Model for stochastic-resonance-type behavior in sensory perception

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(Received 1 June 2001; published 11 February 2002)

Recently it was found that noise could help improve human detection of sensory stimuli via stochastic-resonance-type behavior. Specifically, the ability of an individual to detect a weak tactile stimulus could be enhanced by adding a certain amount of noise. Here we propose, from the perspective of classical signal detection theory, a simple and general model to elucidate the mechanism underlying this phenomenon. We demonstrate that noise-mediated enhancements and decrements in human sensation can be well reproduced by our model. The predicted upper bound of the performance improvement by adding noise is also consistent with the experimental data. We suggest additional experiments to further test the model.

DOI: 10.1103/PhysRevE.65.031904 PACS number(s): 87.19.Bb

The positive role played by noise in nonlinear systems, in particular, stochastic resonance (SR) [1,2], has been widely identified in physical [3,4], chemical [5,6], and physiological systems [7,8]. Recently it was found that noise could also help improve human perception of sensory stimuli [9–11]. Particularly, Collins and co-workers demonstrated through psychophysical experiments that the ability of an individual to detect a weak tactile stimulus could be enhanced by adding a certain amount of noise [9,10], via SR-type behavior.

A standard tool in the psychophysical literature for explaining sensory perception is signal detection theory [12]. How SR-type behavior can arise in the framework of signal detection theory has already been examined by Tougaard [13]. A key assumption in his model is that the sensory response used by the brain for perceptual judgment is determined by an energy mechanism that integrates the squared stimulus amplitude. He assumed that this energy mechanism treats signal and noise equally, and as such, the mean sensory responses to both noise and signal-plus-noise stimuli increase quadratically with the noise level. While such a nonselective energy mechanism may be an adequate model for peripheral receptors, cortical cells that are most likely involved in perceptual judgment do not respond to noise nearly as strongly as to signal [14]. It appears more reasonable to assume that noise increases the variance, instead of the mean, of the cortical response related to perception.

In this paper, we show that SR-type behavior is still present in signal detection theory when the problematic energy assumption is dropped. The new model is not only simpler, but more importantly, it can explain the detailed features of the psychophysical data of Collins *et al.* [9,10], and can make additional, testable predictions. We also compare two different versions of signal detection theory and show that only one of them is consistent with the experimental data.

In the psychophysical experiments of Collins *et al.*, a standard two-alternative forced-choice paradigm was used to measure human performance under different noise levels. In each trial, either a noise stimulus alone (drawn from a zero-mean Gaussian distribution) or a signal-plus-noise stimulus was presented, and subjects had to indicate whether the signal was present or not. The noise level was varied by changing the standard deviation of the noise stimuli in different blocks of trials. Subjects' performance was measured by the percentage of correct responses (percent correct) over many repeated trials at each noise level. The best performance was found at a nonzero noise level for most subjects. (Note that a trial was called a "presentation" and a block of trials was called a "trial" in Refs. [9,10].)

According to signal detection theory, the noise (N) stimuli and the signal-plus-noise (SN) stimuli will generate corresponding sensory responses in the brain. The distributions of the N and SN responses will be denoted by $P_N(x)$ and $P_{SN}(x)$, respectively. For simplicity, such distributions are usually assumed to be one-dimensional [12], with x viewed as the neuronal firing rate pooled across all relevant cells in the brain. Based on the central limit theorem, it is reasonable to assume that both $P_N(x)$ and $P_{SN}(x)$ are normally distributed. Since the SN stimuli only differ from the corresponding N stimuli by a fixed, nonzero signal strength, the means of $P_N(x)$ and $P_{SN}(x)$ satisfy $\mu_N < \mu_{SN}$. Furthermore, since the signal has to be weak in the context of SR (see below), it is reasonable to assume that $P_N(x)$ and $P_{SN}(x)$ have the same standard deviation σ. Obviously, σ depends both on the internal noise in the sensory system and on the external stimulus noise. When the external noise level is increased, σ should increase accordingly. In the following, we will simply use σ as an indicator of the stimulus noise level while assuming the internal noise level is fixed. In contrast to the energy mechanism of Tougaard [13], we further assume that the mean sensory responses μ_N and μ_{SN} are determined by the signal strength only, and remain the same when σ is changed, as shown schematically in Fig. 1.

Signal detection theory postulates that in order to decide whether the signal is present or not in a given trial, the brain has to compare the sensory response in that trial [drawn from $P_N(x)$ or $P_{SN}(x)$] with a relatively stable internal criterion c_r, marked by the vertical line in Fig. 1. If the response is larger than c_r, the answer will be "yes"; otherwise it will be "no."

With these assumptions, the percent-correct measure is simply the percentage of trials for which a subject answers "yes" when the signal is present (hits) or answers "no" when the signal is absent (correct rejections). It is easy to see from Fig. 1 that for experiments [such as those of Collins *et al.*] with an equal number of N and SN trials at each noise

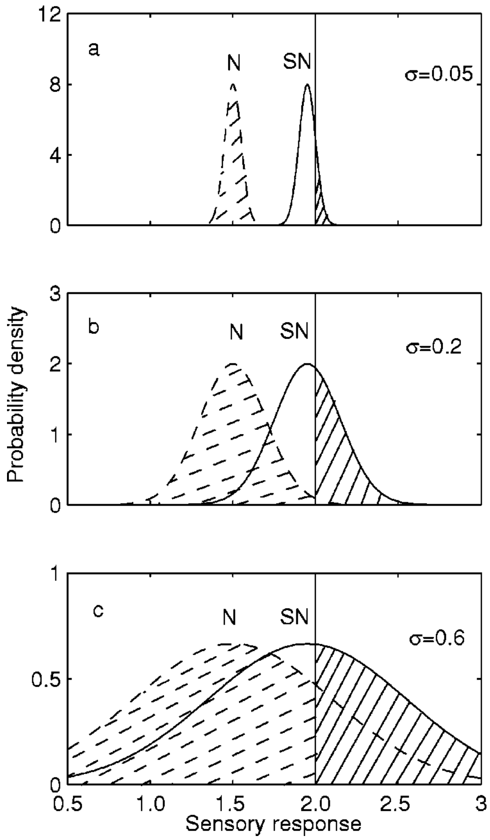

FIG. 1. Probability distributions of sensory responses (in arbitrary units) to *N* and *SN* stimuli at three noise levels σ. Note that different vertical scales are used in the three panels. The criterion c_r is indicated by a vertical line. Within the *SN* distribution the area shaded by solid lines to the right of the criterion represents the proportion of hits, and within the *N* distribution, the area shaded by dashed lines to the left of the criterion represents the proportion of correct rejections. The parameters for the plots are $c_r = 2.0$, $\mu_{SN} = 1.95$, $\mu_N = 1.5$, and (a) $\sigma = 0.05$; (b) $\sigma = 0.2$; (c) $\sigma = 0.6$.

level, the percent correct, p, is given by

$$p = 50\int_{c_r}^{+\infty} P_{SN}(x)dx + 50\int_{-\infty}^{c_r} P_N(x)dx \tag{1}$$

$$= 50 + 25\left[\mathrm{erf}\left(\frac{c_r - \mu_N}{\sigma\sqrt{2}}\right) - \mathrm{erf}\left(\frac{c_r - \mu_{SN}}{\sigma\sqrt{2}}\right)\right], \tag{2}$$

where $\mathrm{erf}(\cdot)$ is the error function. By letting $\partial p/\partial\sigma = 0$, we find that the percent correct is maximum at the noise level given by

$$\sigma = \sqrt{\frac{(2c_r - \mu_{SN} - \mu_N)(\mu_{SN} - \mu_N)}{2\ln[(c_r - \mu_N)/(c_r - \mu_{SN})]}}. \tag{3}$$

Since $\mu_{SN} > \mu_N$, this expression has a real positive solution if and only if

$$c_r > \mu_{SN}. \tag{4}$$

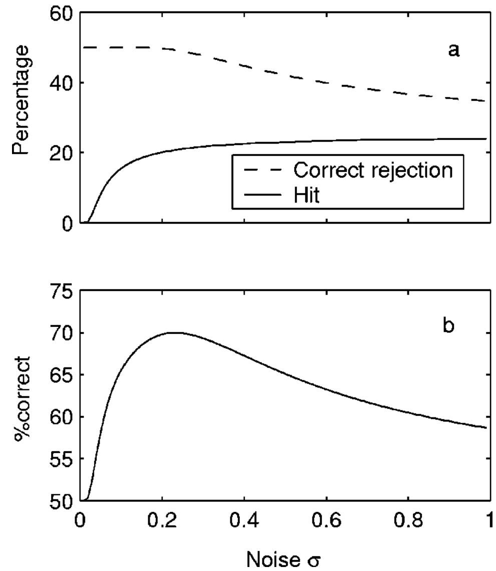

FIG. 2. SR-type behavior in sensory detection. The parameters of the plots are the same as in Fig. 1. (a) The percentage of hits and correct rejections, and (b) the percentage of total correct responses (hits plus correct rejections).

That is, the system can show SR-type behavior if and only if a subject's decision criterion is larger than the mean sensory response to signal-plus-noise, as indicated in Fig. 1. This is easy to understand intuitively. Under the condition $c_r > \mu_{SN}$, when the noise level is low, correct responses mainly come from correct rejections [Fig. 1(a) and Fig. 2(a)]. With somewhat higher noise levels, though the proportion of correct rejections drops slightly, the proportion of hits grows more rapidly [Fig. 1(b) and Fig. 2(a)], resulting in a net increase of the total correct responses. If the noise level continues to increase, however, the proportion of hits will saturate and that of correct rejections will start to fall off quickly [Fig. 1(c) and Fig. 2(a)]. As a result, the correct responses will decrease overall. Taken together, the percent-correct measure as a function of the noise level has a peak, as shown in Fig. 2(b), which is characteristic of SR-type behavior. The fast rise and slower fall of the curve closely resemble the actual experimental data [9,10].

It is well known that the percent correct also depends on the decision criterion c_r [12]. By letting $\partial p/\partial c_r = 0$, we find that the performance reaches a maximum at a c_r given by

$$c_r = \frac{\mu_N + \mu_{SN}}{2}. \tag{5}$$

That is, the optimal criterion is midway between the mean noise response and the mean signal-plus-noise response. Since $\mu_N < \mu_{SN}$, Eq. (5) contradicts the SR condition $c_r > \mu_{SN}$. Therefore, SR could not occur if subjects were always able to choose an optimal decision criterion [13]. However, while μ_N and μ_{SN} can be reduced to arbitrarily small values by choosing arbitrarily weak *N* and *SN* stimuli, it seems reasonable to assume that there is a lower bound for c_r that a subject can set in his/her decision process due to the finite precision of biological systems. Therefore, Eq. (5)

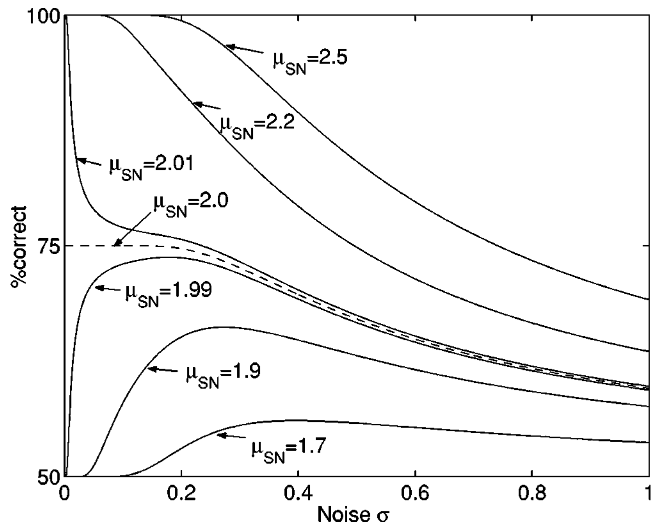

FIG. 3. The percent-correct measure as a function of the noise level at different signal strengths μ_{SN}. All other parameters of the plot are the same as in Fig. 1. The dashed curve represents the borderline case $\mu_{SN}=c_r=2.0$ for SR-type behavior.

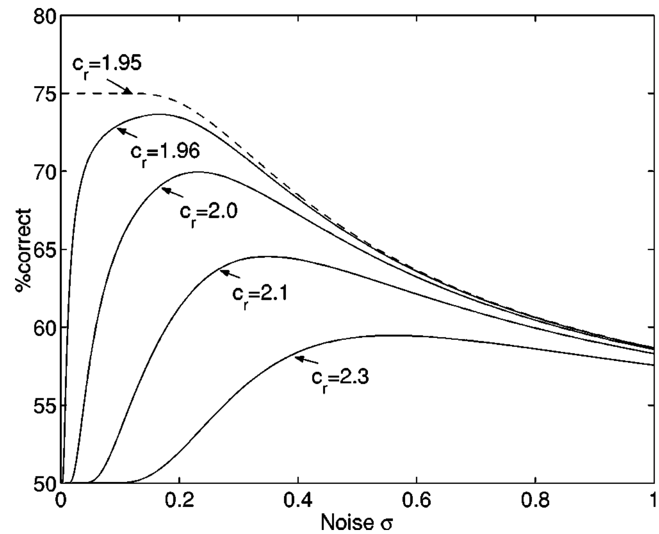

FIG. 4. The percent-correct measure as a function of the noise level at different criteria c_r. All other parameters of the plot are the same as in Fig. 1. The dashed curve represents the borderline case $c_r=\mu_{SN}=1.95$ for SR-type behavior.

should fail and the SR condition $c_r > \mu_{SN}$ is most likely to hold under weak external stimulation, which was the condition in the actual experiments [9,10]. A related point is that subjects' criteria are usually different from the optimal criteria although there is a correlation between the two [12].

A specific prediction we can make is that when SR is observed in experiments with an equal number of N and SN trials, the percent correct performance measure cannot exceed 75%. This is because when $c_r > \mu_{SN}$, the arguments of the two error functions in Eq. (2) are both positive, and therefore the functions lie in the range of $[0,1)$. Consequently, their difference cannot exceed 1, and the whole expression cannot exceed 75. The maximum value 75 is approached when c_r approaches μ_{SN}, and is much larger than μ_N. Remarkably, this prediction is consistent with the reported psychophysical data [9,10]. Tougaard's theory [13] does not make this prediction; indeed, Fig. 2(c) of his paper showed a peak percent correct well above 80%. The reason can be traced to his energy assumption which makes both μ_N and μ_{SN} increase with noise. Consequently, a given criterion can become an optimal criterion in his model at a particular noise level [see his Fig. 1(d), which corresponds to the peak in his Fig. 2(c)].

Collins *et al.* also varied the signal strength in their experiments [10]. We assume that the mean sensory response to signal plus noise (μ_{SN}) is a monotonically increasing function of the signal strength, and in Fig. 3 we plot Eq. (2) as a function of σ for various μ_{SN} while fixing the other parameters. It is clear from the figure that as long as $c_r > \mu_{SN}$, the system shows robust SR-type behavior. In contrast, when the signal is strong enough such that $c_r \leqslant \mu_{SN}$, SR does not occur as noise can only hinder performance. This result is consistent with the experimental finding that at higher signal strength, the performance decreases monotonically with increasing noise [10]. For the borderline case $c_r = \mu_{SN}$ (dashed line in Fig. 3), Eq. (2) indicates that the performance reaches a maximum of 75% at $\sigma \to 0$. Since we showed above that with SR, the performance cannot exceed 75%, SR cannot be observed when the performance is 75% or higher before adding noise. In the psychophysical literature, a threshold is often defined as the stimulus strength needed for reaching a 75% correct level. With this definition, we can conclude that SR cannot be observed with suprathreshold stimuli. This is in good agreement with classical SR theory where SR is defined as a noise-induced enhancement of weak, subthreshold input signals [1,2].

Different subjects usually set different internal criteria when performing psychophysical experiments. We therefore also plot Eq. (2) as a function of σ for various c_r in Fig. 4. It is clear from the figure that when c_r is set just above μ_{SN}, the SR-type behavior is more pronounced while higher values of c_r tend to diminish the peak size. This result is consistent with the observed variability among subjects, and may explain why for a given signal strength some subjects showed a significant peak in the performance curve while others did not [9,10]. It is also known that subjects' criteria can be induced to change by giving them proper instructions [12]. For example, the criteria can be lowered if subjects are told that hits are more important than correct rejections. Figure 4 then suggests that under identical stimulus conditions, the noise level necessary to reach maximum performance should vary when subjects' criteria are manipulated through instructions.

In the above derivations, we have assumed an equal number of N and SN trials, as in the actual experiments [9,10]. However, the results can be easily extended to the general case where the proportion of N and SN trials at each noise level are p_N and $p_{SN}=1-p_N$, respectively. Specifically, Eq. (2) should then be written as

$$p=50+50\left[p_N \mathrm{erf}\left(\frac{c_r-\mu_N}{\sigma\sqrt{2}}\right)-p_{SN}\mathrm{erf}\left(\frac{c_r-\mu_{SN}}{\sigma\sqrt{2}}\right)\right], \quad (6)$$

and the optimal conditions specified by Eqs. (3) and (5) should be replaced by

$$\sigma = \sqrt{\frac{(2c_r-\mu_{SN}-\mu_N)(\mu_{SN}-\mu_N)}{2\ln[p_N(c_r-\mu_N)/p_{SN}(c_r-\mu_{SN})]}}, \tag{7}$$

and

$$c_r = \frac{\mu_N+\mu_{SN}}{2} + \frac{\sigma^2\ln(p_N/p_{SN})}{\mu_{SN}-\mu_N}. \tag{8}$$

From Eq. (7), the optimal noise level now depends on p_N and p_{SN}, and the condition for SR becomes

$$c_r > \mu_{SN}, \tag{9}$$

$$(p_N-p_{SN})c_r > p_N\mu_N - p_{SN}\mu_{SN}. \tag{10}$$

The first inequality is the same as before, and the second inequality can either set an upper or lower bound on c_r, depending on the sign of p_N-p_{SN}. The best performance under SR cannot exceed $50(1+p_N)$ percent. Equation (8) indicates that the optimal c_r is no longer equal to the mean of μ_N and μ_{SN}, but instead, it depends on the noise level and can take any value by properly choosing p_N and p_{SN}.

So far we have used a version of signal detection theory in which subjects are assumed to make decisions by setting a criterion c_r along the sensory response (x) axis [12,13]. An alternative version is to assume that a subject's decision is based on a likelihood ratio, defined as [12]:

$$l(x) = P_{SN}(x)/P_N(x), \tag{11}$$

for each sensory response x. In other words, the brain is assumed to first transform a raw sensory response x into a likelihood ratio $l(x)$. Accordingly, a likelihood-ratio criterion $c_l(\geqslant 0)$ is assumed to be set by the brain such that if $l(x) > c_l$ in a given trial, a subject answers "yes, there is a signal," and answers "no" otherwise. This version of the theory is conceptually identical to the previous one except that here the decision criterion is assumed to be set along the likelihood-ratio axis, while previously, the criterion was set along the raw sensory response axis.

With our earlier assumption that $P_{SN}(x)$ and $P_N(x)$ are Gaussian distributions of the same standard deviation but different means, it is easy to show that $l(x)$ is a monotonically increasing, exponential function of x, and c_l is related to c_r according to

$$c_r = \frac{\sigma^2\ln c_l}{\mu_{SN}-\mu_N} + \frac{\mu_{SN}+\mu_N}{2}. \tag{12}$$

Were the above expression independent of the noise level σ, the two versions of the theory would have produced the same noise dependence for the percent-correct measure, and thus the same SR-type behavior. Instead, for a given c_l, the equivalent c_r is in general a function of the noise level σ according to Eq. (12). Consequently, a fixed c_l criterion implies a variable c_r criterion as σ varies, and vice versa. Therefore, the two versions of the theory are expected to have different SR-type behavior.

Inserting Eq. (12) into Eq. (6), and then letting $\partial p/\partial\sigma = 0$, we find that the optimal noise level under a fixed likelihood-ratio criterion is given by

$$\sigma = \sqrt{\frac{(p_N+c_lp_{SN})(\mu_{SN}-\mu_N)^2}{2(p_N-c_lp_{SN})\ln c_l}}. \tag{13}$$

Since the numerator is always positive, the condition for SR-type behavior (i.e., a real, positive solution for optimal σ) is

$$(p_N-c_lp_{SN})\ln c_l > 0. \tag{14}$$

In Collins *et al.*'s experiments [9,10], $p_N = p_{SN} = 0.5$ and this inequality reduces to $(1-c_l)\ln c_l > 0$, which cannot be satisfied for any c_l. Therefore, the SR-type behavior observed experimentally is consistent with fixing the criterion on the response axis, but not on the likelihood-ratio axis. Furthermore, when $p_N = p_{SN} = 0.5$, it is easy to show that the sign of $\partial p/\partial\sigma$ with fixed c_l is determined by

$$\frac{\partial p}{\partial\sigma} \propto 2(1-c_l)\ln c_l - \frac{(\mu_{SN}-\mu_N)^2(1+c_l)}{\sigma^2}, \tag{15}$$

which is always negative for any $\mu_{SN} > \mu_N$ and $c_l \geqslant 0$. This means that under the fixed likelihood-ratio criterion, the percent correct as a function of noise can only decrease monotonically in experiments with an equal number of N and SN trials. This is contradicted by the actual data of Collins *et al.* It is not meaningful to conclude, however, that the subjects in their experiments used the response criterion (c_r) instead of the likelihood-ratio criterion (c_l), since for each c_r, there is always an equivalent c_l (and vise versa) according to Eq. (12). Rather, the conclusion should be that the subjects must have used a *fixed* c_r instead of a *fixed* c_l under different noise levels.

Although both c_r and c_l are commonly used in theoretical considerations, there is only a standard psychophysical procedure for estimating the dimensionless c_l (often called β) [12]. Rewrite Eq. (12) as

$$c_l = \exp\left[\frac{1}{\sigma^2}\left(c_r - \frac{\mu_{SN}+\mu_N}{2}\right)(\mu_{SN}-\mu_N)\right], \tag{16}$$

and note that under the SR condition of a fixed $c_r > \mu_{SN}$, the terms in both parentheses are positive. We can therefore make the prediction that when SR-type behavior is observed in experiments with equal number of N and SN trials, c_l measured under increasing noise levels should decrease monotonically.

If $p_N \neq p_{SN}$, then it is possible to have SR-type behavior with a fixed likelihood-ratio criterion. Specifically, when

$$p_N > p_{SN} \quad \text{and} \quad 1 < c_l < p_N/p_{SN}, \tag{17}$$

or when

$$p_N < p_{SN} \quad \text{and} \quad p_N/p_{SN} < c_l < 1, \tag{18}$$

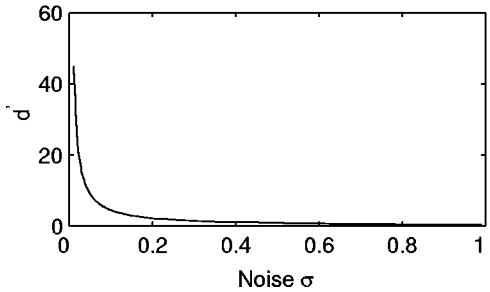

FIG. 5. The detectability d' plotted as a function of the noise level. The parameters are the same as in Fig. 1.

an optimal noise level exists according to Eq. (14).

By letting $\partial p/\partial c_l = 0$, we can also find that the optimal likelihood-ratio criterion is given by [12]

$$c_l = p_N / p_{SN} . \tag{19}$$

Under this condition, there is no solution to the optimal noise level in Eq. (13) regardless of whether $p_N = p_{SN}$ or not. Therefore, similar to the case with the response criterion, SR-type behavior could never occur if the likelihood-ratio criterion were always optimal.

Since the percent-correct measure depends on the criterion type and value, psychophysicists sometimes prefer to use detectability, defined as $d' = (\mu_{SN} - \mu_N)/\sigma$, as a criterion-free measure of the performance. d' can be estimated by counting hits and correct rejections in an experiment [12]. It is obvious from the definition that d' can only decrease monotonically with the increasing noise level σ, as shown in Fig. 5. This conclusion was also reached by Tougaard previously under his energy assumption [13].

It is worth noting that although we have focused on distinguishing signal from noise, our theory can obviously be extended to the situation of differentiating two different signals. In addition, our theory is independent of any specific sensory modality, and should be applicable to SR-type behavior of sensory perception in general. Finally, our theory can be further extended to the case where $P_N(x)$ and $P_{SN}(x)$ are not assumed to have equal standard deviations although the expressions will become more complex.

In summary, we have proposed a general model, in the framework of signal detection theory, to elucidate the mechanism underlying the SR-type behavior recently found in human sensory perception. We have demonstrated that the psychophysical data [9,10] can be explained by the fixed response criterion under different noise levels in signal detection theory but not by the fixed likelihood-ratio criterion. Our model is simpler than that of Tougaard [13] as we have used straightforward sensory response distributions and eliminated the need to assume a nonselective energy mechanism. Both the noise-mediated enhancements and decrements, and the characteristics of the performance curves as a function of the noise level found experimentally [9,10] can be well reproduced by our model. In agreement with classical SR theory and the experimental conditions, the model shows that SR-type behavior in sensory perception is present only for weak, subthreshold input stimuli. The predicted performance upper bound for SR is also consistent with extant psychophysical data [9,10]. The model further predicts that when SR-type behavior is observed in experiments with an equal number of N and SN trials, the likelihood-ratio criterion measured under increasing noise level should decrease monotonically, and that the noise level necessary to reach maximum performance should vary if subjects' criteria are changed by giving them different instructions in different blocks of trials. Finally, the model predicts that the d' measure should always decrease with increasing noise even in those experiments where the percent-correct measure shows SR-type behavior. Experimental tests of these predictions should help determine the adequacy of the model.

This work was supported by the National Institutes of Health.

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