The Perceptual Magnet Effect as an Emergent Property of Neural Map Formation

Frank H. Guenther and Marin N. Gjaja

Boston University
Center for Adaptive Systems and
Department of Cognitive and Neural Systems
677 Beacon Street
Boston, MA, 02215
Fax Number: (617) 353-7755

email: guenther@cns.bu.edu

Running title: Magnet Effect and Neural Maps

Journal of the Acoustical Society of America (1996) vol. 100, pp. 1111-1121.

ABSTRACT

The perceptual magnet effect is one of the earliest known language-specific phenomena arising in infant speech development. The effect is characterized by a warping of perceptual space near phonemic category centers. Previous explanations have been formulated within the theoretical framework of cognitive psychology. The model proposed in this paper builds on research from both psychology and neuroscience in working toward a more complete account of the effect. The model embodies two principal hypotheses supported by considerable experimental and theoretical research from the neuroscience literature: (1) sensory experience guides language-specific development of an auditory neural map, and (2) a population vector can predict psychological phenomena based on map cell activities. These hypotheses are realized in a self-organizing neural network model. The magnet effect arises in the model from language-specific nonuniformities in the distribution of map cell firing preferences. Numerical simulations verify that the model captures the known general characteristics of the magnet effect and provides accurate fits to specific psychophysical data.

Frank Guenther is supported in part by the Alfred P. Sloan Foundation, the National Institutes of Health (1 R29 DC02852-01), and the Office of Naval Research (ONR N00014-95-1-0409). Marin Gjaja is supported in part by the National Science Foundation (NSF IRI 94-01659) and the Office of Naval Research (ONR N00014-95-1-0409 and ONR N00014-95-0657).

1. Introduction

The perceptual magnet effect (Kuhl, 1991) is one of the most actively discussed topics in the recent speech perception literature (e.g., Davis and Kuhl, 1994; Fox, Flege, and Munro, 1995; Iverson, Diesch, Siebert, and Kuhl, 1994; Iverson and Kuhl, 1994, 1995; Kuhl, 1991, 1995; Kuhl, Williams, Lacerda, Stevens, and Lindblom, 1992; Lacerda, 1995; Polka, 1995; Sussman and Lauckner-Morano, 1995). Roughly speaking, the effect is characterized by a warping of perceptual space such that acoustic patterns near phonemic category centers are perceived as closer together than equally spaced acoustic patterns that are further away from phonemic category centers. Because the effect is language-specific, it is assumed that newborn infants will not show the effect (although other, language-independent biases might exist at birth; see Polka, 1995), but by six months of age a language-specific magnet effect arises (Kuhl, 1991; Kuhl et al., 1992) and is apparently maintained through adulthood (Kuhl, 1991).

Previous attempts to explain this effect have typically been formulated within the theoretical framework of cognitive psychology. Kuhl (1995) proposes a native language magnet (NLM) model of infant perceptual development that includes an account of the magnet effect. Kuhl's account assumes that a phonetic "prototype" for each sound category exists in memory and plays a unique role in speech perception: it functions like a "perceptual magnet" for other sounds in the category that "attracts" these sounds so that they sound more similar to the prototype itself. The explanation put forth by Lacerda (1995) suggests that the effect occurs as an emergent property of an exemplar-based categorization process. Infants store exemplars of each category and compare new inputs to these exemplars. The perceived distance between two inputs is related to the relative number of exemplars from different categories in the immediate neighborhoods of the inputs. Lacerda's model assumes no special prototype (cf. Kuhl's explanation) and magnet effect properties arise due to the distribution of examples that the infant experiences.

In contrast to these psychological explanations, this article provides an explanation for the magnet effect using tools from computational neuroscience. This explanation arises from natural extensions of neural principles used to study other sensory and motor modalities in the brain. The claim is that the magnet effect is a simple consequence of the formation of neural maps in the auditory system. These maps are assumed to develop according to the same principles believed to be involved in map formation for other modalities such as vision (e.g., Grossberg, 1976; Kohonen, 1982; von der Malsburg, 1973) and somatic sense (e.g., Gaudiano, Olson, Tal, and Fischl, 1993; Pearson, Finkel, and Edelman, 1987; Sutton, Reggia, Armentrout, and D'Autrechy, 1994). In this account, exposure to a particular language leads to nonuniformities in the distribution of the firing preferences of map cells, and this nonuniformity leads to the magnet effect. It is further hypothesized that a second well-known theoretical tool from neuroscience, the *population vector* (Georgopoulos, Caminiti, Kalaska, and Massey, 1983; Georgopoulos, Kalaska, Crutcher, Caminiti, and Massey, 1984), can be used to predict psychological events based on the cell activities of the auditory map. Because this account posits explanations for the nature of memory and perception in terms of the properties of neural systems, it also represents an attempt at a direct linkage of concepts from cognitive psychology to concepts from neuroscience.

Although the current work can in some respects be interpreted as a neuroscientific account of Kuhl's (1991, 1995) magnet effect explanation (see Section 3) and, to a lesser degree, Lacerda's (1995) model, many important differences exist. Like the explanations of Kuhl and Lacerda, the current model assumes that the magnet effect is related to the distribution of speech sounds experienced by an infant in the first stages of life. In contrast with Kuhl's explanation, however, stored category prototypes do not play a direct or special role in the current model's account of the magnet effect. Instead, perceptual warping occurs due to nonuniformities in the distribution of firing preferences of cells in an auditory neural map, which in turn are the result of nonuniformities in the distributions of sounds experienced by the infant. The current model

is similar to Lacerda's model in that no special prototype is needed to explain the effect, but the two models differ in many other aspects. First, Lacerda's explanation requires that the infant has labeled exemplars; that is, the infant must know the category to which each stored sound belongs. An explanation that does not require linguistic category knowledge probably better captures the phenomenon when one considers that the effect is already present by six months of age, likely before infants have developed awareness of phonemes as linguistic units (Kuhl, 1995). The current explanation does not require any knowledge of the linguistic categories of experienced sounds; exposure to the statistical distribution of sounds in the native language is all that is needed to produce the effect. Thus, the magnet effect is treated as a simple perceptual phenomenon rather than a higher-level phenomenon involving linguistic categories. Second, Lacerda assumes that experienced sounds are stored in memory individually. This explanation becomes cumbersome when one realizes that infants have likely experienced hundreds of thousands of vowels by six months of age (Kuhl, 1995), suggesting that an increasingly large amount of memory must be devoted to the process of vowel perception. In the current explanation, however, inputs are not stored explicitly but instead modify the firing preferences of a fixed number of cells in a neural map. The distribution of the experienced inputs affects the distribution of these firing preferences, but memory requirements do not increase with the number of experienced sounds since the number of cells and synaptic weights used in the map are fixed. Third, Lacerda's model uses rather complex calculations to determine category membership and perceived distance. In the current model, however, the effect arises from calculations that are believed by many to be basic properties of neural systems.

The next section describes the model and motivates its two main assumptions: (1) language-specific auditory experience leads to a nonuniform auditory map, and (2) the population vector provides a means for predicting perceptual effects from neural activities in this map. In Section 3, numerical simulations are used to show that the model captures the main known aspects of the magnet effect, including a shrinking of perceptual space near phonemic category centers (Kuhl, 1991), an expansion of perceptual space away from centers (Kuhl, 1995), and language-specificity in this warping (Kuhl et al., 1992). The simulation results reported in this section include accurate fits to data from psychophysical studies of the magnet effect. This section also includes a discussion of an apparently paradoxical aspect of the magnet effect highlighted by the current model: unlike the results of many other studies which show better discrimination for heavily experienced stimuli, the magnet effect is characterized by *worse* discrimination for more typical vowel stimuli. Finally, Section 4 relates a magnet effect description in psychological terms to the current model's description in neuroscientific terms and places the model in the context of a larger modeling framework of speech development and production called DIVA (Guenther, 1994, 1995a,b).

2. Model Description

A schematic view of the model is provided in Figure 1. The model uses two layers of neurons, referred to as the formant representation and the auditory map, connected by a set of adaptive weights. For clarity, only a subset of the pathways projecting from the formant representation to the auditory map are shown; however, all formant representation cells project to all auditory map cells in the actual implementation. Similarly, the competitive interactions implied by the inhibitory connections (marked by "-" signs) are assumed to occur between all cells in the map. These competitive interactions are not explicitly modeled but are instead subsumed in the auditory map cell firing properties as discussed below.

Formant Representation. The model assumes that peripheral auditory processing yields a neural representation of the formant values of speech sounds. The simulations reported here used formants measured in mels; nearly identical results were obtained in unreported simulations using formants in Hertz. A normalized, agonist-antagonist neural representation was used for each formant. Specifically, the neural representation of the formants for a sound was defined as follows:

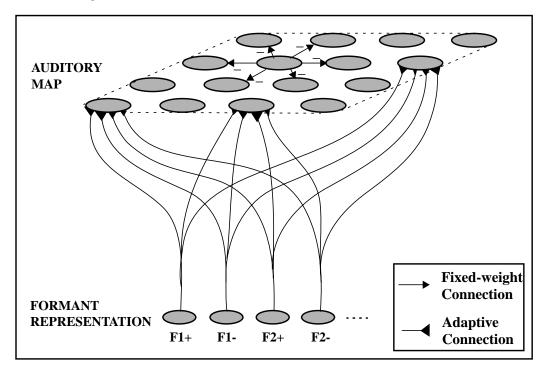


FIGURE 1. Schematic of the model. Input sound patterns activate cells at the formant representation level. These cells project through adaptive synaptic weights to cells in an auditory map. The adaptive weights determine the firing preferences of cells in the auditory map. During early exposure to sounds from a particular language, these weights self-organize such that the distribution of firing preferences of auditory map cells reflects the distribution of sounds in the language. The non-uniformity of this distribution of map cell firing preferences leads to the magnet effect in the model.

$$x_i^+ = \frac{F_i - F_{i \text{ MIN}}}{\sqrt{(F_i - F_{i \text{ MIN}})^2 + (F_{i \text{ MAX}} - F_i)^2}}$$

$$\bar{x_i} = \frac{F_{i \text{ MAX}} - F_i}{\sqrt{(F_i - F_{i \text{ MIN}})^2 + (F_{i \text{ MAX}} - F_i)^2}}$$
(1)

where the index i indicates the formant number, x_i^+ and x_i^- are the activities of the antagonistically paired cells coding the i^{th} formant, F_i is the value of the i^{th} formant in Mels or Hertz, F_i^- MIN is the minimum value of the i^{th} formant in the simulations, and F_i^- MAX is the maximum value of the i^{th} formant. The constants F_i^- MIN and F_i^- MAX are parameters that insure that the cell activities x_i^+ and x_i^- vary between 0 and 1. (All parameter values used in the simulations are reported in the Appendix.) Each simulation used only two formants, either F1 and F2 or F2 and F3.

The normalized, agonist-antagonist formant representation of Equation 1 was chosen to insure that the total activity in the formant representation was the same regardless of the formant values of the input sound. For example, a low value of F1 leads to a small value of x_1^+ and a large value of x_1^- , whereas a high value of F1 leads to a large value of x_1^+ and a small value of x_1^- . If the antagonist cells x_i^- were not included, input sounds with low formants would not produce much activity in the formant representation,

and this would lead to an undesirable bias in the learning process described below. Agonist-antagonist neural representations are common in biological nervous systems.

It is important to note that similar results would be expected for many different neural representations of formant values. For example, von der Malsburg (1973), Pearson et al. (1987), and Sutton et al. (1994) describe self-organizing neural maps that use very different input representations from the one used here. It is further expected that the main results reported herein will hold with input representations that include more than the first two formants; this limited representation was used to simplify the simulations and graphical presentation of simulation results.

Auditory Map. In keeping with most models in the neural network literature, the input to each cell in the auditory map is calculated as the dot product of the input vector (i.e., the neural representation of formant values) and the vector of weights projecting to the map cell. When an input is received, the L cells in the map with the largest input are allowed to remain active, and the activities of all other nodes in the map are set to zero. This process approximates the effects of competitive interactions between map cells (Grossberg, 1976; Kohonen, 1982; von der Malsburg, 1973), and the inhibitory synaptic connections believed to mediate this type of competition are seen in primary sensory areas of cortex, including auditory cortex, somatosensory cortex, and visual cortex (Kandel, Schwartz, and Jessell, 1991). During training, L is a monotonically decreasing function of time, as implemented in the self-organizing feature map of Kohonen (1982). When testing the network, a fixed value of L is used. The activity levels of the L map cells with the largest input are assumed to be proportional to the sizes of their inputs:

$$m_{j} = \frac{\sum_{i} x_{i}^{+} z_{ij}^{+} + x_{i}^{-} z_{ij}^{-}}{M}$$
 (2)

where m_j is the activity of the j^{th} map cell, z_{ij}^+ and z_{ij}^- are modifiable synaptic weights projecting from the i^{th} antagonistic cell pair of the formant representation to the j^{th} map cell, and M is the number of cells in the map.

The learning process used to adjust the synaptic weights between formant representation cells and cells in the auditory map is defined by the following "instar" learning equation (Grossberg, 1969):

$$\frac{dz_{ij}^+}{dt} = \alpha m_j (x_i^+ - z_{ij}^+)$$

$$\frac{dz_{ij}^{-}}{dt} = \alpha m_j (x_i^{-} - z_{ij}^{-})$$
(3)

where α is a learning rate parameter. This is essentially the same learning law that is used in many other models of map formation, including the models of von der Malsburg (1973), Grossberg (1976), and Kohonen (1982). Nearly identical learning laws have also been put forth by neurophysiologists to explain observed synaptic strength changes in areas such as visual cortex (Rauschecker and Singer, 1979, 1981) and hippocampus (Levy and Steward, 1979); see Levy and Desmond (1985) for a short review.

One key property of this model is that the distribution of firing preferences of auditory map cells comes to reflect the distribution of the inputs used to train the model (see Kohonen, 1982), which in turn reflect the distribution of sounds in a particular language. This represents one of the two main hypotheses embodied by the model, and in Section 3 we will see how this property leads to the magnet effect in model simula-

tions. Such experience-based nonuniformities in the distribution of cell firing preferences have been identified by neurophysiologists studying sensory maps in several different modalities. Probably the most wellknown examples of this phenomenon come from studies of visual cortex. For example, limiting visual experience to one eye in kittens leads to many more cells in V1 devoted to the working eye than in normal kittens (Wiesel and Hubel, 1963). Studies of kittens reared in an environment consisting only of contours oriented in one direction (e.g., vertical stripes) indicate that more cells become tuned to the heavily experienced stimulus than to contours of other orientations (e.g., Rauschecker and Singer, 1981). Several neural network models utilizing competitive interactions in neural maps similar to the model proposed here have been used to explain many of these results (e.g., Grossberg, 1976; Kohonen, 1982; von der Malsburg, 1973). Analogous neurophysiological results have been found in somatosensory cortex, where topographic map reorganization results from peripheral nerve damage (Kaas, Merzenich, and Killackey, 1983) or preferential stimulation of certain digits (Jenkins, Merzenich, and Ochs, 1984; Jenkins, Merzenich, Ochs, Allard, and Guíc-Robles, 1990). Again, several neural models using competitive learning have been proposed to explain these data (e.g., Gaudiano et al., 1993; Pearson et al., 1987; Sutton et al., 1994). Moreover, studies from auditory cortex, more relevant to the current model, have shown similar results. Reorganization of auditory cortex topography after partial cochlear lesions has been reported in guinea pigs (Robertson and Irvine, 1989) and cats (Irvine, Rajan, Wize, and Heil, 1991), and Recanzone, Schreiner, and Merzenich (1993) showed that repeated exposure to tones in a particular frequency range during learning of a discrimination task in owl monkeys resulted in an increase in the number of auditory cortex cells tuned to the trained frequency. The current model's hypothesis that the distribution of auditory map cell firing preferences reflects the distribution of sounds in an infant's native language is very much in keeping with these results.

The Population Vector. After the model described in the preceding paragraphs is trained by exposure to a set of sounds approximating the distribution of sounds in a particular language, we are left with the problem of interpreting map cell activities in perceptual terms. The second major hypothesis of the current model is that a population vector (e.g., Georgopoulos et al., 1983, 1984) can be used to predict psychological phenomena from the pattern of neural activities in this map. This population vector is calculated as follows. Each cell in the current model's auditory map will be maximally activated by a particular vector in formant space (e.g., a particular F1-F2 pair). This formant vector is the one whose neural representation at the first stage of the model is parallel to the vector of weights projecting to the auditory map cell. This is clear when one considers that the input to each map cell is the dot product of the neural representation vector and the cell's afferent weight vector, and the dot product of two vectors is maximal when the angle between them is zero. The formant vector that maximally activates the j^{th} auditory map cell will be referred to as its *preferred stimulus* and denoted as F_j . It is assumed that the perceived sound can be derived from the pattern of cell activities at the auditory map using the following population vector equation:

$$\vec{F}_{perceived} = \frac{\sum_{j} m_{j} \vec{F}_{j}}{\sum_{i} m_{j}}$$
(4)

Population vectors of this form have been used by neuroscientists to predict behavioral and psychological phenomena from the ensemble of cell firing rates in a neural map. The population vector was originally formulated to interpret single cell recording data from the arm map region of motor cortex in monkeys performing reaches to targets (Georgopoulos et al., 1983, 1984). In these studies, a preferred movement direction is calculated for each cell by finding the spatial movement direction which results in maximal firing of the cell. The firing levels of many cells are measured while producing the same spatial reach. The population vector is calculated by multiplying each cell's firing rate by it's preferred direction vector, then sum-

ming this quantity over all the cells. The resulting vector has been shown to point in the direction of the actual movement with significant accuracy (e.g., Georgopoulos et al., 1984; Georgopoulos, Kettner, and Schwartz, 1988). The population vector has been similarly used to study cell responses related to reaching in premotor cortex and Area 5 of posterior parietal cortex; see Kalaska and Crammond (1992) for a recent review.

Why do these population vector analyses work? To provide one possible answer to this, it is useful to consider models of motor cortical function during reaching movements. In two recent neural network accounts of reaching (Bullock, Grossberg, and Guenther, 1993; Burnod et al., 1992), it is assumed that motor cortical cells are activated by upstream mechanisms coding the desired spatial direction of movement, and the contribution of each motor cortical cell to downstream mechanisms that command joint rotations is a vector in joint velocity space that would move the hand in the desired spatial direction. The net effect of all active motor cortical cells is summed at the cells commanding joint rotations, with the size of a motor cortical cell's contribution being proportional to its firing rate. In these models, therefore, the joint rotations that move the arm are formed as a weighted average of the contributions of the motor cortical cells in a manner very similar to the weighted averaging that produces the population vector.

Since the landmark reaching studies of Georgopoulos and colleagues, the population vector has been used to interpret activity patterns across neuronal populations during many different tasks in many different modalities. Schwartz (1994) showed that the population vector could be used to accurately reconstruct spiral drawing movements from the activities of a population of cells in motor cortex. Lee, Rohrer, and Sparks (1988) used a population vector to interpret the coding of eye movements by superior colliculus neurons. Georgopoulos, Lurito, Petrides, Schwartz, and Massey (1989) used a population vector analysis to demonstrate the well-known psychological phenomenon called mental rotation (Shephard and Metzler, 1971). In this study, monkeys were required to move in a direction differing by 90 degrees from the direction indicated by lights in a target array. Georgopoulos et al. showed that the motor cortex population vector starts out pointing in the direction of the target light, then rotates through 90 degrees just before movement onset to point in the direction of the actual movement. The population vector has also been used to study sensory systems. Hess (1992) demonstrated that head orientation can be obtained by population vector analysis of the activities of otolith afferent signals. Steinmetz, Motter, Duffy, and Mountcastle (1987) interpreted the activities of visual neurons in parietal cortex using a population vector. Vogels (1990) showed that a population vector analysis of visual cortex neurons can achieve an accuracy of line orientation discrimination that is as good as behaviorally measured just noticeable differences, even with broadly tuned cells with large response variabilities. Zohary (1992) extended this work in a modeling study showing that a population vector analysis could accurately extract information about a single stimulus dimension, although the response of a single visual cortical cell could not reliably be used to extract this information due to the fact that many stimulus dimensions are coded by each cell.

In summary, the two main hypotheses embodied by the current model receive significant support from various studies in the computational neuroscience literature. The hypothesis that linguistic experience results in nonuniformities in the firing preferences of cells in an auditory map is supported by a large number of neurophysiological studies of auditory, somatosensory, and visual cortices, and many neural models similar to the one posited here have been used to explain this phenomenon. The hypothesized utility of the population vector for predicting psychological phenomena from the ensemble of cell activities in a neural map is also supported by several neurophysiological and modeling studies of different tasks in different modalities. The next section provides further support for these hypotheses through model simulations that yield close fits to results from psychophysical studies of the magnet effect.

3. Simulations

The model defined in the preceding section was implemented in computer simulations, and its performance was compared to the results of several psychophysical studies of the perceptual magnet effect. Random initial weight vectors chosen from a uniform distribution over the input space were used in all simulations. The model was then trained with formant input vectors chosen from Gaussian distributions centered on phonetic categories (see Appendix for details). Between 400 and 1000 inputs from each category were used to train the network for each simulation. Gaussian distributions with zero covariance were chosen for simplicity; qualitatively similar results to those reported here were obtained for a wide range of parameter choices, and similar results would also be expected for many single-peaked distributions other than Gaussian distributions with zero covariance. It is important to note that the model self-organizes given only the input vectors without any information regarding their category membership; i.e., the input vectors are not labeled according to which phonetic category they belong. Within this explanation, therefore, it is not necessary for an infant to be capable of identifying sounds as members of phonetic categories in order to develop the magnet effect.

Simulation 1. The first simulation investigated a study of stimulus discrimination in Japanese and English adult listeners when presented with stimuli in or near the American English phonemic categories /r/ and /l/, as reported in Iverson and Kuhl (1994) and Kuhl (1995). (The English /r/ and /l/ categories do not have direct correlates in Japanese.) The input stimuli, psychophysical results, and model results are shown in Figure 2. This study used stimuli that were evenly spaced in F2-F3 space near the locations of the phonemic categories /r/ and /l/ (see Figure 2(A)) and required subjects to indicate perceived similarity of stimuli. Results from American adults indicated a perceptual warping around the phonemic categories (shown in Figure 2(B)), whereas the results from Japanese adults did not indicate warping around the categories.

First, the model's response to the input stimuli was tested without training on /r/ and /l/ stimuli. The untrained map is meant to approximate the auditory maps of Japanese listeners, who presumably do not train on many instances centered at American English /r/ and /l/. The results of this simulation are shown in Figure 2(C), which plots the "perceptual results" obtained using the population vector to interpret the ensemble of auditory map cell activities. As with the Japanese listeners in the Iverson and Kuhl (1994) study, no perceptual clustering is seen around the American /r/ and /l/ categories. The model was then trained with input vectors from Gaussian distributions centered on the left-most stimulus from the middle row of Figure 2 (corresponding to /r/) and the right-most stimulus from the middle row (corresponding to /l/). This simulation corresponds to an American adult, whose auditory map has developed in the presence of many instances of /r/ and /l/. Interpreting the map activities using the population vector results in the warped map shown in Figure 2(D), which shows a remarkable similarity to the results of Iverson and Kuhl (1994) for Americans (Figure 2(B)). Most notably, a strong perceptual clustering occurs near the centers of the phonemic categories. Furthermore, as one moves away from the category centers, the pattern of warping seen in the model remains very similar to the pattern seen in the human subjects. A final point of interest from this simulation concerns what happens in the region between the /r/ and /l/ categories. Kuhl (1995) reports that the perceptual distances of Americans were expanded in this area relative to Japanese speakers. Comparing Figure 2(C) to Figure 2(D) clearly shows that the model also possesses this property. This result highlights a reasonable rationale for why evolution would favor a learning process that leads to a warped perceptual map: for a limited number of neurons, a warped representation makes it easier to distinguish stimuli from different categories at the cost of less behaviorally relevant within-category discrimina-

Understanding the model's performance requires a brief investigation of the effects of training on the adaptive weights in the network. It was mentioned earlier that the "preferred stimulus" for a cell in the auditory

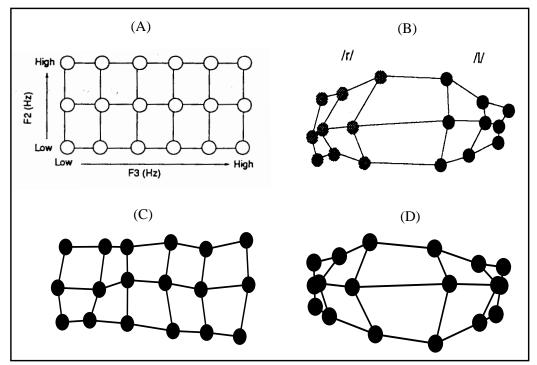


FIGURE 2. Simulation of the Iverson and Kuhl (1994) study of perception near /r/ and /l/ categories. (A) The stimuli used to test subjects were evenly spaced (adapted from Kuhl, 1995). (B) Perceptual results when the test stimuli were presented to American subjects in the Iverson and Kuhl study (adapted from Kuhl, 1995). Stimuli located near the sound categories were perceived as closer together than stimuli located between categories. (C) Simulation results when the test stimuli were presented to an untrained network. As reported by Iverson and Kuhl (1994) for Japanese speakers, the model produces no systematic warping near the /r/ and /l/ categories. (D) Simulation results when the test stimuli were presented to a network trained with many American English /r/ and /l/ inputs. The pattern of perceptual warping is remarkably similar to the warping seen in the American subjects of Iverson and Kuhl (1994).

map is the stimulus that produced an input vector (i.e., formant representation) that was parallel to the vector of weights projecting to the auditory map cell. A cell's preferred stimulus vector can thus be equated to its afferent weight vector, and changing the weights during learning therefore changes the distribution of preferred stimuli across F2-F3 space. Kohonen (1982) demonstrated how a self-organizing feature map can allocate the afferent weight vectors of map cells according to the distribution of input patterns used to train the network. This is illustrated for the current model in Figure 3, which shows the distributions of preferred stimuli before training (top) and after training (bottom). The weight vectors before training were chosen randomly from a uniform distribution, as indicated by the relative uniformity of the distribution of preferred stimuli over F2-F3 space. Training using inputs distributed around the /r/ and /l/ categories leads to peaks in the weight vector distribution at the category centers, as shown in the bottom half of Figure 3. It is interesting to note that the neurophysiological study of Recanzone et al. (1993) found similar peaks in the distribution of auditory cortex cell firing preferences after repeated training on a small range of tonal frequencies, with more than six times as much cortical area devoted to the heavily experienced stimuli in trained monkeys compared to untrained monkeys.

Now consider what happens if we apply a formant input that is centered directly on the peak corresponding to r/ in the bottom plot of Figure 3. The population vector of the map's activities is simply equal to the input vector. This is because the weighted average will have the most inputs from cells whose weight vectors represent this "ideal" r/, and the contributions of cells tuned to either side of the ideal will essentially cancel out due to the approximate symmetry of the preferred stimulus distribution around the peak. This

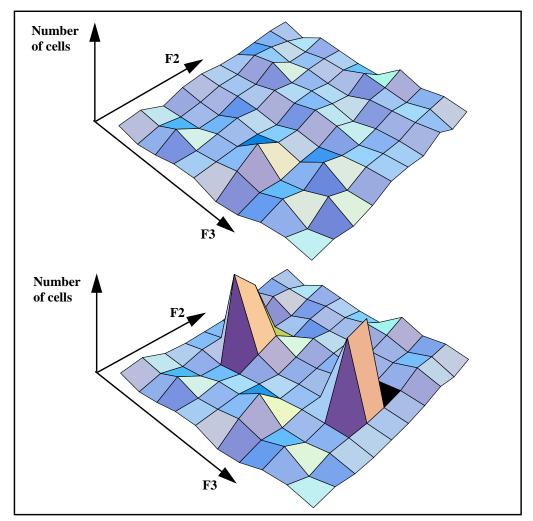


FIGURE 3. Distribution of the preferred stimuli of auditory map cells over F2-F3 space before training (top plot) and after training with /r/ and /l/ inputs (bottom plot). The peaks in the distribution after training correspond to the regions of formant space that were most heavily experienced during training.

"perceptual result" is indicated by the left-most data point in the middle row of Figure 2(D). Next, if an input pattern somewhat to the right of this ideal /r/ in F2-F3 space is applied (i.e., an input with a higher F3 than an ideal /r/), the cells representing this formant vector will be maximally active, but the distribution of somewhat active cells on either side is skewed: there are more somewhat active cells to the left of these cells than to the right. Thus, the weighted average computed by the population vector is skewed to the left as well. That is, the population vector is closer to the ideal for the phoneme than the input is. This is indicated by the second cell from the left in the middle row of Figure 2(D), which is closer to the left-most point than the corresponding input is to the ideal /r/ input. In other words, the network "perceives" the new input to be closer to /r/ than it actually is due to the skewed distribution of weight vectors.

Simulation 2. The second simulation serves mainly to highlight similarities between the current model and certain aspects of the NLM model of Kuhl. Kuhl (1995) hypothesized that by 6 months of age, infants have built up "stored representations, which reflect the distributional characteristics of the vowels the infants have heard" (p. 135). Schematics of these hypothesized representations from Kuhl (1995) are shown in the top row of Figure 4 for Swedish infants (left), English infants (center), and Japanese infants (right). Gaussian distributions centered at the vowel categories shown in the top row were used to generate training

inputs for three language-specific simulations. The second row shows the preferred stimuli for all map cells after training in the three cases. Here, we see clusters of cells with preferred stimuli near the vowel categories; these clusters correspond to peaks in the distribution of preferred stimuli as shown for the two-category case in Figure 3. It is interesting to note that this distribution of preferred stimuli of auditory map cells, or, equivalently, the distribution of afferent weight vectors, constitutes a stored representation that reflects the distributional characteristics of the vowels that the network has "heard", as suggested by Kuhl and schematized in the top row of Figure 4. Finally, the third row of Figure 4 shows the perceptual results when a uniform grid of inputs in formant space is applied to the network. The "stored representation" manifested by the auditory map cells' stimulus preferences results in the magnet effect, evidenced by the language-specific warping of perceptual space near the vowel categories in the bottom row of Figure 4.

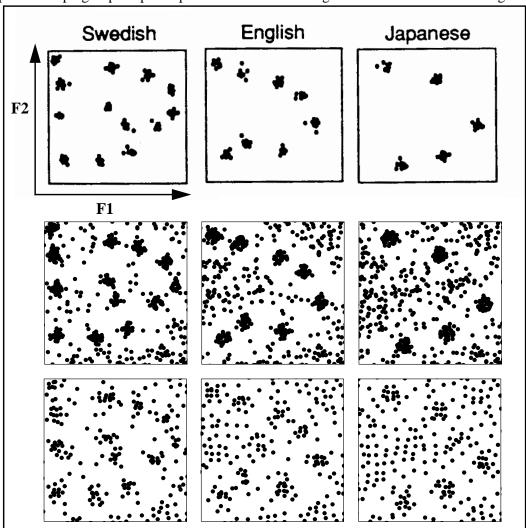


FIGURE 4. (Top row). Schematic of stored vowel representations after exposure to the native language in a Swedish speaker (left), an English speaker (center), and a Japanese speaker (right) as hypothesized by Kuhl (adapted from Kuhl, 1995). (Second row.) Locations of preferred stimuli of auditory map cells in F1-F2 space after training for each of the three languages. (Third row.) Perceptual results when network is tested with a uniform grid of inputs in formant space. Perceptual warping is evidenced by the clusters at the vowel categories for each of the three languages.

Simulation 3. The third simulation looks more closely at the warping of perceptual space near a single category. Kuhl (1991) studied the abilities of adults, six month old infants, and monkeys to discriminate

between synthesized vowel stimuli. The results for adult subjects will be addressed here to avoid the confounding problems caused by difficulties in measuring the perceptions of infants. Each trial started by presenting subjects with a referent speech sound once per second. In half of the trials, the speech sound was switched at some point to a new sound that was different from the first sound, and in the other half the sound was not changed. Subjects were asked to indicate when they detected a change in the sound. A subject was said to generalize if the sound changed but the subject did not respond. The referent sound was either a prototype of the phonemic category /i/ or a non-prototypical sound further away from the category center. The test stimuli were located at radii of 1, 2, 3, or 4 steps away from the referent sound (where each step consisted of a 30 Mel increase in radius from the category center), and the non-prototype referent sound was located at a radius of 4 steps from the prototype referent sound.

Figure 5 shows the results for adult subjects in the Kuhl (1991) study. The top curve represents the percent generalization of stimuli located 1, 2, 3, and 4 steps away from the prototype referent sound, and the bottom curve represents the corresponding results for the non-prototype referent sound. The most salient characteristic of this study is that subjects were more apt to generalize sounds near the prototype than sounds near the non-prototype.

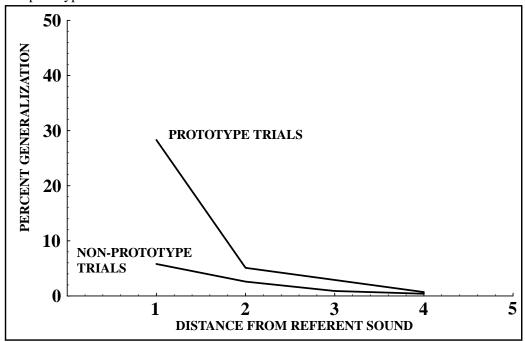


FIGURE 5. Generalization results for adults from the study of Kuhl (1991). Subjects were much more likely to generalize sounds near a prototypical instance of the /i/ category than they were to generalize sounds near a non-prototype.

In order to simulate this experiment using the current model, one must first come up with a method for measuring "percent generalization". The most reasonable choice is to assume that percent generalization varies as some monotonic function of the distance between the referent sound and the test sound in perceptual space. Relatedly, Flanagan (1955) measured the ability of subjects to discriminate vowel-like sounds as a function of the distance between them in formant space. Two main results are of note from this study: (1) the functions relating percent generalization to distance in formant space were typically exponentially decaying or slightly sigmoidal in shape, and (2) the exact form of the function varied significantly with the location of the referent stimulus in formant space. The results in one part of formant space are depicted in Figure 6. (Note that Flanagan plots "percent judgments different" rather than percent generalization, resulting in curves that are flipped with respect to the corresponding percent generalization curves.)

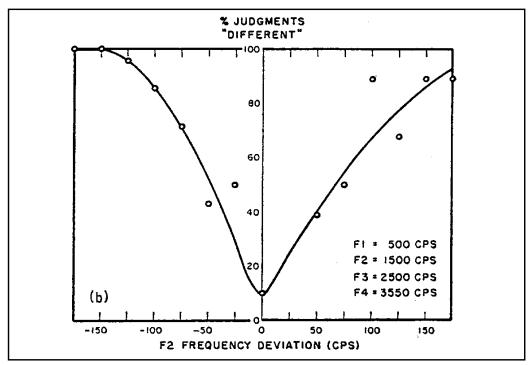


FIGURE 6. Function relating the discriminability of two vowel-like sounds to frequency differences in one region of formant space (adapted from Flanagan, 1955).]

In keeping with Flanagan's results, we assume a generalization function that falls off exponentially with distance from the referent sound. The final difficulty we must deal with is finding the exact shape of the function near the /i/ category. Note that one must assume that percent generalization varies as a function of distance in *perceptual* space rather than distance in formant space; otherwise the magnet effect would not exist at all since equally spaced sounds in formant space would always lead to the same amount of generalization. However, we do not have a direct measure of a stimulus's position in perceptual space given its position in formant space. Therefore, in order to get a reasonable generalization function we assumed that perceptual space is relatively unwarped in the region near the non-prototype in Kuhl's (1991) study and then defined an exponentially decaying function which passed through the Kuhl (1991) non-prototype data points shown in Figure 5 (see Appendix for details). Because Kuhl did not plot percent generalization values for the trials in which the distance between the referent sound and the test sound was zero, we made one final assumption concerning this function, which was that generalization scores are near 100% when the test and referent sounds are the same.

Once we have the function relating percent generalization to perceived distance, the simulation of Kuhl's (1991) experiment is straightforward. For this simulation a single Gaussian distribution of inputs centered at the /i/ category was presented during training. The test stimuli of Kuhl (1991) were then applied to the network and percent generalization was calculated based on perceived distance using the exponentially decaying function described above. The results of this simulation are shown in Figure 7, along with Kuhl's (1991) results. Again, the model produces a very accurate fit to the psychophysical results.

A paradoxical aspect of the magnet effect. We conclude this section with a brief investigation of a seemingly paradoxical attribute of the magnet effect that has not been treated by previous models: unlike the results of many other studies which show better discrimination for heavily experienced stimuli (e.g., Prosen, Moody, Sommers, and Stebbins, 1990; Recanzone et al., 1993; Zwislocki, Maire, Feldman, and Rubin, 1958), discrimination is *worse* for heavily experienced vowel stimuli (i.e., those near vowel cate-

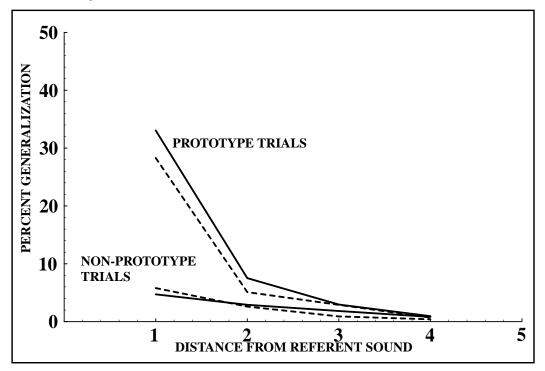


FIGURE 7. Comparison of the model's generalization properties after learning (solid lines) to the results of Kuhl (1991) for adult subjects (dashed lines).

gory centers) than for less frequently experienced vowel stimuli. Furthermore, it is quite likely that larger cortical areas are devoted to prototypical vowel stimuli than non-prototypical vowel stimuli (see discussion of neurophysiological studies of sensory map formation in Section 2). The fact that discrimination is worse for more prototypical vowels is thus apparently at odds with neurophysiological data indicating that larger areas of cortical representation are typically accompanied by increased discrimination capabilities in the somatosensory system (e.g., Penfield and Rasmussen, 1950), visual system (e.g., Kandel, Schwartz, and Jessell, 1991) and auditory system (e.g., Recanzone et al., 1993).

The current model provides a potential explanation for this phenomenon. To understand this explanation, first note that it is very likely that the larger the number of cells devoted to a particular region of input space in a neural map, the more tolerant the neural representation will be to noise in the responses of individual cells in this region. This is supported by modeling studies indicating that the susceptibility of a population vector representation to random variations in the responses of individual cells decreases as the number of cells increases (e.g., Vogels, 1990; Zohary, 1992). In contrast, the simulations in this section have shown that the peak in the distribution of cell firing preferences at the center of a vowel category in the model leads to a warping of the population vector representation toward the category center, which in turn reduces discriminability near the category center. Thus, the larger number of cells devoted to stimuli near the center of a vowel category may contribute to two competing effects: (1) an increase in the system's tolerance to noise in individual cells that contributes to an *increase* in discriminability near the category center, and (2) a magnet effect that contributes to a decrease in discriminability near the category center. As described earlier, the magnet effect occurs in the model due to an asymmetry in the number of active cells whose preferred stimuli fall near the probe stimulus. Figure 8 schematizes this and highlights an implication of this hypothesis: the more sharply peaked the distribution, the greater the asymmetry along the slope, and, therefore, the more the percept of a stimulus will be warped toward the peak. In other words, more sharply peaked distributions produce stronger magnet effects.

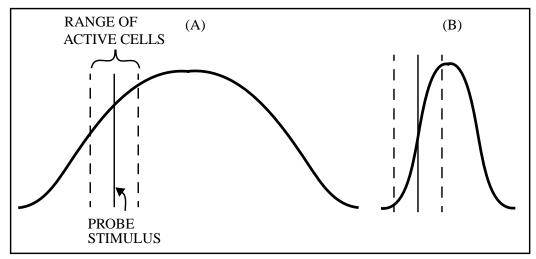


FIGURE 8. The magnet effect arises in the model due to an asymmetry in the number of active cells whose preferred stimuli fall on either side of a probe stimulus. (A) For a broadly peaked distribution of preferred stimuli, the number of active cells closer to peak (i.e., to the right of the probe) is only moderately larger than the number of active cells further away from the peak. This leads to a moderate warping of the population vector toward the peak, corresponding to a moderate magnet effect. (B) For a more sharply peaked distribution the asymmetry is greater, resulting in a much larger magnet effect.

This property leads to a hypothesis regarding the apparent paradoxes mentioned above. The multiply peaked nature of the distribution of vowel sounds in a language may lead to a neural map with a distribution of preferred stimuli that is more sharply peaked than the distributions of cells in neural maps representing other, less "categorical" stimuli, and these sharper peaks would result in much stronger magnet effects. The distortion due to these stronger magnet effects may overcome the tendency for better discrimination due to the noise tolerance that accompanies larger cortical representations. The formation of neural maps with this property also makes sense from a behavioral standpoint: when allocating neural resources to stimuli that fall into natural categories like vowels, it is typically more important to do so in a way that allows better discrimination between categories than within a category. Future research will further explore this hypothesis.

4. Concluding Remarks

This paper proposes a model of the perceptual magnet effect that is formulated as a neural network, thereby allowing the interpretation of psychological descriptions of the magnet effect in terms of the properties of neural systems. Kuhl and others have described the magnet effect as involving a stored representation of a category prototype, i.e., an exemplar whose perceptually measured goodness is maximal for that category. This prototype serves as a sort of anchor whose functional role as a perceptual magnet serves to strengthen category cohesiveness (e.g. Kuhl, 1991, p. 99). In the current account, the "stored representation" of vowels is simply the set of synaptic weights projecting to the auditory map cells. "Category prototypes" are stimuli located at the peaks in the distribution of map cell firing preferences (see Figure 3), which in turn reflect peaks in the distribution of sounds in a particular language. Category "goodness" can be equated to the number of cells in the map which are preferentially activated by an exemplar, with the prototype preferentially activating the most cells of any stimulus in the region of formant space surrounding a phonemic category. The "magnet effect" itself is a warping of perceptual space resulting from a non-uniform distribution of the preferred stimuli of map cells, and "category cohesiveness" describes the

psychological result of the multiply peaked form of this nonuniformity: inputs near the peaks of the distribution are perceived as closer together than inputs near the valleys.

Numerical simulations illustrate the model's ability to explain general characteristics of the magnet effect and accurately reproduce specific psychophysical data. Although the model contains a relatively large number of cells and synaptic weights, only three free parameters were available to fit the data; the learning rate α, the neighborhood size L, and the variance of the Gaussian distributions used to generate the training inputs. Furthermore, all simulations used the same values of α and Gaussian variance; only the neighborhood size L was changed slightly between simulations 1 and 2, owing to the differing number of auditory map cells in these simulations. The function used to translate distance in perceptual space to percent generalization provided some additional fitting power for the third simulation, but this function was in fact very constrained by existing data: an exponential function was chosen to match the form of Flanagan's (1955) data, and the exponential was constrained to pass through the non-prototype data points of Kuhl (1991). Despite the model's simplicity, it captures the salient known aspects of the magnet effect (i.e., a shrinking of perceptual space near phonemic category centers, an expansion of perceptual space away from centers, and language-specificity in this warping), and it provides close fits to the psychophysical results of Kuhl (1991) and Iverson and Kuhl (1994). The model also requires no assumptions about the abilities of infants to identify sounds as members of linguistic categories and therefore has no trouble explaining why the magnet effect is evident in six month old infants.

This model is envisioned as a component of a larger computational modeling framework of speech development, perception, and production called DIVA (Guenther, 1994, 1995a,b). The DIVA model posits a direct link between perception and production during babbling that leads to the formation of speech sound targets that take the form of regions in a speech planning space. Placing the current work within the context of DIVA suggests a scenario in which the sharpening of perceptual representations of phonemic categories, inherent to the current model due to the sharpening of the peaks in the distribution of preferred stimuli of auditory map cells, leads to a progressive sharpening of the production target regions for these same categories. A similar link between perception and production has been hypothesized by Kuhl and Meltzoff (1995) and gains some support from their study showing that repeated exposure to a particular vowel leads to increased productions of that vowel during babbling in infants as young as 12-20 weeks of age. These issues will be investigated further in future work that will incorporate the current model into the DIVA framework.

The model described in this article proposes that the perceptual magnet effect arises as a natural consequence of the formation of neural maps in the auditory system. The model's simplicity stems from its reliance on only two fundamental hypotheses, both of which are supported by a variety of neurophysiological and computational studies: (1) sensory experience leads to language-specific nonuniformities in the distribution of the firing preferences of cells in an auditory map, and (2) the population vector can be used to predict psychological phenomena based on the pattern of cell activities in this map. By fusing concepts from neurosocience and psychology, this study expands the research opportunities for examining the magnet effect. It is hoped that continued work bridging these fields will lead to a more complete understanding of the processes underlying speech development, perception and production.

Appendix: Simulation Parameters

The following parameter values were used for all simulations: $\alpha = 0.04$, $F_{1 \text{ MIN}} = 100 \text{ mels}$, $F_{1 \text{ MAX}} = 1100 \text{ mels}$, $F_{2 \text{ MIN}} = 200 \text{ mels}$, $F_{2 \text{ MAX}} = 2200 \text{ mels}$, $F_{3 \text{ MIN}} = 300 \text{ mels}$, and $F_{3 \text{ MAX}} = 3300 \text{ mels}$. For each phonemic category, the training inputs were chosen from a Gaussian distribution whose mean was chosen to coincide with the phonemic category center as indicated by the original experiments. The vari-

ances of the Gaussians were 20 mels in the F1 dimension, 40 mels in the F2 dimension, and 60 mels in the F3 dimension. The covariances of the Gaussians were zero.

The auditory map for simulation 1 consisted of 500 cells. The neighborhood L started at 35 cells and decreased linearly to 1 cell during training. A neighborhood of 30 cells was used to test the network. The auditory map for simulations 2 and 3 consisted of 1500 cells. L started at 40 and decreased linearly to 1 during training. A neighborhood of 35 cells was used to test the network.

Because training inputs were chosen from Gaussian distributions which have unlimited extent, it was possible to generate a very small percentage of inputs whose formant values were outside the formant ranges defined by the $F_{i \ \rm MIN}$ and $F_{i \ \rm MAX}$ values. When this occurred, the offending input was removed from the training set.

The function relating percent generalization to perceptual distance in simulation 3 was:

percent generalization =
$$\exp(4.605 - 5.341d + 3.463d^2 - 1.087d^3 + 0.117d^4)$$

where d is the perceptual distance between two inputs measured in 30 mel steps. For example, if the difference between the population vector values produced by the model for two inputs was 30 mels, then d = 1, as in the Kuhl (1991) data plots reproduced in Figures 5 and 7. As described in Section 3, the exponential form of this equation was chosen to qualitatively match the results of Flanagan (1955), and a quartic exponential was chosen to insure that the function passed exactly through all four non-prototype data points from the Kuhl (1991) study.

5. References

- Bullock, D., Grossberg, S., and Guenther, F.H. (1993). A self-organizing neural model of motor equivalent reaching and tool use by a multijoint arm. *Journal of Cognitive Neuroscience*, **5**, pp. 408-435.
- Burnod, Y., Grandguillaume, P., Otto, I., Ferraina, S., Johnson, P.B., and Caminiti, R. (1992). Visuomotor transformations underlying arm movements toward visual targets: A neural network model of cerebral cortical operations. *Journal of Neuroscience*, **12**, pp. 1435-1453.
- Davis, K., and Kuhl, P. (1994). Tests of the perceptual magnet effect for American English /k/ and /g/. *Journal of the Acoustical Society of America*, **95**(5), Pt. 2, p. 2976.
- Flanagan, J.L. (1955). A difference limen for vowel formant frequency. *Journal of the Acoustical Society of America*, **27**, pp. 613-617.
- Fox, R.A., Flege, J.E., and Munro, M.J. (1995). The perception of English and Spanish vowels by native English and Spanish speakers: A multidimensional scaling analysis. *Journal of the Acoustical Society of America*, **97**, 2540-2551.
- Gaudiano P., Olson S., Tal D., and Fischl B. (1993). A neural network model of dynamic receptive field reorganization. *Society for Neuroscience Abstracts*, **19**, p. 809.
- Georgopoulos, A.P., Caminiti, R., Kalaska, J.F., and Massey, J.T. (1983). Spatial coding of movement: A hypothesis concerning coding of movement direction by motor cortical populations. *Experimental Brain Research Supplementum*, **7**, pp. 327-336.

- Georgopoulos, A.P., Kalaska, J.F., Crutcher, M.D., Caminiti, R., and Massey, J.T. (1984). The representation of movement direction in the motor cortex: Single cell and population studies. In Edelman, G.M., Gall, W.E., and Cowan, W.M. (eds.): *Dynamic aspects of cortical function*. New York: Wiley.
- Georgopoulos, A.P., Kettner, R.E., and Schwartz, A.B. (1988). Primate motor cortex and free arm movements to visual targets in three-dimensional space. II. Coding of the direction of movement by a neuronal population. *Journal of Neuroscience*, **8**, pp. 2928-2937.
- Georgopoulos, A.P., Lurito, J.T., Petrides, M., Schwartz, A.B., and Massey, J.T. (1989). Mental rotation of the neuronal population vector. *Science*, **243**, pp. 234-236.
- Grossberg, S. (1969). On learning and energy-entropy dependence in recurrent and nonrecurrent signed networks. *Journal of Statistical Physics*, **1**, pp. 319-350.
- Grossberg, S. (1976). Adaptive pattern classification and universal recoding: I. Parallel development and coding of neural feature detectors. *Biological Cybernetics*, **23**, pp. 121-134.
- Guenther, F. H. (1994). A neural network model of speech acquisition and motor equivalent speech production. *Biological Cybernetics*, **72**, pp. 43-53.
- Guenther, F.H. (1995a). Speech sound acquisition, coarticulation, and rate effects in a neural network model of speech production. *Psychological Review*, **102**, pp. 594-621.
- Guenther, F.H. (1995b). A modeling framework for speech motor development and kinematic articulator control. In Elenius, K., and Branderud, P. (eds.): *Proceedings of the XIIIth International Congress of Phonetic Sciences*, vol. 2, pp. 92-99. Stockholm: KTH and Stockholm University.
- Hess, B.J.M. (1992). Three-dimensional head angular velocity detection from otolith afferent signals. *Biological Cybernetics*, **67**, pp. 323-333.
- Irvine, D.R.F., Rajan, R., Wize, L.Z., and Heil, P. (1991). Reorganization in auditory cortex of adult cats with unilateral restricted cochlear lesions. *Society for Neuroscience Abstracts*, **17**, 1485.
- Iverson, P., Diesch, E., Siebert, C., and Kuhl, P.K. (1994). Cross-language tests of the perceptual magnet effect for /_I/ and /_I/. *Journal of the Acoustical Society of America*, **96**(5), Pt. 2, p. 3228.
- Iverson, P., and Kuhl, P.K. (1994). Tests of the perceptual magnet effect for American English /r/ and /l/. *Journal of the Acoustical Society of America*, **95**(5), Pt. 2, p. 2976.
- Iverson, P., and Kuhl, P.K. (1995). Mapping the perceptual magnet effect for speech using signal detection theory and multidimensional scaling. *Journal of the Acoustical Society of America*, **97**, pp. 553-562.
- Jenkins, W.M., Merzenich, M.M., and Ochs, M.T. (1984). Behaviorally controlled differential use of restricted hand surfaces induce changes in the cortical representation of the hand in area 3b of adult owl monkeys. *Society for Neuroscience Abstracts*, **10**, p. 665.
- Jenkins, W.M., Merzenich, M.M., Ochs, M.T., Allard, T., and Guíc-Robles, E. (1990). Functional reorganization of primary somatosensory cortex in adult owl monkeys after behaviorally controlled tactile stimulation. *Journal of Neurophysiology*, 63, pp. 82-104.

- Kaas, J.H., Merzenich, M.M., and Killackey, H.P. (1983). The reorganization of somatosensory cortex following peripheral-nerve damage in adult and developing mammals. *Annual Review of Neuroscience*, 6, pp. 325-356.
- Kalaska, J.F., and Crammond, D.J. (1992). Cerebral cortical mechanisms of reaching movements. *Science*, **255**, pp. 1517-1523.
- Kandel, E.R., Schwartz, J.H., and Jessell, T.M. (1991). *Principles of Neural Science* (third edition). New York: Elsevier.
- Kohonen, T. (1982). Self-organized formation of topologically correct feature maps. *Biological Cybernetics*, **43**, pp. 59-69.
- Kuhl, P.K. (1991). Human adults and human infants show a 'perceptual magnet effect' for the prototypes of speech categories, monkeys do not. *Perception & Psychophysics*, **50**, pp. 93-107.
- Kuhl, P.K. (1995). Mechanisms of developmental change in speech and language. In Elenius, K., and Branderud, P. (eds.): *Proceedings of the XIIIth International Congress of Phonetic Sciences*, vol. 2, pp. 132-139. Stockholm: KTH and Stockholm University.
- Kuhl, P.K., and Meltzoff, A.N. (1995). Vocal learning in infants: Development of perceptual-motor links for speech. In Elenius, K., and Branderud, P. (eds.): *Proceedings of the XIIIth International Congress of Phonetic Sciences*, vol. 1, pp. 146-149. Stockholm: KTH and Stockholm University.
- Kuhl, P.K., Williams, K.A., Lacerda, F., Stevens, K.N., and Lindblom, B. (1992). Linguistic experience alters phonetic perception in infants by 6 months of age. *Science*, **255**, pp. 606-608.
- Lacerda, F. (1995). The perceptual-magnet effect: An emergent consequence of exemplar-based phonetic memory. In Elenius, K., and Branderud, P. (eds.): *Proceedings of the XIIIth International Congress of Phonetic Sciences*, vol. 2, pp. 140-147. Stockholm: KTH and Stockholm University.
- Lee, C., Rohrer, W.H., and Sparks, D.L. (1988). Population coding of saccadic eye movements by neurons in the superior colliculus. *Nature*, **332**, pp. 357-360.
- Levy, W.B., and Desmond, N.L. (1985). The rules of elemental synaptic plasticity. In Levy, B., Anderson, J.A., and Lehmkuhle, S. (eds.): *Synaptic Modification, Neuron Selectivity, and Nervous System Organization* (pp. 105-121). Hillsdale, NJ: Erlbaum.
- Levy, W.B., and Steward, O. (1979). Synapses as associative memory elements in the hippocampal formation. *Brain Research*, **175**, pp. 233-245.
- Pearson, J.C., Finkel, L.H., and Edelman, G.M. (1987). Plasticity in the organization of adult cerebral cortical maps: A computer simulation based on neuronal group selection. *Journal of Neuroscience*, **7**, pp. 4209-4223.
- Penfield, W., and Rasmussen, T. (1950). *The Cerebral Cortex of Man: A Clinical Study of Localization of Function*. New York: Macmillan.
- Polka, L. (1995). Developmental patterns in infant speech perception. In Elenius, K., and Branderud, P. (eds.): *Proceedings of the XIIIth International Congress of Phonetic Sciences*, vol. 2, pp. 148-155. Stockholm: KTH and Stockholm University.

- Prosen, C.A., Moody, D.B., Sommers, M.S., and Stebbins, W.C. (1990). Frequency discrimination in the monkey. *Journal of the Acoustical Society of America*, **88**, pp. 2152-2158.
- Rauschecker, J.P., and Singer, W. (1979). Changes in the circuitry of the kitten visual cortex are gated by postsynaptic activity. *Nature*, **280**, pp. 58-60.
- Rauschecker, J.P., and Singer, W. (1981). The effects of early visual experience on the cat's visual cortex and their possible explanation by Hebb synapses. *Journal of Physiology*, **310**, pp. 215-239.
- Recanzone, G.H., Schreiner, C.E., and Merzenich, M.M. (1993). Plasticity in the frequency representation of primary auditory cortex following discrimination training in adult owl monkeys. *Journal of Neuroscience*, **13**, pp. 87-103.