



## Position-specific effects within the SERIOL framework of letter-position coding

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*Abstract.* In the SERIOL (sequential encoding regulated by inputs to oscillations within letter units) framework, letter position within a word is encoded by the temporal firing pattern of letter units. As opposed to channel-specific schemes, a letter unit can potentially represent any position. This lack of positional specificity is consistent with studies showing that priming can occur across different positions within a letter string (Grainger and Jacobs 1991, *European Journal of Cognitive Psychology*, **3**: 413–434, Peressotti and Grainger 1995, *Perception of Psychophysics*, **57**: 875–890). However, these studies also showed that same-position priming is more robust than this cross-position priming. This result seems inconsistent with non-position-specific letter units. Here we give an explanation of these results under the SERIOL framework. Using mathematical models, we show that broadly tuned feature detectors and an activation gradient can account for the complex experimental data on position-specific and cross-position letter priming.

*Keywords:* neural encoding, computational modelling, letter position.

### 1. Introduction

How does the brain encode the order of letters within a word? For example, how is the word ‘from’ encoded to distinguish it from the word ‘form’? Recent computational models of word recognition have used one of two approaches to the coding of letter position. In a *channel-specific* scheme, it is hypothesized that different sets of letter units exist for each string position. That is, there are separate units representing ‘A’ in the first position, ‘A’ in the second position, etc. (McClelland and Rumelhart 1981, Coltheart *et al.* 1993, Whitney *et al.* 1996). Encoding the string ‘from’ corresponds to activating the unit for ‘F’ in the first set, ‘R’ in the second set, ‘O’ in the third set, and ‘M’ in the fourth set. In *context-unit* encoding, the basic unit is not a single letter, but rather a group of ordered letters, usually trigrams (Seidenberg and McClelland 1989, Mozer and Behrmann 1992). For example, the string ‘from’ would be represented by activating units representing ‘\_FR’, ‘FRO’, and ‘ROM’, and ‘OM\_’ where ‘\_’ represents a word boundary.

There are problems with both proposals. A disadvantage of the channel-specific scheme is that it demands a high degree of item redundancy, requiring a representation of each letter in each possible position. Moreover, it is not consistent with recent studies indicating that relative order among sets of letters, not their absolute position,

is important in letter-position coding (Humphreys *et al.* 1990, Peressotti and Grainger 1999) and that priming across letter positions can occur (Peressotti and Grainger 1995). The context-unit scheme avoids these problems, but the difficult question of how context units themselves become activated has not been addressed.

Previously, we have presented a novel model of letter-position coding that addresses these shortcomings, the SERIOL (sequential encoding regulated by inputs to oscillations with letter units) framework (Whitney and Berndt 1999, Whitney 2001a). In the SERIOL framework, a letter unit can represent any position by virtue of its timing of firing. A context unit (a bigram node) is then activated by a pair of letters that fire in a specific order. Thus, we propose that letter order is represented by context units that are activated by the temporal firing pattern of letter units.

In studies specifically designed to test the channel-specific nature of letter-position coding, there was evidence of cross-position priming. That is, a prime string with a letter in one position could facilitate recognition of that same letter in a different position within a target string (Grainger and Jacobs 1991, Peressotti and Grainger 1995). This finding is consistent with our model because letter units are not channel-specific and can represent any position. However, these studies also showed that same-position priming is more robust than cross-position priming. That is, priming effects were stronger when the primed letter occupied the same position within the prime and target strings. Care was taken in these experiments to present the prime and target strings in different visual locations, so as to rule out the influence of visual overlap. Thus, the researchers concluded that channel-specific letter units were necessary to account for these results.

How then can we account for these position-specific results within a model that does not include channel-specific letter representations, such as the SERIOL framework? We suggest that the position-specific results arose at a pre-orthographic processing level. The goal of this paper is to support this proposal. The organization is as follows. First we review the SERIOL framework. Then we give a detailed review of the experimental results on cross-position versus same-position priming. Then we show, via mathematical modelling, how interactions within the feature and letter levels of our model could produce the pattern of same-position and cross-position results observed in the experiments.

## 2. The SERIOL framework

The proposed model is a theoretical framework. The SERIOL framework specifies the types of representations and computations used by the brain during letter-position coding. Simulations based on various aspects of the SERIOL framework have accounted for a range of experimental results, such as error patterns in patients having acquired dyslexia (Whitney and Berndt 1999), contradictory results on the perceptability of the final letter (Whitney and Berndt 1999, Whitney 2001a), positional patterns of letter perceptibility that vary with visual field, reading direction and dominant cerebral hemisphere (Whitney 2001a) and reaction time patterns for lexical decision on rotated letter strings of varying lengths (Whitney 2001b).

The framework is comprised of five layers of nodes, each having distinct activation dynamics. First we give a brief overview of the entire framework. Then we discuss the layers that are relevant to our topic in more detail.

At the lowest processing layer, the *retinal level*, nodes are precisely topographically organized with respect to visual input from external space. Modelling visual acuity,

activation is highest at the fixation point and falls off as the distance from fixation increases. At the *feature level*, nodes recognize pre-orthographic letter features and are broadly tuned to retinal location. That is, a feature node responds most strongly to input from a preferred retinal location. At this level, the retinal pattern of activation resulting from visual acuity is transformed into a gradient that reflects locational information. This gradient is such that activation decreases from left to right across locations, i.e. the features of the first letter are more highly activated than those of the second letter, which are more highly activated than those of the third, etc. At the *letter level*, nodes recognize individual letters. The varying levels of input from the feature level are converted into a temporal firing pattern across the nodes, in which the firing order tags position. This is accomplished by interaction with a sub-threshold oscillatory cycle, such that the letter node receiving the highest amount of input fires first, the letter node receiving the second highest amount fires next, etc. At the *bigram level*, nodes recognize serially ordered pairs of letters, converting the temporal representation of the letter level to a contextual representation. At the *word level*, nodes recognize sets of bigrams comprising entire words.

Figures 1 and 2 summarize how the string CART would be represented within this framework. Figure 1 diagrams the activation patterns at the retinal and feature levels, while figure 2 displays the letter level to the word level. In summary, at the feature level an activation gradient is established across the features of the letters; at the letter level, C fires, then A, then R, then T; at the bigram level, CA, AR, RT, CR, AT and CT become active; at the word level, CART becomes the most active of the word nodes.

We do not model the processes of feature extraction and letter identification themselves. Rather, our intent is to show that spatiotemporal activation patterns could

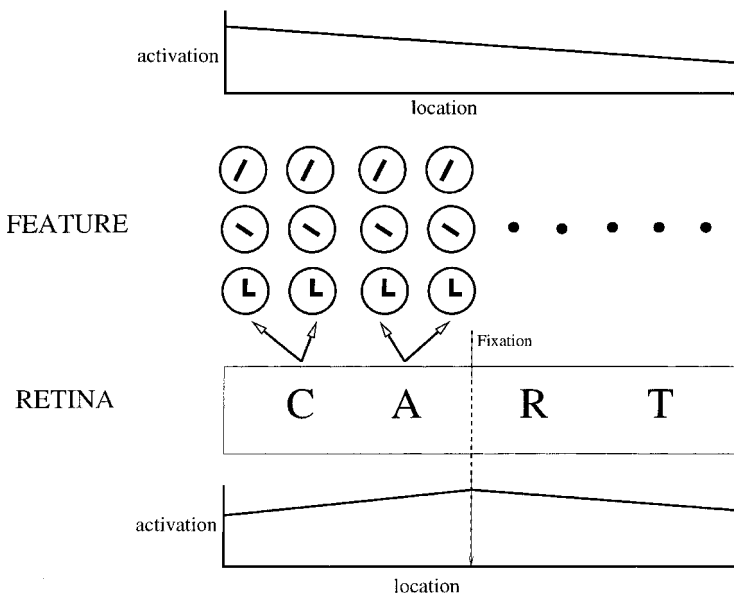


Figure 1. Architecture of the retinal and feature levels of the SERIOL framework. The retinal level is precisely topographically organized with respect to external stimulus, in this case CART. The activation of retinal nodes decreases as distance from fixation increases. Feature nodes are tuned to retinal location. The activation of feature nodes decreases from left to right.

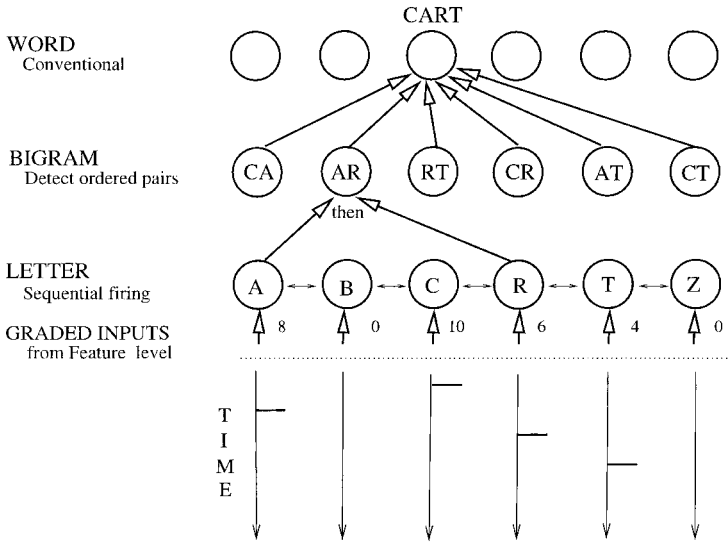


Figure 2. Architecture of the letter, bigram and word levels of the SERIOL framework, with example of encoding the word CART. At the letter level, simultaneous graded inputs are transformed into a sequential firing pattern, as indicated by the timing of firing displayed under the letter nodes. Excitatory connections link the letter nodes and the bigram nodes, which recognize serially ordered pairs of letters. Excitatory connections link the bigram nodes and the word nodes. Activation of word nodes is based on the conventional neural network dot-product model.

be used to encode letter order. Next we describe these patterns in more detail for the feature and letter levels.

### 2.1. Feature level

It is commonly assumed that letters are identified by analysing pre-orthographic features (e.g. lines, and curves). Several studies have indicated that letter features play a role in letter recognition, and that similar features occurring in different locations interact with each other, where the degree of interaction depends on the angular distance between the features (Strangert and Brannstrom 1975, Krumhansl and Thomas 1976, Chastain 1977, Bjork and Murray 1977).

Consistent with the results of these experiments, the feature level of our model is comprised of feature detectors that are tuned to retinal location. There is neurobiological evidence that the response patterns of neurons can be broadly tuned; that is, a neuron responds most strongly to a specific stimulus, and its response falls off as the similarity to this preferred stimulus decreases. For instance, some neurons in the motor cortex are tuned to movement direction. Such a neuron fires most strongly when movement in space occurs in its *preferred direction*. As the direction of movement increasingly differs from this preferred direction, the neuron's firing level decreases (Georgopoulos *et al.* 1982). We propose a similar pattern of activation for feature nodes with respect to retinal location. That is, a feature node is most highly activated when the feature that it recognizes occurs in a certain optimal area of the retina (the feature node's *preferred location*), less strongly activated when that feature occurs near the preferred location, and not at all activated when that feature occurs

far from the preferred location. Each possible feature stimulus is detected by multiple nodes having different preferred locations. This proposal can account for the experimental evidence that similar features interact with each other, where the degree of interaction decreases as the spatial distance between features increases.

We propose that the pattern of activation attained by feature nodes is very different from the pattern of activation at the retinal level. Experimentally, it has been noted that the pattern of perception of letters within a string violates the pattern of visual acuity. Numerous studies of briefly presented letter strings have shown that the initial letter of a string is the most accurately perceived of all the letters, even when the initial letter is far from fixation (Wolford and Hollingsworth 1974, Lefton *et al.* 1978, Hammond and Green 1982, Mason 1982). This pattern cannot be attributed to decreased lateral inhibition for boundary letters; when strings of non-letter symbols are centrally presented, the initial and final symbols are the least well perceived, as would be expected if perception were simply a function of visual acuity (Hammond and Green 1982, Mason 1982). The enhanced perception of the initial symbol also holds for strings of numbers. Thus it appears that a specialized system exists for analysing symbols that commonly occur in strings. This system overrides the effects of visual acuity.

In brief, we propose that this string-processing system operates as follows. The acuity gradient of the retinal level is transformed into a locational gradient at the feature level. For languages read from left to right, the locational gradient is characterized by decreasing activation from left to right across preferred location. That is, feature nodes with the leftmost preferred locations attain the highest level of activation, and activation levels decrease for more rightward preferred locations. (See the activation pattern for the feature layer in figure 1.) At the letter level, this locational gradient is converted into a temporal firing pattern that encodes position.

In the remainder of this section, we describe how the acuity gradient is converted to the locational gradient. Although the following mathematical models do not model processing at this level, we review this conversion process for the sake of completeness. We assume that the mechanism of locational gradient formation is learned during reading acquisition. However, we do not address how this occurs; rather, we describe the processing carried out by a skilled reader. Locational gradient formation depends on two important characteristics of the reader: what scanning direction is employed; and which hemisphere is dominant for language processing. In the following specification, we assume that words are read from left to right (as in English) by a reader having the usual brain organization, that is, left hemisphere dominant. We assume that there is no visual field overlap, so letters falling in the left visual field (LVF) are projected to the right hemisphere (RH), and letters falling in the right visual field (RVF) are projected to the left hemisphere (LH). Letter features are extracted separately in each hemisphere.

Note that for English words, the slope of the acuity gradient in the RVF/LH (i.e. from fixation to the final letter) is in the same direction as our proposed locational gradient, that is, decreasing from left to right. In contrast, the slope of the acuity gradient in the LVF/RH (i.e. from the initial letter to fixation) is in the opposite direction from our proposed locational gradient, that is, increasing from left to right. (For example, compare the activation patterns for the retinal layer and the feature layer in figure 1.) Therefore, we propose that in the LVF/RH, the slope of the acuity gradient is *inverted* as it activates letter features, while the slope of the acuity gradient in the RVF/LH is maintained as it activates letter features. Following callosal transfer,

the resulting two hemispheric gradients are combined, forming a locational gradient which is monotonically decreasing from left to right.

We propose that the slope of LVF/RH acuity gradient is inverted by a combination of excitation and lateral inhibition. This process is displayed in figure 3. We propose that letter features in the LVF/RH become more highly activated by retinal inputs than those in the RVF/LH (see the upper left panel of figure 3). This could occur either by stronger bottom-up connection weights from the retinal level, or by self-excitatory connections for feature nodes in the RH. Within the feature level of the RH, we propose that strong directional lateral inhibitory connections exist such that a feature node inhibits all feature nodes with preferred locations to its right. As a result, letter features corresponding to the first letter receive no lateral inhibition, and inhibition increases strongly as distance from fixation decreases. Thus, the features comprising the first letter attain the highest level of activation (due to strong excitation and lack of lateral inhibition), and activation decreases towards fixation (due to sharply increasing lateral inhibition) (see the upper right panel of figure 3).

In the RVF/LH, we assume that the overall excitation of the feature level by the retinal level is weaker than in the LVF/RH. Directional lateral inhibitory interactions may steepen the slope of the gradient; however, this inhibition need not be as strong as in the RH, since the slope of the acuity gradient in the LH is already in the correct

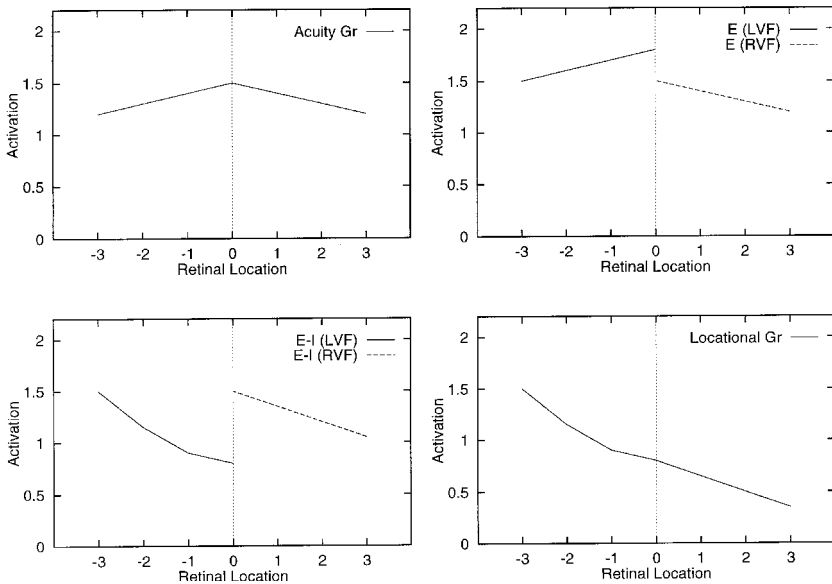


Figure 3. Example formation of the locational gradient across the activations of features. In the first graph (upper left), the acuity gradient of the retinal level is displayed in abstract units of activation. In the next graph (upper right), the effects of hemisphere-specific excitation,  $E$ , at the feature level are shown. Note that in the RVF/LH (retinal location  $\geq 0$ ),  $E$  is equivalent to the acuity gradient, while in the LVF/RH (retinal location  $< 0$ )  $E$  is elevated with respect to the acuity gradient. In the third graph (lower left), the effects of hemisphere-specific leftward lateral inhibition,  $E - I$ , are displayed. Note that inhibition is much stronger in the LVF/RH than in the RVF/LH, and results in inversion of the direction of the slope of the gradient in the LVF/RH. In the final graph (lower right), the hemisphere-specific gradients are joined via interhemispheric inhibition of the RVF/LH's features to form a monotonically decreasing activation gradient across feature locations, the locational gradient.

direction. The two hemispheric gradients are joined when feature information from the RH is transferred to the LH (which is typically specialized for language processing), and the features from the RH inhibit the activations of the LH features. As a result, an activation gradient across all features is created in the LH that is strictly decreasing by left-to-right location (see the lower panels of figure 3). Thus the locational gradient is formed. In Whitney (2001a), we show, via mathematical modelling, how this specification can account for experimentally observed patterns of letter perceptibility that vary with visual field, and we consider other combinations of scanning direction and dominant hemisphere.

## 2.2. Letter level

We propose that the locational gradient of the feature level induces a temporal firing pattern across letter nodes wherein position is represented by the precise timing of firing relative to other letter nodes. This idea is consistent with current neurobiological models of information encoding. Hopfield (1995) has proposed that quantities are represented by the explicit timing of action potentials, rather than by their firing rate. In this *phase-advance* model, encoding neurons undergo internal, sub-threshold oscillations of excitability. The magnitude of an input to such a neuron determines when its potential exceeds the firing threshold. For a small input, threshold is not exceeded until late in the cycle when the cell's oscillation brings its potential near threshold. For a larger input, threshold is exceeded earlier in the cycle. Thus, the size of an input is transformed into a spike timing relative to the oscillatory cycle. This scheme implies that individual spikes are much more important than has traditionally been assumed. Indeed, recent studies have shown that single spikes encode significant amounts of information (Rieke *et al.* 1997), and that spike timing is precise and reproducible at a millisecond time scale (Victor and Purpura 1996, Berry *et al.* 1997; de Ruyter van Steveninck *et al.* 1997).

It has been proposed that oscillatory activity in the brain near 40 Hz (gamma frequencies) is related to cognitive processing (Tiitinen *et al.* 1993). There is evidence that individual 40 Hz waves are related to individual auditory stimuli (Joliot *et al.* 1994). It has been suggested that short-term memories are encoded on 40 Hz sub-cycles of a low-frequency (5–12 Hz) oscillation (Lisman and Idiart 1995). This proposal is consistent with the observation of nested oscillations recorded in the human cortex in response to auditory stimuli (Llinas and Ribary 1993). We suggest that such oscillations also underlie visual language processing. We propose that each letter position corresponds to a successive 40 Hz sub-cycle within an oscillatory period of approximately 200 ms.

This coding scheme does not employ position-specific letter detectors; all feature nodes are connected to all letter nodes. Any letter node can represent any position, depending on the level of input that it receives and the resulting timing of firing. All letter nodes are assumed to undergo synchronous, periodic oscillations of excitability. Due to the locational gradient, the letter node representing the letter in the first position receives the highest level of excitatory input, the second receives the next highest amount, and so on. The letter node receiving the highest level of input fires first because it reaches threshold before the others. The letter node receiving the second highest level of input fires next, etc. Suitable input levels and lateral inhibition assure that only one letter node fires at a time. We assume that a letter node continues to fire until it receives lateral inhibition, and that once a letter node receives inhibition

after it has already fired, it does not fire again in the oscillatory cycle. A precise description of this temporal encoding process is given in Whitney and Berndt (1999).

### 3. Experimental results

Next we discuss the experimental findings. These experiments used non-word target strings to isolate activations at the letter level. They yielded complex patterns of results which we review in detail.

#### 3.1. Grainger and Jacobs (1991)

Grainger and Jacobs (1991) asked subjects to perform an alphabetic decision task, where they were to identify whether or not the character embedded in a string of hash marks was a letter. The target character appeared either in the initial or terminal position of a five-character test string (e.g. '#####' or 'T#####'). Performance was measured as reaction time. The target string was preceded by a briefly presented prime string. In the following discussion, we assume that the target character is a letter.

In addition to the neutral prime ('xxxxx'), there were two types of primes: Letter primes (the target letter embedded in x's) and Word primes (five-letter words). For both types of primes, the target letter could appear either in the same position as in the test string (e.g. prime string 'xxxT' for test string '#####T'), or in the opposite position (e.g. prime string 'TABLE' for test string '#####T'). Two prime exposure durations were used, 16 and 64 ms. Thus there were four variables, each with two possibilities: target letter position in prime string (1 or 5), target letter position in test string (1 or 5), prime type (Word or Letter) and prime duration (16 or 64 ms). To denote conditions, we will use notation of the form *position in prime : position in target : prime type @ presentation duration*. For example, 1 : 5 : W@64 ms refers to the condition where the target letter appears in the first position in the prime string, in the fifth position in the target string, the prime is a Word, and prime presentation duration is 64 ms.

In order to assure that facilitatory effects of prime presentation did not result from physical overlap, the target letter in the prime and test strings occupied different absolute locations on the screen. The prime string was centred in the screen. The test string was presented one line below the prime string. The target letter in the test string was always centred, and was either preceded or followed by hash marks. Thus the target letter in the prime occurred either two characters to the left or right of centre. See figure 4 for examples.

The results were a complex function of all the variables. For prime durations of 16 ms, both Word and Letter primes were facilitatory for both same-position conditions (1 : 1 and 5 : 5), and inhibitory for both cross-position conditions (1 : 5 and 5 : 1). A different pattern emerged for the 64 ms prime exposure duration. Word primes were facilitatory only for the 1 : 1 condition; otherwise, Word primes were inhibitory. Letter primes were facilitatory in the same-position conditions, and showed a trend toward facilitation in the cross-position conditions. In their statistical analysis, the authors collapsed the cross-position conditions, yielding a non-significant facilitatory trend. Looking at each individual condition reveals a 10 ms advantage for the 1 : 5 : L condition, and no advantage for the 5 : 1 : L condition. We shall characterize the 1 : 5 : L condition as facilitatory, and the 5 : 1 : L condition as neutral. These experimental results are displayed in table 1.



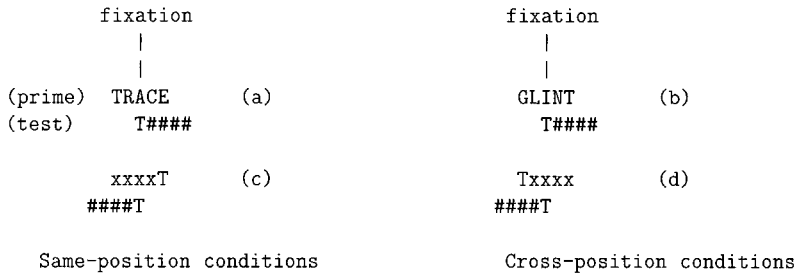


Figure 4. Layout of the presentation in Grainger and Jacobs (1995). Examples (a) and (b) are word primes and (c) and (d) are letter primes. Examples (a) and (c) are instances of same-position conditions since the target letter, T, appears in the same relative position in both prime and test strings, while (b) and (d) are examples of cross-position conditions.

Table 1. Results from Grainger and Jacobs (1991).

<i>Prime</i>	<i>Dur</i>	<i>Fac</i>
1 : 1 : L	16	6
	64	17
1 : 1 : W	16	8
	64	20
5 : 5 : L	16	2
	64	16
5 : 5 : W	16	8
	64	-9
1 : 5 : L	16	-5
	64	10
1 : 5 : W	16	-3
	64	-12
5 : 1 : L	16	-6
	64	0
5 : 1 : W	16	-5
	64	-2

*Prime*—Priming condition, notation as in the text. The top group is comprised of the same-position conditions; the bottom group is comprised of the cross-position conditions. *Dur*—prime presentation duration in milliseconds. *Fac*—facilitation, in milliseconds, relative to the neutral priming condition.

To summarize, same-position priming occurred for all conditions except the 64 ms 5 : 5 : W condition. Cross-position priming occurred only for the 64 ms 1 : 5 : L condition. These experiments indicate that same-position priming is much more robust than cross-position priming, but that cross-position priming can occur. The following experiments provide further evidence for cross-position priming.

### 3.2. Peressotti and Grainger (1995)

Peressotti and Grainger (1995) also asked subjects to perform an alphabetic decision task, where they were to determine whether strings of three characters consisted solely

of letters (e.g. 'TBR' versus 'TB\$'). Primes were also trigrams, consisting of characters from the test string, either in the same order (same-position conditions) or in a different order (cross-position conditions). Different types of cross-position primes were constructed to examine the effects of degree of similarity with the test string. Performance was measured as response time to the test string. In order to assure that facilitation did not result from physical overlap, prime strings and test strings were presented in different sized fonts.

In one set of experiments, cross-position primes were such that no letter occupied the same position as in the test string (e.g. prime 'RTB' for test string 'TBR'). We will designate these as *scrambled* primes. To examine temporal effects, prime exposure duration was varied. The results varied with prime duration. For durations of 33 ms, scrambled primes yielded no significant facilitation, while same-position primes yielded a facilitation of 22 ms. For exposures of 50 ms and 67 ms, cross-position priming did occur with facilitations of 9 and 14 ms, respectively, for the scrambled primes, while the level of same-position priming stayed roughly the same.

In another experiment, cross-position primes were formed by keeping one letter of the test string in the same position, and switching the other two letters (e.g. prime 'TRB' for test string 'TBR'). We will designate these as *switched-position* primes. The position of the unchanged letter was varied, yielding three different conditions. Prime exposure duration was 50 ms. A statistical analysis showed that the amount of facilitation did not vary with the position of the unchanged letter.

In another experiment, *replace* primes were formed by replacing one letter of the test string with a letter not in the test string (e.g. prime 'TBO' for test string 'TBR'). Prime exposure duration was 50 ms. Here results did vary with position of replacement. Replacing the final letter yielded the fastest reaction times, while replacing the middle letter resulted in the slowest reaction times.

A different response paradigm was used in the replace-prime experiment than the previous experiments. The previous experiments were executed under a go/no-go response paradigm, where subjects responded if all characters comprising the target string were letters; otherwise they did not respond at all. The replace primes were executed under a yes/no paradigm. To see if the response paradigm affected the results, the switched-position prime experiment was repeated under the yes/no paradigm. The results were the same as under the go/no-go paradigm: the position of the unchanged letter did not affect the degree of priming. However, the size of the the facilitatory effect was 9 ms less than under the go/no-go paradigm. We use this difference to normalize the size of the replace primes' facilitations, so that facilitations can be compared across all prime types. That is, we add 9 ms to the replace primes' facilitations to bring them in line with those generated under the go/no-go paradigm. The results of all experiments are summarized in table 2.

Overall, the results of Peressotti and Grainger (1995) are similar to those of Grainger and Jacobs (1991). Cross-position priming occurred, but only when prime exposure durations were at least 50 ms. Same-position priming was more robust, occurring even at shorter prime durations, and giving higher levels of facilitation. In order to account for this pattern of results, Peressotti and Grainger (1995) proposed a two-level model consisting of channel-specific letter units and position-independent letter units. Channel-specific letter units are activated prior to position-independent units to account for the temporal priming pattern.

The SERIOL framework incorporates a single set of letter nodes, where position is tagged by timing of firing. Since different positions can be represented by the

Table 2. Results from Peressotti and Grainger (1995).

<i>Type</i>	<i>Prime</i>	<i>Dur</i>	<i>Fac</i>
<i>Same</i>	123	33	22
		50	27
		67	24
<i>Scrambled</i>	312	33	3
		50	9
		67	14
<i>Switched</i>	132	50	20
	321		18
	213		17
<i>Replace</i>	<i>x</i> 23	50	18*
	1 <i>x</i> 3		15*
	12 <i>x</i>		24*

*Type*—type of prime string, *Prime*—form of the prime string, as denoted by the positions of constituent letters with respect to the test string, where *x* denotes a letter not in the test string. For example, 312 indicates that the prime's first letter occurred in the third position in the test string; the prime's second letter occurred in the first position in the test string, etc. *Dur*—prime presentation duration in milliseconds, *Fac*—facilitation, in milliseconds, relative to the neutral condition. \* Normalized value, as explained in the text.

same letter node, cross-position priming at the letter level is possible. However, same-position priming seems at odds with a model that does not include any position-specific letter representations. How then can we account for this finding within our theoretical framework? We propose that the same-position results arose from the pre-orthographic level. Recall that features are tuned to retinal locations. Although the target letter(s) appeared at different physical locations in the prime and test string presentations, we propose that interactions at the feature level could produce the appearance of position-specific priming.

In the following section, we present arguments and mathematical models to support this claim. The modelling is performed at a high level, using functions that are motivated by the SERIOL framework. That is, the modelling is not at the level of individual nodes, since such modelling would be too tedious and would tend to obscure the principles which we are trying to illustrate. Rather, we use functions that describe emergent behaviour, and show how combinations of these functions can replicate the experimental data patterns. The functions are tailored to each experiment in order to model the variables manipulated in that experiment. Thus, we show that combinations of quantities that vary in ways consistent with the SERIOL framework can account for the experimental variations in priming.

## 4. Mathematical models

### 4.1. Grainger and Jacobs (1991)

Recall that in the Grainger and Jacobs (1991) experiments, care was taken to avoid physical overlap between the prime and test strings. The prime string's target letter occurred either two places to the left or right of centre, while the test string's target letter always occurred in the central position, one line below where the prime had

occurred. However, this approach resulted in physical differences in stimulus layout between the same-position and cross-position conditions in the vicinity of the location of the target letter in the prime, specifically in the area below the prime. For the same-position conditions, the location occupied by the target letter in the prime is surrounded by blank space during presentation of the test string. However, for the cross-position conditions, hash marks from the test string presentation appear directly below the location that had been occupied by the prime string's target letter. For example, referring back to figure 4, in the same-position conditions, the locations of Ts in the primes are surrounded by blank space during test string presentation, while for the cross-position conditions, they are bordered by #s appearing immediately below.

As discussed above, several studies have produced evidence that features interact across nearby locations (Strangert and Brannstrom 1975, Krumhansl and Thomas 1976, Bjork and Murray 1977). Consistent with these data, we propose that the activation of the target letter via the prime was influenced by the presence or absence of nearby #s during test string presentation. We assume that the representation of the prime string's features continues to develop during test string presentation. Because the location occupied by the target letter in the prime is not bordered by noise in the same-position conditions, the corresponding letter features can become more highly activated in the same-position conditions than in the cross-position conditions. We assume that such a difference occurs despite the fact that a mask always intervened between the prime and test strings. This assumption is consistent with a finding from a preliminary experiment in Grainger and Jacobs (1991); in that experiment, facilitation occurred only in the condition in which the target letter occupied the same physical location in both the prime and test strings, indicating that effects of physical location can arise despite an intervening mask. Thus, we assume that, under same-position conditions, test string presentation generates less interference to the ongoing activation of the feature nodes of a prime string's target letter (as compared with cross-position conditions). As a result, more total input reaches the target letter node in the same-position conditions, yielding the appearance of position-specific letter priming.

Grainger and Jacobs (1991) concluded that their experimental results support position-specific letter priming. We suggest that this conclusion cannot fully account for the data, since one of the cross-position cases appeared to be facilitatory. Our goal, via computational modelling is to demonstrate that a different interpretation is viable, and in fact allows a quantitative fit to the data. We assume that multiple factors interact in determining the amount of facilitation. We have already argued for inhibitory interference in the cross-position cases. We assume that this effect combines with a facilitatory effect of excitation from the prime presentation, where the amount of facilitation varies in a way that is consistent with the locational gradient of the SERIOL framework, and is not position specific. We also assume that an additional inhibitory effect can arise within the letter level itself, consistent with our assumption of lateral inhibition.

For simplicity, we do not directly model the underlying processes that determine these quantities. Rather, having motivated each of these effects within the SERIOL framework, we make simple assumptions about their form, and demonstrate that these assumptions allow a good fit to these experimental data. The model fits not only the direction of the effect (facilitatory or inhibitory) for each condition, but also the size of the effect (i.e. the difference in average reaction time from the neutral prime

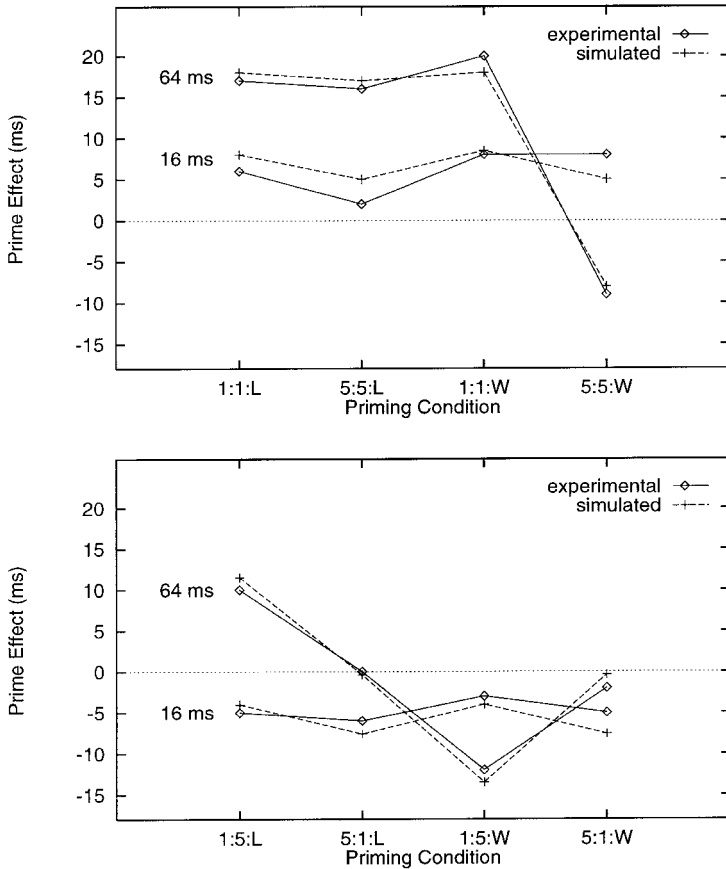


Figure 5. Experimental and modelled results for the Grainger and Jacobs (1991) study. The top graph displays priming for the same-position conditions by prime exposure duration, while the bottom displays those data for the cross-position conditions.

condition). The fit of this model and the corresponding experimental values are displayed in figure 5. The details of the model follow.

We define  $Q$  to be the effect of the prime on the test string relative to the neutral condition (i.e. milliseconds of facilitation or inhibition). We assume that facilitation cannot exceed a certain level. That is,  $Q$  is bounded by a ceiling value, i.e.

$$Q = \min(Q_{\max}, Q_E),$$

where  $Q_{\max}$  is a constant, and the function  $Q_E$  specifies the effect of the prime. This function is of the form:

$$Q_E(t_p, p_p, p_T, type_p) = L^+(p_p, t_p) + F(p_p, p_T, t_p) + L^-(type_p, p_p, p_T, t_p),$$

where  $t_p$  denotes prime presentation duration in milliseconds,  $p_p$  denotes position of the target letter within the prime string (1 or 5),  $p_T$  denotes position of the target letter within the test string (1 or 5) and  $type_p$  denotes whether the prime is of the Word or Letter type.

$L^+$  is a function that represents the effect of bottom-up excitatory input from the feature level to the letter level, where increasing input results in increasing priming facilitation. We assume that input level increases with prime exposure duration; that is, for a given  $p_p$ ,  $L^+$  increases with increasing  $t_p$ . As is consistent with the locational gradient of our underlying theoretical framework, we assume that input level decreases with increasing position; that is, for a given  $t_p$ ,  $L^+$  is larger for  $p_p = 1$  than for  $p_p = 5$ . Note that  $L^+$  does not depend on  $p_T$ , indicating that the amount of facilitation does not depend on whether  $p_p$  matches  $p_T$ , as is consistent with our assumption that letter nodes are not position specific.

Function  $F$  signifies interference at the feature level arising under the cross-position conditions, as discussed above. Thus  $F$  is non-zero only if  $p_p \neq p_T$ . We assume that the effect of this interference is more damaging for longer prime exposure durations; that is,  $F$  increases with increasing  $t_p$ . We assume that the amount of interference is constant with respect to location; that is, for a given  $t_p$  and a mismatch between  $p_p$  and  $p_T$ ,  $F$  does not vary.

Function  $L^-$  denotes lateral inhibitory effects at the letter level resulting from prime presentation. Recall that, within the letter level of the SERIOL framework, lateral inhibitory connections between letter nodes ensure that only one letter node is active at a time. This inhibition becomes relevant when comparing Word primes with Letter primes. We assume that  $L^-$  is zero for Letter primes, since letter nodes representing hash marks do not exist, so there are no letter nodes to provide lateral inhibition to the target letter node. In contrast, for Word primes, lateral inhibitory letter-level effects are possible.

We assume that the prime presentation duration provides a multiplicative component in functions  $L^+$  and  $F$ . That is, there are functions  $L_p^+$ ,  $L_t^+$ ,  $F_p$  and  $F_t$  such that

$$L^+(p_p, t_p) = L_p^+(p_p) * L_t^+(t_p)$$

$$F(p_p, p_T, t_p) = F_p(p_p, p_T) * F_t(t_p).$$

In order to accommodate the experimental results, we do not restrict  $L^-$  to this form. Fitting to the data yielded the following:

$$Q_{\max} = 18 \text{ ms}$$

$$L_p^+(p_p) = \begin{cases} 1.7 & \text{if } p_p = 1 \\ 1.0 & \text{if } p_p = 5 \end{cases} \quad L_t^+(t_p) = 0.25 * t_p + 1 \text{ ms}$$

$$F_p(p_p, p_T) = \begin{cases} 0 & \text{if } p_p = p_T \\ -1.0 & \text{if } p_p \neq p_T \end{cases} \quad F_t(t_p) = 0.1 * t_p + 11 \text{ ms}$$

$$L^-(type_p, p_p, p_T, t_p) = \begin{cases} 0 \text{ ms} & \text{if } type_p = \text{Letter or } t_p = 16 \text{ ms or } p_T = 1 \\ -25 \text{ ms} & \text{if } type_p = \text{Word and } t_p = 64 \text{ ms and } p_T = 5. \end{cases}$$

These equations are consistent with the above specifications.  $L^+(1, t_p)$  is larger than  $L^+(5, t_p)$ , corresponding to locational gradient;  $L^+(p_p, 16 \text{ ms}) < L^+(p_p, 64 \text{ ms})$ , corresponding to increasing excitation with increasing exposure duration. The interference term  $F$  is increasing with exposure duration, and is independent of position (given a mismatch). The lateral inhibition term is only non-zero for the two conditions 1 : 5 : W@64 ms and 5 : 5 : W@64 ms (a possible explanation of which is discussed below), consistent with the assumption that it is zero for all Letter conditions.

Experimentally, all same-position conditions were facilitatory, except for the 5 : 5 : W@64 ms condition. In the mathematical model, this pattern arose because none of the same-position conditions received cross-position interference, and only 5 : 5 : W received lateral inhibition. Experimentally, the only facilitatory cross-position condition was 1 : 5 : L@64 ms. In the model, the only cross-position condition for which excitation was greater than overall inhibition was the condition for which excitation was maximal and lateral inhibition was zero (namely 1 : 5 : L@64 ms). This occurred because excitation grew more quickly with increasing prime presentation duration than did cross-position interference. For all other cross-position conditions,  $L^+ \leq -(F + L^-)$ , resulting in neutral or inhibitory effects, and recreating the experimental pattern.

Note that in the fit to the data, lateral inhibition is non-zero only when the target letter is in the final position of the test string and prime duration is 64 ms. It is interesting that this quantity depends on the target-letter position in the test string, rather than in the prime string. What could be the underlying mechanism? We suggest that it is a matter of timing. The following discussion assumes a Word prime. We use the term *prime-string's letter nodes* to refer to letter nodes that receive input as a result of prime string presentation; similarly for *test-string's letter nodes*. If prime presentation does not provide sufficient excitation for its letter nodes to reach threshold and fire before the test-string's letter nodes fire, there will be no lateral inhibitory effects resulting from the prime. We suggest that when  $t_p = 16 \text{ ms}$ , this is the case for all conditions; the brief presentation does not provide sufficient excitation for the prime-string's letter nodes to fire before the test-string's letter nodes fire. What about when  $t_p = 64 \text{ ms}$ ? We propose that, for certain conditions, the longer prime presentation allows the prime-string's letter nodes to fire before the test-string's target letter node. Recall that, in the SERIOL framework, letter nodes fire sequentially; the node representing the first letter fires before the node representing the fifth letter. We propose that when  $p_T = 1$ , the test-string's target letter node fires before the prime-string's letter nodes (as in the 16 ms conditions). However, when  $p_T = 5$ , the test-string's target letter node fires later, after the prime-string's letter nodes have fired and have induced lateral inhibition. Thus, this dependence on test-string position is consistent with the foremost assumption of the SERIOL model, namely sequential firing of letter nodes.

In summary, we assumed that the amount of bottom-up input depends on prime duration and target letter position in the prime string. This input can be inhibited when test string presentation interferes with feature-level activation of the prime's target letter. Lateral inhibition can occur between letter nodes once they have commenced firing. A summation of these effects yields a good fit to the complex experimental data of Grainger and Jacobs (1991).

#### 4.2. Peressotti and Grainger (1995)

We propose that interactions between the prime and test strings at the feature level also account for the difference between same-position and cross-position priming in the experiments reported by Peressotti and Grainger (1995). We assume that priming can occur at both the feature level and the letter level. As is consistent with the assumption of features tuned to preferred locations, feature priming is graded with respect to location of the feature in space. That is, the occurrence of a feature in one location makes it easier for the representation of the same feature in a nearby location to become activated later. The degree of facilitation falls off with increasing distance.

We will use the term *location* to refer to location on the retina, and *position* to refer to a letter's ordinal position within a string. We propose that what appear to be position-specific results in Peressotti and Grainger (1995) are actually location-approximate results. That is, the occurrence of a feature in the prime string facilitates activation of the same nearby feature in the test string. A correlation between retinal location and string position yielded the appearance of position-specific effects. We demonstrate that a model based on location can account for the results.

In the experiments, both the prime and test string were presented centrally, with the test string's letters twice as large as those in the prime string (6 mm versus 3 mm in width). Primes and test strings were presented in the same case and font. For simplicity, we consider all of a letter's features to be located at the letter's centre. We take the first letter of the prime string to be located at  $-3$ , the second to be at  $0$  (fixation) and the third to be at  $3$ . In accordance with the larger size of the test string's letters, the locations for its letters are  $-6$ ,  $0$  and  $6$ , respectively. We use  $R_p(x)$  to denote the location of the letter in the  $x$ th position in the prime string. Similarly,  $R_T(x)$  denotes the location for the test string. For example,  $R_p(1) = -3$  and  $R_T(1) = -6$ . See figure 6.

Note that the correlation between location in the prime and location in the test string is not strictly position-specific. That is, it is *not* the case that for a certain position, its location in the prime is uniquely closest to its location in the test string. For example, the prime's first letter is equally close (at a distance of  $3$ ) to both the test string's first and second letters, because  $R_T(1) = -3$ , with  $R_p(1) = -6$  and  $R_p(2) = 0$ ; the distance from  $-3$  to  $-6$  is the same as from  $-3$  to  $0$ . Analogously, the prime's third letter is equally close to both the second and third letters of the test string. The second letter of the prime is closest to a single letter of the test string, namely the second letter (location  $0$  versus location  $0$ ). Thus the second letter of the prime is the only letter for which the closest letter in the test string is unambiguously in the same position. Despite this, we show that a model based on feature location can account for the apparent position-specific results of Peressotti and Grainger (1995). The results are displayed in figures 7 and 8. The details of the model follow.

Figure 6. Retinal locations for prime and test strings from Peressotti and Grainger (1995). Prime strings were presented with the first letter at location  $-3$ , the second at  $0$  and the third at  $3$ . Letters of the test strings were presented at  $-6$ ,  $0$  and  $6$ , respectively.



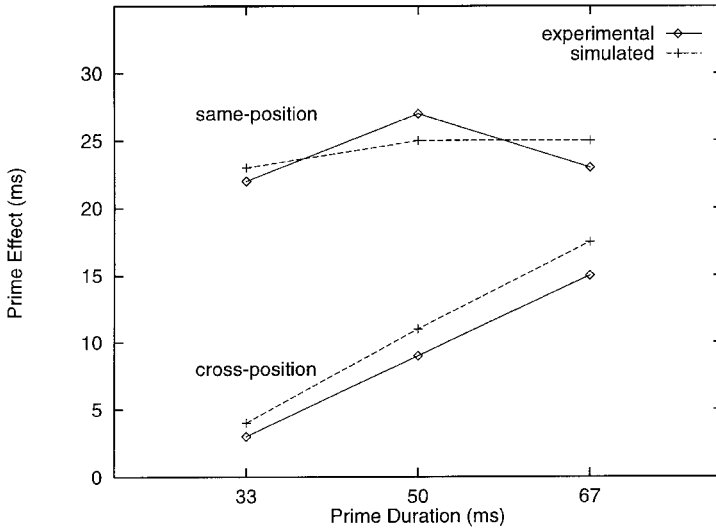


Figure 7. Experimental and modelled results for the Peressotti and Grainger (1995) study. This graph displays variation in priming by prime exposure duration for two types of primes. Same-position primes were identical to the test string, while cross-position primes were *scrambled* primes comprised of the test string's letters, with no letter in the same position as in the test string.

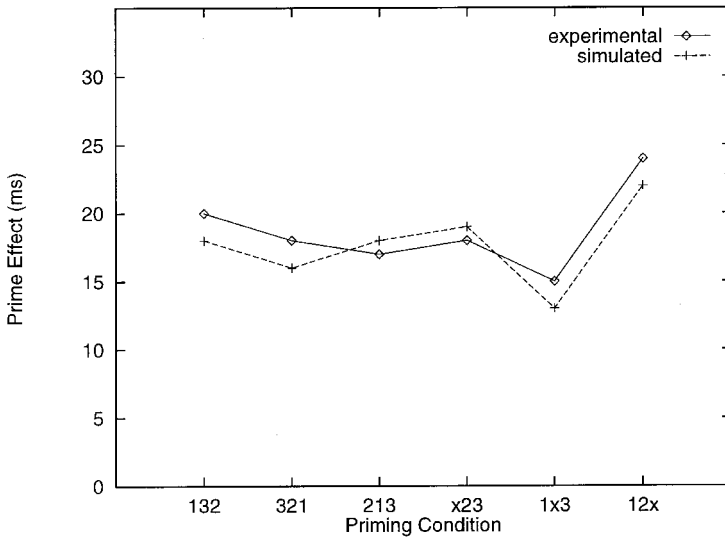


Figure 8. Experimental and modelled results for the Peressotti and Grainger (1995) study. This graph displays priming for various priming conditions, where a prime is denoted by the positions of its letters in the test string, and 'x' denotes a letter not in the test string. The first three prime types are instances of *switched* primes, while the other three are instances of *replace* primes. Prime exposure duration was 50 ms.

We use  $D$  to denote the distance between a letter's location in the prime and in the test string. That is,

$$D(p_T, P_P(p_T)) = |R_T(p_T) - R_P(P_P(p_T))|,$$

where  $p_T$  denotes position in the test string and  $P_P(x)$  denotes the position within the prime string of the  $x$ th letter of the test string. For example, if the first letter of the test string appears in the third position in the prime string,  $P_P(1) = 3$ , and  $D(1, P_P(1)) = | -6 - 3 | = 9$ , since  $R_T(1) = -6$  and  $R_P(3) = 3$ . If the letter does not appear in the prime,  $P_P(p_T) = \infty$ , and  $D(p_T, \infty) = \infty$ . Facilitation at the feature level is assumed to be a decreasing function of  $D$ . For simplicity, we assume feature-level facilitation between similar letters is negligible compared with feature-level facilitation between identical letters, and we ignore feature-level inhibition between different letters.

The mathematical model for the Peressotti and Grainger experiments follows the same form as for the Grainger and Jacobs experiments, wherein facilitation for a letter is the sum of effects within the feature level ( $F$ ), excitation from the feature level to the letter level ( $L^+$ ) and lateral inhibition within in the letter level ( $L^-$ ). Here, the feature-level interactions depend on the function  $D$  (i.e.  $F$  is a decreasing function of  $D$ ), and we take  $L^-$  to be a constant, while the constraints on  $L^+$  are the same (as in the previous model). The total amount of facilitation for a string is the sum of the facilitations for each letter, giving:

$$Q_E = \sum_{p_T=1}^3 (F(D(p_T, P_P(p_T))), t_p) + L^+(P_P(p_T), t_p) + L^-.$$

As above we assume that the effect of prime presentation duration provides a multiplicative component to the  $F$  and  $L^+$  functions, and that the actual facilitation,  $Q$ , is given by bounding  $Q_E$  by  $Q_{\max}$ . Fitting these functions to the data yielded the modelled values, as displayed in figures 7 and 8:

$$Q_{\max} = 25 \text{ ms} \quad L^- = -2 \text{ ms}$$

$$F_p(D(p_T, P_P(p_T))) = \begin{cases} 15 & \text{if } D = 0 \\ 7 & \text{if } D = 3 \\ 3 & \text{if } D = 6 \\ 0 & \text{if } D \geq 9 \end{cases} \quad F_t(t_p) = 1 \text{ ms}$$

$$L_p^+(P_P(p_T)) = \begin{cases} 8 & \text{if } P_P = 1 \\ 4 & \text{if } P_P = 2 \\ 2 & \text{if } P_P = 3 \\ 0 & \text{if } P_P = \infty \end{cases} \quad L_t^+(t_p) = (t_p - 33 \text{ ms}) / 35.$$

Thus using a single set of parameters, we have constructed a mathematical model which replicates the results of a variety of experiments described in Peressotti and Grainger (1995). In order to capture the patterns of cross-position and same-position

priming with prime exposure duration, we used different time courses for the function  $F$  (which dominates in the same-position conditions) and the function  $L^+$  (which dominates in the cross-position conditions):  $F_t$  is constant, while  $L^+p$  is an increasing function of  $t_p$ . This indicates that the feature-level influence has reached its maximal value by 33 ms, while the letter-level influence has not. This is consistent with the underlying framework, in which feature nodes become activated prior to letter nodes; feature nodes attain their maximal activations before letter nodes do.

This account is similar to that of Peressotti and Grainger (1995), who argued that position-specific letter units become activated before position-independent letter units. However, while both accounts involve two levels of representation, we need only invoke one level of letter units in addition to feature units, while the Peressotti and Grainger account requires two levels of letter units in addition to sub-orthographic units (which, based on experimental evidence discussed above, are presumably required in any model). Thus, our model provides a more parsimonious explanation of these experimental results.

The mathematical model also replicated the pattern for different types of cross-position primes. All switched primes gave similar levels of facilitation because the amounts of letter-level priming for each condition were identical, and the amounts of feature-level priming were similar. The model captured the positional nature of the replace prime results. At the feature level, an inherent characteristic of the model is that the most facilitatory condition occurs when the same letter occupies the middle position in both the prime and the test strings (because the distance between prime and target locations is minimized). This predicts the experimental finding that a prime differing from the test string at the middle positions is less facilitatory than primes differing at the other positions. At the letter level of our model, the final letter receives the least input. As a result, replacement of the final letter has the least detrimental effect relative to a same-position prime; that is, it is the most facilitatory replacement condition, as observed experimentally.

## 5. Discussion

We suggest that the topic of letter-position coding has not received the attention that it deserves. This is a circumscribed problem, yet it offers a window on to representational strategies that may be relevant to higher level processing. Encoding letter position to subserve word recognition entails composing constituent entities to form a whole, a common theme in many aspects of cognitive processing. In letter-position coding, the constituent entities are limited to the letters of the alphabet, and the combinatorics are limited to position within a one-dimensional array. Thus, we suggest that this is a tractable problem which offers an avenue of investigation into the realm of high level representations. To this end, we have constructed neurobiologically plausible theoretical framework for letter-position coding that unifies a wide range of experimental data (Whitney and Berndt 1999, Whitney 2001a, b). Because this framework does not include position-specific letter units, it may seem inconsistent with experimental results which seem to indicate that position-specific letter priming occurs (Grainger and Jacobs 1991, Peressotti and Grainger 1995). We have proposed that feature detectors tuned to location may underlie this position-specific priming, and have constructed mathematical models that give good fits to these experimental data. Our framework can account for the cross-position versus same-position priming results using a single level of position-independent letter nodes, in conjunction with

locally tuned feature nodes. Thus, we have shown that position-specific letter representations are not necessary to account for these data.

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