

Using Bayes' Rule to Model Multisensory Enhancement in the Superior Colliculus

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The deep layers of the superior colliculus (SC) integrate multisensory inputs and initiate an orienting response toward the source of stimulation (target). Multisensory enhancement, which occurs in the deep SC, is the augmentation of a neural response to sensory input of one modality by input of another modality. Multisensory enhancement appears to underlie the behavioral observation that an animal is more likely to orient toward weak stimuli if a stimulus of one modality is paired with a stimulus of another modality. Yet not all deep SC neurons are multisensory. Those that do exhibit the property of inverse effectiveness: combinations of weaker unimodal responses produce larger amounts of enhancement. We show that these neurophysiological findings support the hypothesis that deep SC neurons use their sensory inputs to compute the probability that a target is present. We model multimodal sensory inputs to the deep SC as random variables and cast the computation function in terms of Bayes' rule. Our analysis suggests that multisensory deep SC neurons are those that combine unimodal inputs that would be more uncertain by themselves. It also suggests that inverse effectiveness results because the increase in target probability due to the integration of multisensory inputs is larger when the unimodal responses are weaker.

1 Introduction ---

The power of the brain as an information processor is due in part to its ability to integrate inputs from multiple sensory systems. Nowhere else has neurophysiological research provided a clearer picture of multisensory integration than in the deep layers of the superior colliculus (SC) (see Stein & Meredith, 1993, for a lucid review). Enhancement is a form of multisensory integration in which the neural response to a stimulus of one modality is augmented by a stimulus of another modality. We propose a probabilistic

theory of the functional significance of multisensory enhancement in the deep SC that can account for its most important features.

The SC is a layered structure located in the mammalian midbrain (Wurtz & Goldberg, 1989). The deep layers receive inputs from various brain regions composing the visual, auditory, and somatosensory systems (Edwards, Ginsburgh, Henkel, & Stein, 1979; Cadusseau & Roger, 1985; Sparks & Hartwich-Young, 1989). The deep SC integrates this multisensory input and then initiates an orienting response, such as a saccadic eye movement, toward the source of the stimulation. Neurons in the SC are organized topographically according to the location in space of their receptive fields (auditory, Middlebrooks & Knudsen, 1984; visual, Meredith & Stein, 1990; somatosensory, Meredith, Clemo, & Stein, 1991). Individual deep SC neurons can receive inputs from multiple sensory systems (Meredith & Stein, 1983; 1986b; Wallace & Stein, 1996). There is considerable overlap between the receptive fields of individual multisensory neurons for inputs of different modalities (Meredith & Stein, 1996). The responses of multisensory deep SC neurons are dependent on the spatial and temporal relationships of the multisensory stimuli.

Stimuli that occur at the same time and place can produce response enhancement (King & Palmer, 1985; Meredith & Stein 1986a, 1986b; Meredith, Nemitz, & Stein, 1987). Multisensory enhancement is the augmentation of the response of a deep SC neuron to a sensory input of one modality by an input of another modality. Percent enhancement (% *enh*) is quantified as (Meredith & Stein, 1986a):

$$\% \text{ enh} = \left(\frac{CM - SM_{\max}}{SM_{\max}} \right) \times 100, \quad (1.1)$$

where CM and SM_{\max} are the numbers of neural impulses evoked by the combined modality and best single modality stimuli, respectively. Multisensory enhancement is dependent on the size of the responses to unimodal stimuli. Smaller unimodal responses are associated with larger percentages of multisensory enhancement (Meredith & Stein, 1986b). This property is called inverse effectiveness (Wallace & Stein, 1994). Percentage enhancement can range upwards of 1000% (Meredith & Stein, 1986b). Yet not all deep SC neurons are multisensory. Respectively, in cat and monkey, 46% and 73% of deep SC neurons studied receive sensory input of only one modality (Wallace & Stein, 1996). It is not clear why some neurons in the deep SC exhibit such extreme levels of multisensory enhancement, while others receive only unimodal input.

Since the deep SC initiates orienting movements, it is not surprising to find that the orienting responses observed in behaving animals also show multisensory enhancement (Stein, Huneycutt, & Meredith, 1988; Stein, Meredith, Huneycutt, & McDade, 1989). For example, the chances that an orienting response will be made to a stimulus of one modality can be in-

creased by a stimulus of another modality presented simultaneously in the same place, especially when the available stimuli are weak. The rules of multisensory enhancement make intuitive sense in the behavioral context. Strong stimuli that effectively command orienting responses by themselves require no multisensory enhancement. In contrast, the chances that a weak stimulus indicates the presence of an actual source should be greatly increased by another stimulus (even a weak one) of a different modality that is coincident with it.

We will develop this intuition into a formal model using elementary probability theory. Our model, based on Bayes' rule, provides a possible explanation for why some deep SC neurons are multisensory while others are not. It also offers an explanation for the property of inverse effectiveness observed for multisensory deep SC neurons.

2 Bayes' Rule

We hypothesize that each deep SC neuron computes the probability that a stimulus source (target) is present in its receptive field, given the sensory inputs it receives. The sensory inputs are neural and are modeled as stochastic. Stochasticity implies that the input carried by sensory neurons indicating the presence of a target is to some extent uncertain. Thus, we postulate that each deep SC neuron computes the conditional probability that a target is present given its uncertain sensory inputs. We will model the computation of this conditional probability using Bayes' rule.

The model is schematized in Figure 1, in which the deep SC receives input from the visual and auditory systems. We represent these two sensory systems because the bimodal, visual-auditory combination is the most common one observed in cat and monkey (Wallace & Stein, 1996). The results generalize to any other combination. Each block on the grid in Figure 1 represents a single, deep SC neuron. Our model will focus on individual deep SC neurons and on the visual and auditory inputs they receive from within their receptive fields.

We begin with the simplest case: a deep SC neuron receives an input of only one sensory modality. We denote the target as random variable T and a visual sensory input as random variable V . Then we hypothesize that a deep SC neuron computes the conditional probability $P(T | V)$. This conditional probability can be computed using Bayes' rule (Hellstrom, 1984; Applebaum, 1996):

$$P(T | V) = \frac{P(V | T)P(T)}{P(V)}. \quad (2.1)$$

Bayes' rule is a fundamental concept in probability that has found wide application (Duda & Hart, 1973; Bishop, 1995). It underlies all modern systems for probabilistic inference in artificial intelligence (Russell & Norvig, 1995).

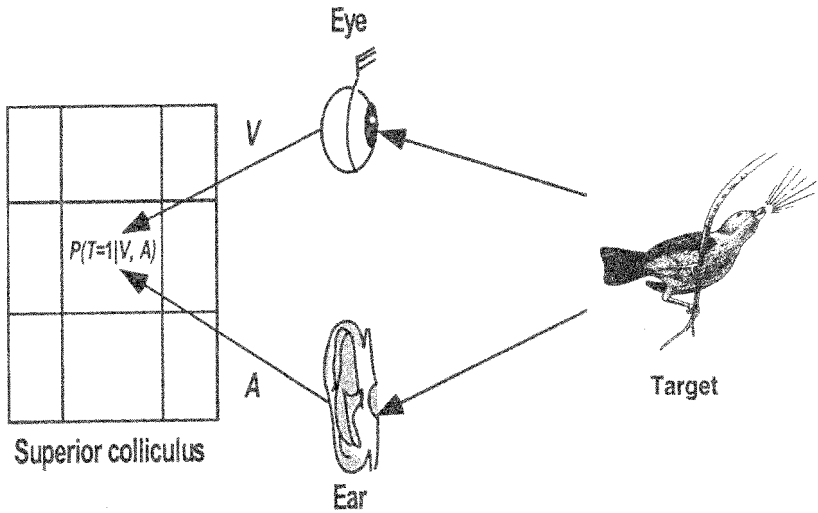


Figure 1: Schematic diagram illustrating multisensory integration in the deep layers of the superior colliculus (SC). Neurons in the SC are organized topographically according to the location in space of their receptive fields. Individual deep SC neurons, represented as blocks on a grid, can receive sensory input of more than one modality. The receptive fields of individual multisensory neurons for inputs of different modalities overlap. V and A are random variables representing input from the visual and auditory systems, respectively. T is a binary random variable representing the target. $P(T = 1 | V, A)$ is the Bayesian probability that a target is present given sensory inputs V and A . The bird image is from Stein and Meredith (1993).

We suggest that a deep SC neuron can be regarded as implementing Bayes' rule in computing the probability of a target given its sensory input. According to equation 2.1, we suppose that the nervous system can compute $P(T | V)$ given some input V because it already has available the other three probabilities: $P(V | T)$, $P(V)$, and $P(T)$. The conditional probability of V given T [$P(V | T)$] is the probability of obtaining some visual sensory input $V = v$ given a target $T = t$ (upper- and lowercase italicized letters represent random variables and particular numerical values of those variables, respectively). In the context of Bayes' rule, $P(V | T)$ is referred to as the likelihood of V given T . The unconditional probability of V [$P(V)$] is the probability of obtaining some visual sensory input $V = v$ regardless of whether a target is present. Thus, $P(V)$ and $P(V | T)$ are properties of the visual system and the environment, and it is reasonable to suppose that those properties could be represented by the brain.

The unconditional probability of T [$P(T)$] is the probability that $T = t$. $P(T)$ is a property of the environment. In the context of Bayes' rule, $P(T)$ is referred to as the prior probability of T . What Bayes' rule essentially does is to modify the prior probability on the basis of input. In Bayes' rule (equation 2.1), $P(T | V)$ is computed by multiplying $P(T)$ by the ratio $P(V | T)/P(V)$. Because $P(T | V)$ can be thought of as a modified version of $P(T)$ based on input, $P(T | V)$ can be referred to as the posterior probability of T . Thus, when computed using Bayes' rule, $P(T | V)$ is referred to as either the Bayesian or the posterior probability of T . It's possible that the prior probability of T [$P(T)$], and its representation by the brain, could change as circumstances dictate. With Bayes' rule, we suggest a model of how the brain could use knowledge of the statistical properties of its sensory systems to modify this prior on the basis of sensory input.

3 Bayes' Rule with One Sensory Input

Equation 2.1 can be used to compute the posterior (Bayesian) probability of a target given sensory input of only one modality. It can be used to simulate the responses of unimodal deep SC neurons. To evaluate equation 2.1, it is necessary to define the probability distributions for the terms on the right-hand side. We define T as a binary random variable where $T = 1$ if the target is present and $T = 0$ if it is absent. We define the prior probability distribution of T [$P(T)$] by arbitrarily assigning the probability of 0.1 to $P(T = 1)$ and 0.9 to $P(T = 0)$. These values are not meant to reflect precisely some experimental situation, but are chosen because they offer advantages in illustrating the principles. Bayes' rule is valid for any prior distribution.

We define V as a discrete random variable that represents the number of neural impulses arriving as input to a deep SC neuron from a visual neuron in a unit time interval. The unit interval for the data we model is 250 msec (Meredith & Stein, 1986b). We define the likelihoods of V given $T = 1$ [$P(V | T = 1)$] or $T = 0$ [$P(V | T = 0)$] as Poisson densities with different means. The Poisson density provides a reasonable first approximation to the discrete distribution of the number of impulses per unit time observed in the spontaneous activity and driven responses of single neurons, and offers certain modeling advantages. The Poisson density function for discrete random variable V with mean λ is defined as (Hellstrom, 1984; Applebaum, 1996):

$$P(V = v) = \frac{\lambda^v e^{-\lambda}}{v!}. \quad (3.1)$$

Example likelihood distributions of V are illustrated in Figure 2A. The likelihood of V given $T = 0$ [$P(V | T = 0)$] is the probability distribution of V when a target is absent. Thus, $P(V | T = 0)$ is the likelihood of V under

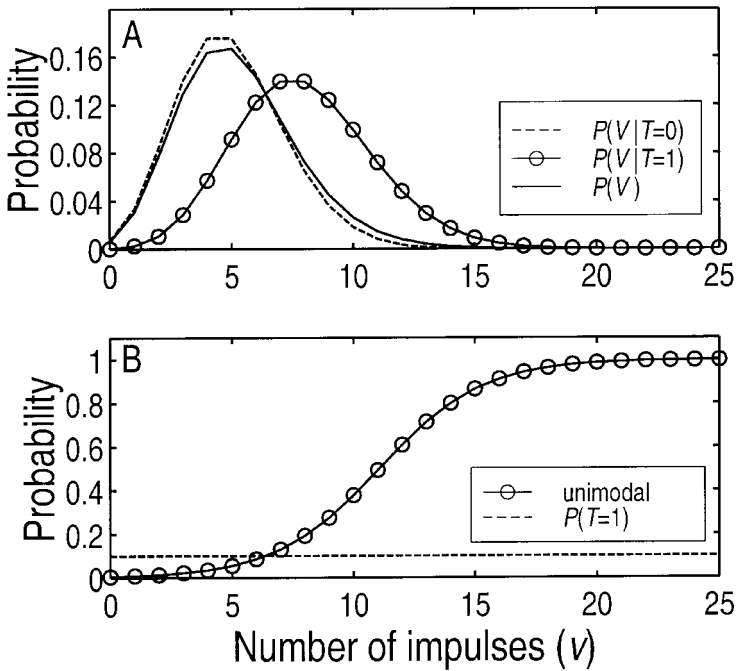


Figure 2: Likelihood distributions and Bayesian probability in the unimodal case. The target is denoted by the binary random variable T . The prior probabilities of the target $[P(T)]$ are 0.9 that it is absent $[P(T = 0) = 0.9]$ and 0.1 that it is present $[P(T = 1) = 0.1]$. The discrete random variable V represents the number of impulses arriving at the deep SC from a visual input neuron in a unit time interval (250 msec). Poisson densities, shown in (A), model the likelihood distributions of V $[P(V | T)]$. A mean 5 Poisson density models the spontaneous likelihood of V [with target absent, $P(V | T = 0)$, dashed line]. A mean 8 Poisson density models the driven likelihood of V [with target present, $P(V | T = 1)$, line with circles]. The unconditional probability of V $[P(V)]$, line without symbols in (A)] is computed from the input likelihoods and target priors (using equation 3.2). The posterior (Bayesian) probability that the target is present given input V $[P(T = 1 | V)]$ is computed using equation 3.3, and the result is shown in (B) (line with circles). The target-present prior $[P(T = 1) = 0.1]$ is also shown for comparison in (B) (dashed line).

spontaneous conditions. It is modeled as a Poisson density (equation 3.1) with $\lambda = 5$ (dashed line). The mean of 5 impulses per 250-msec interval corresponds to a mean spontaneous firing rate of 20 impulses per second. This spontaneous rate is meant to represent a reasonable generic value, but one that is high enough so that the behavior of the model under spontaneous

conditions can be examined easily. The model is valid for any spontaneous rate.

The likelihood of V given $T = 1$ [$P(V | T = 1)$] is the probability distribution of V when a target is present. Thus, $P(V | T = 1)$ is the likelihood of V under driven conditions. The driven likelihood takes into account random variability in the stimulus effectiveness of the target, as well as the intrinsic stochasticity of the sensory neurons. It is modeled as a Poisson density (equation 3.1) with $\lambda = 8$ (line with circles in Figure 2A). The mean of 8 impulses per 250-msec interval corresponds to a mean driven firing rate of 32 impulses per second. Notice that there is overlap between the spontaneous and driven likelihoods of V (see Figure 2A).

Given the prior probability distribution of T [$P(T)$] and the likelihood distributions of V [$P(V | T)$], the unconditional probability of V [$P(V)$] can be computed using the principle of total probability (Hellstrom, 1984; Applebaum, 1996):

$$P(V) = P(V | T = 1)P(T = 1) + P(V | T = 0)P(T = 0). \quad (3.2)$$

Equation 3.2 shows that the unconditional probability of V is the sum of the likelihoods of V weighted by the priors of T . The result is the compound distribution shown in Figure 2A (line without symbols). With $P(T)$ and $P(V | T)$ defined, and $P(V)$ computed from them (equation 3.2), all of the variables needed to evaluate Bayes' rule in the unimodal case (equation 2.1) have been specified.

Our hypothesis is that a deep SC neuron computes the Bayesian (posterior) probability that a target is present in its receptive field given its sensory input. We therefore want to evaluate equation 2.1 for $T = 1$ with unimodal input V :

$$P(T = 1 | V) = \frac{P(V | T = 1)P(T = 1)}{P(V)}. \quad (3.3)$$

We evaluate equation 3.3 by taking integer values of v in the range from 0 to 25 impulses per unit time. For each value of v , the values of $P(V | T = 1)$ and $P(V)$ are read off the curves previously defined (see Figure 2A). The unimodal posterior probability that $T = 1$ [$P(T = 1 | V)$] is plotted in Figure 2B (line with circles). The prior probability that $T = 1$ [$P(T = 1) = 0.1$] is also shown for comparison in Figure 2B (dashed line). For the Poisson density means chosen, the posterior exceeds the prior probability when $v \geq 7$ impulses per unit time (see Figure 2B). For the same values of v ($v \geq 7$), the driven likelihood of V [$P(V | T = 1)$] exceeds the unconditional probability of V [$P(V)$] (see Figure 2A).

Because the target-present prior [$P(T = 1) = 0.1$] is much smaller than the target-absent prior of T [$P(T = 0) = 0.9$], the unconditional probability of V [$P(V)$] is dominated by the spontaneous likelihood of V [$P(V | T = 0)$]

(equation 3.2). This is shown in Figure 2A [$P(V)$, line without symbols; $P(V | T = 0)$, dashed line]. For the priors of T as defined, the ratio $P(V | T = 1)/P(V)$ is roughly equal to the ratio $P(V | T = 1)/P(V | T = 0)$, and computing the posterior probability of the target using Bayes' rule (equation 3.3) is roughly equivalent to multiplying the target-present prior by the ratio of the driven and spontaneous likelihoods of the input. Thus, as the input increases from 0 to 25 impulses per unit time, it changes from being most likely spontaneous to most likely driven (see Figure 2A). On the basis of this increasing unimodal input, Bayes' rule indicates that the target changes from being most probably absent to most probably present (see Figure 2B). We suggest that the sigmoidal curve (Figure 2B, line with circles) describing the Bayesian probability that a target is present given unimodal input V [$P(T = 1 | V)$] is proportional to the responses of individual, unimodal deep SC neurons.

4 Bayes' Rule with Two Sensory Inputs

We can now consider the bimodal case of visual and auditory inputs. We define A as a discrete random variable that represents the number of neural impulses arriving at the SC neuron from an auditory neuron in a unit time interval. The Bayesian probability in the bimodal case (given V and A) can be computed as in the unimodal case, except that in the bimodal case, the input is the conjunction of V and A . The posterior probability that $T = 1$ given V and A [$P(T = 1 | V, A)$] can be computed using Bayes' rule as follows:

$$P(T = 1 | V, A) = \frac{P(V, A | T = 1)P(T = 1)}{P(V, A)}. \quad (4.1)$$

To evaluate Bayes' rule in the bimodal case (equation 4.1) we need to define the likelihoods of A given that a target is present or absent [$P(A | T = 1)$ or $P(A | T = 0)$]. As for V , we define the likelihoods of A given T as Poisson densities with different means.

To simplify the analysis, we assume that V and A are conditionally independent given T . On this assumption, the joint likelihoods of V and A given T [$P(V, A | T)$] can be computed as the products of the corresponding likelihoods of V given T [$P(V | T)$] and of A given T [$P(A | T)$]. For the case in which a target is present,

$$P(V, A | T = 1) = P(V | T = 1)P(A | T = 1). \quad (4.2)$$

Also on the assumption of conditional independence, the unconditional joint probability of V and A [$P(V, A)$] can be computed using the principle of total probability:

$$\begin{aligned} P(V, A) &= P(V | T = 1)P(A | T = 1)P(T = 1) \\ &\quad + P(V | T = 0)P(A | T = 0)P(T = 0). \end{aligned} \quad (4.3)$$

We use the same priors of T as before. With the priors of T and the likelihoods of V and A defined, and the conditional and unconditional joint probabilities of (V, A) computed from them (equations 4.2 and 4.3), we can use Bayes' rule (equation 4.1) to simulate the bimodal responses of deep SC neurons. We evaluate equation 4.1 by taking integer values of v and a in the range from 0 to 25 impulses per unit time. To simplify the comparison between simulated unimodal and bimodal responses, we consider the hypothetical case in which v and a are equal. The results are qualitatively similar when v and a are unequal as long as they increase together.

An example of a bimodal Bayesian probability that a target is present is shown in Figure 3A (line without symbols). In this example, the likelihoods of A are the same as those of V (in Figure 2A). The means of the Poisson densities modeling the spontaneous and driven likelihoods of both V and A are 5 and 8, respectively. The relationship between the Bayesian probability and the inputs in the bimodal case, in which V and A increase together, is qualitatively similar to that in the unimodal case, in which V increases alone. As in the unimodal case (Figure 2), Bayes' rule in the bimodal case indicates that the target changes from being most probably absent to most probably present as the input changes from being most likely spontaneous to most likely driven. In the bimodal case, however, the spontaneous and driven input distributions reflect the products of the individual likelihood distributions of V and A (equations 4.2 and 4.3).

The roughly sigmoidal curves in Figure 3A for the bimodal [$P(T = 1 | V, A)$] (line without symbols) and the unimodal [$P(T = 1 | V)$] (line with circles) Bayesian probabilities are similar in that both rise from 0 to 1 as v and a (bimodal) or v only (unimodal) increase from 0 to 25 impulses per unit time. The difference is that the bimodal curve rises faster. There is a range of values of v over which the probability of a target is higher in the bimodal case, when a is also available as an input, than in the unimodal case with v alone. This can be called the bimodal-unimodal difference (*BUD*) range. Within the *BUD* range, the Bayesian probability that a target is present will be higher in the bimodal than in the unimodal case at the same level of input.

The size of the *BUD* range is related to the amount of overlap between the spontaneous and driven likelihood distributions of the inputs (e.g., Figure 2A). The amount of overlap decreases as the difference between the driven and spontaneous means increases. As an example, the mean of the Poisson density modeling the driven likelihoods of both V and A is changed from 8 to 20. The spontaneous mean for both V and A remains at 5. The unimodal (line with circles) and bimodal (line without symbols) Bayesian probability curves for this example are shown in Figure 3B. The *BUD* range is appreciably smaller in this example, with driven and spontaneous means of 20 and 5 (see Figure 3B) than in the previous example with means of 8 and 5 (see Figure 3A).

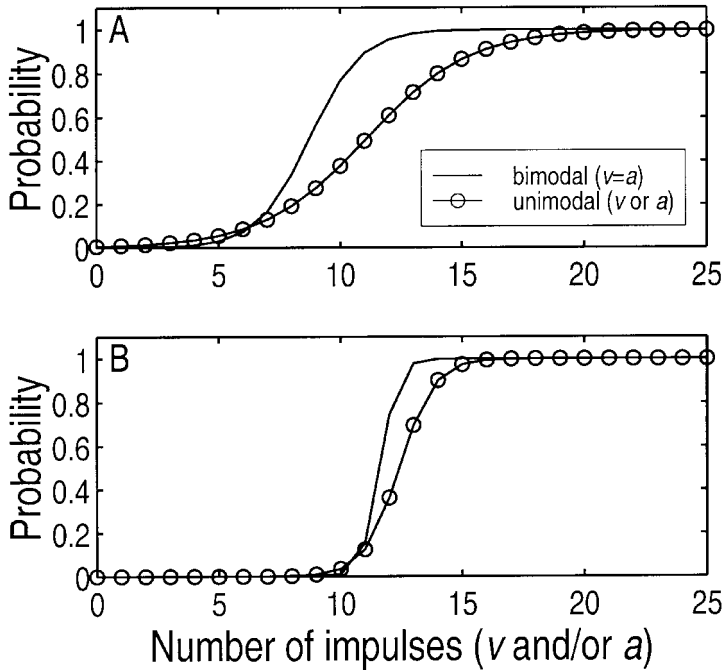


Figure 3: Bayesian target-present probabilities computed in unimodal and bimodal cases. The prior probabilities of the target are set as before [$P(T = 1) = 0.1$ and $P(T = 0) = 0.9$] and the likelihoods of the visual (V) and auditory (A) inputs are modeled using Poisson densities as in Figure 2A. Unimodal Bayesian probabilities (see equation 3.3) are computed as V takes integer values v in the range from 0 to 25 impulses per unit time. Bimodal Bayesian probabilities (equation 4.1) are computed as V and A vary together over the same range with $v = a$. (A) Spontaneous and driven likelihood means are 5 and 8, respectively, for the unimodal case of V only, and for both V and A in the bimodal case. (B) Spontaneous and driven likelihood means are 5 and 20, respectively. The bimodal exceeds the unimodal Bayesian probability over a much narrower range in (B) than in (A). For (A) and (B), lines with circles and lines without symbols denote unimodal and bimodal Bayesian probabilities, respectively.

Comparison of the curves in Figures 3A and 3B illustrates the general finding that the *BUD* range decreases as the difference between the driven and spontaneous input means increases. The *BUD* range is also dependent on the prior probabilities of the target. The influences of changing the spontaneous and driven input means and target priors on the *BUD* range are illustrated in Figure 4. In this figure, the summed difference between the bimodal and unimodal Bayesian probability curves (cumulative *BUD*) is

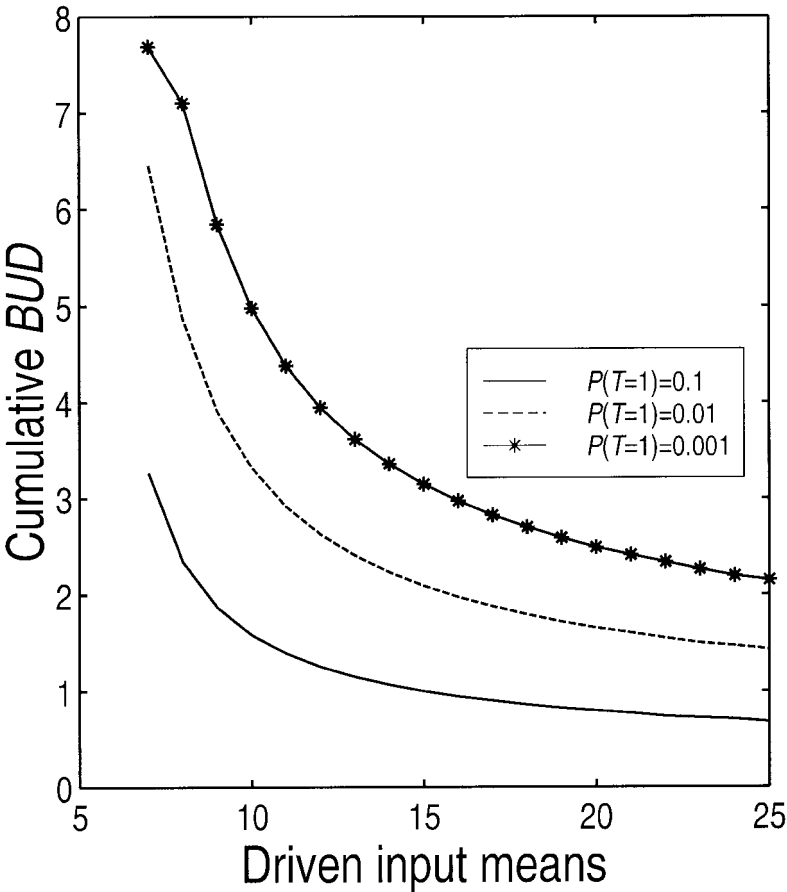


Figure 4: The difference between the bimodal and unimodal Bayesian probabilities decreases rapidly as the difference between the driven and spontaneous input means increases. The spontaneous means for both V and A are fixed at 5 impulses per unit time, and the driven means for V and A are varied together from 7 to 25. Unimodal (equation 3.3) and bimodal (equation 4.1) Bayesian probabilities are computed as v , or v and a together, vary over the range from 0 to 25 impulses per unit time (as in Figure 3). The unimodal is subtracted from the bimodal curve at each point in the input range. The difference (BUD) is summed over the range and plotted. The cumulative BUD is computed with target-present prior probabilities of 0.1 (line without symbols), 0.01 (dashed line), and 0.001 (line with asterisks) (target-absent priors are 0.9, 0.99, and 0.999, respectively).

plotted as the driven means of both V and A are varied together from 7 to 25. The spontaneous means of both V and A are fixed at 5. The target prior distribution is altered so that the target-present prior equals 0.1 (line without symbols), 0.01 (dashed line), or 0.001 (line with asterisks). Figure 4 shows that the cumulative *BUD* decreases as the difference between the driven and spontaneous input means increases. The difference is higher for all means as the target-present prior decreases.

Whether a deep SC neuron receives multimodal or only unimodal input may depend on the amount by which the driven response of a unimodal input differs from its spontaneous discharge. If the spontaneous and driven means are not well separated, then a unimodal sensory input provided to a deep SC neuron indicating the presence of a target would be uncertain and ambiguous. In the ambiguous case, a sensory input of another modality makes a relatively big difference in the computation of the probability that a target is present (e.g., Figure 4 for driven means less than about 15). Conversely, if the spontaneous and driven means are well separated, then a unimodal input provided to a deep SC neuron would be unambiguous. In the unambiguous case, a sensory input of another modality makes relatively little difference in the computation of the probability that a target is present (e.g., Figure 4 for driven means greater than about 15). Unimodal deep SC neurons may be those that receive an unambiguous input of one sensory modality and have no need for an input of another modality.

5 Bayes' Rule with One Spontaneous and One Driven Input ---

To compare the Bayes' rule model with neurophysiological data on multi-sensory enhancement, we must explore the behavior of the bimodal model (equation 4.1) not only for cases of bimodal stimulation, but also for cases where stimulation of only one or the other modality is available. To model the experimental situation in which sensory stimulation of both modalities is presented, we consider the case in which v and a are equal and vary together over the range from 0 to 25 impulses per unit time (as before). This simulates the driven responses of both inputs (both-driven). To model situations in which sensory stimulation of only one modality is presented, we consider the cases in which v or a is allowed to vary over the range, while the other input is fixed at the mean of its spontaneous likelihood distribution (driven/spontaneous).

The results of these simulations are shown in Figure 5A, in which the spontaneous and driven input means are 5 and 8 for both V and A , as before. Because both sensory inputs have the same spontaneous and driven means, the bimodal Bayesian probability curves for the two driven/spontaneous cases are the same. Thus, the curves coincide for the bimodal cases in which v is fixed at 5 while a varies (line with diamonds) and in which a is fixed at 5 while v varies (line with crosses). There is a range of v and a in Figure 5A over which the bimodal Bayesian probability in the both-driven

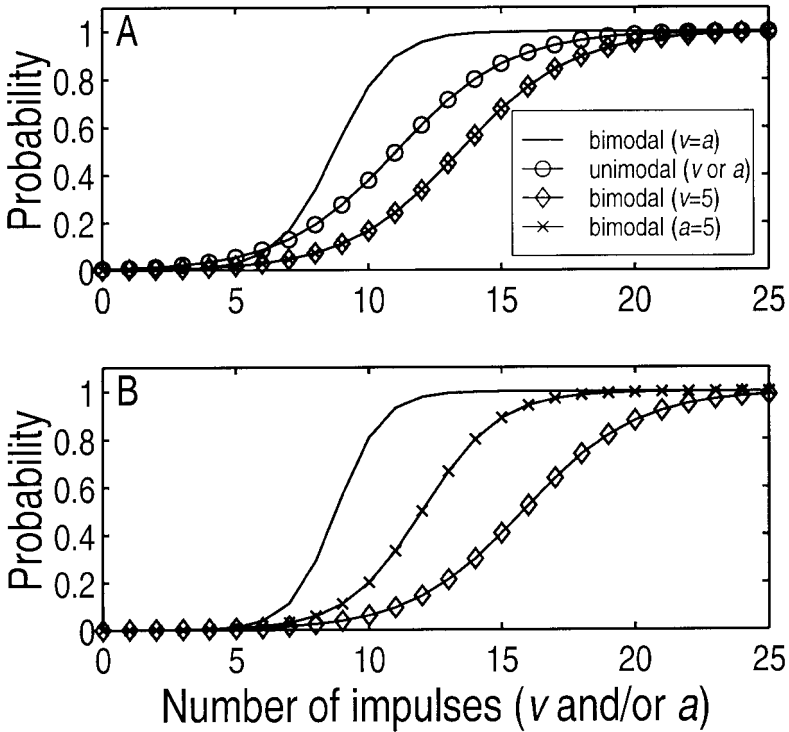


Figure 5: Bimodal Bayesian probabilities (equation 4.1) are computed with both inputs driven or with one input driven and the other spontaneous. Either v and a vary together with $v = a$ (both-driven), or one input varies while the other is fixed at its spontaneous mean of 5 ($v = 5$ or $a = 5$, driven/spontaneous). Target prior probabilities are set as before [$P(T = 1) = 0.1$ and $P(T = 0) = 0.9$] and the likelihoods of inputs V and A are modeled using Poisson densities (as in Figure 2A). (A) The driven input mean is set at 8 impulses per unit time for both V and A . The unimodal Bayesian probability (equation 3.3) is computed for comparison. (B) The driven input mean is 8 for A (as in A) but 10 for V . In (A) and (B), the Bayesian probabilities for the cases where both inputs vary together exceed over a broad range those for which one or the other input is fixed at 5. The driven/spontaneous bimodal Bayesian probability curves are denoted by lines with diamonds for $v = 5$, and lines with crosses for $a = 5$. The both-driven bimodal probability curves ($v = a$) are denoted by lines without symbols, and the unimodal Bayesian probability curve in (A) is denoted by a line with circles, as in Figure 3.

case (line without symbols) exceeds that in the driven/spontaneous cases (lines with diamonds and crosses). This can be called the range of enhancement.

The bimodal curves (both-driven and driven/spontaneous; equation 4.1) are compared in Figure 5A with the corresponding unimodal Bayesian probability curve computed before (equation 3.3). It shows that the Bayesian probabilities in the bimodal, driven/spontaneous cases (lines with diamonds and crosses) are smaller than in the unimodal case (line with circles) for the same inputs v and/or a . This illustrates that Bayes' rule works in both directions. The bimodal probability can be higher than the unimodal probability when the target most likely drives both inputs. Conversely, the bimodal probability can be lower than the unimodal probability when the target most likely drives one input while the other input is most likely spontaneous.

For simplicity, we have considered cases of the bimodal Bayes' rule where the likelihood distributions are the same for inputs of both modalities. The Bayesian analysis presented is valid for any input mean values, as long as inputs that are intended to represent neurons that are activated by sensory stimulation have driven means that are higher than spontaneous means. Figure 5B presents an example of bimodal Bayesian probabilities computed with the same spontaneous means (of 5), but with different driven means of 10 and 8 for V and A , respectively. This case is qualitatively similar to the previous one except that the driven/spontaneous curves do not coincide. The range of enhancement is much larger relative to the curve for which a varies alone while $v = 5$ (line with diamonds) than relative to the curve for which v varies alone while $a = 5$ (line with crosses). There are values of the input for which a driven/spontaneous probability is almost zero while the both-driven probability is almost one.

We hypothesize that the response of a deep SC neuron is proportional to the Bayesian probability that a target is present given its inputs. For the curves in Figures 5A and 5B, the ranges of input over which the bimodal, both-driven probabilities (lines without symbols) exceed the driven/spontaneous probabilities (lines with diamonds and crosses) correspond to ranges of multisensory enhancement. As v and a increase within a range of enhancement, the amount of enhancement increases and then decreases until, above the upper limit of the range, enhancement decreases to zero. This behavior of the bimodal Bayes' rule model can be used to simulate the results of a neurophysiological experiment (Meredith & Stein, 1986b).

The experiment involves recording the responses of a multisensory deep SC neuron to stimuli that by themselves produce minimal, suboptimal, or optimal responses. The simulation is based on the bimodal case shown in Figure 5B, in which the driven means for V and A are different. Inputs for v and a are chosen that give similar minimal, suboptimal, and optimal Bayesian probabilities in the driven/spontaneous case. The both-driven probability is computed using the same, driven input values. The percent-

Table 1: Numerical Values for a Simulated Enhancement Experiment.

| | Driven Input | | Bimodal Bayesian Probability | | | |
|------------|--------------|-----|------------------------------|------------|-------------|---------|
| | v | a | v Driven | a Driven | va Driven | % enh |
| Minimal | 8 | 9 | 0.0476 | 0.0487 | 0.3960 | 713 |
| Suboptimal | 12 | 15 | 0.4446 | 0.4622 | 0.9865 | 113 |
| Optimal | 16 | 21 | 0.9276 | 0.9351 | 1 | 7 |

Notes: Target prior probabilities are set at 0.1 for target present and 0.9 for target absent. The likelihoods of inputs V and A are modeled using Poisson densities with a spontaneous mean of 5 impulses per unit time for both V and A and driven means of 10 for V and 8 for A . With one input fixed at the spontaneous mean, the other input (v or a) is assigned a driven value such that the two driven/spontaneous, bimodal Bayesian probabilities are approximately equal at each of three levels (minimal, suboptimal, and optimal). The both-driven (va) bimodal Bayesian probability is computed using the same driven input values. The percentage enhancement is computed using equation 1.1 in which the both-driven probability is substituted for CM and the larger of the two driven/spontaneous probabilities is substituted for SM_{\max} . The percentage increase in the Bayesian probability (% enh , equation 1.1) when both inputs are driven is largest when the driven/spontaneous Bayesian probabilities are smallest.

age enhancement is computed using equation 1.1, in which the Bayesian, bimodal both-driven probability is substituted for CM and the larger of the two driven/spontaneous probabilities is substituted for SM_{\max} . The values are listed in Table 1.

The results are illustrated in Figure 6, where the bars correspond to the Bayesian, bimodal probabilities in the driven/spontaneous cases (white bar, visual driven (v); gray bar, auditory driven (a)) or in the both-driven case (black bar, visual and auditory driven (va)). Figure 6 is drawn as a bar graph to facilitate comparisons with published figures based on experimental data (Meredith & Stein, 1986b; Stein & Meredith, 1993). Figure 6 shows that in the model, the percentage enhancement goes down as the driven/spontaneous probabilities go up. These modeling results simulate the property of inverse effectiveness that is observed for multisensory deep SC neurons, by which the percentage of multisensory enhancement is largest when the single-modality responses are smallest.

6 Discussion

Multisensory enhancement is a particularly dramatic form of multisensory integration in which the response of a deep SC neuron to a stimulus of one modality can be increased many times by a stimulus of another modality. Yet not all deep SC neurons are multisensory. Those that exhibit the property of inverse effectiveness, by which the percentage of multisensory enhancement is largest when the single-sensory responses are smallest. We hypothesize that the responses of individual deep SC neurons are propor-

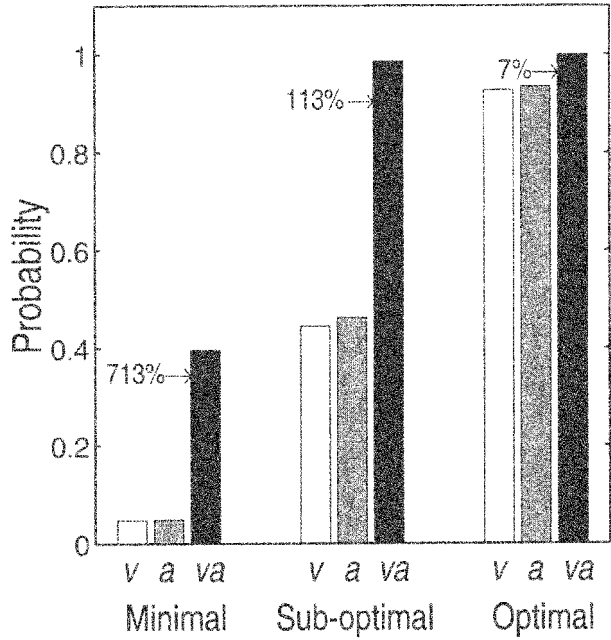


Figure 6: Comparing the driven/spontaneous bimodal Bayesian probabilities at three levels (minimal, suboptimal, and optimal) with the corresponding both-driven probability. Parameters for the target prior and input likelihood distributions are as in Figure 5B. Bimodal probabilities (equation 4.4) are computed when both v and a take various values within the range representing driven responses (va , black bars), or when one input takes the driven value (v , white bars; a , gray bars) but the other is fixed at the spontaneous mean of 5. The percentage increase in the Bayesian probability when both inputs are driven is largest when the driven/spontaneous Bayesian probabilities are smallest. The values are reported in Table 1.

tional to the Bayesian probability that a target is present given their sensory inputs. Our model, based on this hypothesis, suggests that multisensory deep SC neurons are those that receive unimodal inputs that would be more ambiguous by themselves. It also provides an explanation for the property of inverse effectiveness. The probability of a target computed on the basis of a large unimodal input will not be increased much by an input of another modality. However, the increase in target probability due to the integration of inputs of two modalities goes up rapidly as the size of the unimodal inputs decreases. Thus, our hypothesis provides a functional interpretation of multisensory enhancement that can explain its most salient features.

6.1 Hypothesis, Assumptions, and Model Parameters. Our basic hypothesis is that the responses of deep SC neurons are proportional to the probability that a target is present. A similar hypothesis was put forward by Barlow (1969, 1972), who suggested that the responses of feature detector neurons are proportional to the probability that their trigger feature is present. Barlow suggested a model based on classical statistical inference, in which the response of a neuron is proportional to $-\log(P)$ where P is the probability of the results on a null hypothesis (i.e., that the trigger feature is absent). Classical inference differs from Bayesian analysis in many respects, with the main difference being that prior information is used in the latter but not in the former (Applebaum, 1996). In our model, the response of a deep SC neuron is directly proportional to the Bayesian (posterior) probability of a target, based on the prior probability of the target and sensory input of one or more modalities.

We constructed our model so as to minimize the number of assumptions needed to evaluate it. That was our motivation in choosing the Poisson density rather than some other probability density function to represent the visual and auditory inputs, and in considering those two inputs as conditionally independent given the target. The Bayesian formulation is valid regardless of the probability density function chosen to represent the inputs, or whether those inputs are independent or dependent. Our particular construction of the model demonstrates its robustness, since the parameters of other instantiations requiring additional assumptions can easily be set so as to exaggerate the multisensory enhancement effects that we successfully simulate despite the constraints we impose.

Conditional independence given the target implies that the visibility of a target indicates nothing about its audibility, and vice-versa. One can easily imagine real targets for which this assumption is valid and others for which it is not. The advantage of the assumption of conditional independence is that the conditional and unconditional joint distributions of the visual and auditory inputs [$P(V, A | T)$ and $P(V, A)$] are then computed directly from the likelihoods of each individual input and the target priors (equations 4.2 and 4.3). The alternative assumption of conditional dependence carries with it a number of additional assumptions that would have to be made in order to specify how V and A are jointly distributed. The parameters of such a dependent, joint distribution could not be constrained on the basis of available data, but could be chosen in such a way that the simulated multisensory enhancement effects would be greatly exaggerated. Thus, our model construction based on conditional independence of the inputs is more restrictive than the dependent alternative, and conclusions based on it are therefore stronger.

The spike trains of individual neurons have been described using various stochastic processes (Gerstein & Mandelbrot, 1964; Geisler & Goldberg, 1966; Lansky & Radil, 1987; Gabbiani & Koch, 1998). We use the discrete Poisson density to approximate the number of impulses per unit time in

the discharge of individual neurons. Real spike trains can be well described as Poisson processes in some cases but not in others (Munemori, Hara, Kimura, & Sato, 1984; Turcott et al., 1994; Lestienne, 1996; Rieke, Warland, & de Ruyter van Stevenick, 1997). The advantage of the Poisson density is that it is specified using only one parameter, the mean, and this parameter has been reported for neurons in many of the brain regions that supply sensory input to the deep SC. Other densities require setting two or more parameters, which could not be well constrained on the basis of available data but could be chosen in such a way that the simulated multisensory enhancement effects would be greatly exaggerated. Thus, our model construction using Poisson densities to represent the inputs is better constrained than others that would use alternative densities, and conclusions based on it are therefore more robust.

6.2 Unimodality versus Bimodality. Our analysis suggests that whether a deep SC neuron is multisensory may depend on the statistical properties of its inputs. We use two probability distributions to define each sensory input: one for its spontaneous discharge and the other for its activity as it is driven by the sensory attributes of the target. A critical feature of these distributions is their degree of overlap. The more the spontaneous and driven distributions of an input overlap, the more uncertain and ambiguous will that input be for indicating the presence of a target.

Our model suggests that if a deep SC neuron receives a unimodal input for which the spontaneous and driven distributions have little overlap, then that neuron receives unambiguous unimodal input and has no need for input of another modality. Conversely, if a deep SC neuron receives a unimodal input for which the spontaneous and driven distributions overlap a lot, then that neuron receives ambiguous unimodal input. Such a deep SC neuron could effectively disambiguate this input by combining it with an input of another modality, even if the other input is also ambiguous by itself. About 45% of deep SC neurons in the cat and 21% in the monkey receive input from two sensory modalities (Wallace & Stein, 1996). An input of a third modality could provide further disambiguation. About 9% of all deep SC neurons in the cat and 6% in the monkey receive input of three modalities. Inputs to the deep SC are likely to vary in the degree to which their spontaneous discharges and driven responses overlap. For example, sensory neurons vary in their sensitivity, and overlap would occur for those that are less sensitive to stimulation. Sensory inputs would therefore vary in their degree of ambiguity. This could explain why some deep SC neurons are unimodal while others are multimodal (Wallace & Stein, 1996).

6.3 Spontaneous Activity. In the model, the Bayesian probability of a target increases from zero to one as the input increases. We suggest that the responses of individual deep SC neurons are proportional to this Bayesian probability. The Bayesian probability is zero or nearly zero for inputs that are

most likely spontaneous. For the example shown in Figure 2, the Bayesian probability is nearly zero even for an input of 16 impulses per second (4 impulses per 250-msec interval). The spontaneous activity of deep SC neurons is also zero or nearly zero, despite the fact that most of the neurons that supply input to the deep SC have nonzero spontaneous firing rates.

The spontaneous rates of neurons in some of the cortical and subcortical visual and auditory regions that project to the deep SC range from zero to over 100 impulses per second (anterior ectosylvian visual area in anesthetized cat, 1–8 Hz: Mucke, Norita, Benedek, & Creutzfeldt, 1982; pretectum in anesthetized cat, 1–31 Hz: Schmidt, 1996; retinal ganglion cells in anesthetized cat, 0–80 Hz: Ikeda, Dawes, & Hankins, 1992; superior olivary complex in anesthetized cat, 0–140 Hz: Guinan, Guinan, & Norris, 1972; inferior colliculus in alert cat, 2–54 Hz: Bock, Webster, & Aitkin, 1971; trapezoid body in anesthetized cat, 0–104 Hz: Brownell, 1975). For the unanesthetized rabbit, mean spontaneous rates of 36.1 ± 37.8 (SD) and 11.1 ± 11.4 (SD) impulses per second have been observed for single neurons in the superior olivary complex and inferior colliculus, respectively (D. Fitzpatrick and S. Kuwada, pers. comm.). Although neurons discharge spontaneously in most of the regions that provide inputs to the deep SC, most deep SC neurons exhibit low or zero spontaneous discharge, in both the anesthetized preparation and the alert, behaving animal (Peck, Schlag-Rey, & Schlag, 1980; Middlebrooks & Knudsen, 1984; Grantyn & Berthoz, 1985). In the context of the model, we would interpret this low level of deep SC neuron activity as indicating that the probability of a target is low when the inputs are spontaneous.

6.4 Driven Responses. The driven responses of deep SC neurons are influenced by a multidimensional array of stimulus parameters in addition to location in space. For visual stimuli these can include size, and rate and direction of motion (Stein & Arigbede, 1972; Gordon, 1973; Peck et al., 1980; Wallace & Stein, 1996). For auditory stimuli, factors influencing driven responses include sound frequency, intensity, and motion of the sound source (Gordon, 1973; Wise & Irvine, 1983, 1985; Hirsch, Chan, & Yin, 1985; Yin, Hirsch, & Chan, 1985). Specificity for these parameters is most likely derived from the sensory systems that provide input to the deep SC. In the model, we represent input activity as the number of impulses per unit time, which increases monotonically as the optimality of the sensory stimulus increases. The multidimensional array of stimulus parameters, as well as the multiplicity of input sources, raises the possibility of enhancement within a single sensory modality. For example, a visual input specific for size might enhance another visual input specific for direction of motion. The basic model, which includes only one input from each of two sensory modalities, can be generalized to include arbitrarily many inputs of various modalities and specificities.

The Bayesian probability increases as the input increases, and is one or nearly one for inputs that are most likely driven. A Bayesian probability of one could correspond to the maximum activity level of deep SC neurons. The model suggests that unimodal input could maximally drive individual deep SC neurons, even those that are multisensory (e.g., Figure 5). However, in order for some inputs to drive deep SC neurons maximally, they would have to attain very high activity levels. For example, when the auditory input alone is driven in Figure 5B (line with diamonds), it does not produce a Bayesian probability of one even when it has attained 80 impulses per second (20 impulses per unit time). It is possible that some unimodal inputs are unable to attain the activity levels needed to drive deep SC neurons maximally, regardless of the optimality of the unimodal stimulus. The maximal response of a multimodal neuron to such unimodal input would be less than its maximal bimodal or multimodal response. Neurophysiological evidence suggests that this may be the case for some deep SC neurons (Stein & Meredith, 1993).

6.5 Multisensory Enhancement and Inverse Effectiveness. When the responses of deep SC neurons are interpreted as being proportional to the Bayesian probability of a target, then multisensory enhancement is analogous to an increase in that probability due to multimodal input. The strength of the evidence of a target provided to a deep SC neuron is related to the size of its driven input. If a driven input of one modality is large, a deep SC neuron receives overwhelming evidence on the basis of that input modality alone. The probability of a target would be high, and driven input of another modality will not increase that probability much. Conversely, if a driven input of one modality is small, then the evidence it provides to a deep SC neuron is weak, and the probability of a target computed on the basis of that input alone would be small. In that case, the probability of a target could be greatly increased by corroborating input of another modality. According to the probabilistic interpretation, the amount of multisensory enhancement should be larger for smaller unimodal inputs.

The experimental paradigm actually used to demonstrate multisensory enhancement would accentuate this effect. Typically in studying a multisensory deep SC neuron, the response to stimuli of two modalities presented together is compared with the response to a stimulus of either modality presented alone (Meredith & Stein, 1986b; Stein & Meredith, 1993). According to the model, the response of a bimodal, deep SC neuron to a unimodal stimulus would be proportional to the probability of a target given that one input is driven and the other is spontaneous. This bimodal, driven/spontaneous probability is lower than that which would be computed by a unimodal deep SC neuron receiving only the driven input (see Figure 5A). The both-driven bimodal probability can be increased greatly over the driven/spontaneous bimodal probabilities, especially when the driven/spontaneous probabilities are smaller.

Thus, the amount of increase in target probability due to the integration of multimodal sensory inputs goes up rapidly as the responses to unimodal inputs decrease. This relationship is illustrated in Figures 5 and 6. It is analogous to the phenomenon of inverse effectiveness, which is the hallmark of multisensory enhancement in deep SC neurons (Stein & Meredith, 1993). The property of inverse effectiveness is precisely what would be expected on the basis of the hypothesis that deep SC neurons use their multisensory inputs to compute the probability of a target.

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