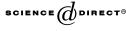


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Facilitative orthographic neighborhood effects: The SERIOL model account

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Abstract

A large orthographic neighborhood (N) facilitates lexical decision for central and left visual field/right hemisphere (LVF/RH) presentation, but not for right visual field/left hemisphere (RVF/LH) presentation. Based on the SERIOL model of letter-position encoding, this asymmetric N effect is explained by differential activation patterns at the orthographic level. This analysis implies that it should be possible to negate the LVF/RH N effect and create an RVF/LH N effect by manipulating contrast levels in specific ways. In Experiment 1, these predictions were confirmed. In Experiment 2, we eliminated the N effect for both LVF/RH and central presentation. These results indicate that the letter level is the primary locus of the N effect under lexical decision, and that the hemispheric specificity of the N effect does not reflect differential processing at the lexical level.

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1. Introduction

In studying cognition, experimental psychologists often investigate visual word recognition, because it involves both sensory and language processing, and stimuli

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can easily be manipulated at both these levels. Physical aspects of the stimuli can be adjusted by varying size, contrast, font, and retinal location. Lexical aspects of the stimuli can be manipulated by controlling variables such as length, frequency, and spelling-to-sound regularity.

Another lexical property that is often investigated is neighborhood size (N) (Coltheart, Davelaar, Jonasson, & Besner, 1977), the number of words that can be formed by changing one letter of the target word to a different letter. For example, the word LANE has many neighbors (BANE, CANE, LATE, LACE, LINE, LONE, LAND, etc.), while the word SHED has few neighbors. As Andrews (1997) pointed out, such experiments provide critical evidence on selectional processing in lexical access.

In lexical decision experiments, a large neighborhood yields a facilitative effect for low-frequency English words. That is, responses to high-N words are faster than responses to low-N words, called the *N effect* (for a review, see Andrews, 1997). Although some lexical decision experiments have failed to demonstrate this N effect, Andrews (1997) notes these divergent results can be attributed to systematic features of the stimuli; the N effect appears to be influenced by language and context. However, all lexical-decision experiments in English for low-frequency words using unblocked stimuli have shown a facilitative effect of large N (Andrews, 1989, 1992; Forster & Shen, 1996; Holcomb, Grainger, & O'Rourke, 2002; Huntsman & Lima, 2002; Johnson & Pugh, 1994; Lavidor & Ellis, 2002a; Sears, Hing, & Lupker, 1995). In an ERP lexical decision experiment, Holcomb et al. (2002) have shown that items (words and pseudo-words) with many orthographic neighbors generated stronger negativity (larger N400s) than similar items with relatively fewer neighbors. This activity was related to a facilitative N effect for words and to inhibitory N effects for pseudo-words as measured by RTs. Holcomb et al. (2002) argued that the fact that the effects of neighborhood size were in the same direction for words and pseudo-words suggests that ERPs are tapping into some basic processing of these stimuli that is affected by number of orthographic neighbors.

The finding of facilitation for high-N for positive responses in lexical decision is somewhat surprising, as lateral inhibition within the word level is usually assumed. Such inhibition would imply that increased similarity to other words should slow reaction times, rather than speed them. Several explanations for the locus of this unexpected facilitation have been proposed.

Facilitation could arise at the letter level through top-down feedback, as in the Interactive Activation Model (McClelland & Rumelhart, 1981). That is, neighbors may send excitation back to the letter level, which in turn speeds activation of the target word.

Alternatively, facilitation could arise solely within the word level, as in the Multiple Read-Out Model (MROM) (Grainger & Jacobs, 1996). In the MROM, positive lexical-decision responses are taken to be influenced by two factors: the maximal activation of a single lexical item, and the total activation across lexical items. That is, if total activation at the word level exceeds a threshold, a positive response can be generated without the precise identification of a single item. Thus, high-N may speed reaction times by increasing total word-level activation.

This total-activation threshold is taken to be modifiable according to the statistics of the stimuli, which would account for differing influences of N under variations of non-word difficulty.

Another possible locus of facilitation is the phonological level, either through general feedback to the target word or specifically via word bodies (Ziegler & Perry, 1998). Of course, facilitation may result from multiple sources (Reynolds & Besner, 2002). Thus the source of facilitation in the N effect remains an open question.

The strength of the N effect can be influenced by the neighbor's frequencies, and the spread of positional differences of the neighbors (Mathey & Zagar, 2000; Pollatsek, Perea, & Binder, 1999; Pugh, Rexer, Peter, & Katz, 1994). In some cases, the existence of a higher frequency neighbor can be inhibitory (Grainger, O'Regan, Jacobs, & Segui, 1992). N also affects other tasks such as naming, where facilitative effects have been found (Andrews, 1997; Peerman & Content, 1997; Reynolds & Besner, 2004), and dwell times in naturalistic reading, where inhibitory effects have been found (Perea & Pollatsek, 1998; Pollatsek et al., 1999), while for semantic categorization, N has little effect (Forster & Shen, 1996).

Thus the influence of neighbors varies with their properties and with the task. There are two possibilities for the source of variation with task. One possibility is that different tasks index different aspects of word-level activations. For example, lexical-decision may index total word-level activation, as in the MROM model, while other tasks may index target-word activation. Alternatively, all tasks may index target-word activation level. Such variations could then be explained under a general framework in which neighbors engender two opposing forces on the target—an inhibitory one, probably due to competition within the word level, and an excitatory one, of currently unknown origin(s). It is likely that the balance of these influences could be altered by the task and the stimuli, accounting for these differing results. Furthermore, a task which depends more directly on lexical activation level (e.g., lexical decision) may simply be more sensitive to this variable than a task that requires additional processing (e.g., semantic classification).

N also affects reaction times to pseudo-words in lexical decision. High-N pseudowords are rejected more slowly than low-N pseudo-words (Coltheart et al., 1977; Carreiras, Perea, & Grainger, 1997; Ziegler & Perry, 1998). In this case, the effect of high-N could not result specifically from target activation, as there is no target. Rather, the effect must stem from more general aspects of word-level activation.

While orthographic neighbors are associated with a range of phenomena, we seek to understand the nature of the observed facilitative effects of N in particular. We focus on the lexical-decision task, which is not confounded by the demands of phonological assembly. Our goal is not to give a full account of N effects across tasks, nor to provide a full account of the lexical-decision process. Rather, we focus on the more narrow issue of the mechanisms underlying the well-established facilitative N effect.

Investigation into this N effect has recently been extended to lateralized presentation (Lavidor & Ellis, 2002a), where an N effect was found for presentation to the left visual field (LVF), but not the right visual field (RVF) This result was replicated in another experiment which included central (CVF) presentation. For a single set of stimuli, there was an N effect for the CVF and LVF, but not the RVF (Lavidor & Ellis, 2002b). Understanding this $VF \times N$ -effect interaction should shed light on the nature of the facilitation underlying the N effect.

First, we consider the standard explanation of hemifield asymmetries. Due to the routing of the optic nerves at the optic chiasm, stimuli occurring in the RVF are initially projected to the left hemisphere (LH), while stimuli presented in the LVF are projected to the right hemisphere (RH). Therefore, visual-field asymmetries, such as the length effect (Bouma, 1973; Melville, 1957; Young & Ellis, 1985) and positional error patterns (Hellige, Cowin, & Eng, 1995), been take to reflect hemisphere-specific modes of lexical access, with parallel processing of letters in the RVF/LH and less efficient, non-parallel processing in the LVF/RH.

Interestingly, for the N effect, the CVF patterns with the LVF/RH, not the more efficient RVF/LH. Therefore, the observed interaction of the N effect with visual field could not have arisen simply because of less efficient processing in the LVF/RH. As most neighbors differ from each other in the first position (in the four-letter English stimuli used in experiments showing the N effect), could differences in the acuity of the first letter of the target could explain the interaction with visual field? Again, the asymmetry is in the wrong direction. Acuity of the initial letter is highest in the CVF and lowest in the LVF, yet they pattern together.

An alternative account of hemisphere-specific lexical access is provided by the Split Fovea model, in which granularities of sub-lexical units differ (Monaghan, Shillcock, & McDonald, 2004). The model develops differing granularities under the assumption that initial letters fall more frequently in the LVF, while final letters fall more frequently in the RVF. The differing statistics of the initial versus final letters makes it more efficient for the "LVF/RH" to operate over multi-letter units, and for the "RVF/LH" to operate over single-letter units. (However, see Whitney (2004) for arguments against the underlying assumptions of the Split Fovea model.) Neighborhood effects may be stronger in the RH because a multi-letter representation is more sensitive to context than is a single-letter representation (Monaghan, pers. comm.).

Such analyses of hemifield effects based on differences in lexical access rest upon the assumption the information initially projected to a single hemisphere continues to be processed by that hemisphere until the point of lexical access. However, imaging studies indicate that brain activity becomes left-lateralized at a pre-lexical level (in inferotemporal cortex) during visual word recognition (Cohen et al., 2000; McCandliss, Cohen, & Dehaene, 2003; Tarkiainen, Helenius, Hansen, Cornelissen, & Salmelin, 1999). In line with these results, masking studies suggest that information is transferred from the RH to the LH at the feature level during visual word recognition (Moscovitch, 1983, 1986). This suggests that there is a single orthographic route to the lexicon; a pre-lexical representation is formed in the LH, independently of presentation location. However, a single route seems at odds with the hemispheric specificity of the N effect. How could the influence of neighborhood size vary with visual field, if the process of lexical access does not differ with visual field?

To answer this question, Whitney (2004) proposed an account of the asymmetry of the N effect under the SERIOL model of letter-position encoding, which employs a single orthographic route to the lexicon. This model specifies how the early, retino-

topic representation of a string is progressively converted into an abstract representation of letter order (Whitney, 2001a; Whitney & Berndt, 1999). This processing requires hemisphere-specific transformations at the feature level, which could potentially explain the effect of visual field. This account hinges on differences in activation patterns, and leads to highly specific predictions about how to create or negate the N effect via positional manipulations of letter contrast.

Using similar logic, we have already shown that activation patterns underlie the asymmetry of the length effect (Whitney & Lavidor, 2004). It has long been known that word length affects performance in the LVF/RH, but not in the RVF/LH (Bouma, 1973; Melville, 1957; Young & Ellis, 1985). Based on predictions from the SERIOL model, we were able to negate the usual LVF length effect in lexical decision and to create an RVF length effect, by brightening the second and third letters of the stimuli, and dimming the sixth letter (if present). This is the first time that the LVF length effect has been abolished, demonstrating that the asymmetry of the length effect arises from hemisphere-specific activation patterns, rather than hemisphere-specific modes of lexical access.

In this paper, we test the predictions of the SERIOL model regarding the influence of contrast manipulations on the asymmetry of the N effect. This analysis indicates that it should be possible to create or abolish the N effect simply by dimming the inner or outer letters of four-letter words, and these predictions were confirmed in two experiments. The otherwise unexpected prediction that contrast manipulations should have these effects is unique to the SERIOL model. No other model is capable of generating such an analysis, and so these results provide strong support for the SERIOL model. Thus the present findings illuminate the processing carried out by the orthographic/lexical route in visual word recognition, and further demonstrate how a single mode of lexical access can nevertheless give rise to visual-field asymmetries. Furthermore, no account that explains the N effect at a level of processing higher than the orthographic level can accommodate our experimental results. Thus the present findings also illuminate the locus of the N effect. The success of the model in generating these novel results illustrates the importance of realistic computational approaches in the study of cognitive psychology.

In the following, we first review the model and the explanation of the asymmetry of the N effect. After discussing the resulting predictions in detail, we present the experiments, and conclude with a general discussion of the results and their implications.

2. Review of the SERIOL framework

It is well known that neural representations increase in abstractness as distance from sensory cortical areas increases. The SERIOL model offers a theory of the representational transformations carried out in the processing stream extending from the early visual areas to lexical access. This requires specification of how a retinotopic representation is transformed into a location-invariant, abstract encoding of letter order, and how that encoding then activates the lexical level. Given the scope of this endeavor, and the goal of providing a realistic account of what the brain is actually doing, it should not be surprising that the resulting model is somewhat complex.

The model provides a theory of such processing in the skilled reader, under the assumption that the brain solves the problem of letter-position encoding in a standard way. That is, we assume that innate representational mechanisms and learning algorithms give rise to similar processing strategies across (non-dyslexic) readers. The SERIOL model specifies the proposed outcome of such learning. (For conjectures on how this learning might occur, see Whitney & Cornelissen (2005)).

We note that the following is a review of a model that has already been fully specified. The model was not in any way designed to account for the N effect and the related visual-field asymmetry. As discussed in the following section, the only additional assumptions necessary for explaining the N effect are related to consideration of top-down feedback. We first give a brief overview of the model, and then present it in more detail. For brevity, we do not include supporting experimental evidence for our underlying assumptions; such arguments can be found elsewhere (Whitney, 2001a, 2001b, 2002; Whitney & Berndt, 1999).

The SERIOL framework is comprised of five layers: edge, feature, letter, bigram, and word. In the following, we use the term *node* to refer to a processing unit in the model. Within each layer, a letter's activation corresponds to the total amount of activity across nodes participating in the representation of that letter.

The edge layer corresponds to the earliest levels of visual processing, where receptive fields are small, and there is an activation pattern resulting from differences in acuity. It is well known that the number of retinal and cortical cells representing a fixed area of space decreases as distance from fixation increases. Thus, the number of edge nodes representing a letter is taken to decrease as eccentricity increases. Due to this acuity gradient, letter activations are highest near fixation, and fall off as distance from fixation increases.

At the feature level, nodes are more broadly tuned to retinal location. As discussed in more detail below, it is proposed that the acuity gradient is converted into an activation pattern, dubbed the *spatial gradient*, in which activation level decreases across the string from left to right. For example, for the stimulus BIRD, B's features become the most highly activated, I's the next most activated, R's the next, and D's the least. The ability to create this spatial gradient would be learned during reading acquisition (Whitney & Cornelissen, 2005).

The spatial gradient then interacts with letter nodes that oscillate in excitability, inducing sequential firing at the letter level. That is, B fires, then I, then R, and then D. Thus a retinotopic representation is converted into a location-invariant, serial encoding of letter order. This conversion also results in varying letter activation levels, as we discuss below. The basic capacity to create a location-invariant representation by mapping space onto time via oscillatory cells is taken to be innate.

We assume that this representation of letter order subserves separate orthographic and phonological routes to the lexicon. We concentrate on the orthographic route. The letters then activate nodes which represent ordered letter pairs. Such a bigram node is activated any time that its constituent letters fire in the proper order. Thus, in our example, bigram nodes representing BI, IR, and RD, as well as those corresponding to non-contiguous letter pairs (BR, BD, and ID), become activated. A bigram node's activation level depends on its constituent letter activations and the time lag between the firing of those letters. The basic capacity to represent spatial relationships between the components of an object via ordered pairs is also taken to be innate. Bigrams then activate word-level representations via weighted connections. See Fig. 1 for a summary of the processing levels and their associated activation patterns.

Next, we discuss the proposed mechanisms underlying the representational transformations performed in each layer. Because our account of the N effect depends primarily on the feature and letter levels, we focus on processing at those layers, and present a brief summary of the higher levels.

2.1. Edge to feature levels

Mounting evidence from behavioral and Transcranial Magnetic Stimulation studies indicates that the representation of the fovea is initially split across the cerebral hemispheres, with no overlap along the vertical meridian (Brysbaert, 1994; Brysbaert et al., 1996; Lavidor & Walsh, 2003). These studies are in line with neuroanatomical arguments against such a bilateral representation, as discussed by Leff (2004). Given the high resolution of modern brain-imaging techniques, a bilateral representation in primary visual cortex should be detectable if it were present, yet no imaging study has found evidence for such a representation (Leff, 2004). Thus, available evidence indicates that letters immediately to the left of fixation initially go to the RH, and letters to the right, go to the LH. Therefore, the representation of a centrally fixated word is initially split across the hemispheres (Brysbaert, 2004). This has implications for how the spatial gradient is created at the feature level.

The proposed spatial gradient is monotonically decreasing from the first letter to the last letter. We assume that during reading acquisition, a top-down attentional gradient is initially employed, and the visual system then learns to create this activation gradient in a bottom-up manner (Whitney & Cornelissen, 2005), yielding the spatial gradient. We now describe the resulting string-specific processing proposed for the conversion of the acuity gradient into the spatial gradient.

Note that acuity *increases* from the first letter to the fixated letter (i.e., in the LVF). Therefore, the slope of the acuity gradient in the RH is in the opposite direction to that required for the spatial gradient. As a result, the acuity gradient's slope in the LVF/RH must be *inverted* as letter features are activated. In contrast, acuity *decreases* from the fixated letter to the final letter (i.e., in the RVF), as desired for the spatial gradient. Thus, the acuity gradient's slope in the LH can be maintained as letter features are activated. As a result, processing at the feature level differs across hemispheres, with the RH performing more extensive transformations.

First, we discuss this RH processing. The increasing acuity gradient must be inverted to form the decreasing spatial gradient. The number of cells that can represent an area of space is fixed. Therefore, this inversion occurs via adjustment of firing rates. We propose that RH features become more highly activated by bottom-up inputs than LH features. This could occur either via higher connection weights from the edge to feature level, or stronger feedback excitation from a feature node to itself.

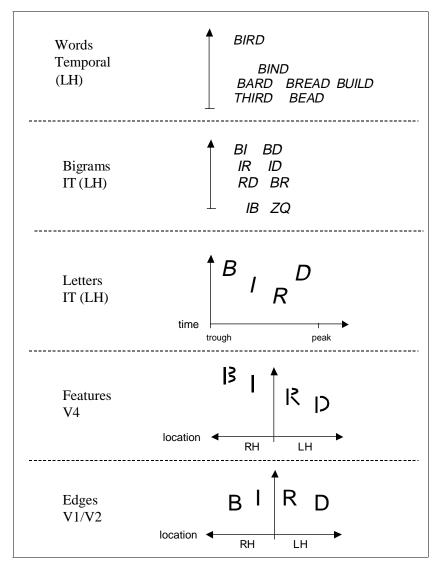


Fig. 1. Example of the encoding of the BIRD through the various levels of processing. Each area is associated with an approximate brain area (IT = inferotemporal cortex). The proposed activity pattern for the relevant units at each level is illustrated, where the vertical axis of each graph corresponds to activation level. At the two earliest levels, units are tied to retinal location. At the letter layer, units are organized by firing order. Here, *trough* denotes the point of lowest excitability in the oscillatory cycle, and *peak* denotes the point of highest excitability. At the highest levels (bigram and word), there is no topographic or temporal organization to the encoding. At these levels, relative activations of some units not directly encoding the stimulus are included for reference. We discuss in more detail below how these activation patterns arise.

This stronger bottom-up RH excitation would be learned in response to more attention being directed to the initial letters of a word (Whitney & Cornelissen, 2005), allowing the first letter's features to reach a high level of activation even if they are far from fixation. (See bottom panel of Fig. 2.) This proposal is consistent with the finding that at large eccentricities, an initial letter is perceived better in the LVF than in the RVF, even if the LVF initial letter is *farther* from fixation than the RVF initial letter (Bouma, 1973; Estes, Allemeyer, & Reder, 1976).

We also propose that strong directional lateral inhibitory connections develop within the RH feature level such that each node inhibits other nodes to its right.

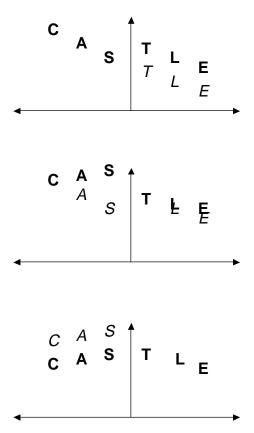


Fig. 2. Illustration of the formation of the spatial gradient at the feature level, illustrating the effects of hemisphere-specific excitation (bottom frame), hemisphere-specific directional inhibition (middle frame), and cross-hemispheric inhibition (upper frame). The axes are the same as those for the feature layer in Fig. 1. Here, for clarity and simplicity, we use a longer example stimulus, CASTLE, and do not draw individual features. In each frame, the boldface letters represent the activation pattern prior to the illustrated transformation, and the italics represent the result of the transformation. The initial activation pattern (lower frame, bold letters) corresponds to the acuity gradient from bottom-up input. The final result (upper frame, bold letters in LVF/RH and italicized letters in RVF/LH) is a monotonically decreasing activation gradient. For clarity, we show these transformations occurring sequentially, although they would actually occur interactively.

Thus, inhibitory input increases as letter position increases, because more and more features send inhibition from the left. This strong directional inhibition overrides the slope of the acuity gradient, inverting it (see middle panel of Fig. 2). So the features comprising the first letter attain a high level of activation (due to strong excitation and lack of lateral inhibition), and activation decreases towards fixation (due to sharply increasing lateral inhibition).

In the LH, we assume that 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, although some directional inhibition may steepen its slope.

In addition to inhibition within hemispheres, there is also inhibition across hemispheres. The RH features inhibit the LH features, bringing the activations of the LH features lower than those of the RH. Thus the two halves of the spatial gradient are meshed to create a strictly decreasing activation gradient from the first to the last letter (see top panel of Fig. 2).

In summary, there are three important components to spatial gradient formation: (1) hemisphere-specific excitation—RH features receive more excitation that LH features; (2) hemisphere-specific directional inhibition—features inhibit other features to the right, with much stronger such inhibition in the RH; and (3) cross-hemispheric inhibition—RH features inhibit LH features. As discussed in Whitney (2001a), these assumptions on spatial gradient formation explain a wide range of data on letter perceptibility concerning the influence of string position, retinal location, and reading direction.

2.2. Feature to letter levels

At the letter level, retinal location is abstracted away to yield a serial encoding of string position. Crucially, we assume that all letter nodes undergo synchronous, sub-threshold oscillations of excitability. The spatial gradient interacts with the letter nodes' temporal excitability gradient, resulting in a sequential firing (Hopfield, 1995; Lisman & Idiart, 1995). Early in the oscillatory cycle, the excitability of the letter nodes is low. Thus, only the letter node receiving the highest level of input can exceed threshold and fire (i.e., B in our BIRD example). As excitability increases over time, the letter node receiving the next highest level of input can fire (i.e., I), and so on (see Fig. 3). An active letter node inhibits all other letter nodes, and continues to fire until inhibited by a subsequent letter node.

The assumption of lateral inhibition between letter nodes raises the question how a new letter node can ever start to fire, since all inactive nodes are 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 decreases enough that a different letter node can start to fire. When active node receives lateral inhibition, it becomes strongly inhibited.¹

¹ This in turn raises the question of how a repeated letter is represented. We assume that there is a pool of nodes for each letter, and that each instance of a letter activates a different subset of that pool.

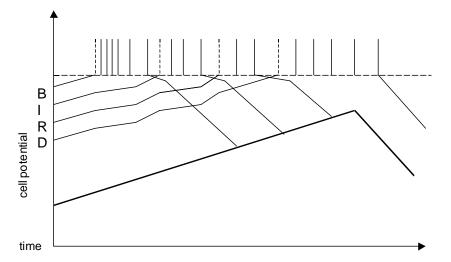


Fig. 3. Illustration of serial firing at the letter level for the stimulus BIRD, for groups of cells comprising the representations of B, I, R, and D. The thick line represents the base oscillation in excitability, while the horizontal dashed line represents firing threshold (not drawn to scale). Density of vertical lines ("spikes") above firing threshold represent overall firing rate, not individual neural spikes. For clarity, the first "spike" for each new letter is shown in dashed lines. The activation of each letter unit is proportional to the total number of "spikes" for that letter. The varying amounts of cell potential for different letters reflect input levels corresponding to the spatial gradient. Thus, the spatial gradient interacts with the oscillatory cycle to induce serial firing at the letter level.

The varying activation levels from the spatial gradient continue to affect the higher levels of processing. 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 one, a letter's activation depends both on its own level of input (which determines its firing rate), and the level of input to the next letter (which determines its firing duration). As a result, letter activations are generally decreasing across the string, except at the final letter. This final-letter advantage occurs because the final letter can fire longer than the internal letters (until the end of the oscillatory cycle), since it is not inhibited by a subsequent letter (see Fig. 3). Although we assume a monotonically decreasing activation gradient at the feature level, there is a different pattern at the letter level, one that is consistent with the well-known advantage for the final letter.

In summary, the level of input to a letter determines when it can fire with respect to the oscillatory cycle. Therefore, the spatial gradient induces serial firing at the letter level. The activation of a letter increases with its firing rate (which depends on its input level), and its firing duration (which depends on when it is inhibited by a subsequent letter).

2.3. Letter to word levels

The relative timing of pairs of letters then serves as the basic unit of lexical access, consistent with experimental evidence showing that the relative ordering of letters,

not their absolute string position, is important (Grainger & Whitney, 2004; Humphreys, Evett, & Quinlan, 1990; Perea & Lupker, 2003; Peressotti & Grainger, 1999; Schoonbaert & Grainger, 2004). That is, the temporal encoding activates bigram nodes, and the activity across bigram nodes is consolidated to activate words. 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 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. The input to a word node is then calculated in the usual way, as the dot-product of the input and weight vectors.

This access via weighted bigrams provides a new definition for lexical similarity. Two words will be the most similar when they share the most highly weighted bigrams, regardless of string length. For example, the words LANE and LANCE are highly similar under this metric, because LANCE contains all the bigrams in LANE, in essentially the same positions. LANE and LATE are less, but still very, similar because they match on the most highly weighted bigrams. In contrast, LANE and CANE are only moderately similar, since they do not match on the important first/second and first/last bigrams. Simulations have shown that differences in bigram activation patterns allow the system to differentiate between two words even when one word is contained within another, as in the LANE/LANCE example (Whitney & Berndt, 1999).

Thus, we would claim that the true measure of orthographic neighborhood size should be broader than the N metric; it should include words that differ in length from the target, and similarity should depend of position of mismatch (Perea, 1998). However, our goal is to explain previous experimental results that have been generated under the N metric. Therefore, we too will use the N metric.

3. Analysis of the N effect

Next, we review the explanation of the asymmetry of the N effect, which was first presented in Whitney (2004). We note that, while the following analysis may not be immediately obvious given the SERIOL model, it is nonetheless a direct outcome of a consideration of the tenets of the model. In fact, when Whitney undertook the goal of explaining the asymmetry of the N effect under the constraints of the model, this account was the only one she could generate that both explained the experimental results and was consistent with the model.

Although the SERIOL model focuses on the bottom-up processing stream, we do not mean to rule out top-down activation. Indeed, our analysis of the N effect depends on such activation. We propose that excitation from the word level back to the letter level is the source of the N effect in lexical decision (Whitney, 2004). The oscillatory cycle driving the letter level is taken to fall in the theta band (4–8 Hz) (Klimesch, 1996; Klimesch et al., 2001; Lisman & Idiart, 1995). Thus, an individual cycle would take 125–250 ms, allowing multiple cycles to occur during lexical decision. That is, the

letter-node sequence may fire multiple times. Input to the letter level is primarily bottom-up during the first oscillatory cycle. There may be top-down input to letter nodes during the first cycle, as word nodes are progressively activated, but we assume that the strongest influence occurs during subsequent cycles. After the first cycle is complete, the target word node and its neighbors will be among the most highly activated. On subsequent cycles, top-down input from these word nodes to the letter nodes will then have a maximal effect. We propose that such top-down input is the source of the N effect, as in the account based on the Interactive Activation Model; this top-down input affects letter-node activations, which in turn affect the continuing evolution of word-node activations. This feedback also takes the form of a gradient. That is, the first letter receives the most top-down excitation, the second letter receives the next most, etc. Such a gradient may be necessary for serial output of letters during spelling.

In the SERIOL model, the feature level is the last point of hemisphere-specific processing, in line with Moscovitch (1983, 1986). Therefore, we propose that differences in feature-level activation patterns underlie the hemispheric specificity of the N effect. More specifically, we propose that hemispheric differences arise from the formation of the spatial gradient, coupled with the processing which converts the spatial gradient into a serial firing pattern. Due to these dynamics, increased top-down input to the letter level (from high-N) has a facilitative effect for LVF/RH presentation, but not for RVF/LH presentation.

First, we focus on the spatial gradient formation. The hemisphere-specific transformations that are required to create the spatial gradient for a fixated word have ramifications for parafoveally presented words. Acuity gradient inversion in the LVF/RH normally operates on a small number of letters of high acuity. For a string at a large eccentricity in the LVF, these mechanisms may fail to create a smoothly decreasing spatial gradient, as follows. Strong inhibition from the first letter to the low-acuity second and third letters makes their activations quite low. However, as acuity increases for the final letters, lateral inhibition becomes insufficient, and their activations remain too high. Thus there is a sharp decrease in activation across the early string positions, and then a flattening, see Fig. 4. In contrast, the spatial

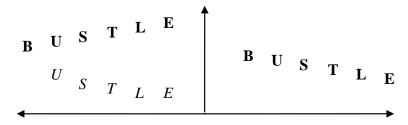


Fig. 4. Spatial gradient formation for parafoveal presentation. The boldface letters represent the activation pattern following increased bottom-up excitation. In the LVF/RH, all letters do not reach the maximal activation level, because bottom-up input levels are lower than for central fixation. Strong lateral inhibition from the first letter has a large effect on the second and third letters, because of their low levels of bottom-up input. Due the lower activations of the initial letters and the increasing activation levels of the final letters, lateral inhibition fails to create a smoothly decreasing gradient (italicized letters). In the RVF/LH, the spatial gradient remains smoothly decreasing because it is based on the acuity gradient.

gradient remains smoothly decreasing for RVF presentation, since it is largely based on the acuity gradient. The existence of such differing activation patterns is supported by observed differential positional patterns of letter perceptibility with visual field (Wolford & Hollingsworth, 1974). A computational model based on these principles closely replicated the observed patterns (Whitney, 2001a).

However, Jordan, Patching, and Thomas (2003) have claimed that such visual-field asymmetries are an artifact of incorrect fixations. They demonstrated that a visual-field asymmetry vanished when subjects were required to precisely maintain central fixation (within 7.5 min of arc) for 1 s before the stimulus could appear. However, fixation errors cannot explain the qualitatively different patterns that emerged under the uncontrolled and controlled versions of the experiment. As discussed by Nazir (2003), it is likely that the stringent demands of the fixation task itself altered attentional and perceptibility patterns. Indeed, in a study where subjects were trained to maintain central fixation (under somewhat less stringent conditions than above), there were strong differences across the visual fields even at an exposure duration of 2.4 s (Estes et al., 1976). The resulting perceptibility patterns are consistent with stronger left-to-right inhibition in the LVF/RH.

To summarize, the differing patterns of acuity and inhibition in the LVF/RH and the RVF/LH create spatial gradients with different shapes. In the RVF/LH, the spatial gradient is smoothly decreasing. In the LVF/RH, the spatial gradient is steep at early string positions (two and three) and then flattens out.

Next, we focus on the dynamics of the conversion of the spatial gradient to serial firing at the letter level. We will denote a currently firing letter node as L - 1, and the node that is to fire next as L. The time at which L can start to fire is limited both by lateral inhibition from L - 1, and the level of excitatory input to L. When the firing rate of L - 1 exceeds a certain level, L cannot start to fire, due to the constant lateral inhibition generated by L - 1. At some point, the firing rate of L - 1 and the resulting lateral inhibition will decrease to a level which would give L the opportunity to fire. At this point, there are two possibilities. (1) If L receives enough excitatory input to cross threshold, it can fire. In this case, lateral inhibition from L - 1 was the limiting factor on when L could start to fire; additional excitatory input to start firing immediately, its activation is delayed until its excitability increases enough (via the oscillatory cycle) to cross firing threshold. L - 1 will then continue firing until L can cross threshold. In this case, the limiting factor was the amount of excitatory input; if L had received more excitatory input, it could have started firing sooner.

Because bottom-up excitation (from the spatial gradient) to the second letter node is relatively lower in the LVF than in the RVF, we propose that firing of that letter is limited by excitatory input in the LVF, while its firing is limited by lateral inhibition in the RVF. That is, a second letter in the LVF *cannot* start to fire as soon as constant lateral inhibition has abated, because it does not receive enough excitatory input to do so. In contrast, a second letter in the RVF *does* receive enough bottom-up input to start to fire at the earliest opportunity. Therefore, increased excitatory input (from the top down via high-N) has an effect in the LVF, but not the RVF. In the LVF, the effect of the second letter firing earlier is to increase its activation level, and decrease the first letter's activation level (since it stops firing sooner). We assume that such a decrease at the first letter has little effect, because its activation is already very high. Thus increased top-down excitation for LVF/RH presentation increases the second letter's activation, while essentially maintaining the first letter's activation. The increased activation is carried forward to the bigram and word levels, allowing the target word to reach response threshold sooner, reducing reaction time. This same effect occurs in the CVF, because the first and second letters fall in the LVF/RH. Because the firing of the second letter is not affected in the RVF/LH, the N effect does not occur for that presentation location.

Although we think that the second letter is the primary locus of the N effect, the third letter could also play a role, especially under LVF presentation. If the firing rate of the third letter is initially slow enough that it is possible for the next letter to cut it off at any time, activation of the third letter will be quite low if the fourth letter cuts off its firing too soon. This would occur if the input level to the fourth letter is almost as high as to the third letter. This may be the case for LVF presentation, due to the flattening of the spatial gradient. However, this would not be the case for the CVF, because the activation levels of the third and fourth letters' features are determined by the rapidly decreasing acuity gradient. Thus, under LVF presentation, top-down excitation from high-N may also increase the activation of the third letter. (Of course, feedback excitation would also increase the input level to the fourth letter, but the third letter would get a bigger boost than the fourth under a top-down gradient.) Such top-down input would have less effect for central presentation, because the third letter's input level is already much higher than the fourth letter's.

In summary, the SERIOL model posits stronger feature-layer, left-to-right inhibition for the LVF/RH than for the RVF/LH. For LVF and CVF presentation, we propose that such strong inhibition from the first letter to the second letter makes excitatory input the limiting factor in the activation of the second letter node. Therefore, top-down excitation from high-N can increase the second letter's activation. In the RVF/LH, the second letter already fires as early as possible, so additional excitation has no effect. Thus there is an N effect for the LVF and the CVF, but not the RVF. In addition, top-down excitation may also increase activation of the third letter for LVF presentation.

4. Experiment 1

In the first experiment, we concentrate on the asymmetry of the N effect. Because we propose that differences in bottom-up activation patterns underlie this asymmetry, changes to these activation patterns should modulate the N effect. If it were possible to create the LVF/RH activation pattern in the RVF/LH, and vice versa, the asymmetry of the N effect should switch to give an N effect in the RVF but not the LVF. Such manipulations of activation patterns could be accomplished by adjusting contrast levels at specific string positions. In the following, we consider four-letter words under unilateral presentation. The RVF/LH's feature-level activation pattern could be replicated in the LVF/RH by slightly dimming the outer letters. Dimming the first letter should decrease directional inhibition from that letter, mimicking the weaker left-to-right inhibition in the LH. Dimming the final letter should mimic a decreasing acuity gradient. Therefore, this manipulation should produce a smooth, RVF-like spatial gradient in the LVF, and should negate the usual N effect. Conversely, the LVF/RH's activation pattern could be mimicked in the RVF/LH by slightly dimming the internal letters, to give a steep, then flattening spatial gradient. This should induce the N effect in the RVF.

To test these predictions, we performed a lateralized lexical-decision experiment of low-N versus high-N words, with two different patterns of dimmed input, in addition to the control (undimmed) condition. In the *inner-dimmed* condition, the contrast of the second and third letters was reduced. In the *outer-dimmed* condition, the contrast of the first and fourth letters was reduced. The goal was to dim letters enough to alter activation patterns, but not enough to impact perceptibility. Thus we sought to influence reaction times, without affecting accuracy. Our account of the N effect allows precise predictions concerning the expected effects of these manipulations.

The following predictions are derived from reasoning about the underlying principles of our account of the N effect, rather than from simulations. First we give an overview of the expected patterns, and then present the predictions formulaically. Of course, under the control conditions, we'd expect to see faster RTs for high-N than low-N in the LVF, but no difference in the RVF. Next we consider how dimming should affect RTs, with respect to the corresponding control conditions.

4.1. LVF

4.1.1. Outer-dimming

As discussed above, this should create a smooth spatial gradient. What is the RT for a smooth gradient in the LVF? It is given by the high-N control condition (because top-down input from high-N compensates for the usual, non-smooth gradient). So, under outer-dimming, high-N and low-N should both equal the high-N control condition, giving no N effect.

4.1.2. Inner-dimming

This exacerbates the usual non-smoothness of the gradient. Therefore, the N effect should remain, perhaps with an overall increase in RTs.

4.2. RVF

4.2.1. Inner-dimming

This should replicate the non-smooth LVF gradient. High-N should compensate for this non-smoothness. Therefore, the high-N inner-dimmed condition should equal the RVF control conditions (which give the RT for a smooth gradient). In the low-N condition, the non-smoothness will remain, giving an increased RT and an N effect.

4.2.2. Outer-dimming

This will decrease the input levels to the first and fourth letter nodes somewhat, but their activations should remain relatively high. Unlike the LVF, dimming the first letter should have little effect on the second letter's feature-level activation, due to the lack of strong left-to-right inhibition. Dimming the fourth letter may increase the activation of the third letter node somewhat, although not as much as in the LVF (because the spatial gradient is already smoothly decreasing, due to the acuity gradient). Thus, overall we would expect little effect of dimming the outer letters in the RVF.

These predictions can be quantified as follows. Let R be the reaction time for the non-dimmed, RVF, low-N condition, L be the additional time cost of presentation to the non-dominant hemisphere, and Z be the cost of a non-smooth gradient (low activation of the second and third letters). The expected reaction times for the other control conditions are

RVF, high-N = R LVF, high-N = R + L LVF, low-N = R + L + Z.

4.3. LVF

4.3.1. Outer-dimming

Activation of the outer letter nodes will decrease slightly, but this should not have a large effect, as their activations should remain relatively high. Activation of the second letter node should increase, because the strong left-to-right inhibition from the first letter is reduced at the feature level (providing more bottom-up input to the second letter node). Activation of the third letter node should also increase (because its firing will not be cut off as soon by the fourth letter node). Thus, for the low-N condition, the cost of low internal-letter activation (Z) is removed, giving R + L, while the high-N condition remains R + L. Therefore there should be no N effect under outer-dimming. Note the counterintuitive prediction that such stimulus degradation should produce *facilitation* for low-N (relative to the undimmed control). Essentially, dimming the outer letters should increase activation of the inner letters, mimicking the effect of top-down input to high-N words under the control condition. Thus the low-N outer-dimmed condition should be equivalent to the high-N control condition.

4.3.2. Inner-dimming

There should be no change in the overall bottom-up activation pattern, although further reducing input to the internal letters could create an additional cost. We would expect an N effect to remain, while RTs for both N conditions may increase (compared to the control condition).

4.4. RVF

4.4.1. Inner-dimming

This manipulation will reduce bottom-up input to the internal letters. For high-N, top-down input will compensate, so high-N should remain the same as the control

condition, giving R. However, for low-N, there is no compensation, so the internalletter activation cost is induced, giving R + Z. Thus an N effect should emerge.

4.4.2. Outer-dimming

As in the LVF, there should be little direct cost on the external letters. However, activations of internal letters will not change much in this VF (because there is weaker feature-level left-to-right inhibition, and the spatial gradient is already smoothly decreasing across the final letters, due to the acuity gradient). Therefore, there should be little effect overall, so both the high-N and low-N conditions should remain the same as the control condition, giving R.

In summary, we predict that outer-dimming should decrease reaction times for the LVF low-N condition, and inner-dimming should increase reaction times for the RVF low-N condition. Inner dimming may increase reaction times for the LVF conditions. Dimming in other conditions should have little effect. Therefore, outer-dimming should negate the LVF N effect, via facilitation for low-N. Inner-dimming should create an RVF N effect, via inhibition of low-N. See Fig. 5 for a graphical presentation of our predictions, under the simplest assumptions—that inner-dimming incurs no additional cost in the LVF, and that L and Z are of the same magnitude. The latter assumption is consistent with the results of Lavidor and Ellis (2002a), in which both were on the order of 30 ms.

5. Method

5.1. Participants

Nineteen native English speakers participated in the experiment. All had normal or corrected-to-normal vision and were aged 18–26 (mean age 19.4, SD = 1.6). Each participant received either a course credit or £2. All participants were right-handed and scored at least 80 on the Edinburgh test (Oldfield, 1971). Nine were males, 10 females.

5.2. Design and materials

5.2.1. Stimuli

The word stimuli were 78 4-letter English content words (nouns and verbs). Half of the words had fewer than 10 orthographic neighbors (mean no. of neighbors 6.2). These words formed the low-N group. The remaining words all had more than 12 neighbors (mean 17.0).² These formed the high-N group. As is usually the case for

² Some reviewers commented that the average N value of the low-N group (6.2) reflects a medium, rather than low, value. However since our high-N value is higher than the values employed in other relevant studies (e.g., Holcomb et al. (2002) used mean N of 14 for the high-N group and mean N = 3.71 for the low-N group), the difference between the high-N and low-N values was sufficient, and indeed produced the predicted results.

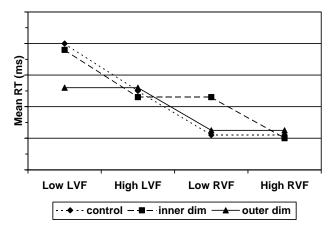


Fig. 5. Predicted reaction-time pattern for the different experimental conditions, under the assumptions that dimming the internal letters in the LVF incurs no additional cost, and that L (cost of presentation to LVF) and Z (cost of low excitation to internal letters) are both on the order of 30 ms, based on the results of Lavidor and Ellis (2002a).

English words, neighbors most frequently differed from their respective target words in the first position. The low-N and high-N groups were matched on written frequency, which was low (mean 10 occurrences per million, Kucera & Francis, 1967), imageability (mean 512), and age of acquisition (mean 360). Each group was divided into three sets, to allow rotation through the three different presentation conditions (control, inner-dimmed, or outer-dimmed). These 6 sets of 13 words each were also matched for written word frequency, imageability, and age of acquisition. The stimuli are given in Appendix A.

Under our proposal that the N effect arises from feedback from the word level to the letter level, followed by feed-foward effects from the letter level specifically to the target word, we focus on words because non-words do not provide a target. Therefore, the non-words were created such that they would amplify the N effect for words (based on Sikaluk, Sears, & Lupker, 2002), and N was not varied for the non-words. The non-words were generated from a different pool of 4-letter words by altering one or two letters, usually replacing the vowels with consonants (however bigrams were always orthographically legal). There was no special effort to match N size of the non-words as they served mainly as the context for the words; however to keep chance performance at 50% level we presented the non-words at the same illumination conditions as the real words.

All stimuli were presented in 14-point Helvetica lower-case font, appearing as high contrast (c = 0.72) white letters on a gray background of 4 cd/m². In the inner-dimmed condition, light-gray patches were projected on the 2nd and 3rd letters of the presented target, so the contrast between the letter and the background color was decreased by 33%; thus these letters were dimmer than the rest of the word. Similarly, two light-gray patches dimmed the 1st and 4th letters in the outer-dimmed condition. In the control condition, no letters were dimmed. See Fig. 6 for an example of the presentation conditions. The stimuli were presented for 180 ms, at a



In the inner-dimmed condition, the contrast of the second and third letters was reduced.



In the outer-dimmed condition, the contrast of the first and fourth letters was reduced.



Fig. 6. Examples of the three presentation conditions used in Experiment 1.

displacement of 2.5° from the fixation point to the center of the word or non-word. The displacement was to the left or to the right of a central focus point (LVF and RVF, respectively).

5.2.2. Design

Each subject was assigned to one of the three versions of the experiment. The different versions rotated the word sets across the experimental conditions (many- and low-N words in control, inner-dimmed, and outer-dimmed conditions). Each target stimuli was presented once to each visual field. The within-subject factors for words were N size (high, low), visual field (RVF, LVF) and presentation condition (control, inner-dimmed or outer-dimmed). Each combination of the within-subject variables was repeated 13 times, so total number of trials per subject was 156.

5.3. Procedure

Stimulus presentation was controlled by an IBM Pentium computer on 17" SVGA display. The participants sat at a viewing distance of 50 cm, with the head positioned in a chin rest. The experiment was designed using Super-Lab version 2.

Each session began with 10 practice trials to introduce the task, followed by 24 additional practice trials of centrally presented letter strings, where the task was to perform lexical decision. Thirty-six additional practice trials presented words and non-words either to the left or to the right of the fixation point. Each trial began with + appearing in the center of the screen for 400 ms. For the first trial, the + remained for 2000 ms, and disappeared when the target word was presented. The + would again reappear to allow projection of the next target word. Targets were briefly presented for 180 ms (either a word or a non-word), to the left or to the right of the focus point. The participant's task was to decide, as quickly and as accurately as possible, whether the stimulus was a legal English word or a non-word. Participants responded by pressing one of two available response keys, labeled 'word' and 'non-word' on a standard 'QWERTY' keyboard. For half of the participants, the response 'word' was made by pressing the 'N' key, and 'non-word' by pressing the 'V' key. For the other half, the response keys were reversed. The participants were randomly assigned to one of the two response options.

6. Results

Since the main manipulation of orthographic neighborhood was designed for the word stimuli, the repeated measures analysis with N (high, low), visual field (right, left) and presentation condition (control, inner-dimmed or outer-dimmed) as the within-subjects variables were conducted only for words. RTs of less than 150 ms and more than 1400 ms were discarded either as anticipatory or excessively lengthy (discarded trials occurred infrequently, less than 2% of the total). Mean reaction times for correct responses are summarized in Table 1, and presented graphically in Fig. 7.

	LVF low-N	LVF high-N	RVF low-N	RVF high-N
Control				
Mean RT	620	595	569	566
SD	72	70	67	66
% Error	19	15	18	18
Inner-dimmed				
Mean RT	611	590	590	569
SD	72	69	73	69
% Error	20	17	18	15
Outer-dimmed				
Mean RT	592	598	555	558
SD	70	84	80	75
% Error	14	20	11	15

Table 1

Mean reaction times (and standard deviations) for word targets in ms and error scores as a function of target orthographic neighborhood size, visual field, and presentation condition for Experiment 1

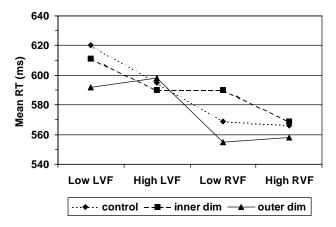


Fig. 7. Mean reaction times for word targets in ms as a function of target orthographic neighborhood size, visual field, and presentation condition (Experiment 1). LOW denotes low-N size, HIGH denotes high-N size.

6.1. Reaction times

Visual field had a significant effect $[F_1(\cdot 1, 18) = 7.2, p < .05; F_2(1, 76) = 6.4, p < .05]$, with RVF words (mean RT = 567 ms) responded to faster than LVF words (mean RT = 601 ms). Presentation type and neighborhood size interacted $[F_1(2, 36) = 4.18, p < .05; F_2$ not significant]. We examined the simple effects of N for each visual condition separately and found that the N effect was significant both in the control condition [F(1, 18) = 5.9, p < .05] and the inner-dimmed condition [F(1, 18) = 8.2, p < .05], but not the outer-dimmed condition.

The interaction between presentation type, visual field, and orthographic neighborhood size was also significant $[F_1(2,36) = 6.3, p < .01; F_2(2,152) = 6.0, p < .01]$. Post hoc Bonferroni (p < .05) comparisons (over subjects and items) yielded that for LVF words, the N effect occurred under both the control and inner-dimmed conditions, but not the outer-dimmed condition. For RVF words, the N effect emerged only under the inner-dimmed condition.

6.2. Error rates

Average error rate was 16%, and the patterns were similar to the RT data. However, no significant effects of visual field, N size, or presentation condition were found (see mean error rates in Table 1).

7. Discussion

The hemispheric specificity of the N effect was replicated for the control conditions, with faster reaction times to high-N than low-N words in the LVF/RH, but not the RVF/LH. In the LVF/RH, dimming the outer letters negated the N effect, via facilitation (relative to the control condition) for low-N, but not high-N. In the RVF/LH, outer dimming had no effect. In the RVF/LH, dimming the inner letters created the N effect via inhibition for low-N, but not high-N. In the LVF/RH, innerdimming had no effect. A comparison of Figs. 5 and 7 shows that the experimental results closely match the predicted pattern.

8. Experiment 2

Experiment 1 showed the predicted patterns for hemifield presentation. It should also be possible to negate the N effect for CVF presentation via a contrast manipulation. However, a different manipulation may be required, since the third letter may be less affected in the CVF than in the LVF. Recall that we propose that input is too high to the fourth letter for LVF presentation, cutting off firing of the third letter. Therefore, dimming the fourth letter would be helpful in mimicking the effect of top-down input from high-N. However, for CVF presentation, the fourth letter would already receive considerably less input than the third letter may not be helpful, because the spatial gradient is already steeply decreasing. Therefore, we initially ran a pilot study to determine what manipulation would negate the CVF N effect. This study indicated that dimming both outer letters did not remove the N effect, while dimming only the first letter did. This difference in suitable dimming patterns between the LVF and CVF is consistent with the proposed differing shapes of the spatial gradient. In Section 9.4, we consider the implications of the different dimming patterns in more detail.

In Experiment 2, we sought to negate the N effect for LVF and CVF presentation within a single study. In the *dimmed* condition, the outer two letters were dimmed for LVF and RVF presentation, while only the first letter was dimmed for CVF presentation. The respective control conditions remained the same as in Experiment 1. We expected to replicate the results from the outer-dimmed conditions in Experiment 1, and to negate the CVF N effect by facilitating responses to low-N words.

9. Method

9.1. Participants

Twenty-five native English speakers participated in the experiment. All had normal or corrected-to-normal vision and were aged 18–28 (mean age 19.6, SD = 1.9). Each participant received either a course credit or £2. All participants were righthanded and scored at least 80 on the Edinburgh test (Oldfield, 1971). Eleven were males, 14 females.

9.2. Design and materials

9.2.1. Stimuli

The stimuli of Experiment 1 were used here (see Appendix A).

9.2.2. Design

Each subject was assigned to one of the three versions of the experiment. The different versions rotated the word sets across the experimental conditions. The withinsubject factors for words were N size (high, low), visual field (RVF, LVF or centre) and presentation condition (control or outer-dimmed). Each combination of the within-subject variables was repeated 13 times. The outer-dimmed condition included dimming of the two external letters for the RVF and LVF presentations, and dimming the first letter for the centrally presented stimuli.

9.2.3. Procedure

The procedure was similar to Experiment 1's procedure.

9.3. Results

Since the main manipulation of orthographic neighborhood was designed for the word stimuli, the repeated measures analysis with N (high, low), visual field (right, left, and centre) and presentation condition (control or outer-dimmed) as the within-subjects variables were conducted only for words. The results of one participant were not included in the analysis due to low-accuracy performance (below chance level). RTs of less than 150 ms and more than 1400 ms were discarded either as anticipatory or excessively lengthy (discarded trials occurred infrequently, about 2% of the total). Mean reaction times for correct responses are presented in Table 2 and Fig. 8.

9.3.1. Reaction times

Table 2

Visual field had a significant effect $[F_1(2, 46) = 10.3, p < .01; F_2(2, 152) = 8.1, p < .01]$, with centrally presented words (mean RT = 478 ms) yield fastest responses, followed by RVF words (mean RT = 536 ms), than by LVF words (mean RT = 567 ms), post hoc differences were analyzed employing Bonferroni comparisons (p < .05).

The interaction between presentation type, visual field, and orthographic neighborhood size was also significant $[F_1(2,46) = 5.8, p < .01; F_2(2,152) = 4.9,$

Mean reaction times (and standard deviations) for word targets in ms and error scores as a function of target orthographic neighborhood size, visual field, and presentation condition for Experiment 2

-						
	LVF few N	LVF many N	CVF few N	CVF many N	RVF few N	RVF many N
Control						
Mean RT	582	560	495	472	537	540
SD	59	65	57	60	71	66
% Error	16	12	10	8	13	11
Outer-dimn	ned (1st and 4th	h letters, 1st lette	r for the CVF)			
Mean RT	558	570	471	479	536	533
SD	63	62	58	55	59	60
% Error	14	15	9	10	13	11

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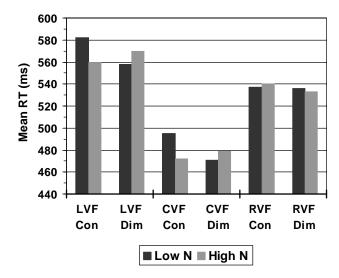


Fig. 8. Mean reaction times for word targets in ms as a function of target orthographic neighborhood size, visual field, and presentation condition (Experiment 2). CON denotes the control condition, and DIM denotes the dimmed condition.

p < .05]. Post hoc Bonferroni (p < .05) comparisons yielded that for LVF and CVF words, the N effect occurred for the control condition, but not the outer-dimmed condition. For RVF words, there was no N effect in any condition.

9.3.2. Error rates

Average error rate was 11%, and the patterns were similar to the RT data. However, no significant effects of visual field, N size, or presentation condition were found.

9.4. Discussion

In the control condition, N effects for the CVF and LVF, but not the RVF, were replicated. The dimmed condition for the LVF and RVF (wherein the outer letters were adjusted) replicated the results from Experiment 1— the LVF N effect was negated via facilitation for low-N, while dimming had no effect in the RVF. Crucially, the CVF dimmed condition (wherein only the first letter was adjusted) negated the N effect, via facilitation for low-N, but not high-N. Thus the predicted results were achieved.

The finding from pilot studies that dimming the outer letters in the CVF did not abolish the N effect would seem to indicate that there was a deleterious effect of dimming the fourth letter, for which top-down input from high-N compensated, giving an N effect. This is consistent with the claim that input to fourth letter is relatively too high in the LVF but not the CVF. However, we have also assumed that dimming the outer letters should have little direct inhibitory effect, because the corresponding letter-node activations would remain relatively high. The results from both experiments are consistent with this assumption, as there was no effect of outer-dimming in the RVF. But now there is something of a conflict—the implication of a deleterious effect of dimming the final letter in the CVF, but not the LVF or RVF.

Perhaps, it is the case that dimming the fourth letter does have an inhibitory effect in general (due to reduced activation of the fourth letter-node), and the net effect of dimming that letter depends on the relative level of input to the third letter node. For LVF presentation, where the spatial gradient is proposed to be quite shallow across the third and fourth letters (due to incomplete inversion of the acuity gradient), the facilitative effect of increased firing time for the third letter (due to delayed firing of the fourth letter) may dominate. For RVF presentation, where the spatial gradient is proposed to be steeper across the final positions (due to the decreasing acuity gradient), dimming the fourth letter may create some facilitation at the third letter, which cancels an inhibitory effect at the fourth letter, giving no overall effect. It is well known that the slope of the acuity gradient increases as eccentricity decreases. Therefore, the spatial gradient across the final letters should be even steeper for CVF presentation than for RVF presentation. In this case, dimming the fourth letter may provide no benefit at the third letter (because it could already fire for a relatively long time), so there is a net inhibitory effect due to reduced activation of the fourth letter. Increased top-down input to the fourth letter due to high-N may then compensate for this effect. Thus, the RVF outer-dimming results may reflect cancellation of inhibitory and excitatory effects rather than an absence of such effects.

10. General discussion

Experiments 1 and 2 showed that it is possible to create or negate the N effect by altering bottom-up activation patterns via contrast manipulations, as predicted. In Experiment 1, we succeeded in reversing the asymmetry of the N effect; the N effect was abolished in the LVF and created in the RVF. In Experiment 2, we succeeded in abolishing the N effect in both the LVF and CVF. While the proposed underlying mechanisms may seem somewhat complex, we note that a simple explanation of our results does not suffice. It cannot be the case that dimming the outer letters was facilitative for LVF, low-N words simply because the internal letters were unmasked at a very low level. In that case, there should have been a similar effect in the RVF, yet none was found. It could not be the case that such RVF facilitation did not occur simply because the stimuli were less degraded than in the LVF, as we demonstrated a facilitation in the least degraded location, the CVF. The fact that the LVF and CVF N effects were abolished via facilitation of low-N words indicates that we have replicated the facilitation normally generated by high-N words. Moreover, the creation of an RVF N effect by dimming the internal letters indicates that the reason that such an effect does not normally occur is that those letters are usually more highly activated. This places the locus of the $VF \times N$ -effect interaction squarely at the level of hemisphere-specific, orthographic activation patterns. The SERIOL model explains the source and nature of these patterns.

We also note that the explanation of these effects is entirely based on a pre-existing model. The representations and the transformations in the SERIOL model were originally independently motivated by the architecture of the visual system, the results of behavioral experiments, and theories of neural information processing based on neurobiological experiments, brain-imaging studies, and mathematical considerations (Whitney, 2001a). Whitney later set out to construct an account of the VF × N-effect interaction that would be consistent with the existing model. After much analysis, Whitney was only able to construct a single account of this interaction under the strong constraints placed by the model on any such explanation (Whitney, 2004). This account generated very precise predictions, which have been presented and verified here. The only change from the original model (Whitney, 2001a) is the explicit consideration of top-down excitation. No other model could have generated these unexpected and counterintuitive predictions, which have allowed the N effect to be created or abolished for the first time. Next, we consider the implications of our results for various issues in visual word recognition.

10.1. Locus of the facilitative N effect

The fact that manipulations of contrast modulated the N effect indicates that its primary locus is the letter level. Other accounts of the N effect based on total word-level activations (Grainger & Jacobs, 1996) or phonological representations (Ziegler & Perry, 1998) cannot explain the demonstrated effects of manipulating the visual properties of letters.

However, the MROM model (Grainger & Jacobs, 1996) accounts for a range of data in lexical decision, such as sensitivity to stimulus characteristics, based on the idea that threshold to total word-level activations can be dynamically modified. How then could such sensitivity be explained under our account of the N effect? It may be the case that threshold to *single* items can be dynamically altered. Although the MROM model assumes that this is not the case, such an assumption is not necessarily well founded. For example, it seems reasonable that the single-item threshold driving initiation of a saccade may be higher for proofreading than for rapid scanning of text. Similarly, a single-item threshold driving lexical decision may also be sensitive to task demands which are influenced by stimulus characteristics.

We suggest that variations in the N effect with task and stimuli can be accounted for by dynamic setting of a single-item threshold, changes to the balance of inhibitory and excitatory influences, and differences in task sensitivity to single-item lexical activation levels. We discuss in more detail below how language, neighbor frequency and position of mismatch may change the balance of excitatory and inhibitory factors, although a full account of all N and lexical-decision effects is beyond the scope of this article.

However, some have argued against a letter-level locus of the N effect (Browosky & Besner, 1993; Reynolds & Besner, 2004) based on the absence of an interaction between stimulus quality and word frequency in lexical decision (Balota & Abrams, 1995; Browosky & Besner, 1993; Stanners, Jastrzembski, & Westbrook, 1975). That is, when letter contrast is uniformly low, the cost of this degradation does not vary

with the frequency of the target word. If there were feedback from the word level to the letter level, this should cause an interaction between stimulus quality and a lexical attribute, such as frequency. The lack of such an interaction has been taken as indicating that processing is staged, rather than interactive. That is, computations are completed at the letter level before being passed on to the word level, as opposed to a continuous interaction between levels.

However, we point out that this finding is not inconsistent with our model, or our experimental results. Note that the SERIOL model is not a fully interactive; letter activations only occur at specific time intervals. Although we have not fully specified all the timing relationships between levels, the implicit assumption is that there is gating between the feature and letter levels. The induction of the correct firing order at the letter level depends on the proper activation pattern at the feature level. Thus, the feature level must settle into this pattern before it activates the letter level. If the letter nodes were activated while the feature level input must be passed to the letter level at the start of an oscillatory cycle. Therefore there has to be some co-ordination between the feature and letter levels, so that feature level activation affects the letter level at the right time. Thus, we assume a staged activation. So, the effects of uniformly low stimulus quality may be resolved before the feature level is allowed to activate the letter level, consistent with the lack of interaction between overall stimulus quality and frequency.

However, this does not rule out the possibility of feedback from the word level affecting the letter level at a later point in processing. Such feedback would not interact with overall effects of stimulus quality, which have been resolved prior to activation of the letter level. However, this feedback would interact with the resulting activation pattern passed forward from the feature level. Consistent with this scenario, we have demonstrated an interaction between the N effect and positional manipulations of letter contrast. Thus, we have demonstrated an interaction between a lexical attribute and stimulus quality, indicating that feedback from the word to letter level does occur, and is the primary source of the N effect in lexical decision.

It has been observed that a facilitative effect of N is not present for high-frequency target words (Andrews, 1989; Sears et al., 1995). Why might this be the case? While an explanation of this interaction falls beyond the scope of the SERIOL model, we offer one possibility. It is generally assumed that lexical activation of high-frequency words occurs more quickly than low-frequency words. Due to this faster activation, there may be a ceiling effect, where increased input from the letter level (from feedback due to high-N) has little additional influence on the activations of word nodes representing high-frequency words. That is, the activation rate of a low-frequency word node may be more sensitive to small differences in the amount of input than the activation rate of a high-frequency word. Similarly, the lack of an irregularity effect for high-frequency words (Paap & Noel, 1991; Seidenberg, Waters, Barnes, & Tanenhaus, 1984) as been taken to arise from the faster activation of their lexical representations (Coltheart, Rastle, Perry, Langdon, & Ziegler, 2001; Paap & Noel, 1991; Whitney, Berndt, & Reggia, 1996).

Andrews (1997) noted that the N effect appears less strong in French and Spanish than in English (e.g., Carreiras et al., 1997). Our conclusion that feedback excitation to the letter level is the primary source of the N effect can potentially account for such a linguistic difference. Under the assumption that the reading lexicon also provides the spelling lexicon (Burt & Tate, 2002), spelling could be represented by connections from a word node back to the letter nodes. In languages with shallower orthographies than English, such as Spanish and French, it is less necessary to encode spelling via word-to-letter connections, since spelling is predictable from phonology. Therefore, excitatory word-to-letter connections may be weaker in such languages. That is, spelling may depend more on phonology-to-orthography than on word-to-orthography connections. If top-down connections are weaker, excitation from high-N would be reduced in these languages, accounting for a reduced facilitative influence of N.

10.2. Orthographic similarity

Our proposal that the internal letters are the primary source of the N effect implies that the position of difference between a target and its neighbor should matter. A neighbor should be most facilitative when it matches on the internal letters. Indeed, there are experimental results consistent with this analysis (Ziegler & Perry, 1998). In those experiments, N was held constant while the number of words matching the target's body (body neighbors, BN) was varied, and, in another set of words, BN was held constant while N was varied. In the BN manipulation, high BN was facilitative, (as compared to low BN). In the N manipulation, high-N had no effect. Thus facilitation depended on a large number of body neighbors, not N-metric neighbors, in line with the proposed importance of the internal letters. Since BN and N are usually highly correlated, these results suggest that the standard N effect results from body neighbors. Of course, body neighbors would also send top-down excitation to the final letter. However, under the assumption of a top-down activation gradient, topdown input to the second and third letters would be stronger, and these effects would dominate.

Under the bigram encoding, a word node corresponding to body neighbor would not become highly activated, because it likely would not match on the important first letter. Thus, we propose that the N effect occurs as a result of top-down input to letter nodes via the summed excitation of a large number of *moderately* active word nodes. This leaves open the possibility of an inhibitory effect for a *highly* activated non-target word node, as would be expected from lateral inhibition within the word level.

This proposal explains observed influences of higher frequency neighbors. In French, the existence of a higher frequency neighbor mismatching a five-letter target at the fourth letter has an inhibitory effect, while one mismatching at the second letter does not (Grainger et al., 1992). Under the SERIOL model, a neighbor mismatching at the fourth letter would be highly activated by the target, since all of the highly weighted bigrams are matched. In contrast, a neighbor mismatching at the second letter would be less activated (and would provide less lateral inhibition)

within the word level), since some highly weighted bigrams are not matched. Thus, a neighbor mismatching on the fourth letter could provide much stronger lateral inhibition to the target than one mismatching on the second letter, accounting for the observed results. In a similar vein, Perea (1998) has shown that a neighbor prime mismatching a five-letter target in the third or fourth positions is inhibitory, while one mismatching in other positions is not. This pattern could not have resulted from the activation level of the neighbor, as each neighbor was directly activated to same degree by the prime. However, it may be the case that inhibitory connection weights are stronger between more similar words, to facilitate competition where it matters most. Thus, these results may reflect such learned relationships between words. A word formed by transposing two letters of the target, such as SALT and SLAT, is also highly activated under the bigram metric, because most of the bigrams are shared (Grainger & Whitney, 2004). This accounts for the finding that having such a transposed-letter neighbor can be inhibitory (Andrews, 1996).

Thus, the graded similarity levels that emerge from the bigram encoding can account for seemingly contradictory findings on the effects of words that are similar to a target word, where facilitative, inhibitory, and null effects have all been observed. Inhibitory effects can occur for high-frequency neighbors that are highly activated under the bigram metric, especially in shallow-orthography languages where topdown excitatory effects may be weaker. Excitatory effects can occur when a large number of neighbors are moderately activated, so that the target word does not receive strong lateral inhibition, and top-down excitatory effects dominate. As lowerfrequency neighbors would yield lower lexical activation levels, this suggests that lower-frequency neighbors should be the primary source of the facilitative N effect, which seems to be the case (Paap & Johansen, 1994; Pollatsek et al., 1999).

10.3. Locus of visual field asymmetries

The fact that the normal visual-field \times N-effect interaction was overridden by our manipulations demonstrates that it does not reflect inherent hemispheric differences at the level of lexical access. These results disprove an account of the N asymmetry based on hemisphere-specific granularities of sub-lexical units (Monaghan et al., 2004; Monaghan, pers. comm.), as it should not be possible to reverse the asymmetry under such an account. Rather, we have shown that an asymmetric word-level effect can result from differences in processing near the visual level. As discussed in Section 1, we have also demonstrated that similar manipulations of letter contrast can reverse the asymmetry of the length effect (Whitney & Lavidor, 2004).

These results demonstrate that hemispheric asymmetries at the lexical level do not necessarily entail different modes of lexical access. Rather, hemisphere-specific activation patterns are the cause of these asymmetries. Thus, the locus of visual-field effects seems to be lower in the processing stream than is commonly assumed, consistent with brain-imaging data showing that processing becomes left-lateralized at a pre-lexical level (Cohen et al., 2000; McCandliss et al., 2003; Tarkiainen et al., 1999). Our results and the brain-imaging data suggest that it is inappropriate to use visual half-field studies to investigate linguistic-level hemispheric specificity. As such

studies are widely used for such a purpose, it is quite important to clarify the source of observed asymmetries. In future work, we will try to extend our findings to semantic asymmetries in order to further support our claim that hemifield differences reflect activation patterns at the orthographic level, rather than specialization at the lexical level and above.

10.4. Letter-position encoding

Our highly specific, counterintuitive predictions were based on the details of spatial gradient formation from the SERIOL model. The confirmation of these predictions provides strong support for the idea that letter-position encoding employs a spatial activation gradient, the formation of which requires hemisphere-specific processing, giving differing activation patterns across the visual fields. Although our experimental results do not directly confirm the claim that the spatial gradient induces a serial encoding of letter order, the proposed dynamics do explain why top-down feedback has no effect when the internal letters already receive a relatively high level of excitatory bottom-up input.

In sum, the experiments presented here help answer key questions in visual word recognition, shedding light on the locus of the N effect, the nature of orthographic similarity, the source of hemispheric asymmetries, and the neural mechanisms of let-ter-position encoding. These results also demonstrate the feasibility of bridging the neural and cognitive levels via the close integration of modeling and experimental work.

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Low-N			High-N		
Set A	Set B	Set C	Set A	Set B	Set C
beau	arch	babe	bush	beam	bite
cube	aunt	coal	cage	bolt	boot
earl	chop	crab	cone	deer	cake
germ	disc	gasp	dent	duck	cart
gulf	duel	grip	dusk	dump	dock
heap	fork	jerk	hank	gang	hail
howl	lamb	lens	herd	gore	hint

Appendix A. Stimuli for Experiments 1 and 2

(continued on next page)

Low-N			High-N	High-N		
Set A	Set B	Set C	Set A	Set B	Set C	
newt	menu	liar	hind	hose	hush	
oath	omen	oven	hump	lime	joke	
palm	plug	raid	mall	maze	leak	
shed	prey	riot	mule	pump	mist	
soap	roar	sand	nail	rent	port	
swim	suds	sigh	rust	rope	rake	

Appendix	A.	(continued)
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