewed other common objects. These results demonstrate that this special fusiform area, later named fusiform face area (FFA), is selectively involved in the perception of faces. Moreover, neuroimaging is sensitive to deeper sources than other non-invasive methods. For instance, Labar et al (1998) found that the neural activity in amygdala, a place located deep in medial temporal lobe, correlated with the degree of acquisition during fear conditional learning in individual participants.

Although hemodynamic neuroimaging can present various cortical areas underlying different behavior (see the review by Cabeza & Nyberg, 2000), its relatively poor temporal resolution is its Achilles' heel. The temporal resolution for PET is at the level of minutes while fMRI is at the level of seconds (Menon et al., 1995), yet word comprehension occurs in less than a second. Because we are specifically interested in neural dynamics underlying word reading , electrophysiological recordings are more appropriate to research the hierarchical processing of word identification (see the review by Wilson, Leuthold, Lewis, Georgopoulos, & Pardo, 2005).

3.1.2 Using MEG to measure the dynamics of word identification

Providing precise timing information, the non-invasive electrophysiological measures of EEG and MEG have been widely used and demonstrated to be useful tools in cognitive neuroscience research (Hillyard, 2000; Posner & Desimone, 1998; Rugg & Coles, 1995). The relatively direct mapping of neural population activity and the superior temporal resolution allow these electrophysiological measures to illuminate the nature of nerual activity that supports cognitive functions. Furthermore, because these measures are themselves passive, requiring no action by the participant, they provide a covert unbiased window on the underlying processes.

Under the assumption that the same processes are consistently performed by the same cortical structures whenever specific cognitive functions are performed, the neurons that underlie these cognitive functions activate accordingly and their electromagnetic properties change from the resting state. EEG and MEG directly record these electromagnetic responses from the postsynapses of neurons that activate synchronously (Hämäläinen, Hari, Ilmoniemi, Knuutila, & Lounasmaa, 1993). Thus, electrophysiological methods can provide a reliable measure of this electromagnetic field. As illustrated in Figure 3-1A, the recorded magnetic field in MEG as measured at different scalp locations can be positive (i.e., a source) or negative (i.e., a sink): the red and green contour lines represent the source (coming out of surface) and sink (going into the surface) of the magnetic field. These signals can indicate different cognitive processes depending on which and when a neural source is measured. However, because the pattern of the recorded magnetic field is the summation of neurons in different cortical areas, it measures the summation of different processes.

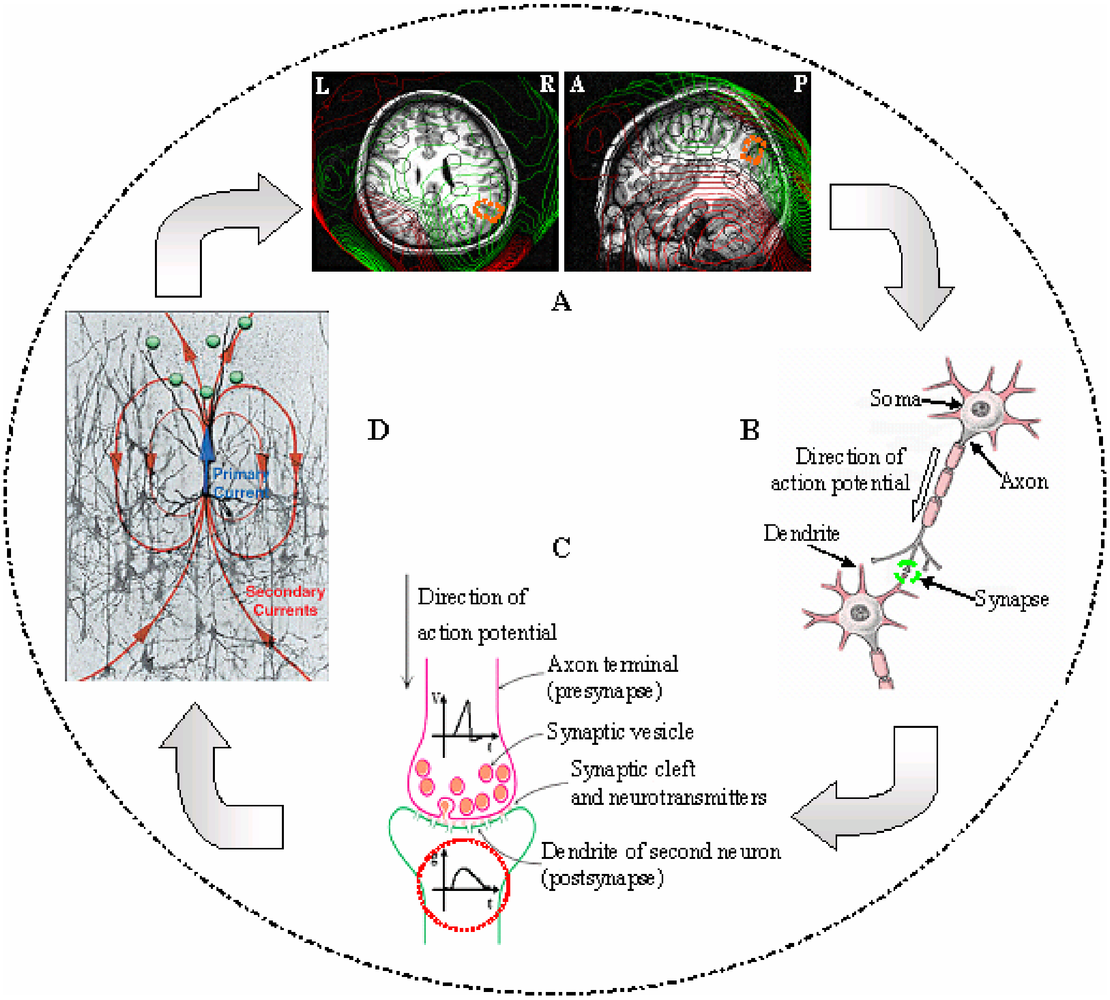

Figure 3-1 The underlying neural mechanisms for the signals recorded by electrophysiological methods (MEG/EEG). A. MEG iso-field maps of a typical M170 response distributed over anatomical MRI of a representative participant. The figure shows an axial view (L: left, R: right) and a sagittal view (A: anterior, P: posterior), the dipole-like pattern (red: sink, green: source) in the iso-field maps distributed over the temporal-occipital conjunction. Each open circle stands for one sensor in MEG facility. An area of human cortex (gray matter) is highlighted in an orange dotted rectangle. B. A cartoon represents the structure of pyramidal cells, which is believed the sources of the signal from cortical layer IV recieved by non-invasive electrophyiological methods. After accumulating enough inputs, the action potential is generated in hillock near soma and propagated along the myelin axon. The action potential needs to cross a synapse to reach the dendrite of the second neuron. A synapse is highlighted in green dotted circle. C. A cartoon of a typical synapse. When action potential travels along the axon and finally reaches the terminal, neurotransmitters are released from synaptic vesicles into synaptic cleft. Neurotransmitters diffuse quickly and bind to receptors on the dendrite of the second neuron. As a result, the current conductance is increased and potential in postsynapse is changed accordingly based on different types of channels are opened. The excitory postsynaptic potential (EPSP) occurs if the sodium ion channels are open, while the inhibitory postsynaptic potential (IPSP) occurs if the chorine ion channels are open. D (adopted from Baillet, Mosher, & Leahy, 2001). EPSPs are generated at the apical dendrites of a cortical pyramidal cell (green dots). They trigger a current that flows through the volume conductor from the cell body to the apical dendrite. The primary current (blue) takes the shortest path and secondary currents (red) close the current loop. EEG recording is sensitive to both the primary and secondary currents while

MEG recording is more sensitive to the primary current. Because the apical dendrites of pyramidal cells tend to be perpendicular to the cortical surface, the electrical current is also perpendicular to the cortical surface. When millions of postsynapses accumulate EPSP synchrously, which usually can be achieved in a 1mm^2 cortex, the sum of electric/magnetic activity is recorded by the sensors placed near the scalp (the iso-field map in A).

At the cellular level, the origin of this electromagnetic activity is believed to be pyramidal cells in cortex layer IV. A typical neuron includes three functional parts (Figure 3-1B): the dendrites, where the inputs arrives; the cell body (soma), in which input accumulates towards generation of an action potential; and the axon along which the action potential transmits. When an action potential reaches the terminal of the axon, the effect of this potential needs to cross the synapse to reach the dendrite of the receiving neuron, and this signal transfer is achieved by a series of chemical processes (Figure 3-1C). The result of these chemical processes (i.e., neurotransmitter release and post-synaptic binding), is the opening of ion channels in the postsynaptic dendrite, which establishes a temporary currents both in intracellular and extracellular conductors (Figure 3-1D). Scalp EEG is sensitive to both primary and secondary currents while the magnetic fields that MEG measures are more sensitive to the primary current (Barth, Sutherling, & Beatty, 1986). To be observed by the sensors placed near scalp, the current produced by a single postsynapse is not enough. However, because the apical dendrites of pyramidal cells tend to be perpendicular to the cortical surface, a large number of dendrites can simultaneously produce currents in a similar direction that flow perpendicular to the cortical surface. Hence, the recorded electromagnetic signals near the scalp are the result of aggregated activity of millions of pyramidal cells that exhibit excitatory postsynaptic potential synchronously (Baillet, Mosher, & Leahy, 2001).

Because of the superior temporal resolution and relative direct measure of neural activity, electrophysiological recordings are ideal for tracking a series of mental operations that occur in a cascade manner in word identification within hundreds of milliseconds after the visual word onset (see the review by Halgren et al., 2002). Moreover, magnetic fields are less distorted by the skull and scalp than electric fields, and so MEG obtains a better spatial resolution than EEG. Moreover, MEG measures absolute magnetic fields rather than voltage potential difference, which avoids the problem of different results with difference reference comparisons. Therefore, MEG is an excellent tool for measuring the dynamics in word identification.

3.1.3 Limitations of electrophysiological recordings

The human brain is a highly distributed system and many cortical areas are simultaneously active during any task. Non-invasive surface recordings, such as scalp electroencephalography (EEG) and magnetoencephalography (MEG), use many sensors to record the voltage potentials or magnetic field responses near the surface of the head that arise from the underlying mixture of cortical sources. Each sensor in these recording methods receives a mixed signal from all neural sources and the contribution of each source depends both on the distance to that source and the relative orientation of that source (Hämäläinen, Hari, Ilmoniemi, Knuutila, & Lounasmaa, 1993). Given the mixture of underlying neural sources, it is inaccurate to assume a one-to-one mapping between sensors (or local groups of sensors) and underlying sources. In particular, a change in response for a particular sensor could be due to a change in the magnitude of response of the dominant neural source, or it might instead be due to a change in the distribution of the neural sources as different cortical areas are recruited in the different conditions of interest.

The inherent ambiguity between response magnitude and cortical distribution could be addressed with equivalent dipole modeling (Baillet & Garnero, 1997) or blind source separation algorithms, such as independent component analysis (ICA) (Makeig, Jung, Bell, Ghahremani, & Sejnowski, 1997). However, due to the 3-dimensional nature of passive electrophysiological recordings (as opposed to 2-D manipulated cortical slices with fMRI), there exists a so-called “inverse problem”, which refers to the infinite possible cortical solutions to a particular data pattern across the sensors (Mosher, Leahy, & Lewis, 1999). These techniques tackle the inverse problem through simplifying assumptions, such as an assumed number of dipoles/components and independence from moment to moment and trial to trial. The accuracy of these techniques strongly relies upon these assumptions, which are known to be false in many circumstances. For instance, synchronization between cortical areas during auditory or visual detection tasks (Baudena, Halgren, Heit, & Clarke, 1995; Halgren, Baudena, Clarke, Heit, Liegeois et al., 1995; Halgren, Baudena, Clarke, Heit, Marinkovic et al., 1995) implies that different cortical sources are temporally dependent rather than independent.

The ambiguity that arises from only considering select sensors is compounded by averaging across subjects because the same sensor may reflect entirely different mixtures of cortical sources for each individual. Nevertheless, sensor selection and subject averaging remain common practices in EEG experiments (e.g., Dehaene & Naccache, 1998; Wilding & Rugg, 1996) and few EEG studies address this issue directly (although see Campanella et al., 1999; Whittingstall, Stroink, & Dick, 2004). For instance, it has been demonstrated that anatomical differences in the cortex directly relate to EEG scalp recording differences (Basile et al., 2006). Beyond anatomical differences, tissue conductivity volume conduction differences also play an important role in the magnitude and pattern of scalp potentials (Nunez & Srinivasan, 2006). In contrast to this situation with EEG, the role of individual differences is carefully considered in the study of neuroanatomy and functional magnetic resonance imaging (fMRI). For instance, current practice in fMRI normalizes against neuroanatomical differences by employing inflation techniques that map each individual brain onto a canonical brain that is flattened such that sulci can be visualized in a 2D plane (Fischl, Sereno, & Dale, 1999). Analogous to this canonical brain mapping with fMRI, we present a simple technique that normalizes EEG or MEG responses across all sensors against the 'standard' response pattern for that individual.

In light of individual differences, EEG and MEG typically go to one of two extremes. EEG analyses often average over many participants, making sure to keep scalp electrodes in the same position in relation to the external parts of the head, with the hope that this produces a systematic positioning in relation to the brain, or at least sufficient data to overcome the differences that might otherwise confound the results with a smaller number of participants. In contrast, systematic positioning of sensors in relation to the head is all but impossible with MEG. Therefore, MEG typically involves analyzing the results from a small number of participants separately (e.g., Xu, Liu, & Kanwisher, 2005), with no method for combining the results across individuals. This avoids the potential errors caused by averaging across individual differences who have different neuroanatomy (e.g., Liu & Ioannides, 1996), but makes it impossible to use inferential statistics to make claims about the general population.

Traditional EEG and MEG results based on single sensors or small groups of sensors can nevertheless reliably identify whether conditions are different from each other, but cannot ascertain 1) whether the observed differences reflect the addition/subtraction of new cortical sources or 2) whether the observed differences are due to increases or decreases in response magnitude of the underlying sources. Our technique can address these functionally important questions through the multivariate comparison of the entire array of sensors in experimental conditions against a standard response pattern for each individual. For EEG this makes exact placement of electrodes less important and for MEG this allows comparison across individuals.

The above discussion focused on the role of individual differences and the inherent ambiguity between pattern similarity and response magnitude. In addition to these concerns, many experimental paradigms introduce a third problem by using short inter-stimulus intervals between presentations, which results in measurements that reflect the combination of fast cortical responses to the current stimulus and slower responses from previous stimuli. However, this problem is all but unavoidable considering that many of the most widely used and informative designs in behavioral psychology rely upon short latencies between stimuli (e.g., Di Lollo, Enns, & Rensink, 2000; Kanwisher, 1987; Levin & Simons, 1997; Posner, Snyder, &

Davidson, 1980; Raymond, Shapiro, & Arnell, 1992). Complicated experimental and mathematical techniques can be employed to address this issue of overlapping electrophysiological waveforms (Woldorff, 1993). However, our simple multivariate comparison technique may also help in such situations considering that comparisons can be done separately in relation to fast (e.g., P100) and slow (e.g., N170) standard responses so as to partially untangle the combined pattern.

Similar to ICA and dipole modeling and similar to multivariate analyses in fMRI (Kriegeskorte, Goebel, & Bandettini, 2006; Norman, Polyn, Detre, & Haxby, 2006), our technique uses the entire pattern across all the sensors. Our approach is also analogous to the use of a "localizer task" in functional magnetic resonance imaging (fMRI) studies (e.g., Kanwisher, Tong, & Nakayama, 1998) in that it compares responses to a standard reference. In fMRI experiments, an initial task is often used to locate a particular cortical region of interest for that individual. Subsequent experimental conditions are then analyzed in terms of this region. By analogy, we include a condition that defines a 'standard response' for each individual (i.e., a pattern over all sensors in some baseline condition at a chosen time following the stimulus), against which we compare the response pattern in experimental conditions. We advocate both a measure of pattern similarity to the standard response as well as the projected magnitude "in the direction of the standard response". Next, we present the mathematical details for calculating these measures and then we demonstrate their effectiveness using data from a word priming study that recorded high density evoked MEG.

3.2 Measures of similarity and magnitude

Measures of similarity and magnitude can be calculated for any two patterns across the sensors, such as with two different experimental conditions, but they are most effective when there is a standard response for comparison. The standard response should measure a response that includes many of the same processes of potential interest that are employed in the experimental conditions, but remain free of overlapping waveforms and other complications. The situation that defines the standard response should be similar to the experimental conditions in terms of the stimuli, level of attention, task demands, salience, task relevance, etc. In the example to follow, the experimental conditions of interest were immediately repeated versus novel words and the standard response was generated from a highly attended prime word presented in isolation for a sufficiently long duration.

We define the entire multivariate pattern of sensors in one condition to be $\vec{A}$, which is an n-dimensional column vector where n is the number of sensors (i.e., all analyses are in "sensor space"). Then, the response in some other condition, $\vec{B}$, can be compared for its similarity as defined by the n-dimensional angle (Equation 1) as well as its magnitude in the direction of $\vec{A}$ through the geometric projection of $\vec{B}$ onto $\vec{A}$ (Equation 2).

$$\cos\theta = \frac{\vec{A}^T \vec{B}}{|\vec{A}||\vec{B}|} \qquad \text{(Eq. 1)}$$

According to Equation 1, the value of cosine θ gives an index of the spatial similarity between the pattern across the sensors in two experimental conditions, A and B. We refer to use of this measure as the ‘angle test’. Similar to a correlation measure, the cosine of the angle ranges between -1 and +1, with -1 indicating completely opposite, +1 indicating completely similar, and 0 indicating dissimilar (perpendicular). This measure has the advantage that it is unaffected by the magnitude of the response. For example, if two conditions have identical response patterns across the sensors, but the response magnitude for one condition is twice as large, this comparison technique will reveal that the angle between them is 0, and, thus, the cosine of the angle is 1.0 (i.e., perfectly similar). If the angle test reveals that there is no statistically reliable difference in the spatial similarity between two conditions (below we discuss a technique for assessing statistical reliability), this suggests that the distribution of underlying cortical sources is similar between the two conditions. The distribution of cortical sources might change in exactly the right way to produce the same pattern across the sensors, but such a coincidence is of low probability, particular when the number of sensors is large. Thus, a high value on the angle test is likely to correspond with a similar mix of cortical responses. Conversely, if the angle test reveals that the spatial similarity of the sensors is different, then this definitely indicates that the underlying distribution of cortical responses has changed. This second conclusion is assumption free, barring confounding factors such as head position changes between conditions.

$$|\overrightarrow{B}|\cos\theta = \frac{\overrightarrow{A}^{T}\overrightarrow{B}}{|\overrightarrow{A}|} \qquad \text{(Eq. 2)}$$

For the ‘projection test’ based on Equation 2, the magnitude of an experimental condition B is normalized against the standard response A, by projecting $\overrightarrow{B}$ in the direction of $\overrightarrow{A}$. This projection can be used to calculate the magnitude of response for some condition in the direction of the standard response. It is not necessary that the condition of interest be similar to the standard response. However, in order to unambiguously compare two projection values in two different experimental conditions (e.g., B_1 and B_2), the conditions need to be sufficiently similar to each other. Otherwise, any apparent magnitude differences could be due to similarity differences. In other words, a critical first step is to assess whether the conditions are dissimilar with the angle test. Regardless of the observed level of similarity between the conditions, the projection values can be calculated, but if it is found that the conditions are dissimilar, then an obtained difference in the projection values does not unambiguously indicate a magnitude change and instead only indicated something has changed. Nevertheless, even in this situation, the projection test may be useful for normalizing against individual differences.

Because the projection is relation to each individual's "clean" standard response (e.g., the M170 to a word presented in isolation), it should normalize both against each individual differences (e.g., the particular pattern over sensors of the M170 for a particular individual), but, also, against contamination from overlapping waveforms that exist with short latencies between successive stimuli (e.g., the combination of an M170 to a word presented 170 ms ago with the M400 to a prime word presented 570 ms ago). Because this technique normalizes against individual differences, the projection values can be used in traditional inferential statistical tests across the data of multiple participants.

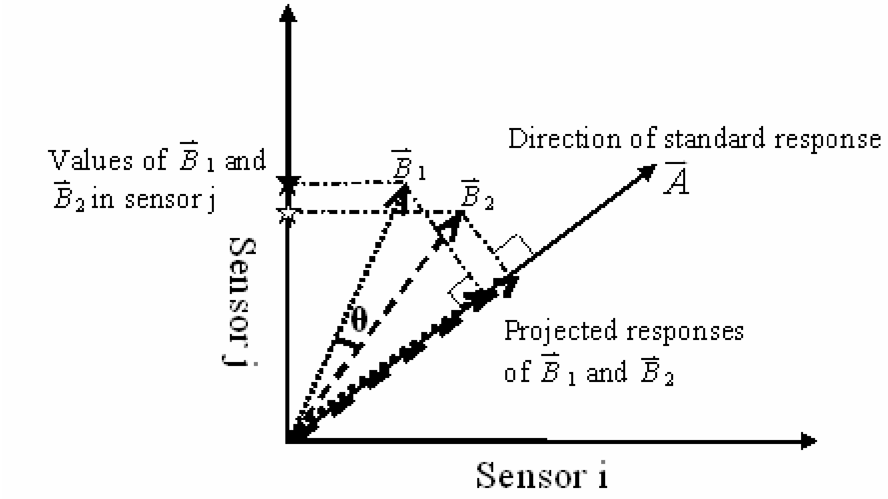

Figure 3-2 Demonstration of the angle test and the projection test with a hypothetical situation involving 2 sensors (i and j). Results are shown for a standard response (the solid line A) and 2 experimental conditions (B_1, dotted line and B_2, dashed line). In this example, the conditions are spatially similar to each other, but are different from the standard response because, unlike the standard response, the experimental conditions include some other overlapping response. The spatial angle (θ) between the experimental conditions indicates whether the experimental conditions represent different response patterns across the 2 sensors. Because the conditions are sufficiently similar to each other (i.e., small angle), the projection onto the standard response indicates response magnitude that normalizes against individual differences and against overlapping waveforms (i.e., the magnitude of response in the direction of the standard response). If the sensor of largest magnitude is selected (i.e., sensor j) it is concluded that B_1 (filled star on vertical axis) is greater than B_2 (open star on vertical axis) but, in contrast, if the projection onto the standard response is analyzed, it is concluded that B_2 (length of dashed arrow) is greater than B_1 (length of dotted arrow).

Figure 3-2 illustrates the angle test and projection test, with a hypothetical example that includes spatial differences between the standard (A) and experimental conditions (B_1 and B_2), as might arise from overlapping waveforms for the experimental conditions. For demonstration purposes, only two sensors are shown (e.g., a 2-D sensor space), but the same logic applies to n sensors defining n dimensions (i.e., a multivariate situation). The angle test between B_1 and B_2 indicates that they are sufficiently similar and, therefore, likely due to the same mixture of underlying cortical sources. Thus, the projection onto the standard response provides a pure measure of magnitude that normalizes against individual differences (i.e., different patterns in the standard response for different individuals) and also normalizes against overlapping waveforms (i.e., extraction of that component of the experimental condition that is in the direction of the standard response, rather than in the direction of the overlapping response). The bold lines along the direction of standard response are the projected normalized responses of experimental conditions. A traditional analysis based on the sensor with the largest response compares sensor j in the two conditions, and concludes that condition B_1 produced a larger response than condition B_2. In comparison, projection of the experimental conditions onto the standard response concludes that condition B_1 produced a smaller response magnitude than condition B_2.

The general procedure for using these measures includes the following steps. 1) identify an appropriate standard response in the experimental design; 2) use the angle test to assess the similarity of conditions of interest; 3) project the experimental conditions onto the standard response to normalize against individual differences and overlapping waveforms. If the answer to step 2 concludes that the conditions are dissimilar, the projection of step 3 is still useful for normalizing, but it does not unambiguously indicate magnitude versus similarity. However, if conditions are not found to be similar according to the angle test, then the projection values unambiguously indicate magnitude and increases versus decreases can be taken to correspondingly indicate increases versus decreases of cortical response.

In order to statistically test each step, a null hypothesis distribution is needed. There are several techniques that could be applied to define a null distribution, although we take the relatively simple approach of comparing the first half versus second half of trials within the experiment for a given condition (i.e., cross-validation over time), versus the same first/second half of trials comparison between conditions. The selected trials could be determined by odd versus even trials, or through repetitive non-parametric bootstrap samples, but first versus second half of the experiment is simple to calculate and includes trends over time in the null distribution. In this manner, the angle and projection tests become simple t-test of between versus within conditions.

Next, we provide an example where these measures were used to assess M170 responses in a short-term repetition paradigm with visually presented words. The response of interest was to the briefly flashed target word. The first word (i.e., the long prime) was used to define a standard response for the M170 in terms of the spatial pattern associated with a single visually presented word. This event was chosen for the standard response because it presented a single highly attended word. First, the angle test was implemented to statistically test the existence of individual differences in the standard response (otherwise there’s no need for a standard response to obtain normalization). Next, the angle test was used to assess the similarity across the 3 different target conditions (*novel*, a target word that is different than both prime words; *short*, a target word that repeats the second prime, which was presented 150 ms prior the target; and *long*, a target word that repeats the first prime, which was presented 2,000 ms prior to the target). Because the target conditions were found to be sufficiently similar to each other, the projection test was used to unambiguously indicate response magnitude. The projection measure normalized the target conditions against the standard response and the results were analyzed across individuals to determine if, in general, target response magnitude varied across the conditions. Essentially, we asked "how much of an M170" occurred in each condition for each individual by using all the data across the entire sensor array as compared each individual's standard M170 to visually presented words.

3.3 An example with MEG: Immediate word repetitions

The example implementation of these techniques, reported next, may seem overly complex. However, this complexity proves to be instructive. A major advantage of these measures is that they can be applied to high density sensor data that varies greatly across individuals (as is the case with MEG data in this example) and that they can be applied to isolate a small response (e.g., the target word presented for just 50 ms) that overlaps greatly with a previous stimulus (e.g., the prime word presented 150 ms before) or overlaps greatly with a subsequent stimulus subsequent stimuli (e.g., the pattern mask presented immediately after the target word). The chosen paradigm is a classic threshold word identification paradigm (e.g., Humphreys, Besner, & Quinlan, 1988), which requires immediately preceding primes, brief targets, and subsequent masks. Therefore, this task is ideal for demonstrating the effectiveness of these measures for untangling the otherwise confusing combination of responses.

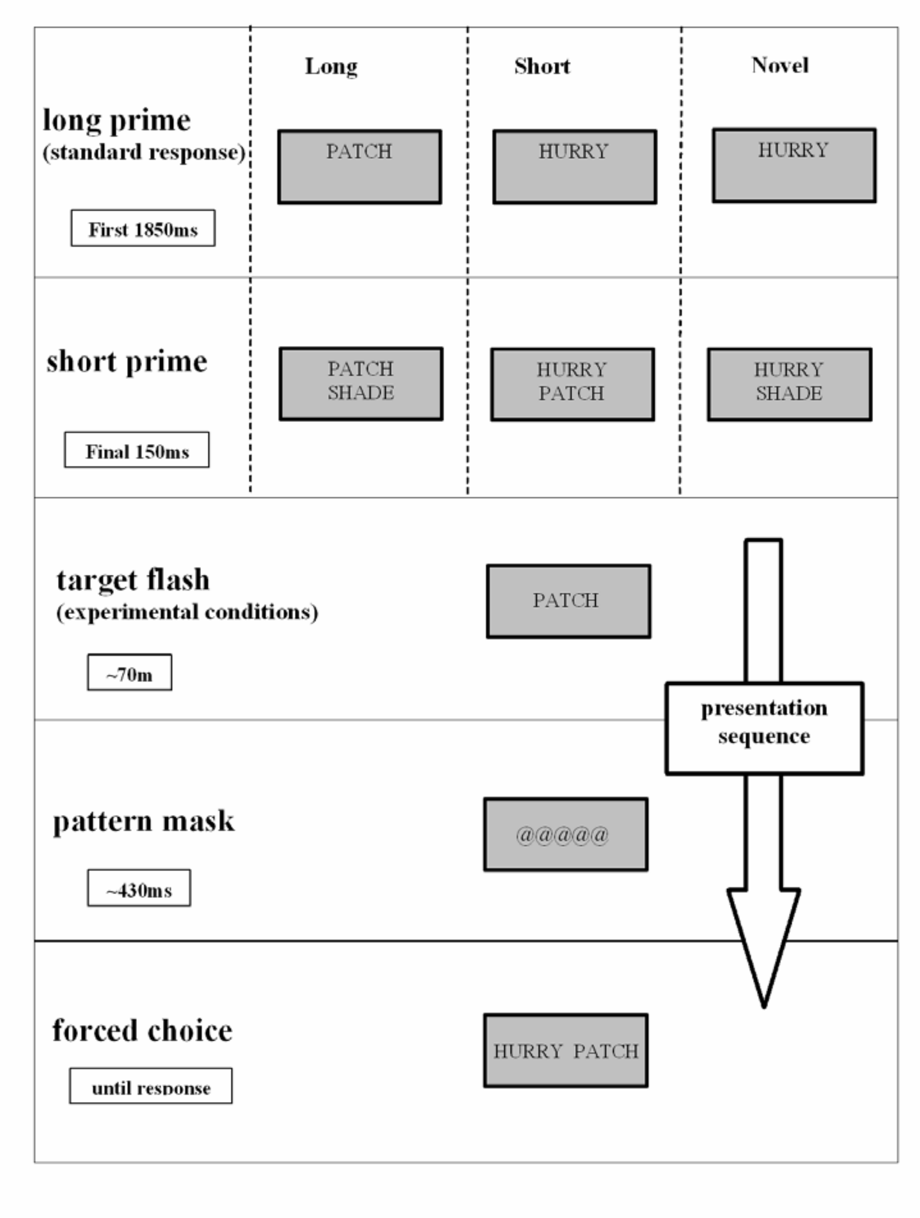

Figure 3-3 Presentation sequence for the reported experiment for demonstrating the projection method. The task of participants was to identify the briefly flashed target word by selecting between two choice words at the end of the trial sequence. Target flash durations were set separately for each individual to achieve threshold performance of 75% correct. The upper prime word appeared first (long prime), remaining onscreen for 1850 ms in isolation, thus providing a standard response. During the final 150 ms prior the target word, the lower prime word appeared (short prime). MEGs to the target flash provided 3 experimental conditions, depending on whether the target was different than both primes, a repeat of the long duration prime, or a repeat of the short duration prime.

This experiment is only summarized here, and is reported in full elsewhere (Huber, Tian, Curran, O'Reilly, & Woroch, in press). As seen in Figure 3-3, the task of the participants was to identify the briefly flashed target word (e.g., PATCH) presented in the center of the screen immediately after the prime words. First, a single prime word appeared above the midline, which provided the standard response (as well as a long duration prime). Next, a second prime word appeared 1850 ms later, below the midline. Finally, these two prime words were replaced by a single target word, which provided the evoked MEG responses for the 3 conditions of interest (a *novel* target, a target that repeated the *short* duration prime, and a target that repeated the *long* duration prime). Target word durations were set at the perceptual threshold for each participant such that accuracy was approximately 75% in forced choice identification (e.g., a choice between HURRY and PATCH).

Humphreys et al. (1988) used a similar paradigm and found differences in the magnitude of immediate repetition priming with masked versus unmasked words. The current paradigm tested these effects by controlling for response bias with two-alternative forced choice testing, rather than naming the briefly flashed target word. With just a single prime, as in the Humphreys et al. studies, comparison of the MEG response to the target following a brief prime versus following a long duration prime would be problematic because only the short duration prime condition involves overlapping waveforms. Furthermore, short versus long duration primes might involve different degrees of alertness. For instance, the abrupt onset of a word may result in a transient attentional response with a different MEG signature that would exist following a brief prime but not following a long duration prime. To address these concerns, the current paradigm presented on every trial a first prime for 2,000 ms (the long prime) as well as a second prime for the final 150 ms (the short prime) before the target. Thus, all conditions are identical up until the target, and any attentional effects should be equivalent.

3.3.1 Individual Differences

The response to the long prime was used as the standard response because the long prime was seen in isolation for 1850 ms as part of the highly attended sequence of events. Figure 3.4A shows the M170 standard response results from all 10 participants, demonstrating different spatial patterns for the M170 to visually presented words.

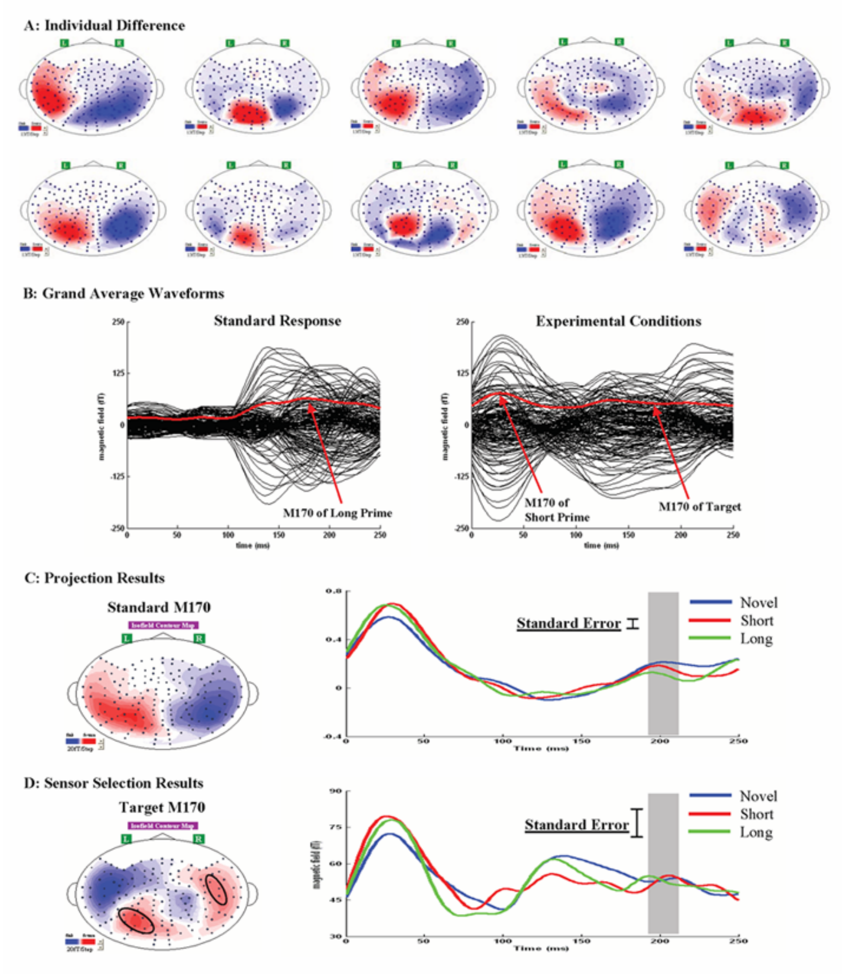

Figure 3-4 Comparison of the results using projection method and channel selection method. A. Spatial patterns of the M170 standard responses for all 10 individuals. In general, individual

differences in the similarity of these patterns were found to be reliable as indicated by a statistical test of the angle between the standard responses across individuals. B. Comparison between the grand averaged waveforms of standard response to the long prime (left), versus the grand averaged experimental response to the target word (right), which immediately followed the second prime. Both figures represented waveforms in 157 channels of grand-average results. The bold red lines in both figures is the Root-mean-square (RMS) of the 157 channels. For the experimental conditions, there is no clear M170 peak, possibly because of individual differences, overlapping waveforms, or because the target word is only presented briefly. C. Projection results. The topographic map is the grand average of the standard M170 responses. The graph shows the average projection measures at each moment in time for 3 different target conditions, with projection calculated separately for each individual according the standard responses in A. D. Traditional sensor selection and Root Mean Square results. The topographic map is the grand average target M170. The 10 sensors with the largest positive magnitude are circled and these were selected to produce traditional sensor selection analyses. The graph shows average Root Mean Square for the selected sensors at each moment in time. The topographic maps in C and D were taken at 176 milliseconds after word onset (the long prime onset for C and the target word onset for D). A comparison of these topographic maps reveals large differences, which suggests that the target response is contaminated by overlapping responses from the second prime, which occurred just 150 ms before the target. The shaded areas in the graphs of both C and D indicate the 22ms average window used for statistical analyses. The error bar in each graph indicates one standard error of the mean difference between novel and repeated words, averaged over the short and long conditions as calculated for the M170 time window. There was no difference among M170 responses of the 3 target conditions using sensor selection. However, the projection measure uncovered the small target M170 peak and revealed that the target word produced less of a cortical response when it repeated the long duration prime.

In order to statistically assess reliability of these individual differences (i.e., are the differences in Figure 3-4A reliable individual differences or just due to sampling noise), the experiment was separated into two halves, and M170 patterns for each half were determined separately in order to obtain a null hypothesis measure of spatial pattern variability. There were 400 trials in the experiment and so standard M170 responses to the first 200 trials were calculated separate from the last 200 trials. The angle test was performed for the 10 within subject comparisons for the data of the 10 participants (i.e., angle between first half and second half for each individual), versus the 45 between subject comparisons (10 choose 2 combinations of first half versus second half when these halves are for different individuals). Using an independent samples t-test, the cosine angle for the between subjects comparison was significantly lower (more dissimilar) than the within subjects comparison, $t(21.5)$ =

7.812, $p < .001$[2]. This indicates that different people have different spatial patterns for the M170 responses to visually presented words. This result highlights the need to normalize against these individual differences.

Although not central to application of these measures, we note that the reported analyses also normalized for individual differences in the timing of the M170 responses. This was done by determining peak M170 times in the standard response waveform to find appropriate M170 temporal offsets for each individual. These individually appropriate times were then used for subsequent tests (i.e., we assumed that these same peak times were applicable to the briefly flashed target words). 22 ms windows were placed around these individually determined M170 peak responses for data averaging purposes, both for the standard responses as well as the target condition responses. Separate statistical tests validated the reliability of these timing differences.

3.3.2 Target Repetition Effects

The 3 target conditions were first compared to each other using the angle test to check if they produced different spatial patterns. Such a finding would indicate that one or more of the conditions involved recruitment of a cortical response not present in the other conditions. Statistical reliability was again determined by dividing the experiment into trials from the first half of the experiment versus trials from the second half of the experiment. The patterns for each half were again compared to

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[2] Because the assumption of equal variances was violated for the independent samples t test ($F = 4.26$, $p < .05$), the degrees of freedom has been appropriately adjusted.

each other with the angle test, with this occurring for first/second half angle measures from the same condition (the within values for null hypotheses) versus first/second half angle measures from different conditions (the between values for experimental conditions). Because this was a comparison of conditions, rather than individuals, these comparisons were calculated within subject (i.e., repeated measures). Because there were 3 conditions, this entailed 3 different possible comparisons between conditions, which were then averaged in comparison to the average of the 3 within condition comparisons, yielding one between conditions measure and one within conditions measure for each participant. In a dependent samples test across the 10 participants, there was no significant difference in the similarity (angle test) of the between conditions comparisons versus the within condition comparisons, $t(9) = -1.216$, $p = 0.255$. This suggests that the same distribution of cortical responses was involved in the 3 target conditions. Thus, the subsequent projection test was taken to indicate magnitude differences rather than pattern differences.

After finding no support for the hypothesis that the 3 conditions were dissimilar, magnitude changes were determined by projecting each condition onto the standard response (i.e., the M170 to the long prime). In doing so, the target word's response was reduced to a single magnitude measure that normalized against individual differences. Besides allowing statistical tests across individuals, this normalization also helped reduce contamination from the ongoing later components (e.g., M400) in response the short prime, which was presented just 150 ms prior to the target. By projecting the target response onto the standard M170, the resultant magnitude more cleanly reflects the M170 component, with the overlapping M400 response to the short prime partially factored out. The degree of success in this decontamination depends on the spatial similarity between the standard response and the unwanted overlapping response. The possible contamination from the M400 to the short prime is highlighted in Figure 3-4B and the topographic maps of 3-4C and 3-4D, which show the grand averaged (i.e., across individuals) standard response 170 ms after the long prime (the waveforms are shown in the first graph of 3-4B and the topographic map is shown in 3-4C). This contamination is seen by comparing these standard responses to the grand average target response 170 ms after presentation of the target (the waveforms are shown in the second graph of 3-4B) and the topographic map is shown in 3-4D). As seen in the figures, these two topographic patterns, which include 4,000 trials, are very different and the M170 waveform to the target appears to be missing as indicated by the Root Mean Square (RMS) shown in the red line.

First, we report the results from the projection measure and, next, we compare these to the results with traditional sensor selection. A repeated measures one-way ANOVA across the 3 priming conditions as applied to the projection test values averaged over a 22 ms window (see Table 3.1 and Figure 3-4C), revealed significant differences for the M170, $F(2,18) = 5.202$, $p < .025$[3]. Subsequent contrasts revealed that the M170 to a repeated word was smaller than the novel condition, but only following a long duration prime, $t(9) = 3.916$, $p < .01$, with no priming effect following a short duration prime, $t(9) = .919$, $p = .382$. This finding replicated the

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[3] After Geisser-Greenhouse correction to the degrees of freedom, there were still significant differences for the M170, $F(1.75,15.72) = 5.202$, $p < .025$.

same result found for the N170 in an ERP experiment with identical design (Huber, Tian, Curran, O'Reilly, & Woroch, in press). Figure 3.4C portrays the projection test results, first showing the standard M170 topographic map and then the projection values at each moment in time for the three conditions. The topographic map shows the grand average standard response for illustrative purposes, but the separate standard responses shown in Figure 3.4A were used for the projections prior to averaging across subjects. The shaded region of the waveform graph indicates the 22 ms window used for statistical analyses and the error bar is the standard error of the mean repetition priming difference averaged across short and long duration priming. Unlike the grand average waveforms in the second graph of Figure 3.4B, which reveal no apparent target M170 response, there is now a definite peak for the M170 in response to the target (as well as an earlier large peak for the M170 to the short prime). Thus, this normalization technique extracted the M170 component from the overlapping waveforms and did so with a separate normalization for each individual, thereby recovering the small M170 peak to the briefly presented and masked target word.

Next, we compare these results to a traditional technique based on sensor selection. We first calculated the grand average response to the experimental conditions at 170 ms (shown in the topographic map of Figure 3-4D) and then selected the 10 sensors with the largest positive magnitude across the 3 conditions (these sensors are circled in Figure 3-4D). Subsequent analyses were performed only for these sensors. Using these sensors, an average M170 response for each individual in each condition was calculated based on the 22 ms time window. Comparing across the 3 priming conditions with this sensor selection measure, a repeated measures one-way ANOVA found no differences, $F(2,18) = .591$, $p = .565$[4] (see Table 3.1 for the raw values and measures of standard error for each analysis technique). The corresponding waveforms in Figure 3-4D may appear to indicate differences between the 3 conditions, but perhaps the most important result in Figure 3-4D is the height of the standard error bar, which is more than twice as large as compared to the projection results in Figure 3-4C. Furthermore, even with the maximal M170 sensors selected, there is no obvious M170 peak to the target, unlike the graph in Figure 3-4C. Thus, the sensor selection results are too unreliable to conclude that there were any effects of priming condition or even that there was an M170 to the briefly presented target.

	M170 (sensor selection)		M170 (projection test)	
	Mean (fT)	standard error	Mean	standard error
Novel	44.829	-	.207	-
Short	40.384	2.896	.176	.034
Long	43.598	4.545	.113 **	.024

Table 3-1 Target M170 results with traditional sensor selection versus the project measure. Doube stars stands for repetition effects significant at the .01 level.

Although traditional sensor selection failed to find any reliable results across individuals, the projection measure not only found reliable results, but, furthermore,

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[4] After Geisser-Greenhouse correction to the degrees of freedom, there was still no significant difference for the M170 using sensor selection, $F(1.54,12.36) = .591$, $p = .527$.

these results replicated N170 ERP results with the same experimental design (Huber, Tian, Curran, O'Reilly, & Woroch, in press). Furthermore, such 'repetition suppression' effects immediately following primes are in agreement with several other published results. For instance, the M170 to a face is likewise smaller in magnitude when presented immediately after a face as compared to objects from other categories (Harris & Nakayama, 2007). Similarly, with a slightly different paradigm using visual words, early repetition effects have been documented for the P150 (Holcomb & Grainger, 2006). However, unlike these previous results, which were based on sensor selection, the current technique unambiguously indicates that smaller MEG values with priming correspond to smaller cortical responses, and are not due to a change in the pattern across sensors.

3.4 Discussion

Using MEG responses to short-term repetition priming of visually presented words as an example data set, we demonstrated the effectiveness of the proposed similarity and magnitude measures. These techniques use all the data from all recorded sensors (i.e., these are multivariate measures), to determine reliable measures of spatial similarity and response magnitude. Calculation of the angle between patterns determined whether conditions produced different patterns, such as would be the case if they involved a different mix of underlying neural sources. Because no differences were found, the projection test indicated response magnitude without worry that apparent differences were due to recruitment of different cortical responses in some conditions but not others. Calculation of the projection between each condition and a standard response provided a magnitude measure that normalized against individual differences and reduced contamination from overlapping responses. We found that 1) individual spatial differences were large and reliable; 2) the conditions of interest where similar to each other in terms of the topographic pattern; and 3) priming reduced the magnitude of the distributed cortical response for the M170 to a target that repeated a long duration prime. In contrast, a traditional analysis based on sensor selection failed to find any reliable effects. We will use this new developed projection method in the following sections to investigate the dynamics in single word identification.

Similar to these measures, registration methods have been developed to handle individual differences (Maintz & Viergever, 1998). For instance, intersubject registration involves mapping one participant's imaging data onto another participant's imaging data and atlas registration involves the registration of each participant's imaging data onto canonical imaging data. Registration has been successfully employed with MEG data to overcome individual difference (e.g., Corouge, Hellier, Gibaud, & Barillot, 2003). However, the angle and projection measures that we employed are more easily implemented and do not require atlas or between subject registration because they instead normalize each person's data against their own standard response.

One limitation of these measures is their inability to localize specific cortical sources. As discussed in the introduction, source localization techniques suffer from limitations due to possibly erroneous simplifying assumptions. Considering the limitations of these source localization algorithms, alternative analysis methods have been proposed that attempt to delineate separate processes rather than separate cortical areas. Similar to our proposed techniques, Haig and Gordon (1995) used spatial projection to provide a measure of response magnitude in different conditions. However, their technique was applied to the subject averaged data rather than separately for each individual. First, they found the spatial pattern corresponding to the average difference between the conditions of interest. Next, the results for each individual were projected onto this difference pattern and inferential statistics were applied to these projection scores from each individual. This is similar to our technique except that we advocate normalizing each individual by their own standard response. Additionally, we suggest that the similarity between conditions needs to be checked before implementing projection in order to rule out changes in cortical recruitment between conditions.

An important statistical concern with scalp EEG and MEG analyses based on individual sensors or groups of sensors is the need to correct for multiple comparisons (i.e., one could continue to select different sensors until a desired result is found). A conservative correction for the pair-wise type I error rate in order to achieve a desired family-wise type I error rate (i.e., the probability that one or more comparisons incorrectly indicates a significant difference), is to use the Bonferonni inequality, in which case the significance level is the desired type I error rate (e.g., .05) divided by the number of sensors or groups of sensors (e.g., 157 for case of the MEG data we reported, requiring that any particular result achieve a probability of .00032 to reach significance). In truth, it is rare that researchers perform this conservative correction because it would require more data collection than is typically feasible. However, multivariate measures across all sensors avoid the problem of multiple comparisons by distilling the data to a single measure of spatial similarity or response magnitude.

Besides spatial similarity and response magnitude, cortical processes can be delineated in their timing. For instance, a study performed by Uhl et al. (1998) examined spatiotemporal patterns in EEG, revealing components at different phases at a given temporal frequency (i.e., different modes). In this manner, the evoked response at a sensor was explained by changes in the distribution of the temporal modes. This again points out the dangers of assuming a one-to-one mapping between sensors and responses of interest; not only does an evoked response reflect a distribution of cortical sources, but the underlying sources may each contain a distribution of temporal patterns. Our technique of spatial similarity and response magnitude is not intended as a competitor to such analyses and is instead complementary. When working with a theory based on the precise timing of cortical processes, such as with spike timing models, or oscillator models and power spectrum effects, then these timing analyses are appropriate. However, when working with a theory based on degree of activation, such as with average firing rate or hemodynamic effects, then spatial similarity and response magnitude are appropriate.

We suggest that these measures provide several distinct advantages over traditional analyses based on individual sensors or groups of sensors. First, they indicate whether the distribution of cortical sources has changed or whether the response magnitude of cortical sources has changed; such a conclusion cannot be made with single sensors or groups of sensors, which can only indicate whether there is a difference. Second, they normalize against individual differences, allowing inferential statistics across participants. Third, by projecting onto a standard response, they reduce the problem of overlapping waveforms that arises in experiments with multiple rapid presentations. Fourth, they distill multi-sensor data to a single number of similarity or magnitude, thus avoiding the statistical problem of multiple comparisons. Fifth, they do not require collection of anatomical information for each individual. Thus, one can calculate these measures without costly structural MRI data. Finally, and perhaps most importantly, these measures are easy to implement and do not require sophisticated software. In the following sections in this chapter, we will use this projection method to facilitate the investigation of dynamics in word identification.

Part II: An MEG study of cue and target responses during speeded category matching

3.5 Introduction

The method of electrophysiological recording has proven to be a feasible tool to investigate the dynamics of cognitive functions (Hillyard, 2000; Posner & Desimone, 1998; Rugg & Coles, 1995). In the following introduction, different process stages in the hierarchy organization of word identification are revealed by electrophysiological recording (Section 3.5.1). Moreover, the different neural processes associated with behavioral dynamics are introduced (Section 3.5.2). By considering the characteristics of electrophysiological method and associated satiation theory proposed in Chapter 2, specific predictions are made in the MEG study of semantic satiation.

3.5.1 The word identification process in electrophysiological studies

The whole process of word identification is a hierarchical process. Similar to the hierarchical organization of the visual object receptive fields of different neurons that become more sensitive to complex features along the ventral pathway (Thorpe & Fabre-Thorpe, 2001), Dehaene et al. (2005) argued that word identification is achieved through a hierarchical architecture. In this hierarchy, the edges and line segments and other primary perceptual elements contained in external visual word are initially processed in visual cortex. The abstract representation of letters and orthography is formed at the second stage in this hierarchical process. The meaning of a word then finally retrieved based on the formed orthography from semantic memory.

Because of this hierarchical architecture, the timing of activity at different process stages is informative to track different mental operations in word identification. Consistent with the theory of hierarchal process in visual word identification, the associated neural activity for successive process stages has been assessed using electrophysiological recording. The major and well-established temporal components are observed in electrophysiological recordings around 100 ms, 170ms and 400ms after the onset of visual word stimuli, which are thought to correspond to perceptual processes, orthographic processes and meaning access, respectively (Bentin, Mouchetant-Rostaing, Giard, Echallier, & Pernier, 1999).

The following review is not intended to cover all aspects of word identification. Rather, it focuses on the major process stages reflected in electrophysiological recording that demonstrate the information process and flow throughout word identification. Moreover, because we will use MEG to investigate the dynamic processing in hierarchical representations, the remaining introduction will focus on the studies with electrophysiological recordings.

3.5.1.1 Perceptual processing: 100ms

The first stage in word identification is to process perceptual information contained in visual words. Basic perceptual features are extracted from the background to form letter representations and this information is then used to construct orthographic information. These perceptual processes happen very quickly and are accomplished in posterior regions of occipital lobe. Tarkiainen et al. (1999) manipulated the level of noise in different stimuli that included different number of letters as well as letter-like symbols. The earliest neural activity occurred around 100 ms after stimulus onset, which was observed in primary visual areas, demonstrated by a dipole fitting method (see the review by Hämäläinen, Hari, Ilmoniemi, Knuutila, & Lounasmaa, 1993). The magnitude of these dipoles increased across different noise levels in different type of stimuli. However, the neural activity of letters and symbols with same length produced equal response magnitude. Hence, this earliest temporal component reflects the computation of low-level visual properties that are used to form abstract letter representations, but does not reflect letter identification.

3.5.1.2 Orthographic processing: 200ms

After the first stage of perceptual processes, the information about the physical properties of letters is passed along to form abstract representations of letters and orthography. The computation for forming the orthography of a word occurs around 200ms after stimulus onset. Schendan et al. (1998) found that the activity of ERP started around 150ms presented differences between the stimuli that contained orthographic features and the ones without any orthography. However, there was no difference in the responses before 200 ms between words and pseudowords, which implies that these early neural processes do not involve the meaning of words.

Letter strings, like faces, are a type of perceptual category that human can easily and efficiently identify. This ability is obtained most likely by the extensive experience of orthographic stimuli throughout lifetime. Similar to the special function of fusiform face area (FFA) in face identification (Kanwisher, McDermott, & Chun, 1997), a special area called visual word form area (VWFA) has been identified, which is located near the FFA (Cohen et al., 2002). An intracranial recording study conducted by Nobre et al. (1994) found that neural activity in inferior temporal lobe exhibited specific temporal activation when viewing words. Words and nonwords evoked equal activity in the posterior fusiform gyrus around 200ms, but faces and other objects did not activate the same area.

The processing in VWFA is thought to represent the formation of abstract orthography in a relatively automatic manner. In a combined EEG and fMRI study, Dehaene et al. (2001) investigated the cortical processing of masked words. They observed less neural activity to the target in left fusiform gyrus around 200ms following an identical masked word, and this suppression effect was independent of the letter cases of the two successively presented words.

In summary, the second major stage in visual word identification is to construct the abstract representation of orthography. This computational process occurs around 200ms after word onset and it is carried out in a special region named

VWFA. Moreover, the construction of this neural representation of orthography can be achieved without awareness.

3.5.1.3 Semantic processing: 400ms

The final stage in word identification is access for the meaning associated with a word. Accessing meaning is indicated by a component occurring after the construction of orthography in electrophysiological recording, which reaches a peak around 400 ms after the onset a word (Brown & Hagoort, 1993; Kutas & Hillyard, 1980). This well investigated and reliable response to words is termed the N400 in the EEG literature and the M400 in the MEG literature.

The sensitivity of the N400 to semantic retrieval has been demonstrated in various electrophysiological experiments. By comparing expected ending words in sentences, such as ‘Mary spreads her bread with butter’, versus unexpected but grammatically valid endings, such as ‘Mary spreads her bread with socks’, Kutas and Hillyard (1984) found that the more predictable a word, the smaller the amplitude of N400. In addition, unexpected words that were semantically related to the expected word, such as ‘Mary spreads her bread with chocolate’, induced lower N400 amplitudes than anomalous ending words, but higher amplitudes than the appropriate words. Similar activity reduction in the N400 was also observed in the responses to the second of a pair of successive words when they were semantically or associatively related (e.g. Bentin, McCarthy, & Wood, 1985; Kiefer, Weisbrod, Kern, Maier, & Spitzer, 1998). Therefore, the evidence indicates that the neural activity occurs around 400ms reflects the process of accessing meaning from semantic memory and how well this information fits into the current retrieval context (Kutas & Federmeier, 2000).

Further studies demonstrated that the N400 response reflects the cumulative processes by which the semantic information is retrieved based on the formed orthographic representation from long-term memory. For example, an activity reduction in N400 magnitude was observed when a target word (e.g., chair) was preceded by a pseudoword that was derived from a semantically related word (e.g., wable) to the target word (Deacon, Dynowska, Ritter, & Grose-Fifer, 2004). These results suggest that the pseudowords with similar orthography can evoke semantic activation as the legal words. Holcomb et al. (2002) also reported a direct relation between orthographic neighborhood size and the amplitude of N400 response. In these studies, orthographic neighborhood size (number of words that have similar spelling) was manipulated in a lexical decision task and a categorization task. By assuming that the words with larger orthographic neighborhood size activate more semantics from long-term memory, they successfully predicted the observation of larger N400 activity following the words with more similar spellings. Therefore, all these results support the claim that the N400 reflects the process of meaning access from semantic memory based on the orthographic cues.

In summary, word identification is a series of successive mental operations, from perceptual process of physical stimulus, to construction of orthographic representation, to meaning access. This hierarchical organization processes information at different levels and transfers information between different processing stages. Although the timing of activity at each processing stage can vary in different experimental setups or tasks (e.g. Sereno & Rayner, 2003), it is generally agreed that there are 3 primary processes that involve in word identification, including perception, orthography and lexical/semantic access, and that these processes can be reflected in electrophysiological recording by different temporal components that occur around 100ms, 200ms and 400ms respectively.

3.5.2 The neural effects of recent experience on word identification

The recent past can affect the current word identification process, resulting in either benefit or detrimental effects depending on the duration of prior presentation. Moreover, the priming effects are apparent at different time in electrophysiological recording due to the hierarchical manner in which information is processed and transferred. Therefore, prime induced adaptation can be used to examine the dynamics in different processing stages of such hierarchical architecture.

3.5.2.1 Neural dynamics

Recent events produce various behavioral effects on current word identification, from benefit to deficit, as we demonstrated in Chapter 2. Similarly, neural activity also exhibit dynamic patterns in responding to repeated stimuli.

The results of neural responses to repeated stimuli are decreases in activity in general. In single neuron recording studies, it has been found that fewer neurons activate for the second of consecutively repeated stimuli (Li, Miller, & Desimone, 1993; Sobotka & Ringo, 1996). Such phenomenon is termed repetition suppression, which is caused either by the activation of fewer neurons (Li, Miller, & Desimone, 1993; Sobotka & Ringo, 1996) or by less output from the same number of neurons, such as with the synaptic depression examined by Tsodyks and Markram (1997).

Inline with the findings in single neuron recording, system level measures also demonstrate the neural suppression. Hemodynamic responses have been found to decrease after repetitive exposure to a stimulus in many fMRI studies (see the review by Henson, 2003). Because of excellent spatial resolution, this neural suppression can be identified in specific areas, depending on what is repeated. Generally, posterior areas exhibit response decrements in perceptual repetition tasks (e.g. Grill-Spector & Malach, 2001) and temporal and frontal areas exhibit response decrements in semantic repetition tasks (e.g. Dale et al., 2000).

Neural suppression at different processing stages can be seen at different times with electrophysiological recording studies. Word repetitions affect early perceptual components that occur before 200ms after stimuli onset in a perceptual identification task (Huber, Tian, Curran, O'Reilly, & Woroch, in press). The N170 responses to the second occurrence of the identical words decreased over occipital and posterior temporal lobe (Figure 3-5). Repetition effects also reflect in later component that associates with semantic processing. The N400 component produced small magnitude after the semantically related repetitions (Holcomb, 1993; Van Petten & Kutas, 1991).

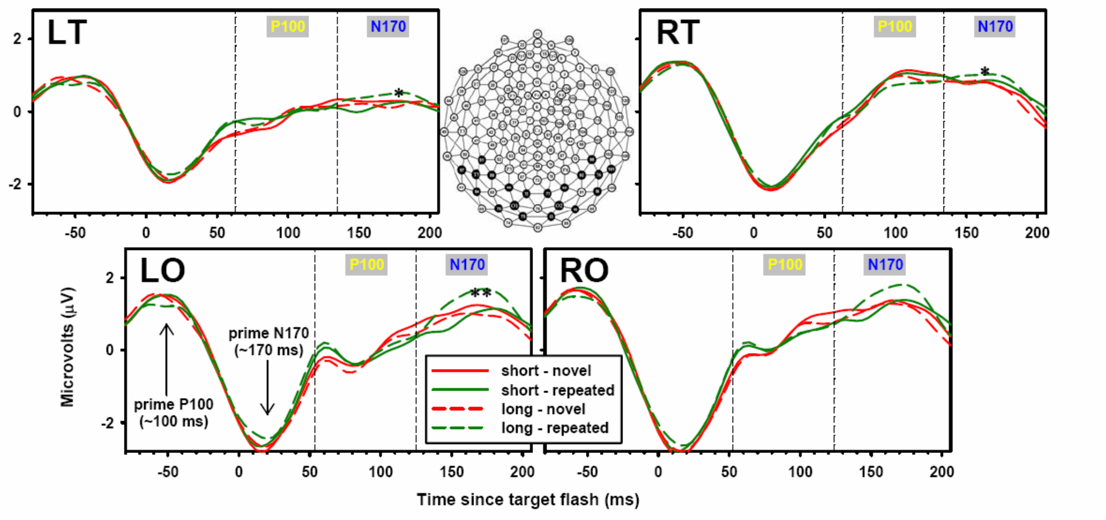

Figure 3-5 Repetition effects in average ERPs responses in a perceptual identification experiment. This results demonstrate the repetition effects occur in the N170 response over left, right temporal regions (LT, RT) and Left occipital region (LO), with the less activity of the repeated target compared with novel target following the prime with long presentation duration, but not following the prime with short presentation duration (adopted from Huber, Tian, Curran, O'Reilly, & Woroch, in press).

In summary, the neural activity decreases across repeated stimuli. This is confirmed by studies of single neuron recording, neuroimaing and electrophysiological studies. Depending on different levels of process where the repetitions present, the neural suppression can be observed in different cortical regions and at different times.

3.5.2.2 Neural mechanism to account for priming benefits and deficits

To link the observed behavioral patterns and the neural suppression activity, different theories have been proposed to account for either the benefit or deficit effects of recent experience. Theories that account for behavioral benefits in repetition paradigm claim that less neural activity in specific processing stages facilitates identification. For instance, sharpening theory links the benefit effects with the neural activity decrement by proposing that only the neurons that optimally represent the feature of a stimulus remain active, while other neurons that are redundant in the representation are deactivated (Desimone, 1996). At the system level, reduced activation also leads to faster settling time during identification (Henson & Rugg, 2003; Noguchi, Inui, & Kakigi, 2004).

The theories that link behavioral responses deficits to neural suppression propose that reduced neural responses reflect inefficient processing. Depending on which processing stage is affected by recent experience, this inefficient processing can occur in different regions and at different times in neural system. Take semantic satiation as an example. Two distinct theories have been proposed to account for the semantic satiation effect. Jakobovits and Lambert (1962) first proposed that repeated exposure reduces neural activity in semantic regions, and this is the reason why meaning is lost. Smith and Klein (1990) also concluded that semantic satiation is caused by fatigue or adaptation in neural systems that underlie the representation of meaning. In contrast, Esposito and Pelton (1971) proposed an alternative theory implicating the effect of recent experience on the perceptual process to account for semantic satiation. Their theory states that semantic satiation arises from inefficient perceptual processing after extensive repetitions

However, few theories simultaneously explain the behavioral dynamic patterns of benefit and deficit effects. One exception is a study by Davelaar et al. (in preparation), which propsed an account based on neural integration and habituation. They found neural habituation effect in a same/different MEG experiment as measured by the M170 response to the target, which was larger when the target word was different from the cue word. By assuming that speeded same/different responses are based on change detection (immediate novelty) as calculated by the activity difference between cue and target, and that priming of cue or target from the last trial results in habituation, this account explained the behavioral results. Specifically, they found that reaction times to different trials with primed cues were faster (enhanced novelty detection) whereas reaction times to different condition trials with primed targets were slower (reduced novelty detection).

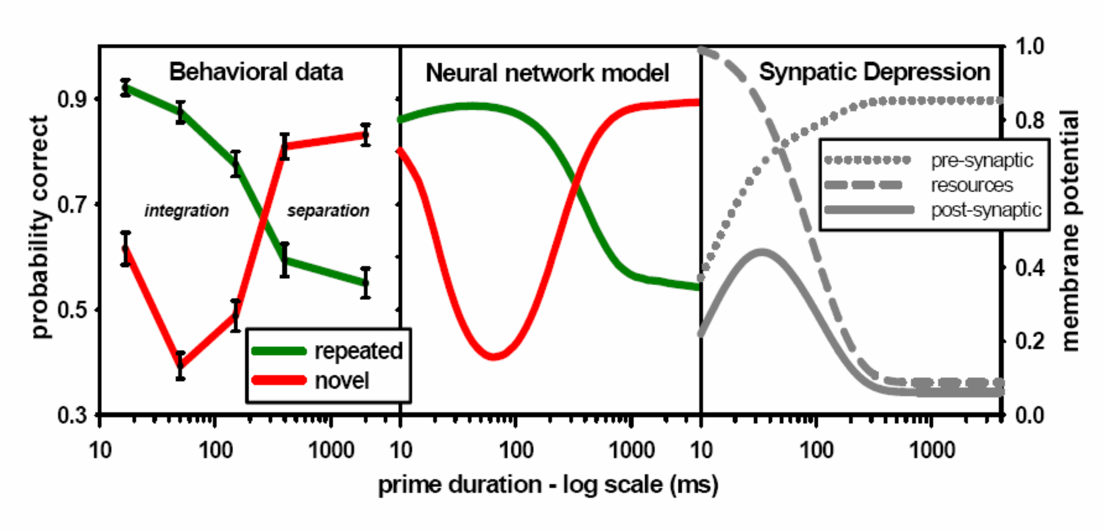

Figure 3-6 Simulation of behavioral transition in an immediate priming study by implementing the mechanism of synaptic depression in a hierarchical neural network. The behavioral responses present a dynamic transition that participants tend to decide the target is the same as the prime with short presentation duration, while judge the target is different from the prime with long presentation duration (the left-hand panel). The right-hand panel demonstrates the role of neural habituation through synaptic depression in the associations, with the activity in postsynapses decrease to an asymptotic level following an initial peak. This activity decrease due to loss of synaptic resources produces a transition from positive to negative priming effects in a hierarchical neural network (adopted from Huber, Tian, Curran, O'Reilly, & Woroch, in press).

Neural habituation in the associations between different stages of processing has been proposed to account for the behavioral transition between benefit and deficit effects in a perceptual identification task. In a computational model with a hierarchical architecture, Huber and O'Reilly (2003) implemented synaptic depression in the associations between orthographic and lexical/semantic processes. They simulated neural resources depletion in associations following long duration primes, but following short duration primes, lingering activation facilitated target processing (Figure 3-6). This hypothesis was tested both in behavioral and electrophysiological studies (Huber, Tian, Curran, O'Reilly, & Woroch, in press). Although this account assume that the neural habituation occurs in the association between orthographic and lexical/semantic processing, this assumption was not directly tested because those experiments always used repetition priming, which fails to identify the particular stage where the habituation occurs. The study reported next seeks to directly test this assumption.

3.5.2.3 A new interpretation of electrophysiological components and semantic satiation predictions

In Chapter 2, we examined the transition from semantic priming benefits to semantic satiation, using a speeded matching task in which a category cue was repeated 10 times in one block of 20 trials. Compared with results from the two subsequent experiments that presented the same number of repetitions in meaning (experiment 2) or orthography (experiment 3), the theory of associative satiation was supported.

Next, we consider how to interpret electrophysiological responses such that we can generate predictions for an MEG experiment on semantic satiation to more directly test the associative satiation theory. As reviewed in Section 3.1.2, MEG measures the fluctuation of postsynaptic potentials, but is not only affected by changes (i.e., satiation) in the processing of the cortical areas directly responsible for a topographic pattern of response. Instead, changes to the MEG signal reflect changes of information transfer efficiency in the projections (associations) to that area (e.g., a change in Y is not directly a change in process X performed by Y, but rather a change in the cortical areas that provide input to Y). For instance, a change to the MEG signal that corresponds to semantic processing cortical areas will primarily reflect a change of output from lexical processing cortical areas. This somewhat complicated supposition follows considering that the signal from postsynaptic potentials underlies electrophysiological measures such as EEG and MEG (Figure 3-7).

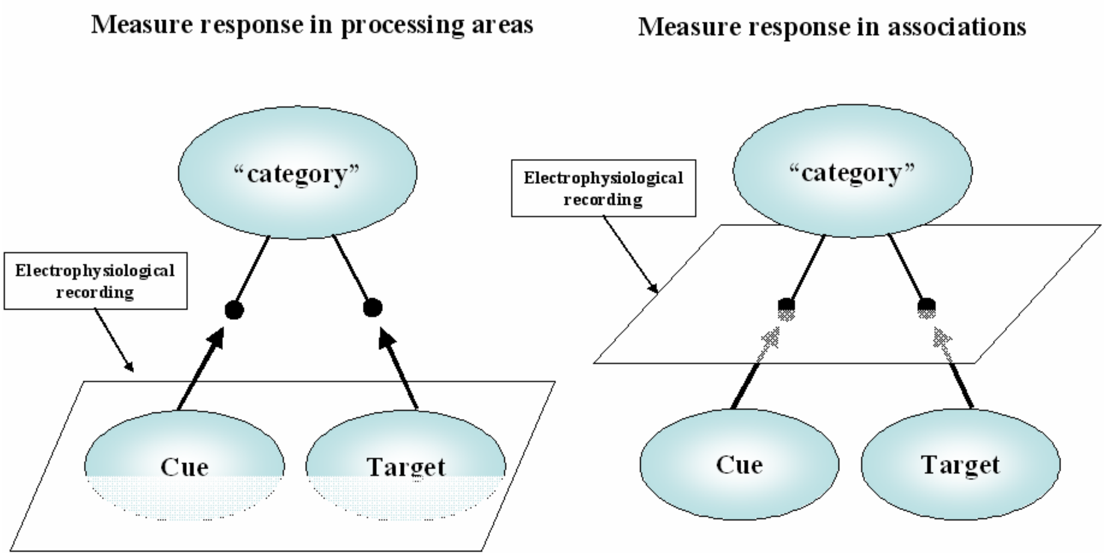

Figure 3-7 Two possibilities for the source underlying electrophysiological recordings at the scalp. Left: scalp recording are traditionally assumed to indicate the nature of processing in the associated cortical area (e.g., identification of the cue and target orthography). Right: careful consideration of the signal underlying scalp recordings leads to a different interpretation. Because scalp potentials are sensitive to extracellular currents along apical dendrites of pyramidal cells, activity is more accurately thought of as the summation of afferent information at a particular cortical area. Therefore, scalp recordings measure the active association to the receiving cortical area, but do not include the processing of that area itself. By this account, the topographic pattern reflects the anatomical position of the receiving cortical area but changes in the magnitude of that pattern of activation reflect changes in the various areas that project to that receiving area. In the current situation, this implies that an area of the cortex processing the semantic content of a category will produces an anatomically specified pattern of responses across the sensors, but changes in that pattern will not directly reflect changes in semantic processing. Instead, these changes will reflect the reception of signals at the semantic area from cortical areas that process the various word tokens (e.g., orthographic or phonemic processing) that might elicit a semantic response.

Several points should be mentioned here. We neither assume that particular cortical areas just processes one cognitive function, nor do we assume that different cognitive functions correspond to different cortical regions. In Figure 3-7, we simplified hierarchical approach with just two processing levels and an association between them. It may be true that these processing levels are separated by intermediate levels, such as with a hidden-layer in neural networks. But we make this simplification to highlight the role of associations. It doesn't really matter whether these associations are for senders and receivers all within the same cortical region or between different cortical regions, or whether these associations are the direct links between processing levels or through intermediate processes.

Hierarchical processing implies that electrophysiological waveforms include several distinct temporal components. For instance, in semantic retrieval, the major temporal components are M100, M170 and M400 that are labeled as the time of peak response relative to the onset of a word (Bentin, Mouchetant-Rostaing, Giard, Echallier, & Pernier, 1999). Because electrophysiological recording are sensitive to the postsynaptic potential, the temporal waveform components primarily reflect changes to the input of the area responsible for the topographic pattern across the sensors (Figure 3-7). Using this novel interpretation, the major components in semantic retrieval processing are illustrated in Figure 3-8, in which cortical locations are just roughly sketched. The M100 is the inputs to the orthographic processing from the outputs of visual processing; the M170 is the input to the lexical/semantic processing from the output of the orthographic processing and the M400 is the input to the decisional processing from the output of lexical/semantic processing.

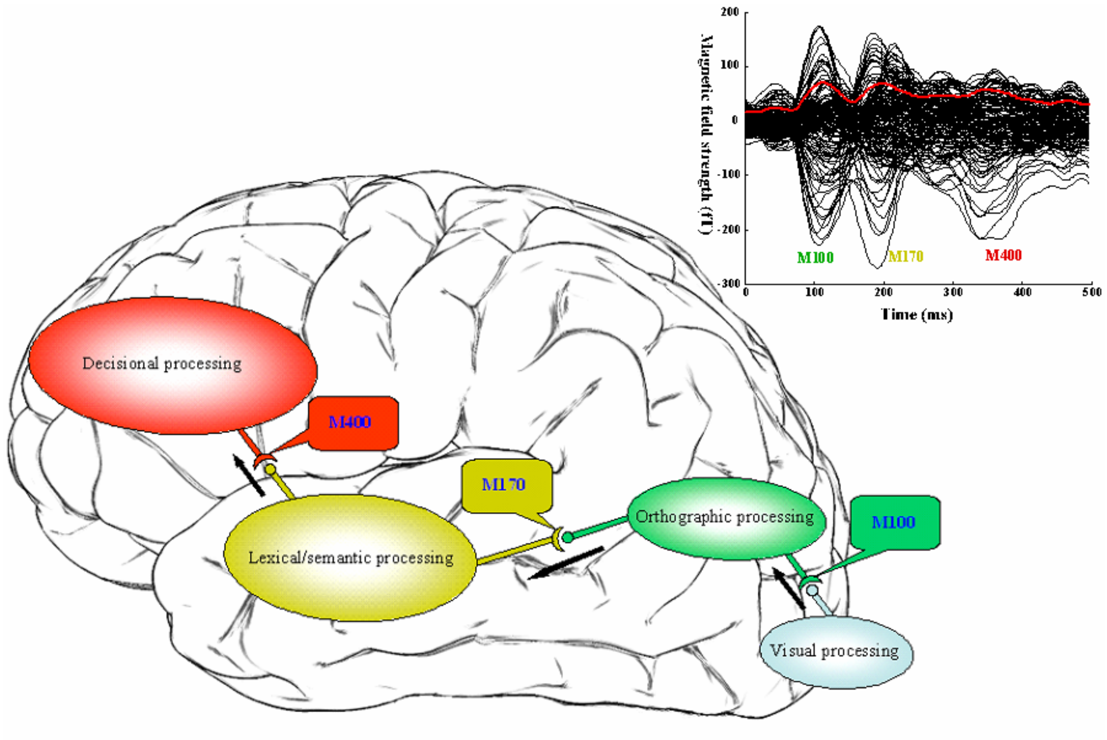

Figure 3-8 Proposed cortical sources for the cascade of evoked MEG responses to a visually presented word. Typically, three MEG waveform components are observed for visually presented words, as highlighted by the graph of evoked magnetic flux for all 157 sensors. These waveforms are labeled by the time at which they typically reach a peak, giving rise to the terms M100, M170 and M400 in MEG. These are thought to have similar sources as the P100, N170 and N400 that are measured with EEG. As seen in Figure 3-7, it is suggested that the source of scalp recordings is the afferent information (e.g., the active association) received at a cortical area. This is shown here by linking the M100, M170, and M400 labels to the receptors of an area. Reading is thought to arise from a cascade of processing that proceeds from low-level visual processing (line segments), to orthographic identification, to lexical/semantic identification, and finally use of retrieved meaning in the task relevant decision. The ovals roughly suggest the cortical areas associated with these processes.

Assuming that repetitions affect the association between different levels of processing, semantic satiation is a suitable domain to test this novel interpretation of electrophysiological results. Based on the theory of associative satiation as well as this novel interpretation of electrophysiological data, we next generate separate predictions for MEG responses to repeated cues and targets using the same experimental design as Experiment 1b (Figure 3-9).

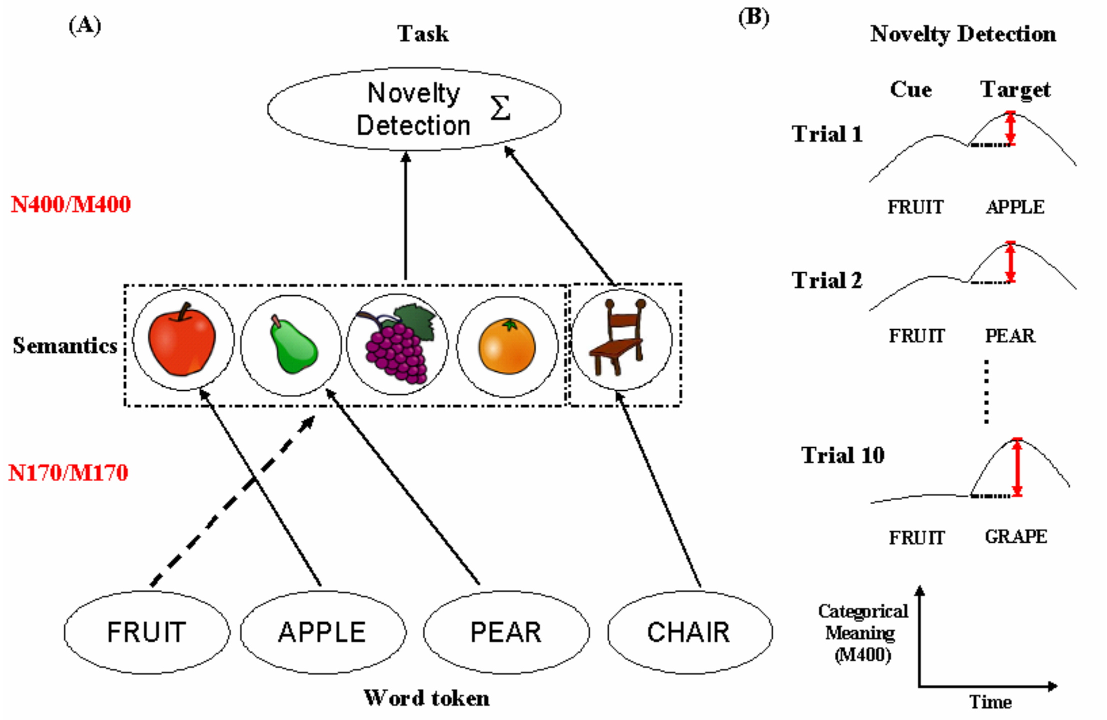

Figure 3-9 Theoretical relation between visually presented word tokens, the semantics elicited by those tokens, and the summed semantics used in the decision process. A) The category label FRUIT projects to the meaning of all fruits whereas exemplars only project to their specific meaning. The association between FRUIT and the meaning of the fruit exemplars is reduced by habituation with repeated presentation of FRUIT, as indicated by the dashed arrow line. All semantic responses project to novelty detection and by summing these projections, the onset of new input is used to discriminate between match and mismatch trials. Assuming that scalp electrophysiological recordings measure associations between processing areas (i.e., input to receiving areas), the labels on the left indicate proposed mappings to waveform responses B) The graphs show the progressively habituated semantic response to the cue word FRUIT and the progressively increased difference in new semantics in response to a categorically matching target word. The latter is highlighted by the red arrows. With this semantic satiation, a target word such as GRAPE produces a burst of new semantic response because the cue FRUIT failed to activate the semantics associated with GRAPE. Therefore, the decision process of detecting the onset of novel semantics is potentially misled to conclude that GRAPE mismatches FRUIT. To avoid incorrect responding on repeated cue trials, participants may slow down. The proposed mapping to waveforms gives rise to the prediction that repeated cues will produce smaller M170 responses (loss of association to meaning) and smaller M400 responses (loss of semantic output due to smaller semantic responses). However, because the target is always a new word, a matching target following a repeated cue is predicted to produce a larger M400 due to an apparent onset of novel semantics (increased magnitude of the red arrows).

Because the M170 is sensitive to changes in orghography, which is the input to the lexical/semantic processing, the M170 response to the cue should decrease across repetitions due to resource depletion in the association between orthographic and lexical/semantic processing (the dotted lines in Figure 3-9A). However, because even in the repeated trials, orthographic features of the target (as opposed to the cue) are not repeated, no change in the M170 responses to the target is expected.

Because the M400 is sensitive to unexpected lexical/semantic events and semantics is the input to higher level processing (including decision), the M400 response to the cue should decrease due to less input from orthographic processing as the associations become inefficient, thus reducing semantic responses. Moreover, we should observe corresponding changes to the target of the same category as the repeated cue. Because a repeated cue fails to produce a robust semantic response with associative satiation, a target for the category will appear to activate new (unexpected) semantic information. According to our novelty account (Davelaar, Tian, Weidemann, & Huber, in preparation) that novelty detection is based on a change in activation to the target, the M400 response to a matching target in the repeated condition will increase (in increasing length of red arrows across repetitions in Figure 3-9B).

Finally, the M100 response is sensitive to changes in visual presentation perception input to the orthographic processing. Due to the relatively long stimulus onset asynchrony between cue and target in this experimental design, the M100 responses to both the cue and target is not expected to vary.

3.6 Experiment 4: testing associative satiation with MEG

We used the same speeded category matching in mixed lists paradigm as Experiment 1b in Chapter 2. The neural responses to the cue and target were measured and the effect of repetitions is assessed qualified in different temporal components as a function of the number of repetitions.

Method

Participants. A total of 13 participants participated in this experiment with compensation. All participants were right handed native English speakers with no history of neurological disorder.

Materials. Sixteen single-word category labels were selected (see Appendix 1a). Twenty single-word exemplars formed a list for each category label (McEvoy & Nelson, 1982; Van Overschelde, Rawson, & Dunlosky, 2004). All words were displayed in upper case Times Roman font, as yellow lettering against a black background, and subtended less than 3 degrees of visual angle. Stimulus materials were projected on a screen inside the MEG chamber. Two 2-button response boxes were used and participants held each of them in one hand. One button on each response box was assigned to a response.

Experimental design and procedure. The experimental design and procedure was the same as in Experiment 1b, except that a blank screen was presented for 500ms between trials instead of feedback. This was done to minimize artifacts caused by eye blinks.

MEG recording. Magnetic signals were measured using a 160-channel (157 data channels and 3 reference channels), whole-head axial gradiometer system (KIT, Kanazawa, Japan). Five electromagnetic coils were attached to the head of participants before the MEG recording to check head position within the MEG. The locations of the coils were determined with respect to three anatomical landmarks (nasion, left and right preauricular points) on the scalp using 3D digitizer software (Source Signal Imaging, Inc.) and digitizing hardware (Polhemus, Inc.). The coils were localized with respect to the MEG sensors, both at the beginning and end of the experiment.

Before the visual word experiment, participants listened to 200 repetitions of 250HZ and 1 kHz, 50 ms sinusoidal tone (ISI randomized between 750 and 1550 ms), with 100 repetitions for each frequency. Auditory-evoked responses to the onset of these pure tones were examined, and the auditory M100 was identified. The auditory M100 is a prominent and robust response, apparent around 100 ms after auditory stimuli onset and has been the most investigated auditory MEG response (for review see Roberts, Ferrari, Stufflebeam, & Poeppel, 2000). A dipole-like pattern (i.e., a source and sink pair) in the magnetic topographic map distributed over the temporal region of each hemisphere was identified for each participant. These auditory dipole patterns were used to verify whether participants were in the proper position.

The MEG data were acquired with a sampling rate of 500 Hz, filtered online between 1 Hz and 200 Hz, with a notch at 60 Hz. Raw data were noise-reduced using time shift PCA method offline (de Cheveigné & Simon, 2007). A 1000 ms time period that was time locked to the cue category label was extracted and averaged over all the trials both across and within different repetition conditions and positions. These data were averaged across all trials for a given individual, and were used as standard response for the angle and magnitude tests. A second 1000 ms time period that was time locked to the target exemplar onset was extracted and averaged within different repetition conditions and positions. Trials with amplitudes >3pT (~5%) were considered artifacts and discarded. The averages were low-pass filtered with cutoff frequency of 20 Hz.

MEG analysis. In part I of this chapter, we developed a projection method to normalize individual differences to run statistics across participants (Tian & Huber, 2008). In this study, the individual standard response $\vec{A}$ was obtained by averaging responses to the cues across all different repetition conditions and positions within each participant. The individual responses to the cue and the target $\vec{B}$ were obtained by averaging responses to the cues or to the targets separately within different repetition conditions and positions. Individual M100, M170 and M400 were identified based on Root-mean-square (RMS) both in the standard response and in the responses to the cue and target in different repetition conditions and positions. We first confirmed that there was no difference between experimental conditions across positions in term of similarity using Eq. 1 in part I of this chapter (angle test). After using magnitude test (projection) to normalize individual difference (Eq. 2 in part I of this chapter), we took the second to tenth trials broken into thirds. The first trials of repeated and nonrepeated conditions were eliminated because there was no difference between these conditions at that point within a block. Therefore, 3 positions were created out of 9 trials in each repetition condition. A repeated measures two-way ANOVA with factors of position (3), and repetition status (2) was carried out for each temporal component (M100, M170 and M400) of the response to the cue. Moreover, the same repeated measures two-way ANOVA was carried out for each temporal component of the response to matching targets.

Results

Similarity test. The temporal components (M100, M170 and M400) both to the cue and to matching and mismatching targets were compared using the angle test to determine if they differed between repeated and nonrepeated at each of the 6 experimental conditions (2 repetition conditions by 3 positions). Statistical reliability was determined by dividing the experiment into trials from the first half versus trials from the second half and the patterns for each half were compared to each other with the similarity test, with this occurring for first/second half angle measures from the same condition (the within values for null hypotheses) versus first/second half angle measures from different conditions (the between values for experimental conditions). Because there were 6 conditions in each group, this entailed 15 possible comparisons between conditions, which were then averaged in comparison to the average of the 6 within condition comparisons, yielding one between-conditions measure and one within-conditions measure for each participant. In a dependent samples t-test across 13 participants, there was no significant difference in the similarity of the between conditions measure versus the within condition measure in temporal components responses to the cue, $t(12) = .828$, $p = .424$; $t(12) = -.188$, $p = .854$; $t(12) = -1.285$, $p = .223$, for M100, M170, M400 respectively. Moreover, there was no significant difference in the similarity of the between conditions measure versus the within condition measure for all temporal components responses to both matching and mismatching targets, for matching targets, $t(12) = .549$, $p = .593$; $t(12) = .841$, $p = .417$; $t(12) = .595$, $p = .563$, while for mismatching targets, $t(12) = 1.222$, $p = .245$; $t(12) = .808$, $p = .435$; $t(12) = .779$, $p = .451$, for M100, M170 and M400 respectively. Therefore, these results suggest that there was no difference in cortical response distribution between repeated and nonrepeated conditions. Thus, the topographic patterns of the responses to the cue and the responses to the matching and mismatching targets were similar enough to allow meaningful magnitude comparisons. In other words, any magnitude differences were taken to indicate changes in the magnitude of the underlying cortical responses rather than differential recruitment of cortical areas in some conditions as compared to other conditions.

Magnitude test. The angle test assessed similarity among patterns, but for this analysis, we were interested in the magnitude of the M100, M170 and M400 responses both to the cue and target words. Therefore, the appropriate measure across all 157 sensors is the projection of the cue word response and target word response onto the standard pattern, as in Equation 2. In the current situation, we determined the grand average of the responses to the cue word as the standard response, $\overline{A}$, while each separate response to the cue in the 6 cue conditions and the target in the 12 target conditions, $\overline{B}$, were projected onto the standard response. Furthermore, the nonrepeated condition (baseline) was subtracted from repeated condition at each list position. Therefore, each participant yielded 3 difference data points across positions for the responses to the cue and the responses to the target in match and mismatch status.

Three repeated measures one-way ANOVA with a factor of 3 different positions were run on the difference data of responses to the cues and targets in match and mismatch conditions. For the responses to the cue, comparing across 3 positions in terms of this magnitude test, the activity in the repeated conditions was significantly lower than that in nonrepeated condition across repetitions (the first column in Figure 3-10), for the M170, $F(2,24) = 4.335$, $p < .05$ and for the M400, $F(2,24) = 4.347$, $p < .05$ but not for the M100 ($F < 1$). The post hoc linear contrast test revealed a decrease in both the M170 and M400, $t(12) = 2.434$, $p < .05$ and $t(12) = 3.225$, $p < .01$. For the comparison across the 3 positions of the response to the target in match trials, the activity in the repeated condition was higher than that in nonrepeated condition (the second column in Figure 3-10), for the M400, $F(2,24) = 3.744$, $p < .05$ but not for the M100 or the M170 (Fs < 1), while there was no difference in mismatch trials for the M100, M170 and M400 (Fs < 1, the third column in Figure 3-10).

In summary, the results were as predicted: The M170 response to the cue decreased across repetitions. However, due to the lack of such repetitions the M170 to the target did not show any change across repetitions and the M400 to the cue decreased across repetitions. Due to the meaning loss of the repeated category, the target in the same category appear to activate a novel category meaning across repetitions, induced the M400 responses to the target of the same category increased across trials. The M170 and M400 decreases to the repeated cue was predicted due to associative satiation, and the M400 increase to the matching target following a repeated cue was predicted due to increased novelty detection.

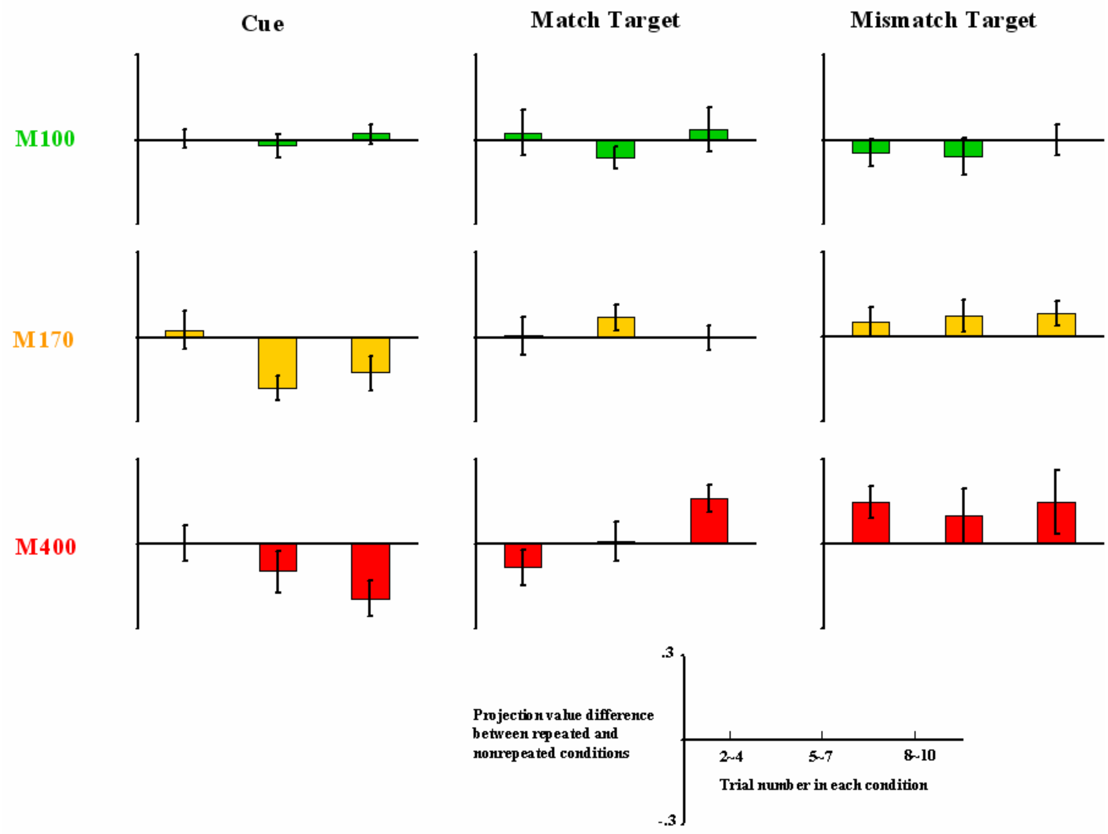

Figure 3-10 MEG response differences for the repeated condition minus the non-repeated condition as a function of trial number. These differences are shown in response to the cue word (left), a matching target word (middle), or a mismatching target word (right). In each case, the M100, M170, and M400 difference is graphed with trial number along the x-axis. MEG magnitude is calculated using the projection method and the M100, M170, or M400 standard response for projection is found by taking the response to the cue word after collapsing across all conditions and all trial numbers. As seen in the first column, both the M170 and the M400 to the repeated cue word decreased as trial number increased. This was predicted because habituation to the repeated cue word produces less input to semantic processing and a resultant smaller input to semantic summation. As seen in the second column, the only effect for a matching target was an increase in the M400. This was predicted under the assumption that the decision process monitors for a change in the summed semantic response (i.e., detection of novel semantics) in order to rapidly decide whether the meaning of the target matches or mismatches the meaning of the cue. Because the semantic response to the cue is lessened in the repeated condition, a matching target erroneously produces the appearance of a change in semantics as indicated by a larger M400 (a burst of new input to the decision area following on the heels of a diminished response to a repeated cue). This erroneously detected semantic change in the repeated match condition is hypothesized to underlie the reaction time deficit; to avoid incorrect responses due to erroneous detection of mismatch, participants slow down for repeated cue word trials. There were no trial number effects for the M100 and no trial number effects for mismatch targets.

3.7 Discussion

This study tested the dynamics of neural processing in associations as the underlying mechanism of semantic satiation using MEG recording. The general results for this study were a decrease in the M170 and M400 responses to the cue and an increase in the M400 response to the target across the repetitions. Based on the assumption that these responses reflect associations between orthography and lexical-semantic processing, and between lexical-semantic and novelty detection, these results (Figure 3-10) confirmed predictions of associative satiation.

According to this account, when presenting repetitions both in orthographic and semantic processes of the cues, the neural resources in the associations for transferring information were depleted by the multiple repetitions as indicated by the decrement in the M170 response. The reduced input to semantic processing led to an activity decrease in the M400 response to the cue. On the other hand, the M170 to the target did not show any significant decrease across multiple trials because every target was a new orthographic form. However, in the match trials of the repeated condition, the same categorical meaning of the target was already satiated during the repetitions of the cue, the system treated the repeated categorical meaning novel rather than familiar. This resulted in an activity increase in the M400 response to the target in the match trials across repetitions. According to novelty detection theory (Davelaar, Tian, Weidemann, & Huber, in preparation), the cognitive system monitors the response to target for a boost in activation (novelty) associated with the level of processing appropriate to the task (semantic processing and the M400 in this case) to detect differences between the cue and target. This activity increase in the

M400 to targets in the match trials is the increase of novelty due to the loss of meaning for the repeated category. This apparent novelty led the cognitive system to possibly conclude that there were categorical differences between cue and target when there were in fact none. This response conflict resulted in a reaction time increase across repetitions in the match trials.

These results might be explained by orthographic habituation to the repeated cue word. However, our Experiment 3 results rule this alterative out because there as no RT slow down in a simple orthographic matching task. We only observed response facilitation that did not change with increasing repetitions. This suggests that the effect of repetitions on orthographic processing were eliminated by the beginning of the next trial, perhaps due to the 3 seconds between trials. The relatively large stimulus onset asynchrony might have allowed orthography to fully recover. However, our account assumes that the information transfer in the associations between orthographic and lexical/semantic processes becomes less and less efficient across trials. This produced the observed response changes across trials in Experiment 1 and in the MEG effects in this experiment.

Our interpretation of the signal observed in electrophysiology may shed light on discrepancies in the literature. According to this interpretation, the M170 response is the input to lexical/semantic processing. Therefore, the M170 is sensitive to both the information processing within orthographic processing and the effects in the associations between orthographic and lexical/semantic processing. Similarly, the M400 response is recorded after the output from lexical/semantic processing as passed to higher level cognitive process, such as decision making. This may explain the location differences of observing lexical/semantic effects in frontal lobes (Holcomb & Grainger, 2006; Kutas & Hillyard, 1984), even through neuropsychological studies place semantic processing in the temporal lobes (Warrington, 2000).

In summary, this study confirmed key predictions of associative satiation. Furthermore, we provided a novel interpretation of different electrophysiological components as reflecting the associations between processes. These findings advance our understanding both for the dynamics of neural processing to visually presented word and the manners in which EEG/MEG measures are interpreted in general.

Chapter 4: General Discussion

The main goal of this paper was to investigate information processing in a complex identification task and how recent events can affect the flow of information, especially by considering transient changes in association strength between different perceptual processes in the service of hierarchical perception (perception at different levels of abstraction). Using word identification as an example task with levels of processing, the phenomenon of semantic satiation demonstrated the effects of recent events on information flow. MEG was used to explore the neural mechanisms underlying the observed behavioral deficit in semantic satiation. This chapter summarizes the results of these studies and discusses their implications.

4.1 Study summary

4.1.1 Behavioral and electrophysiological measures of associative satiation

In Chapter 2, three experiments used a matching task with cue words presented for one second followed by speeded responses to target words. All experiments used lists of 20 trials, with 10 of these trials involving repetitions across trials in different levels and the other 10 trials did not involve any repetition. Experiment 1 used repeated category labels followed by different category exemplars (i.e., category matching), and we found an initial RT facilitation, which became a deficit towards the end of the list. Assuming that this slow down measures semantic satiation, Experiments 2 and 3 tested whether semantic satiation results from repeated category semantics by using different exemplars as cues on every trial (Experiment 2) or whether semantic satiation results from repeated words by changing the task to simple word matching (Experiment 3). Because these two experiments only produced facilitation, this suggests that semantic satiation requires repeating a word while continuing to access the meaning of that word (i.e., a repeated association).

To investigate the underlying neural mechanism of the observed associative satiation, the same experiment as Experiment 1b was replicated while the MEG was recorded in part II of chapter 3. Responses to both the cue and target were analyzed and interpreted in terms of neural habituation in the association between orthographic and lexical/semantic processing across the repetitions. The M170 response to the cue decreased across repetitions, suggesting that there was a reduced association form orthography to lexical/semantic processing due to neural habituation. Moreover, the M400 response to the cue decreased across repetitions presumably due to insufficient input from the orthographic process. In contrast, the M170 response to the target did not show any change across trials presumably target words never repeated. However, the M400 responses to targets on repeated category trials increased with the number of repetitions of the cue. This increase was as predicted by our novelty detection account of same/different judgments (Davelaar, Tian, Weidemann, & Huber, in preparation). The increased M400 responses to targets was expected because matching targets in the repeated category cue condition would appear to excess a new meaning due to lack of meaning access from the cue.

4.1.2 Electrophysiological methods consideration

MEG was used to assess temporal aspects of information processing in word identification.

In part I of Chapter 3, a simple multivariate measures using data from the entire spatial array of sensors was proposed to separate the effects changes in the distribution of neural sources versus changes in the magnitude of neural sources. Furthermore, this technique normalized against individual differences and produced a much less variable measure of response magnitude that could then be compared across individual with traditional inferential statistics. In part II of Chapter 3, these techniques were used both with immediate repetitions of words in perceptual identification and also with the semantic satiation paradigm.

We argued that consideration for the source of electrophysiological recording results in a different interpretation than is typically found in the literature. This new interpretation of temporal components was supported in an MEG experiment using the repeated category paradigm. Assuming that MEG responses reflect the input to cortical areas, rather than processing within those areas, the pattern of results for both cue and target words was as predicted by the proposed associative satiation account.

4.2 Information transfer in hierarchical identification

4.2.1 The benefits of a hierarchical approach to electrophysiology

Previous research identified levels of processing in word identification. However, the role of associations between different processes was not considered in these analyses. This current study suggests that associations and efficiency of information transfer between processing can strongly influence behavior.

This approach generates new interpretations and hypotheses that advance our understanding of cognitive function and neural processing. For instance, consider the role of associations and habituation in the debate of whether the face N170/M170 component reflects a specialized face module (Kanwisher, McDermott, & Chun, 1997) or a distributed process (Haxby, Hoffman, & Gobbini, 2000). By our account, rather than specifying a one-to-one mapping between the N170/M170 and the face processing module, the topographic pattern of the M170 instead reflects the cortical areas that face processing areas project to. Furthermore, changes in the N170/M170 reflect the difference between face perception of the current stimulus as compared to the degree of the face detection for the stimulus immediately prior to the onset of the face. In other words, the M170 is not face perception, but rather the novelty of a face as compared to the perceptual input just prior to the face. Moreover, the face processing area projects to many other cortical areas. For instance, the M170 might be due to the connections between face processing and emotion processing (Storbeck, 2007), such as with facial expressions. The literature suggests that there is an activity decrease when processing inverted faces compared with processing upright faces (see the review by Rossion & Gauthier, 2002). The reason for this decrease may be because inverted faces do not provide social information.

The role of information transfer efficiency in hierarchical processing may also help to resolve some apparent contradictions in cognitive neuroscience research. For instance, the N400/M400 observed with electrophysiological recording is believed to reflect lexical/semantic processing and it is found mainly in frontal electrodes (Halgren et al., 2002; Holcomb & Grainger, 2006; Kutas & Hillyard, 1984). However, lexical/semantic areas are found in the temporal lobe according to neuropsychological research as observed in lesion studies (Warrington, 2000). By our associative interpretation of electrophysiology, this apparent disagreement is to be expected: The source of changes in the N400/M400 is in the lexical/semantic processing areas of the temporal lobes, but it is the reception of these signals in frontal areas that sum to produce a measurable change in scalp electrodes.

4.2.2 Information transfer as a research perspective

Different areas of cognition may benefit by considering the role of information transfer efficiency. For instance, attention and different states of awareness may correspond to different modes of transfer efficiency. A workspace model was recently proposed in which that associations between different cognitive processes were required in demanding tasks (Dehaene, Kerszberg, & Changeux, 2001; Dehaene & Naccache, 2001). Compared with the task in Experiment 1 where the meaning of the words was required, the task of Experiment 3 required less effort because responses only could be based on orthographic matching. The attention required in different tasks may control the routing of information and select the information based on the task demands.

Similarly, different aspects of neural activity may also benefit by considering the flow of information. Beyond firing rate and evoked response magnitude, frequency also carries information on cortical processing. Activity in different cortical areas may oscillate at different frequency (Basar, 1998) and the activity between regions can synchronize together and oscillate at the same frequency (Lachaux, Rodriguez, Martinerie, & Varela, 1999; von Stein & Sarnthein, 2000). The intrinsic working frequency and synchrony are believed to reflect specific human cognitive functions (Basar, Basar-Eroglu, Karakas, & Schurmann, 2001; Klimesch, 1996; Lachaux, Rodriguez, Martinerie, & Varela, 1999; von Stein & Sarnthein, 2000). For instance, the gamma band frequency is proposed to facilitate feature binding (Singer & Strategies, 1999). Likewise, the successful transfer of information between processing may require synchronization across multiple neurons and the connection between cortical areas is perhaps indicated based on similar frequencies. The observed M170 and M400 decrease in part II of Chapter 3 can be used to test this hypothesis. Magnitude changes in different conditions can result from postsynaptic decreases with the same number of neurons active, a smaller number of activated neurons, or from less synchronization among neurons (Rugg & Coles, 1995). Therefore, a spectral analysis is needed to determine if the M170 and M400 decrease was due to the lessening of the neural response magnitude (such as with inhibition or synaptic depression) or due to loss of temporal coherence (loss of synchrony) and whether there was a common frequency between these two temporal components.

In conclusion, a novel account of semantic satiation was proposed based on the claim that associations between levels of processing habituate with recent activity. Support for this account was found using both behavioral studies and MEG recording.

Appendices

Appendix Ia Words used in Experiment 1a

Category labels	VEGETABLE	INSECT	SPORT	MAMMAL	FRUIT	SPICE
Exemplar 1	CARROT	ANT	FOOTBALL	DOG	APPLE	SALT
Exemplar 2	LETTUCE	SPIDER	BASKETBALL	CAT	ORANGE	PEPPER
Exemplar 3	BROCCOLI	BEE	SOCCER	HORSE	BANANA	GARLIC
Exemplar 4	CUCUMBER	MOSQUITO	BASEBALL	LION	GRAPE	SUGAR
Exemplar 5	PEAS	BEETLE	TENNIS	BEAR	PEAR	OREGANO
Exemplar 6	CORN	GRASSHOPPER	HOCKEY	TIGER	PEACH	CINNAMON
Exemplar 7	POTATO	BUTTERFLY	SWIMMING	COW	STRAWBERRY	PAPRIKA
Exemplar 8	CELERY	WASP	GOLF	ELEPHANT	KIWI	BASIL
Exemplar 9	ONION	ROACH	VOLLEYBALL	DEER	PINEAPPLE	VANILLA
Exemplar 10	SPINACH	MOTH	LACROSSE	PIG	WATERMELON	MUSTARD
Exemplar 11	SQUASH	GNAT	RUGBY	GIRAFFE	PLUM	VINEGAR
Exemplar 12	BEAN	COCKROACH	SOFTBALL	RABBIT	GRAPEFRUIT	LEMON
Exemplar 13	CAULIFLOWER	CATERPILLAR	SKIING	GOAT	MANGO	THYME
Exemplar 14	CABBAGE	CENTIPEDE	RUNNING	ZEBRA	CHERRY	CURRY
Exemplar 15	RADISH	CRICKET	GYMNASTICS	MOOSE	CANTALOUPE	NUTMEG
Exemplar 16	ASPARAGUS	WORM	POLO	SHEEP	RASPBERRY	PARSLEY
Exemplar 17	BEET	MANTIS	RACQUETBALL	RACCOON	TANGERINE	CHILI
Exemplar 18	POTATOES	DRAGONFLY	WRESTLING	FOX	NECTARINE	ROSEMARY
Exemplar 19	TURNIP	FLEA	BOWLING	DONKEY	PAPAYA	CHIVES
Exemplar 20	ZUCCHINI	HORNET	BADMINTON	ELK	APRICOT	MARJORAM

Appendix Ia continue

Category labels	FLOWER	BIRD	BEVERAGE	VEHICLE	OCCUPATION
Exemplar 1	ROSE	EAGLE	BEER	CAR	SECRETARY
Exemplar 2	DAISY	ROBIN	VODKA	BUS	MANAGER
Exemplar 3	TULIP	BLUEJAY	WINE	TRUCK	COOK
Exemplar 4	LILY	CARDINAL	RUM	AIRPLANE	POLICEMAN
Exemplar 5	CARNATION	HAWK	WHISKEY	PLANE	ATHLETE
Exemplar 6	DAFFODIL	PARROT	TEQUILA	TRAIN	BANKER
Exemplar 7	DANDELION	SPARROW	GIN	BICYCLE	CARPENTER
Exemplar 8	PANSY	PIGEON	MARGARITA	VAN	JANITOR
Exemplar 9	ORCHID	SEAGULL	CHAMPAGNE	BOAT	THERAPIST
Exemplar 10	PETUNIA	DOVE	SCOTCH	SHIP	SCIENTIST
Exemplar 11	IRIS	PARAKEET	BOURBON	MOTORCYCLE	DOCTOR
Exemplar 12	VIOLET	FALCON	WATER	SUV	TEACHER
Exemplar 13	LILAC	CANARY	COKE	SUBWAY	LAWYER
Exemplar 14	COLUMBINE	OWL	MILK	TAXI	NURSE
Exemplar 15	GERANIUM	DUCK	JUICE	CAB	FIGHTER
Exemplar 16	PEONY	FINCH	SODA	SCOOTER	PROFESSOR
Exemplar 17	AZALEA	WOODPECKER	TEA	HELICOPTER	ACCOUNTANT
Exemplar 18	BEGONIA	FLAMINGO	COFFEE	JEEP	PSYCHOLOGIST
Exemplar 19	CHRYSANTHEMUM	ORIOLE	LEMONADE	MOPED	DENTIST
Exemplar 20	GARDENIA	SWALLOW	PUNCH	JET	ENGINEER

Appendix Ib Words used in Experiment 1b

Category labels	EMOTION	COLOR	UTENSIL	FLAVORING	OCCUPATION	BIRD	SPORT	WEATHER
Exemplar 1	LOVE	BLUE	KNIFE	SALT	DOCTOR	EAGLE	FOOTBALL	TORNADO
Exemplar 2	HAPPINESS	RED	FORK	PEPPER	TEACHER	ROBIN	BASKETBALL	HURRICANE
Exemplar 3	SADNESS	GREEN	SPOON	GARLIC	LAWYER	BLUEJAY	SOCCER	RAIN
Exemplar 4	FEAR	YELLOW	SPATULA	SUGAR	FIREMAN	CARDINAL	BASEBALL	SNOW
Exemplar 5	SORROW	PURPLE	PAN	CHILI	PROFESSOR	HAWK	TENNIS	HAIL
Exemplar 6	ANGER	ORANGE	POT	SPICE	ACCOUNTANT	CROW	HOCKEY	FLOOD
Exemplar 7	DEPRESSION	BLACK	WHISK	CINNAMON	DENTIST	WOODPECKER	SWIMMING	LIGHTNING
Exemplar 8	MAD	WHITE	BLENDER	PAPRIKA	ENGINEER	PARROT	GOLF	BLIZZARD
Exemplar 9	BITTERNESS	PINK	BOWL	KETCHUP	SECRETARY	SPARROW	VOLLEYBALL	FOG
Exemplar 10	CONFUSION	BROWN	LADLE	BUTTER	MANAGER	PIGEON	BOXING	SLEET
Exemplar 11	EXCITEMENT	GRAY	PLATE	BASIL	COOK	SEAGULL	KARATE	MONSOON
Exemplar 12	JEALOUSY	VIOLET	CHOPSTICKS	VANILLA	POLICEMAN	DOVE	RUGBY	THUNDER
Exemplar 13	JOY	INDIGO	TONGS	MUSTARD	ATHLETE	PARAKEET	SOFTBALL	WIND
Exemplar 14	PITY	MAGENTA	OPENER	SESAME	BANKER	FALCON	SKIING	STORM
Exemplar 15	CRYING	TURQUOISE	MIXER	VINEGAR	CARPENTER	CANARY	SURFING	TYPHOON
Exemplar 16	LAUGHTER	MAROON	OVEN	GINGER	JANITOR	OWL	RUNNING	DROUGHT
Exemplar 17	TEARS	TEAL	COLANDER	OIL	THERAPIST	FLAMINGO	GYMNASTICS	CLOUD
Exemplar 18	SMILE	TAN	CUP	THYME	SURGEON	ORIOLE	DIVING	SUNSHINE
Exemplar 19	TENSION	AQUA	STOVE	CURRY	SALESMAN	RAVEN	WRESTLING	GALE
Exemplar 20	SHOCK	FUCHSIA	MICROWAVE	NUTMEG	ARCHITECT	DUCK	BOWLING	DUST

Appendix Ib continue

Category labels	CLOTHING	FISH	ELEMENT	INSTRUMENT	VEHICLE	VEGETABLE	INSECT	MAMMAL
Exemplar 1	SHIRT	SALMON	OXYGEN	DRUM	CAR	CARROT	FLY	DOG
Exemplar 2	PANTS	TROUT	HYDROGEN	GUITAR	BUS	LETTUCE	ANT	CAT
Exemplar 3	SOCKS	EEL	CARBON	FLUTE	TRUCK	BROCCOLI	TERMITE	HORSE
Exemplar 4	UNDERWEAR	BASS	HELIUM	PIANO	AIRPLANE	TOMATO	BEE	LION
Exemplar 5	SHOES	TILAPIA	NITROGEN	TRUMPET	TRAIN	CUCUMBER	MOSQUITO	BEAR
Exemplar 6	HAT	TUNA	GOLD	CLARINET	BICYCLE	PEAS	BEETLE	TIGER
Exemplar 7	SHORTS	SHARK	IRON	SAXOPHONE	VAN	CORN	BUG	COW
Exemplar 8	JACKET	FLOUNDER	SILVER	VIOLIN	BOAT	POTATO	GRASSHOPPER	ELEPHANT
Exemplar 9	SWEATER	HERRING	SODIUM	TROMBONE	SHIP	CELERY	BUTTERFLY	DEER
Exemplar 10	SKIRT	CARP	SULFUR	TUBA	MOTORCYCLE	BEANS	WASP	PIG
Exemplar 11	COAT	COD	ZINC	CELLO	SKATEBOARD	SPINACH	HORNET	GIRAFFE
Exemplar 12	DRESS	GUPPY	COPPER	OBOE	SUBWAY	SQUASH	MOTH	SQUIRREL
Exemplar 13	GLOVES	HALIBUT	CHLORINE	BASS	TAXI	CAULIFLOWER	GNAT	GOAT
Exemplar 14	SCARF	PERCH	NEON	HARP	SCOOTER	CABBAGE	ROACH	MOOSE
Exemplar 15	BLOUSE	TROUT	CALCIUM	HORN	HELICOPTER	RADISH	CATERPILLAR	SHEEP
Exemplar 16	TIE	MARLIN	ALUMINUM	KEYBOARD	JEEP	ASPARAGUS	WEEVIL	CHEETAH
Exemplar 17	BELT	MINNOW	BORON	PICCOLO	MOPED	TURNIP	CRICKET	WOLF
Exemplar 18	TOP	PIKE	LITHIUM	BANJO	SUV	ZUCCHINI	MANTIS	FOX
Exemplar 19	BOXERS	SNAPPER	MERCURY	HARMONICA	JET	ONION	DRAGONFLY	DONKEY
Exemplar 20	JEANS	PIRANHA	MAGNESIUM	TAMBOURINE	CAB	BEET	FLEA	ZEBRA

Appendix II Words used in Experiment 2

type of emotion	color	kitchen utensil	part of human body	occupation	natural earth formation	sport	weather phenomenon
LOVE	BLUE	KNIFE	LEG	DOCTOR	MOUNTAIN	FOOTBALL	TORNADO
HAPPINESS	RED	FORK	ARM	TEACHER	RIVER	BASKETBALL	HURRICANE
SADNESS	GREEN	SPOON	FOOT	LAWYER	OCEAN	SOCCER	RAIN
FEAR	YELLOW	SPATULA	FINGER	FIREMAN	VOLCANO	BASEBALL	SNOW
SORROW	PURPLE	PAN	HEAD	PROFESSOR	LAKE	TENNIS	HAIL
ANGER	ORANGE	POT	TOE	ACCOUNTANT	VALLEY	HOCKEY	FLOOD
DEPRESSION	BLACK	WHISK	EYE	DENTIST	HILL	SWIMMING	LIGHTNING
MAD	WHITE	BLENDER	HAND	ENGINEER	ROCK	GOLF	BLIZZARD
BITTERNESS	PINK	BOWL	NOSE	SECRETARY	CANYON	VOLLEYBALL	EARTHQUAKE
CONFUSION	BROWN	LADLE	EAR	MANAGER	PLATEAU	BOXING	SLEET
EXCITEMENT	GRAY	PLATE	MOUTH	COOK	CRATER	KARATE	MONSOON
JEALOUSY	VIOLET	CHOPSTICKS	STOMACH	POLICEMAN	PLAIN	RUGBY	THUNDER
JOY	INDIGO	TONGS	HEART	ATHLETE	CAVE	SOFTBALL	WIND
PITY	MAGENTA	OPENER	KNEE	BANKER	GLACIER	SKIING	STORM
CRYING	TURQUOISE	MIXER	NECK	CARPENTER	ISLAND	SURFING	TYPHOON
LAUGHTER	MAROON	OVEN	BRAIN	JANITOR	STREAM	RUNNING	DROUGHT
TEARS	TEAL	COLANDER	HAIR	THERAPIST	CLIFF	GYMNASTICS	CLOUD
SMILE	TAN	CUP	ELBOW	SURGEON	DESERT	DIVING	SUNSHINE
TENSION	AQUA	STOVE	SHOULDER	SALESMAN	BEACH	WRESTLING	GALE
SHOCK	FUCHSIA	MICROWAVE	CHEST	ARCHITECT	WATERFALL	BOWLING	DUST

Appendix II continued

article of clothing	part of a building	chemical element	musical instrument	transportation vehicle	vegetable	insect	4-footed animal
SHIRT	WINDOW	OXYGEN	DRUM	CAR	CARROT	FLY	DOG
PANTS	DOOR	HYDROGEN	GUITAR	BUS	LETTUCE	ANT	CAT
SOCKS	FLOOR	CARBON	FLUTE	TRUCK	BROCCOLI	SPIDER	HORSE
UNDERWEAR	WALL	HELIUM	PIANO	PLANE	TOMATO	BEE	LION
SHOES	ROOF	NITROGEN	TRUMPET	TRAIN	CUCUMBER	MOSQUITO	BEAR
HAT	STAIRS	GOLD	CLARINET	BICYCLE	PEAS	BEETLE	TIGER
SHORTS	ELEVATOR	IRON	SAXOPHONE	VAN	CORN	BUG	COW
JACKET	ROOM	SILVER	VIOLIN	BOAT	POTATO	GRASSHOPPER	ELEPHANT
SWEATER	CEILING	SODIUM	TROMBONE	SHIP	CELERY	BUTTERFLY	DEER
SKIRT	BASEMENT	SULFUR	TUBA	MOTORCYCLE	BEANS	WASP	PIG
COAT	BATHROOM	ZINC	CELLO	SKATEBOARD	SPINACH	ROACH	GIRAFFE
DRESS	OFFICE	COPPER	OBOE	SUBWAY	SQUASH	MOTH	SQUIRREL
GLOVES	HALL	CHLORINE	BASS	TAXI	CAULIFLOWER	GNAT	GOAT
SCARF	LOBBY	NEON	HARP	SCOOTER	CABBAGE	COCKROACH	MOOSE
BLOUSE	BRICK	CALCIUM	HORN	HELICOPTER	RADISH	CATERPILLAR	SHEEP
TIE	FOUNDATION	ALUMINUM	KEYBOARD	JEEP	ASPARAGUS	CENTIPEDE	CHEETAH
BELT	ENTRANCE	BORON	PICCOLO	MOPED	TURNIP	CRICKET	WOLF
TOP	ATTIC	LITHIUM	BANJO	MINIVAN	ZUCCHINI	WORM	FOX
BOXERS	CARPET	MERCURY	HARMONICA	FORD	ONION	DRAGONFLY	DONKEY
JEANS	CELLAR	MAGNESIUM	TAMBOURINE	CAB	BEET	FLEA	TURTLE

Appendix III Words used in Experiment 3

Words used in Experiment 3	Category of that word
CORN	vegetable
WASP	insect
GOLF	sport
BEAR	mammal
TAXI	vehicle
COOK	occupation
PITY	emotion
PINK	color
BOWL	utensil
KNEE	Body part
LAKE	earth
SNOW	weather
COAT	clothing
ROOF	building
IRON	chemical
HORN	instrument

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