Hemisphere-specific effects in word recognition do not require hemisphere-specific modes of access

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Abstract

Consistent with converging experimental evidence, we assume that foveal information is initially split across the two cerebral hemispheres. We have previously presented the SERIOL model of letter-position coding, which specifies how the resulting two halves of a letter string are integrated into an abstract representation of letter order. This representation is based on ordered pairs of two letters (bigrams); such a representation is created for input occurring at any location in the visual field. Various studies have shown hemisphere-specific effects in lexical access by using unilateral presentation of stimuli. While the hemisphere-independent means of lexical access in the SERIOL model (via bigrams) may seem inconsistent with these findings, we propose that such effects arise from the hemisphere-specific transformations necessary to create the bigram representation. We provide a theoretical account of the finding that high N (lexical neighborhood size) evokes facilitation in the RH, but not the LH (Lavidor & Ellis, 2002a, 2002b); an experiment discussed elsewhere (Whitney & Lavidor, 2003) has verified key predictions of this account. We also discuss the differing effects of word length across visual fields.
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1. Introduction

There is mounting evidence that there is no overlap of the visual fields along the vertical meridian in humans (Brysbaert, 1994; Brysbaert, Vitu, & Schroyens, 1996; Lavidor, Ellis, Shillcock, & Bland, 2001; Lavidor & Walsh, 2003; Sugishita, Hamilton, Sukuma, & Hemmi, 1994) Rather, the representation of the fovea is initially split across the two cerebral hemispheres. Thus, for a centrally fixated word, letters in the left visual field (LVF) are projected to the right hemisphere (RH), and letters in the RVF are projected to the LH. This raises the question of how the two halves of the string are integrated. Most researchers assume that a canonical, unified representation of the entire string subserves word recognition. Thus, the two halves are integrated prior to lexical access, and the encoding of the letter string does not depend on its presentation location. We will denote this the *hemisphere-independent* assumption.

The hemisphere-independent assumption is consistent with brain-imaging evidence. A small area of LH fusiform cortex, dubbed the Visual Word Form Area (VWFA), is consistently activated during reading; it has been proposed that this area underlies an abstract representation of letter order (Cohen et al., 2000; Cohen et al., 2002). Activation of the VWFA is invariant with respect to visual field and retinal location (Cohen et al., 2000) and is specific to letter strings (Cohen et al., 2002). Its activation does not depend on presentation format; it responds to letter strings in MiXeD cAsE (Polk & Farah, 2002) and to orally spelled words (Booth et al., 2002). Brain lesions limited to the VWFA region are associated with pure alexia, with sparing of lexical retrieval via other modalities (Binder & Mohr, 1992; Damasio & Damasiao, 1983; Leff et al., 2001). Thus experimental evidence points to an abstract representation of letter order in the left hemisphere.

The SERIOL model is the only split-fovea model of lexical access which explains how hemisphere-specific letter input is integrated within the left hemisphere into a unified, abstract representation of letter order. The

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model explains a wide range of data concerning the effects of letter position, visual field, and reading direction on letter perceptability and lexical access (Whitney, 2001a, 2001b, 2002; Whitney & Berndt, 1999).

In contrast, Monaghon, Shillcock, and McDonald, and McDonald (this volume)2003 present a split-fovea model in which the encoding of the string varies with presentation location. We denote this the *hemisphere-specific* model. As a result of positional asymmetries in bigram and letter frequencies coupled with positional input asymmetries in the model, the "LH" and "RH" develop differing representations of letter order. The LH develops a coding based on individual letters, while the RH develops a coarser coding based on bigrams. Thus, the representational grain size depends on the presentation location. The authors propose that such differing representations contribute to observed VF differences in semantic priming.

Experimental investigations into the role of orthography in word recognition have also yielded VF differences. Neighborhood size (N), the number of words that can be formed by changing one letter of the target word (Coltheart, Davelaar, Jonasson, & Besner, 1977), is one lexical property that is often manipulated. In English, lexical decision is generally faster for high N words than for low N words (for a review, see Andrews, 1997). Lavidor and Ellis (2002a, 2002b) have shown that the influence of N is hemisphere dependent. For LVF/RH presentation, high N is facilitatory, as for central presentation. However, for RVF/LH presentation, N has no effect.

Moreover, the lack of influence of orthography in the LH is not limited to the N effect. Chiarello (1985) showed that orthographic priming was larger in the RH than the LH. For target presentation to the RVF/LH in experiment 2 of Lavidor and Ellis (2002a), a centrally presented prime differing from the target by a single letter produced no facilitation relative to an unrelated prime. In contrast, facilitation was observed for target presentation to the LVF/RH. Thus orthography in general seems to have less impact in the LH than the RH.

The hemisphere-specific model could potentially explain these effects based on the differing representations in each hemisphere. For example, neighborhood effects may be stronger in the RH because a bigram representation is more sensitive to letter context than is a single-letter representation (Monaghan, personal communication). It is less obvious how to account for these effects within a hemisphere-independent framework, such as the SERIOL model. How can N and form priming have different effects across the hemispheres if the encoding supporting word recognition is the same for both hemispheres?

The influence of string length also varies with visual field. In the LVF/RH, increasing string length leads to increased reaction times for lexical decision and decreased accuracy for letter identification; in the RVF/LH, increasing string length has little effect (Bouma, 1973; Ellis, Young, & Anderson, 1988; Young & Ellis, 1985). Ellis and colleagues have proposed that these results reflect different modes of access, with non-parallel processing [1] of letters in the RH and parallel processing in the LH. The SERIOL model uses a serial encoding of letter position. How can length have differing effects across the hemispheres if letter processing is always serial?

The goal of this paper is to show how the SERIOL model can account for these effects, based on a differential patterns of activation across units of a single grain size, under a single mode of processing. The organization of the paper is as follows. In the following section, we review the SERIOL model. In Section 3, we discuss how activation patterns in the SERIOL model account for some visual field interactions in other experiments. In Section 4, we present our account of the hemispheric influences on N and form priming; in Section 5, we discuss the length effect.

2. Overview of the SERIOL model

The SERIOL model is a theoretical framework of letter string encoding in the brain. The framework addresses the following questions. How is letter position represented? How is that representation formed from the retinotopic visual input? How does that representation activate the correct word? This framework is meant to describe processing in a mature reader, under the assumption that the proposed representations develop due to processing constraints in the brain. However, this developmental aspect is a direction for future research and is not included in the present framework. Portions of this theory have been implemented in computational models (Whitney, 2001a, 2002; Whitney & Berndt, 1999).

In the following, we summarize the basics of the theory. The SERIOL model is comprised of five layers: retina, feature, letter, bigram, and word. We start at the letter layer, and work upwards to the bigram and word levels, and then downwards to the feature and retina levels.

The most well known model of word recognition, the Interactive Activation model (McClelland & Rumelhart, 1981), uses a position-specific encoding of letter order. That is, there are separate representations of each letter for each string position. The definition of N is based on such a representation. However, priming studies have indicated that encoding at the letter level is not position-specific. A letter in one string position can

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[1] Such sequential processing could occur either from left to right, or from the ends inward.

prime the same letter in different string position, and absolute string position does not have be maintained in order to prime words (Humphreys, Evett, & Quinlan, 1990; Peressotti & Grainger, 1995, 1999). Consistent with this data, we assume a non-position-specific encoding; a letter node can represent that letter in any position. Therefore, the must be some way of associating a letter node with a particular string position. We propose that this is accomplished via firing order. For example, the string *cave* is represented by C firing, then A firing, then V, and then E. This firing pattern is repeated with respect to an oscillatory cycle, as we discuss in more detail below.

A serial encoding of letter order explains the effect of string length on reaction times in lexical decision, as observed in the LVF/RH, and in both VFs for non-standard presentation formats (MiXeD CaSe, non-aligned letters) (Ellis et al., 1988; Lavidor, Ellis, & Pansky, 2002; Young & Ellis, 1985) and for Hebrew (Lavidor, Babkoff, & Faust, 2001). Thus, an absence of a length effect (for RVF presentation in standard format in a left-to-right language) can be considered the exception, rather than the norm. In Section 5, we discuss how a length effect could be absent, despite a serial encoding, under certain conditions. For lexical decision on rotated letter strings (Koriat & Norman, 1985), a serial encoding explains the complex pattern of reaction times with respect to string length and rotation angle, as discussed in Whitney (2002).

Next we consider how this serial encoding activates words. Priming studies have shown that the relative order of letters is highly important; no facilitation occurs if the order of the target word's letters is not preserved for the most part in the prime (Humphreys et al., 1990; Peressotti & Grainger, 1999). Therefore, we assume that the relative timing of pairs of letters serves as the basic unit of lexical access. That is, the temporal encoding activates bigram nodes, and the activity across bigram nodes is consolidated to activate words. A bigram node is activated any time that its constituent letters fire in the correct relative order; the letters do not have to be contiguous in the string. Thus the sequence C, A, V, E activates bigrams CA, CV, AV, CE, AE, and VE. Each bigram node is connected to every word node which represents a word containing that bigram. Each connection is weighted, as we discuss below.

Thus far we have considered how string position is represented at the letter level (serial encoding), and how that representation activates word nodes (via bigrams). But how is this serial encoding generated? We now turn to the proposed mechanism. The input to the letter level comes from the feature level, which is comprised of nodes that are locationally tuned. That is, a feature node responds optimally to a certain feature occurring at a specific retinal location. Consistent with this assumption, several studies have indicated that 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 spatial distance between the features (Bjork & Murray, 1977; Chastain, 1977; Krumhansl & Thomas, 1976; Strangbert & Brannstrom, 1975). We have shown (Whitney, 2001b) that interactions at the feature level could account for what appears to be position-specific letter priming (Grainger & Jacobs, 1991; Peressotti & Grainger, 1995).

We propose that induction of the serial encoding depends on the interaction of two key components: (1) feature-level activations are graded such that activation is monotonically decreasing from the first to the last letter; (2) letter nodes undergo synchronous oscillations of excitability (Hopfield, 1995; Lisman & Idiart, 1995). Thus in our example, C's features would be the most highly activated, A's features the next most, and so on. This pattern of activation is dubbed the *locational gradient*. Early in the oscillatory cycle, the excitability of the letter nodes is low. Therefore, only the letter node receiving the highest level of input (i.e., C) can exceed threshold and fire. See Fig. 1. Then as excitability increases over time, the letter node receiving the next highest level of input can fire (i.e., A), and so on. Thus, parallel activation at the feature level is converted to sequential activation at the letter level. An active letter node inhibits all other letter nodes, and continues to fire until it is inhibited by the firing of the next letter node.[2] Following the model proposed by Lisman and Idiart (1995), we propose that each letter node fires in a 40 Hz subcycle of a 5 Hz oscillatory cycle. See Fig. 2 for an overview of the letter to word processing.

The induction of the serial encoding requires an activation gradient across locationally-tuned units. But how is this locational gradient created? We turn next to the underlying mechanisms. At the retinal level, there is an activation gradient related to acuity—activation is highest at the fixated letter, and falls off as the distance from fixation increases. This acuity gradient must be transformed into the locational gradient. See Fig. 3. Locational gradient formation depends on a reader's scanning direction. In the following specification, we assume that words are read from left to right.

The proposed locational gradient is *decreasing* from left to right. Note that the acuity gradient is *increasing* from left to right in the LVF/RH; that is, the slope is in

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[2] This raises the question how a different letter node can ever start to fire, since all other letter nodes are being inhibited by the firing node. We assume that as a node continues to fire, there is accommodation and its firing rate slows down. Eventually the level of inhibition generated by the firing node will decrease sufficiently that a different letter node can fire. When a node that has been firing receives lateral inhibition, it becomes strongly inhibited. This in turn raises the question of what happens when the same letter appears more than once in a word. We assume that there is a pool of letter nodes for each letter. Each instance of a letter activates a different subset of that pool.
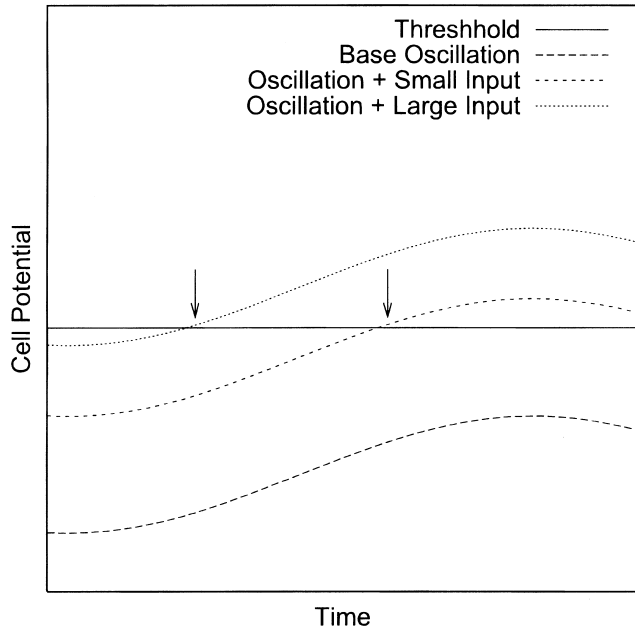
Fig. 1. When a relatively large input is added (top curving line) to the sub-threshold oscillation, the cell potential crosses threshold at the first arrow (action potential not illustrated). If instead, a smaller input is added (middle curving line), the cell potential crosses threshold later in the cycle, at the second arrow.
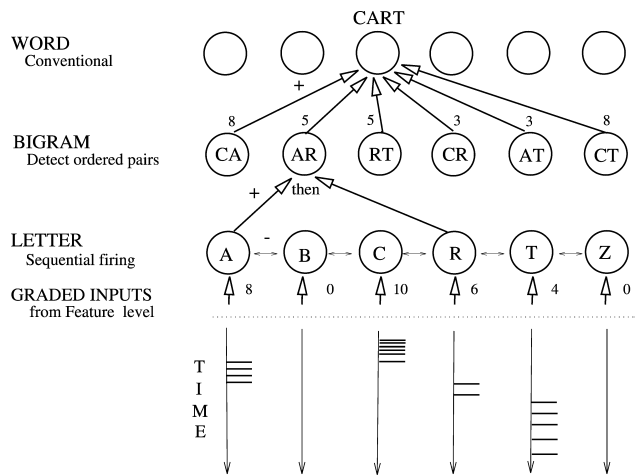

Fig. 2. Architecture of the letter, bigram, and word levels of the proposed theoretical framework, with example of encoding the word CART. At the letter level, simultaneous graded inputs (input values shown next to arrows) create a temporal firing pattern, as indicated by the firing diagram displayed under the letter nodes. Excitatory connections link the letter nodes with the bigram nodes, which recognize ordered pairs of letters. Excitatory connections link the bigram nodes and the word nodes. As discussed below, the amount of feature-level input also determines letter activations. Letter node activations correspond to the total number of spikes (indicated in firing diagram). The activations of the bigrams (shown above the nodes) are determined by the activations of the constituent letters and the amount of time between their activity. Activation of word nodes is determined in the conventional way (dot-product of inputs and connection weights).
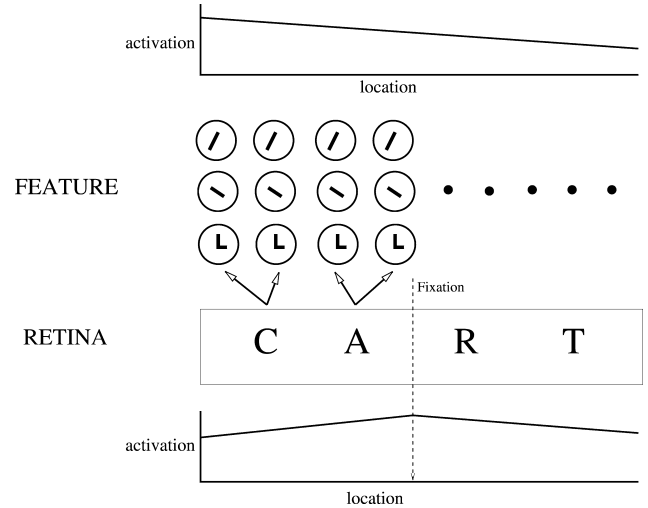

Fig. 3. Architecture of the retinal and feature levels of the proposed theoretical framework. The retinal level is precisely topographically organized with respect to external stimulus, in this case CART. The activation of retinal nodes decreases as distance from fixation increases. Feature nodes are tuned to retinal location. The activation of feature nodes decreases from left to right across locations.

the opposite direction of the locational gradient. In contrast, the acuity gradient is *decreasing* in the RVF/LH, like the locational gradient. Therefore, in the LVF/RH, the slope of the acuity gradient must be reversed or *inverted* as it activates letter features, while in the RVF/LH it is maintained. Thus processing at the feature level is very different across hemispheres, with the RH performing more extensive processing than the LH.

Locational gradient formation is illustrated in Fig. 4. 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 right panel of Fig. 4.) This allows the first letter's features to reach a high level of activation even if they are far from fixation. 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 having preferred locations to its right. Thus, inhibitory input increases as letter position increases, because more and more features send inhibition from the left. This directional inhibition must be sufficiently strong to override the slope of the acuity gradient, inverting it. So the features comprising the first letter attain a high level of activation (due to strong excitation and lack of lateral inhibition from the left), and activation decreases towards fixation (due to sharply increasing lateral inhibition from the left). (See the lower left panel of Fig. 4.)

In the LH, we assume that both bottom-up excitatory and lateral inhibitory inputs are weaker, because the acuity gradient's slope is already in the correct direction. Thus the acuity gradient is essentially maintained at the feature level in the LH, although some weak directional inhibition steepens its slope.
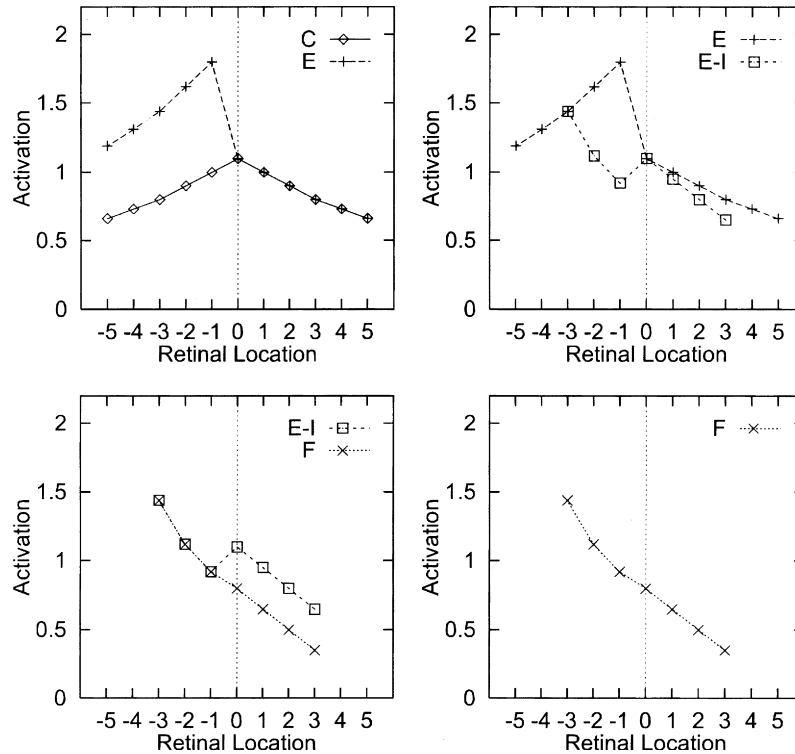
Fig. 4. Example formation of the locational gradient across the activations of features. Features are represented by their preferred location. Fixation is at retinal location 0, with LVF locations <0 and RVF locations >0. In the first graph, the acuity gradient, C, is displayed, with the effects of hemisphere-specific excitation, E. Note that in the RVF/LH, E is equivalent to C, while in the LVF/RH E is elevated with respect to C. In the second graph, E is redisplayed for reference, and the effects of hemisphere-specific lateral inhibition, E–I are displayed for a seven-letter string starting in retinal location −3. 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 acuity gradient in the LVF/RH. In the third graph, E–I is redisplayed, and the hemisphere-specific gradients are joined via interhemispheric inhibition of the LH's features to form a monotonically decreasing activation gradient across feature locations, denoted F. In the next graph, F is redisplayed in isolation for clarity.

In addition to inhibition with hemispheres, there is also inhibition across hemispheres. The RH feature nodes inhibit the LH feature nodes, bringing the activations the LH's leftmost letter's features lower than those of the RH's rightmost letter. As a result, a locational activation gradient which is strictly decreasing from left to right is formed. (See the lower right panel of Fig. 4.)

In summary, there are three important components to the formation of the locational gradient: (1) stronger excitation to the RH (to raise initial letter's activation level); (2) strong rightward lateral inhibition within the RH (to invert the acuity gradient); (3) inhibition from the RH to the LH (to integrate the two halves of the locational gradient). We discuss below how these mechanisms explain observed patterns of letter perceptability.

So, in an overall summary of the SERIOL model, the acuity gradient is modified by hemisphere-specific processing to become a locational gradient. The locational gradient interacts with letter nodes which oscillate in excitability, inducing them to fire sequentially. This serial encoding activates words node via bigram units, which encode ordered letter pairs. We have discussed in more detail elsewhere (Whitney, 2001a) why these transformations are necessary to encode letter order in a way that is robust and consistent with experimental data.

The letter and bigram levels of the model comprise the unified, prelexical representation of the string; we propose that they are realized in the LH in the VWFA. Since the mechanisms for the formation of the locational gradient are hemisphere-specific, they would occur prior to integration within the VWFA. We remain agnostic as the specific form of information transferred from the RH to the LH. RH features might activate analogous LH features, which then activate LH letter nodes, or RH features might directly activate LH letter nodes. We do not rule out the possibility that the locational gradient occurs across location-specific letter nodes (rather than feature nodes), which then activate more abstract LH letter nodes. The central claim is that an activation gradient across some level of locationally-tuned units is converted to the sequential firing of abstract letter units in the LH. For convenience, we have assumed that the locational gradient occurs at the feature level, and that RH feature nodes directly activate LH letter nodes.

3. Activation patterns in the SERIOL model

The varying levels of activation from the locational gradient continue to have an effect through the higher levels of processing. At the letter level, not only do letter nodes receiving high levels of input fire earlier, they fire faster. Since a letter node fires until it is inhibited by the next letter node, its activation level depends both on its own input level (which determines its firing rate), and the level of input to the next letter (which determines firing duration). In general, the higher the input level, the higher the letter activation, with the activation of letters receiving low levels of input being particularly sensitive to duration of firing. Since the final letter is not inhibited by a subsequent letter, it can continue to fire until the end of the oscillatory cycle. Thus even though it fires more slowly than the internal letters, it can reach a higher level of activation because it fires longer. (See Fig. 2.) So at the letter level, activation is decreasing across the string, except for the final letter which attains an activation near that of the first letter. This accounts for observed positional patterns of letter perceptability across strings, where perceptability generally decreases as letter position increases, but rises for the final letter [3] (Hammond & Green, 1982; Lefton, Fisher, & Kuhn, 1978; Mason, 1982; Wolford & Hollingsworth, 1974).

However, the activation of the final letter is highly dependent on when it starts to fire with respect to the oscillatory cycle. For very low levels of input across all the letters, such as with very short presentation durations, the firing of all letter nodes will be shifted towards the end of the oscillatory cycle. As a result, the final letter will have less time to fire, and may have the lowest activation of all the letters. This accounts for the fact that the final letter is sometimes the least well perceived of all the letters; all experiments in which this occurred used extremely brief presentation durations (40 ms or less) (Hellige, Cowin, & Eng, 1995; analysis of error data in Humphreys et al., 1990; five- and six-letter words in Montant, Nazir, & Poncet, 1998). Indeed, increasing exposure duration from 40 to 80 ms within a single experiment preferentially increased the perceptability of the final letter as compared to other positions (Eviatar, 1999).

The letter activations then determine bigram activations. A bigram node's activation is roughly proportional to the product of its constituent letter activations, coupled with sensitivity to the firing delay between those letter nodes when neither letter node is highly activated. As a result, the bigrams encoding the first/second and first/last letters of a string are the most highly activated,

and the those encoding the second/third and second/last letters are the next most highly activated. Weights on bigram-to-word connections record the bigram activation pattern resulting from each word.

Such weights allow the system to differentiate between two words when one is contained within the other. For example, consider HOSE and HORSE. If the bigrams were not weighted, the input *hose* would activate the word node HORSE as highly as the node HOSE, since HORSE contains all the bigrams in HOSE. However, considering activation patterns, the weight on the HE-to-HOSE connection is larger than the weight on HE-to-HORSE, because the E for *hose* becomes more highly activated than the E for *horse*. Also, the weight on OS-to-HOSE is larger than the weight on OS-to-HORSE, since a bigram responding to the second and third letters is more highly activated than one responding to the non-contiguous second and fourth letters. These differences in connection weights allow *hose* to activate HOSE more than HORSE. A simulation showed that weighted bigrams allow correct recognition of all single syllable English words, and a "lesion" this system accurately reproduced the error patterns of subjects with acquired dyslexia (Whitney & Berndt, 1999).

Because the processing required for formation of the locational gradient varies with hemisphere, we would expect some differences in the resulting hemispheric gradients. Next we look at a variety of experimental results which we claim reflect such differences.

We have proposed that feature-level activations are boosted in the RH (as compared to the LH) in order to raise the initial letter's input to a high level. This predicts that, for identical distances from fixation, an initial letter should be perceived better in the LVF than in the RVF. Indeed, such a systematic LVF advantage has been observed for initial letters at large eccentricities (Bouma, 1973; Estes, Allemeyer, & Reder, 1976; Legge, Mansfield, & Chung, 2001).

Next we consider activation patterns across string positions. In one study, subjects were to report the letters comprising a nine-letter string (Wolford & Hollingsworth, 1974). In order to de-confound the effects of retinal location and string position, the location of the string's initial letter was systematically varied from −12 to 5 letter widths from fixation. These experimental data are shown in the upper panels of Fig. 5, displayed to focus on the effect of increasing the number of letters to the left of a given retinal location. These perceptability curves vary with VF. To summarize, in the RVF, increasing string position leads to steadily decreasing perceptability at the target location. In contrast, in the LVF, increasing string position initially leads to a sharp decrease in perceptability (in going from position 1 to 2 and from 2 to 3), but then there is less and less effect as more and more letters are added to the left. This non-linearity increases as distance from fixation increases.

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[3] There is usually an increase in perceptability at the fixated letter. In our model, this could arise from a lack of smoothness in the locational gradient at the fixated letter where the two halves of the locational gradient are joined.
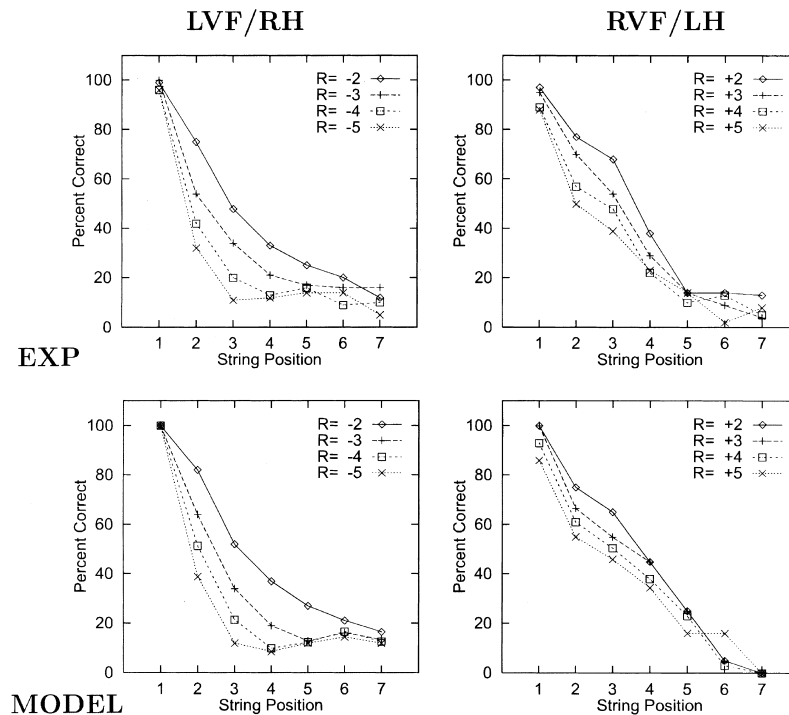
Fig. 5. Experimental and modeled results for interaction of string position and retinal location from Wolford and Hollingsworth (1974). Graphs display percent correct at each string position for various retinal locations, R. The upper graphs display experimental data, and the lower graphs display the model's results.

The general decrease in perceptability with increasing position is consistent with our proposal for directional inhibition in the feature layer. We suggest that the variations across visual fields stem from differences in inhibition levels and in acuity patterns. At early string positions, the stronger directional inhibition in the RH is apparent; this inhibition over-compensates for the acuity gradient, so perceptability falls off more rapidly at positions 2 and 3 in the LVF than in the RVF. [4] In the LVF, each letter added to the left *decreases* in acuity. Therefore, each new letter is less and less able to exert inhibition on the target letter. This accounts for the flattening of the perceptability curves with increasing string position. In contrast, in the RVF, each additional letter *increases* in acuity (as long as it still falls in the RVF), resulting in a sustained decrease in perceptability at the target letter. These assumptions on directional inhibition allow a computational re-creation of the observed patterns, as displayed in the lower panels of Fig. 5.

Nazir and colleagues (Nazir, Ben-Boutayab, Decoppet, Deutsch, & Frost, this volume2003) also argue that reading induces specialized low-level visual processing. In support of this claim, they demonstrated interactions

between reading direction and VF effects under letter identification tasks. For fixation on the first versus last letter of a five-letter string, there was a RVF/LH advantage in English, while there was no interaction with VF in Hebrew. However, for fixation on the central letter of a nine-letter string, a different pattern emerged; there was a LVF/RH advantage for English, and a RVF/LH advantage for Hebrew.

These results are what would be expected under our proposals. For lateralized presentation, there is an RVF/LH advantage in English because LVF/RH presentation entails degradation both from callosal transfer and from the high inhibition levels necessary for acuity-gradient inversion, while RVF/LH presentation entails neither transfer nor inversion. For Hebrew, inversion should occur in the LH (rather than the RH), since the initial letters fall into the RVF. Thus, inversion and transfer occur in opposite hemispheres, balancing each other and yielding no effect of visual field. For central presentation, there is a LVF/RH advantage in English because the RH letters inhibit the LH letters (to join the two halves of the locational gradient). This inhibition occurs in the opposite direction in Hebrew, yielding a RVF/LH advantage.

Error patterns have also been taken as evidence for hemisphere-specific modes of processing (Hellige et al., 1995; Hellige & Scott, 1997; Marks & Hellige, 1999). In these experiments, subjects were to identify extremely briefly displayed CVC trigrams presented in a vertical

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[4] Since acuity falls off more and more slowly as eccentricity increases, this over-compensation is to be expected at large eccentricities, assuming that the strength of directional inhibition is fairly constant within a hemisphere.

column, with each letter upright. For LVF/RH presentation, subjects made many more errors involving the last letter than the first letter of the string. For RVF/LH presentation, this finding was attenuated: there were relatively more errors on the first letter and fewer errors on the last letter, resulting in a more even distribution of errors across the string. There was also a strong effect of visual field on accuracy, with more total errors in the LVF/RH than in the RVF/LH. These patterns were taken to be evidence of parallel processing of strings by specialized linguistic modules in the LH, and less efficient, serial processing in the RH.

However, a counterintuitive result arose when input was directed to both hemispheres simultaneously. For bilateral presentation, the error pattern was more similar to LVF/RH pattern than to the RVF/LH pattern (Marks & Hellige, 1999). Thus, even though the LH was more effective than the RH at performing the task, the RH seemed to dominate when stimuli were presented to both hemispheres simultaneously. It is difficult to understand why the less efficient hemisphere should dominate under the "modes of processing" model.

Based on locational gradient formation, we offer an explanation of these results that accounts for both the unilateral and bilateral patterns. Despite the unorthodox vertical format, we assume that encoding processes similar to those used for horizontal presentation are invoked. Hellige and colleagues, in their analyses, also assume that the data from these experiments are relevant to normal string processing. More specifically, we assume that the letters are mentally projected to the canonical horizontal position, and then the rotated image is processed as usual. However, since all letters were presented roughly at the same distance from fixation, there is no acuity gradient. Therefore, effects of directional inhibition are isolated.

The proposed within-hemisphere directional inhibition accounts for the differing unilateral error patterns. In the RH, starting with a flat acuity gradient should yield a very steep locational gradient, due to strong rightward inhibition. In the LH, starting with a flat acuity gradient should yield a very shallow locational gradient, due to the weak rightward inhibition. Thus the final letter will receive much less bottom-up input in the RH than in the LH. This accounts for the greater percentage of final-letter errors in the LVF/RH.

The proposed across-hemisphere inhibition accounts for the similarity of the bilateral error pattern to the LVF/RH pattern. Recall that the RH features inhibit the LH features to form a monotonically decreasing locational gradient. We propose that under bilateral stimulation, the LVF/RH features inhibit the RVF/LH features as usual. Thus the input from the LVF/RH dominates due to the way in which hemispheric representations of letter strings are normally integrated.

This analysis implies that hemispheric error patterns should vary with reading direction. For languages read from right to left, the patterns should be reversed, since acuity-gradient inversion should then occur in the RVF/LH. This is precisely the finding reported in a study of Hebrew readers performing the trigram identification task; for those readers, the percentage of final-letter errors was greater in the RVF/LH than in the LVF/RH, and the bilateral pattern was the same as the RVF/LH (Eviatar, 1999). For languages that are read from top to bottom, there should be no hemispheric asymmetry, since acuity gradient inversion should occur along the vertical axis, not the horizontal axis. Indeed, a study of Japanese kana, for which the vertical orientation is normal, showed no differences between the LVF/RH, RVF/LH, and bilateral patterns (Hellige & Yamauchi, 1999). These findings are inconsistent with a "modes of processing" account, but are predicted by the locational gradient account.

Thus we conclude that these error patterns are not attributable to serial versus parallel processing. Rather, hemispheric differences stem from the direction of slope of the acuity gradient relative to that of the required locational gradient. Similarly, we propose that the visual field interactions for N and form priming are not the result of different hemisphere-specific types of representations. Rather, the interactions stem from different patterns of activation over the same type of representation, as we discuss next.

4. The SERIOL model and the hemispheric influence of orthography

We assume that the RVF absence of N and form priming effects both stem from the same underlying cause. This assumption is justified on the basis of simplicity; there is no evidence to motivate a more complicated explanation in which each arises for independent reasons.

We start by discussing possible sources of the facilitation observed for high N, first considering direct interactions between word nodes. Most models of word recognition assume lateral inhibition between word representations, allowing the most highly activated word to silence its competitors. We assume that inhibitory connections between very similar words are stronger than between less similar words. This assumption is consistent with experimental results on TL pairs, words which differ from one another by the transposition of two letters, such as *salt* and *slat*. Priming a TL word with its TL partner is inhibitory, as compared to priming with an unrelated word (Andrews, 1996). Under the SERIOL model, a TL word is very similar to its TL partner, since most bigrams are shared between the two words. Thus these experimental results indicate that a

word that is very similar to the target provides more inhibition than an less similar word.

Therefore, it is somewhat surprising that high N results in facilitation rather than inhibition. In fact, the data is conflicting; some studies do show inhibitory effects (Carreiras, Perea, & Grainger, 1997; Grainger, 1990; Grainger, O'Regan, Jacobs, & Segui, 1989, 1992; Huntsman & Lima, 1996; Perea & Pollatsek, 1998). Andrews (1997) noted that most of these experiments were in French or Spanish; the effect of N seems to be language dependent. We assume that high N produces both facilitatory and inhibitory effects via different mechanisms and that the relative importance of these opposing effects can be influenced by some property of language.

Several explanations for the source of the facilitatory effect have been proposed. One is based on feedback excitation by spreading activation, such as in the Interactive Activation model (McClelland & Rumelhart, 1981). When the target word partially activates many non-target word nodes, these nodes send excitation back to the letter level. The increased activation of the letter nodes then causes the target word node to become activated more quickly.

The multiple read-out model assumes that a task which does not require unique identification of a single word, such as lexical decision, can benefit from increased activation at the word level (Grainger & Jacobs, 1996). Under this proposal, an affirmative response in lexical decision is speeded when the total activation across the words is higher.

A third explanation is based on phonological influences from word bodies (Ziegler & Perry, 1998). In English, many high N words share the same body (rime) with other words. The rime is a good predictor of the phonological realization of the vowel, which is highly variable in English. Therefore, words with many body neighbors will tend to share the same pronunciation of the vowel, and this shared phonology may speed lexical access.

Next we evaluate these proposals with respect to the assumption that the facilitatory effect of N is modulated by language. In the multiple read-out model, it is difficult to see how language would modulate the way in which total word level activations influence an affirmative response in lexical decision. In the rime model, the relative importance of the rime would have to vary with language. While this is quite plausible, the assumption that phonology underlies the N effect is not consistent with experimental evidence on phonological priming. Chiarello (1985) demonstrated that such priming is obtained in the RVF/LH and not the LVF/RH. If the N effect were mainly phonological, then it should occur for the LH and not the RH. However, as discussed above, the opposite result occurs. Under the feedback account, the strength of excitatory word-to-letter connections

would have to be higher in English than in other languages. This is certainly plausible, since the mapping from phonology to orthography is less regular in English than in French or Spanish. Thus, in a language where spelling is less well determined by a word's phonology, stronger top-down connections could exist to encode spelling. Therefore, we conclude that most likely source of facilitation is via top-down feedback to the letter level.

Our proposal for positional activation patterns, coupled with the above assumption on word-level lateral inhibition, imply that the position of difference between a target and its neighbors should matter. Facilitation should be maximal if most neighbors differ in the first position, because a mismatch in the first position minimizes lateral inhibition within the word level. Recall that the first/last and first/final bigrams have the highest weights. If a neighbor mismatches on the first letter, it is not very similar to the target and will not provide strong lateral inhibition. Therefore top-down excitation to the letter level will dominate. In contrast, a neighbor that mismatches on the third letter is very similar to the target, because it shares the most highly weighted bigrams. Therefore, the net effect of such a neighbor should be inhibitory.

There is experimental evidence consistent with this analysis. The rime model makes similar predictions, since it assumes that the effect of high N comes from neighbors matching the target's body, called *body neighbors*. A body neighbor does not have to be the same length as the target. To test this model, Ziegler and Perry (1998) held N constant, while manipulating BN (number of body neighbors); they also held N constant, while manipulating BN. For the BN manipulation, they predicted that high BN words should be facilitated with respect to low BN words. Our account gives the same prediction, because there will more word nodes sending top-down excitation, without much increase in inhibition within the word level, since most body neighbors do not match on the crucial first letter. Fpr the N manipulation, they predicted no facilitation for high N, since facilitation via BN is held constant. We predict inhibition for high N, since there should be more highly activated non-target word nodes (those matching the target on the first, second, and last letters), which should provide strong inhibition. As predicted, high BN was facilitatory. In the N manipulation, high N was inhibitory, but this result was not statistically reliable. Thus both models are consistent with these results.

They also performed the same manipulation with nonword targets, predicting that high BN should be inhibitory (based on increased phonological similarity to real words), as should high N (based on increased orthographic similarity to real words). High N was indeed slower than low N. However, for the BN manipulation, there was no effect at all (identical RTs for both

conditions). This result is more consistent with our model, under the assumption that only highly activated word nodes influence response latency to a nonword. A word node that is a body neighbor is usually not highly activated, as indicated above. Thus manipulating BN should not increase the number of highly active word nodes, so it should not affect nonword reaction times.

Our assumption that the locus of N effects, and accordingly form priming effects, is at the letter level is also consistent with experimental evidence (Dehaene, Le Clec', Poline, Le Bihan, & Cohen, 2002) showing that the occurrence of form priming is associated with a change of activity level in the VWFA, which has been associated with the abstract representation of letter order, as discussed above. In the following, we will refer to additional excitatory input to the letter level generated by either by high N or a prime as *priming input*. Under these assumptions, something about RVF/LH presentation prevents priming input from affecting letter activations in a way that decreases reaction time.

We propose that this occurs as a result of hemisphere-specific activation patterns, coupled with the dynamics that convert the locational gradient into serial activation at the letter level. First we discuss those dynamics in more detail. The time at which a non-initial letter node can start to fire is limited both by lateral inhibition coming from the prior letter, and by its own level of excitatory input. We assume that lateral inhibition prohibits firing for a fixed amount of time. When this inhibition wears off, a letter node can fire if it receives enough excitatory input to cross threshold. If not, its firing is delayed until the increase in excitability (resulting from the oscillatory cycle) brings it across threshold.

As discussed above, the dropoff in perceptability in going from position 1 to position 2 is larger in the LVF/RH than in the RVF/LH (see Fig. 5), as is consistent with stronger rightward inhibition at the feature level in the RH. We propose that this difference underlies the hemisphere-specific effects of N and form priming, as follows. For RVF/LH presentation, the relatively high level of input to the second letter allows it to start firing at the first possible opportunity (when inhibition from the first letter wears off). Therefore, a slight increase in excitatory input (from priming input) has no effect. In contrast, for RVF/LH presentation, the second letter does not fire at the first opportunity, because the amount of bottom-up excitatory input is lower (due to strong rightward inhibition within the feature level). Therefore, priming input allows the second letter to cross threshold and fire sooner. The effect is to decrease the first letter's activation level (since it stops firing sooner), and increase the second letter's activation level. We assume that such a decrease at the first letter has little effect, because its activation level is already very high. The increased activation of the second letter is

carried forward to the bigram and word levels, allowing the target word node to reach response threshold sooner. Thus, priming input has a facilitatory effect for LVF/RH presentation. This same effect occurs for central presentation, since the first and second letters fall in the LVF/RH. In contrast, for RVF/LH presentation, priming input has no effect since bottom-up input is already high enough that lateral inhibition is the limiting factor at the second letter.

Note that we do not claim that the second position is the most important in absolute terms. That honor goes to the first and last positions. Rather we claim that the second position is preferentially affected by lateral inhibitory patterns evoked by different presentation locations. This predicts that manipulation of bottom-up input to the second letter (relative to the other letters) should modulate the influence of N. Indeed, we have experimentally demonstrated that the N effect can be created in the RVF/LH or obliterated in LVF/RH via positional manipulations of letter contrast (Whitney & Lavidor, 2003).

Thus, in order to explain the differential effects of orthography across visual fields, it is not necessary to assume that LVF and RVF presentations generate *qualitatively* different types of representations, as in a hemisphere-specific model. Rather, *quantitative* variations in activation levels are the source of the hemispheric specificity of the N effect (Whitney & Lavidor, 2003).

We conclude this section by comparing the SERIOL model to the hemisphere-specific model (Monaghan et al., this volume). While that model gives some interesting results, we suggest that they are based on questionable assumptions. In that model, a split input layer (representing each visual field) feeds to a split hidden layer (representing each hemisphere), which feeds to an output layer. Each half of the input layer has four slots. The model is trained on every four-letter word in English. The representations which the hidden layer develops are tied to the location of the stimulus on the input layer; there is no generalization across input locations. As a result, there is no abstract representation of the letter order; each word has to be presented at every possible input location during training. [5] This lack of a location-invariant sublexical representation is inefficient and is contrary to most models of word recognition. Note that even position-specific representations of letter order (such as the Interactive Activation model) are location-invariant; it is assumed that the retinal

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[5] This holds when the output is not predictable from the input, as in mapping from orthography to semantics. When the output is predictable, as in mapping from orthography to orthography, generalization does occur (in terms of responding to an untrained input), but there still is no location-invariant representation of letter order in the hidden layer.

location of the input is abstracted away to give a word-centered representation of letter position. The prevailing assumption of a location-invariant representation is supported by data on the VWFA, which is unaffected by the visual field and retinal location of the input (Cohen et al., 2000).

However, the claims of the hemisphere-specific model depend directly on this undesirable lack of a location-invariant representation. The hemisphere-specific representations develop from the interaction of differing letter position frequencies with input locations. The use of symmetric "visual fields" creates a differential distribution of letter position with visual field (e.g., the first letter falls in the LVF 80% of time—on four out of the five possible presentation locations). The initial letters fall more often into the LVF, so the RH hidden layer develops representations based primarily on their distributional frequencies. Similarly, the end letters fall more often into the RVF, so the LH hidden layer develops representations tuned to their frequencies. These differing representations are the source of the model's results.

Moreover, these locational assumptions are inconsistent with actual fixation patterns when reading text. It has been demonstrated that the perceptual span (availability of letters required for normal reading speed) is highly asymmetric, with a width of four letters in the LVF, and 14 letters in the RVF (Rayner, 1975). When an unfixated word in the RVF can be identified, it is skipped (never fixated); this happens for about 50% of four-letter words (Rayner & McConkie, 1976). When a four-letter word is fixated, fixation falls on the first letter about 20% of the time (McConkie, Kerr, Reddix, & Zola, 1988). So the first letter of a four-letter word actually appears in the LVF only 40% of the time (i.e., 0.5 (likelihood of word being fixated) × 0.8 (likelihood of fixation occurring after the first letter)). Thus, the initial letter of a four-letter word is not more likely to fall into the LVF, contrary to the frequency assumptions which drive the model's results.

In contrast, the SERIOL model assumes an abstract representation of letter order, and describes how this representation is derived from the input. The hemisphere-specific results in the model do not depend on frequency assumptions, but rather arise directly from the processing required to induce the serial encoding of letter order. The proposed transformations account for complex patterns of letter perceptability arising from the interaction of letter position, retinal location, reading direction, and presentation duration as described above and elsewhere (Whitney, 2001a, 2001b, 2002; Whitney & Berndt, 1999); the hemisphere-specific model cannot explain these results. Therefore, we suggest the SERIOL model provides a more realistic account of how the two halves of a string are reunited.

5. Length effects

As discussed in Section 1, VF also modulates the influence of string length: there is a length effect in the LVF/RH, but not in the RVF/LH. First we discuss how length could fail to effect lexical-decision reaction times, despite a serial encoding of letter order. We assume that for a "yes" to be generated in lexical decision, a word node must accrue sufficient activation to exceed a response threshold. We suggest that, for a short word, the final letter must fire for an extended period before the target word node reaches threshold. In contrast, for a longer word, response threshold is reached sooner after the final letter starts to fire, because the target has received more input from the previous letters (since there were more of them). Thus, the limiting factor is the total input to the target word node, rather than the time at which the final letter begins to fire. We propose that this is the scenario in the RVF/LH; the delayed firing of the final letter for longer words is balanced out by the increased total input.

We had previously proposed that the length effect in the RH resulted from increased settling times during acuity gradient inversion (Whitney, 2001a). This analysis was based on the occurrence of the length effect in the LVF/RH, but not the RVF/LH, for RH-dominant readers (Brysbaert, 1994), suggesting that inversion, not inter-hemispheric transfer, is the source of the length effect. This analysis implies that the length effect should reverse for right-to-left readers; there should be a length effect in the RVF/LH, and not the LVF/RH. However, recent experiments show that this is not the case; for lexical decision in Hebrew, a length effect did occur in the LVF/RH (Lavidor et al., 2001, 2002). These studies gave conflicting results for the RVF/LH: a length effect emerged in one (Lavidor et al., 2001), but not the other (Lavidor et al., 2002).

Therefore, we revise our analysis to encompass these data. We propose that the serial encoding of letter position manifests itself when the locational gradient becomes non-optimal. We assume that bigram-to-word weights are proportional to bigram activations triggered by a a steadily decreasing locational gradient (resulting from a fixated word). When the locational gradient is not steadily decreasing, bigram activations will form a pattern that is different from this learned weight vector. As a result, other words that are similar to the target may become more highly activated than usual, yielding increased lateral inhibition to the target. The final letter then becomes more important in raising the target word node above threshold; reaction time becomes limited by the final letter reaching a certain activation level, revealing the serial nature of the encoding.

For example, consider the words *hear* and *heart*. The weight on the HR-to-HEAR connection is very high, since those are the first and last letters; in contrast, the

weight on HR-to-HEART is quite low. Now consider the input H E A R T, when R's activation abnormally high. There will be a larger increase in the activation of HEAR than of HEART in response to R, due to the magnitude of the HR weight. Therefore, HEAR will send more inhibition to HEART than usual, so the T will have to fire longer than usual before HEART is brought above response threshold. Thus when activation is less narrowly focused on the target word, more information is required from the final letter.

As discussed previously, acuity-gradient inversion creates a non-linear gradient at large eccentricities. We propose that callosal transfer also creates non-linearity in the locational gradient by causing increasing degradation with decreasing activation. Thus callosal transfer preferentially degrades the final letters. As a result, the firing of the final letter is delayed more and more as string length increases, directly causing an increase in reaction times. So callosal transfer causes a length effect by altering both the overall shape, and the steepness of the locational gradient. The change in shape causes increased lateral inhibition at the word level, while the increase in steepness causes the final letters to take longer to fire.

Next we look at the role of these processes on reaction times for readers with differing characteristics, starting with LVF/RH presentation. For LH-dominant readers, both inversion and transfer apply, so there is a large length effect. For RH-dominant readers, only inversion is required, so there is a smaller length effect than for LH-dominant readers, as observed in Brysbaert (1994). For Hebrew readers (Lavidor et al., 2001, 2002), transfer alone creates a length effect.

Next we consider RVF/LH presentation. For LH-dominant readers, neither transfer nor inversion is required, so the locational gradient remains smoothly decreasing and there is no length effect. For RH-dominant readers (Brysbaert, 1994), why was not there a length effect (due to callosal transfer from the LH to the RH)? The RH-dominant group was comprised of subjects with lower-than-normal LH dominance, possibly including subjects with bilateral language abilities. Perhaps language could also be processed in the LH, so callosal transfer was not required. For Hebrew readers, a length effect should emerge in the RVF/LH due to inversion. We suggest that conflicting evidence on this point is due to differing word lengths. The study which did show a length effect (Lavidor et al., 2001) used six-letter words, while the study that did not (Lavidor et al., 2002) used a maximum of five letters. Perhaps the locational gradient did not become sufficiently non-linear to elicit a length effect at this shorter word length.

Furthermore, a comparison of French versus Hebrew using the naming task (Nazir, Kajii, Frost, & Osaka, 2003) yielded the expected pattern. In French, there was a much larger length effect in the LVF than in the RVF; in Hebrew, length effects were equivalent across VFs.

These results are consistent with an earlier study in Hebrew. which showed strong length effects on accuracy (in lexical decision) and reaction times (in naming), independent of VF (Koriat, 1985). Thus, the majority of studies (three out of four) which investigated lateralized length effects in Hebrew showed no interaction with visual field. These findings are consistent with our proposal that, in a right-to-left language, callosal transfer (from the RH) and acuity-gradient inversion (in the LH) independently create length effects, via production of non-optimal locational gradients. In contrast, in left-to-right languages, transfer and inversion both originate in the RH, giving a strong length effect in the LVF, but none in the RVF.

A non-hemisphere-specific way of manipulating the locational gradient is via presentation format. For example, when letters are not horizontally aligned, the locational gradient should be flatter than usual, since directional inhibition should be impaired. Indeed, a format in which letters randomly appeared slightly above or below the horizontal yielded a length effect in the RVF/LH (Ellis et al., 1988; Young & Ellis, 1985). MiXeD CaSe also yields a length effect in the RVF/LH (Lavidor et al., 2002). This format should result in a gradient that is less smooth than usual, since the features of the lower-case letters will be less highly activated than those of the upper-case letters.

Thus we are able to provide a more parsimonious explanation of length effects than the modes of processing model, which posits two different routes of word recognition (Ellis et al., 1988). We suggest that there is a single means of lexical access via a serial encoding of letter position. When the locational gradient is optimal, this serial encoding is not evident; otherwise it is.

The modes of processing model has also been invoked to explain reaction time patterns for rotated letter strings (Lavidor et al., 2001). In that study, Hebrew readers performed lateralized lexical decision on rotated strings under two different formats. In one format, the string was rotated as a whole, resulting in tilted letters. In the other, the letters remained upright as they were translated above the horizontal. Rotation angle was varied from 0° to 90°, in increments of 15°, and string length was either three or six letters.

An idealization of the data, displaying the significant effects, is given in Fig. 6; the data are collapsed over string lengths. For angles ⩽ 45°, there was no interaction with format; there was a RVF/LH advantage for angles ⩽ 30°, while reaction times were equivalent across VFs for 45°. For the larger angles, there was an interaction with format. In the tilted condition, reaction times remained equivalent across VFs. In the upright condition, a sharp increase in reaction times occurred for both VFs, but at differing angles. This increase occurred at smaller angle in the RVF/LH (60°) than in the LVF/RH (90°). Thus, for 60° and 75°, reaction times
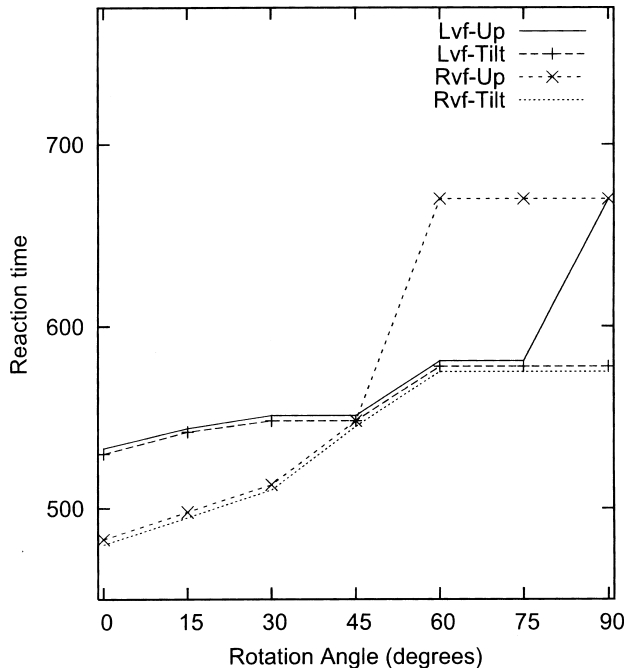
Fig. 6. Idealization of the data from Experiment 1 of Lavidor et al. (2001) using a piecewise linear fit to show significant effects, which are summarized in the text.

were actually faster for presentation to the non-dominant hemisphere. In general, reaction times were longer for six-letter than three-letter words. The only interaction of string length with other variables was that this LVF/RH advantage was significant for six-letter, but not three-letter, words.

Lavidor and colleagues propose that this overall pattern reflects different modes of processing: for angles ≤ 30° in the RVF/LH, the efficient, parallel mode applies, while the inefficient mode is required in all other conditions. However, this does not explain the LVF/RH advantage. If both hemispheres used the same inefficient mode of processing, neither hemisphere (or perhaps the dominant hemisphere) should have an advantage.

In contrast, this LVF/RH advantage for large angles in the upright format falls naturally out of our proposal for locational gradient formation. As rotation angle increases, directional inhibition becomes less effective because there is less horizontal overlap between the letters. At large enough angles, normal locational gradient formation will fail, causing a shift to less automatic processing, and increased reaction times. However, the angle at which this shift occurs should differ across hemispheres. For Hebrew, the slope of the acuity gradient in the LVF/RH is in the same direction as the locational gradient, so the acuity gradient suffices until there is no gradient. This explains the large jump in reaction times at 90°. In the RVF/LH, the acuity gradient is in the wrong direction. Thus locational gradient formation fails at a smaller angle (i.e., 60°). Inversion is more likely to fail when more letters are involved, due to increased weakness of the first letter compared to the last letter. Therefore, the LVF/RH advantage is more pronounced for longer words.

For the tilted format, we propose that the letter string as a whole is mentally rotated to the horizontal; then normal locational gradient formation is invoked. Therefore, there is no angle at which inversion fails, but rather there is gradually increasing degradation due to mental rotation. We suggest that for angles >30°, this degradation becomes the dominating factor, yielding similar reaction times across hemifields.

Thus we agree that there are two modes of processing reflected in this data. However, we propose that a shift from one mode to another occurs a different points and for different reasons than Lavidor and colleagues. They propose that a shift occurs at 45° in the RVF/LH conditions because the string is no longer perceived as being in a standard format. In contrast, we propose that shifts occur at 60° (RVF/LH) and 90° (LVF/RH) in the upright conditions because acuity-gradient inversion fails. We note that the patterns in the data are more consistent with our account. The increase in reaction times for the upright conditions is quite large, indicating an abrupt shift; the increase for the RVF/LH conditions is smaller and fits into a trend of increasing reaction times with rotation angle.

6. Conclusion

Brain imaging (ERP and fMRI) indicates that hemifield presentation of a letter string activates V4 in the contralateral hemisphere at about 160 ms post-stimulus. After this point, processing is identical for both hemifields: the VWFA in the LH lights up at 200 ms, followed by activation of a bilateral frontoparietotemporal network (Cohen et al., 2000). In contrast, behavioral experiments show hemifield-dependent results with respect to lexical-level factors (i.e., length, N, form priming), as we have discussed. These results may seem contradictory at first. The last point of hemisphere-specific processing is a visual area; it is unclear how differences at the visual level could influence factors at the lexical level. Resolving this contradiction, we have discussed how hemispheric differences in visual processing (i.e., locational gradient formation) could account for the results of these behavioral experiments. Predictions based on this account of the N effect have been experimentally confirmed (Whitney & Lavidor, 2003).

References

Andrews, S. (1996). Lexical retrieval and selection processes: Effects of transposed-letter confusability. *Journal of Memory and Language, 35*, 775–800.

Andrews, S. (1997). The effect of orthographic similarity on lexical retrieval: Resolving neighborhood conflicts. *Psychonomic Bulletin & Review, 4*, 439–461.

Binder, J., & Mohr, J. (1992). The topography of callosal reading pathways. A case-controlled analysis. *Brain, 115*, 1807–1826.

Bjork, E. L., & Murray, J. T. (1977). On the nature of input channels in visual processing. *Psychological Review, 84*, 472–484.

Booth, J. R., Burman, D. D., Meyer, J. R., Gitelman, D. R., Parrish, T. B., & Mesulam, M. M. (2002). Functional anatomy of intra- and cross-modal lexical tasks. *Neuroimage, 16*, 7–22.

Bouma, H. (1973). Visual interference in the parafoveal recognition of initial and final letters of words. *Vision Research, 13*, 767–782.

Brysbaert, M. (1994). Interhemispheric transfer and the processing of foveally presented stimuli. *Behavioural Brain Research, 64*, 151–161.

Brysbaert, M., Vitu, F., & Schroyens, W. (1996). The right visual field advantage and the optimal viewing position effect: On the relation between foveal and parafoveal word recognition. *Neuropsychology, 10*, 385–395.

Carreiras, M., Perea, M., & Grainger, J. (1997). Orthographic neighborhood effects on visual word recognition in Spanish: Cross-task comparisons. *Journal of Experimental Psychology: Learing, Memory, and Cognition, 23*, 857–871.

Chastain, G. (1977). Feature analysis and the growth of a percept. *Journal of Experimental Psychology: Human Perception and Performance, 3*, 291–298.

Chiarello, C. (1985). Hemisphere dynamics in lexical access: Automatic and controlled priming. *Brain and Language, 26*, 146–172.

Cohen, L., Dehaene, S., Naccache, L., Lehericy, S., Dehaene-Lambertz, G., Henaff, M., & Michel, F. (2000). The visual word form area: spatial and temporal characterization of an initial stage of reading in normal subjects and posterior split-brain patients. *Brain, 123*, 291–307.

Cohen, L., Lehericy, S., Chochon, F., Lemer, C., Rivaud, S., & Dehaene, S. (2002). Language-specific tuning of visual cortex? Functional properties of the visual word form area. *Brain, 125*, 1054–1069.

Coltheart, M., Davelaar, E., Jonasson, J. T., & Besner, D. (1977). Access to the internal lexicon. In S. Dornic (Ed.), *Attention and performance, Vol. VI: The psychology of reading*. London: Academic Press.

Damasio, A., & Damasiao, H. (1983). The anatomic basis of pure alexia. *Neurology, 33*, 1573–1583.

Dehaene, S., Le Clec', H. G., Poline, J. B., Le Bihan, D., & Cohen, L. (2002). The visual word form area: a prelexical representation of visual words in the fusiform gyrus. *Neuroreport, 13*, 321–325.

Ellis, A. W., Young, A. W., & Anderson, C. (1988). Modes of word recognition in the left and right cerebral hemispheres. *Brain and Language, 35*, 254–273.

Estes, W. K., Allemeyer, D. H., & Reder, S. M. (1976). Serial position functions for letter identification at brief and extended exposure durations. *Perception & Psychophysics, 19*, 1–15.

Eviatar, Z. (1999). Cross-language tests of hemispheric strategies in reading nonwords. *Neuropsychology, 13*, 498–515.

Grainger, J. (1990). Word frequency and neighborhood frequency effects in lexical decision and naming. *Journal of Experimental Psychology: Learing, Memory, and Cognition, 29*, 228–244.

Grainger, J., & Jacobs, A. M. (1991). Masked constituent letter priming in an alphabetic decision task. *European Journal of Cognitive Psychology, 3*, 413–434.

Grainger, J., & Jacobs, A. (1996). Orthographic processing in visual word recognition: A multiple readout model. *Psychological Review, 103*, 518–565.

Grainger, J., O'Regan, J., Jacobs, A., & Segui, J. (1989). On the role of competing word units in visual word recognition. *Perception & Psychophysics, 45*, 189–195.

Grainger, J., O'Regan, J., Jacobs, A., & Segui, J. (1992). Neighborhood frequency effects and letter visibility in visual word recognition. *Perception & Psychophysics, 51*, 49–56.

Hammond, E. J., & Green, D. W. (1982). Detecting targets in letter and non-letter arrays. *Canadian Journal of Psychology, 36*, 67–82.

Hellige, J. B., Cowin, E. L., & Eng, T. L. (1995). Recognition of CVC syllables from LVF, RVF, and central locations: Hemispheric differences and interhemispheric interactions. *Journal of Cognitive Neuroscience, 7*, 258–266.

Hellige, J. B., & Scott, G. B. (1997). Effects of output order on hemispheric asymmetry for processing letter trigrams. *Brain and Language, 59*, 523–530.

Hellige, J. B., & Yamauchi, M. (1999). Quantitative and qualitative hemispheric asymmetry for processing Japanese kana. *Brain and Cognition, 40*, 453–463.

Hopfield, J. J. (1995). Pattern recognition computation using action potential timing for stimulus representation. *Nature, 376*, 33–36.

Humphreys, G. W., Evett, L. J., & Quinlan, P. T. (1990). Orthographic processing in visual word identification. *Cognitive Psychology, 22*, 517–560.

Huntsman, L., & Lima, S. (1996). Orthographic neighborhood structure and lexical access. *Journal of Psycholinguistic Research, 25*, 417–429.

Koriat, A. (1985). Lateralization effects in reading pointed and unpointed Hebrew. *British Journal of Psychology, 76*, 161–173.

Koriat, A., & Norman, J. (1985). Reading rotated words. *Journal of Experimental Psychology: Human Perception and Performance, 11*, 490–508.

Krumhansl, C. L., & Thomas, E. A. C. (1976). Extraction identity and location information from briefly presented letter arrays. *Perception & Psychophysics, 20*, 243–258.

Lavidor, M., Babkoff, H., & Faust, M. (2001). Analysis of standard and non-standard visual word format in the two hemispheres. *Neuropsychologia, 39*, 430–439.

Lavidor, M., & Ellis, A. (2002a). Word length and orthographic neighborhood size effects in the left and right cerebral hemispheres. *Brain and Language, 80*, 45–62.

Lavidor, M., & Ellis, A. (2002b). Orthographic neighborhood effects in the right but not in the left cerebral hemisphere. *Brain and Language, 80*, 63–76.

Lavidor, M., Ellis, A., Shillock, R., & Bland, T. (2001). Evaluating a split processing model of visual word recognition: Effects of word length. *Cognitive Brain Research, 12*, 265–272.

Lavidor, M., Ellis, A. W., & Pansky, A. (2002). Case alternation and length effects in lateralized word recognition: Studies of English and Hebrew. *Brain and Cognition, 50*, 257–271.

Lavidor, M., & Walsh, V. (2003). A magnetic stimulation examination of orthorgraphic neighborhood effects in visual word recognition. *Journal of Cognitive Neuroscience, 15*, 354–363.

Leff, A., Crewes, H., Plant, G., Scott, S., Kennard, C., & Wise, R. (2001). The functional anatomy of single-word reading in patients with hemianopic and pure alexia. *Brain, 124*, 510–521.

Lefton, L. A., Fisher, D. F., & Kuhn, D. M. (1978). Left-to-right processing of alphabetic material is independent of retinal location. *Bulletin of the Psychonomic Society, 112*, 171–174.

Legge, G. E., Mansfield, J. S., & Chung, S. T. (2001). Psychophysics of reading XX: Linking letter recognition to reading speed in central and peripheral vision. *Vision Research, 41*, 725–743.

Lisman, J. E., & Idiart, M. A. P. (1995). Storage of 7+−2 short-term memories in oscillatory subcycles. *Science, 267*, 1512–1515.

Marks, N. L., & Hellige, J. B. (1999). Effects of bilateral stimulation and stimulus redundancy interhemispheric interaction. *Neuropsychololology, 13*, 475–487.

Mason, M. (1982). Recognition time for letters and nonletters: Effects of serial position, array size, and processing order. *Journal of Experimental Psychology, 8*, 724–738.

McClelland, J. L., & Rumelhart, D. E. (1981). An interactive activation model of context effects in letter perception: Part 1. An account of basic findings. *Psychological Review, 88*, 375–407.

McConkie, G. W., Kerr, P. W., Reddix, M. D., & Zola, D. (1988). Eye movement control during reading: I. The location of initial eye fixations on words. *Vision Research, 28*, 1107–1118.

Monaghon, P., Shillock, R., & McDonald, S. (2003). Hemispheric asymmetries in semantic processing. *Brain and Language,* this issue.

Montant, M., Nazir, T. A., & Poncet, M. (1998). Pure alexia and the viewing position effect in printed words. *Cognitive Neuropsychology, 15*, 93–140.

Nazir, T., Ben-Boutayab, N., Decoppet, N., Deutsch, A., & Frost, R. (2003). Reading habits, perceptual learning, and recognition of printed words. *Brain and Language,* this issue.

Nazir, T. A., Kajii, N., Frost, R., & Osaka, N. (2003). Script characteristics modify the way we perceive isolated words: Visual field effects in the perception of French, Hebrew, Kanji, and Hiragana words. In preparation.

Perea, M., & Pollatsek, A. (1998). The effects of neighborhood frequency in reading and lexical decision. *Journal of Experimental Psychology: Human Perception and Performance, 24*, 767–779.

Peressotti, F., & Grainger, J. (1995). Letter-position coding in random consonant arrays. *Perception & Psychophysics, 57*, 875–890.

Peressotti, F., & Grainger, J. (1999). The role of letter identity and letter position in orthographic priming. *Perception & Psychophysics, 61*, 691–706.

Polk, T., & Farah, M. (2002). Functional MRI evidence for an abstract, not perceptual, word-form area. *Journal of Experimental Psychology: General, 131*, 65–72.

Rayner, K. (1975). Parafoveal identification during a fixation in reading. *Acta Psychologia, 4*, 271–282.

Rayner, K., & McConkie, G. (1976). What guides a reader's eye movements. *Vision Research, 16*, 829–837.

Strangbert, B., & Brannstrom, L. (1975). Spatial interaction effects in letter processing. *Perception & Psychophysics, 17*, 268–272.

Sugishita, M., Hamilton, C. R., Sukuma, I., & Hemmi, I. (1994). Hemispheric representation of the central retina of commissurotomized subjects. *Neuropsychologia, 32*, 399–415.

Whitney, C. (2001a). How the brain encodes the order of letters in a printed word: the SERIOL model and selective literature review. *Psychonomic Bulletin & Review, 8*, 221–243.

Whitney, C. (2001b). Position-specific effects within the SERIOL framework of letter-position coding. *Connection Science, 13*, 235–255.

Whitney, C. (2002). An explanation of the length effect for rotated words. *Cognitive Systems Research, 3*, 113–119.

Whitney, C., & Berndt, R. S. (1999). A new model of letter string encoding: Simulating right neglect dyslexia. *Progress in Brain Research, 121*, 143–163.

Whitney, C., & Lavidor, M. (2003). Why a large neighborhood does not facilitate word recognition in the left hemisphere. Submitted.

Wolford, G., & Hollingsworth, S. (1974). Retinal location and string position as important variables in visual information processing. *Perception & Psychophysics, 16*, 437–442.

Young, A. W., & Ellis, A. W. (1985). Different methods of lexical access for words presented in the left and right visual hemifields. *Brain and Language, 24*, 326–358.

Ziegler, J., & Perry, C. (1998). No more problems in Coltheart's neighborhood: resolving neighborhood conflicts in the lexical decision task. *Cognition, 68*, B53–B62.