A common framework for discriminability and perceived intensity of sensory stimuli

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Abstract

The perception of sensory attributes is often quantified through measurements of discriminability (the ability to detect small stimulus changes), as well as through direct judgements of appearance or intensity. Despite their ubiquity, the relationship between these two measurements remains controversial and unresolved. Here, we propose a framework in which they arise from different aspects of a common representation. Specifically, we assume that judgements of stimulus intensity (e.g., through rating scales) reflect the mean value of an internal representation, and discriminability reflects the ratio between the derivative of the mean value and the internal noise amplitude, as quantified by the measure of Fisher Information. A unique identification of internal representation properties can be achieved by combining the two measurements. As a central example, we show that Weber's Law of perceptual discriminability can co-exist with Stevens' power-law scaling of intensity ratings (*for all exponents*), when the noise amplitude increases in proportion to the representational mean. We extend this result beyond Weber's range by incorporating a more general and physiology-inspired form of noise, and show that the combination of noise properties and discriminability measurements accurately predicts intensity ratings across a variety of sensory modalities and attributes. Our framework unifies two major perceptual measurements - discriminability and rating scales, and proposes a neural interpretation for the underlying representations. Additionally, our framework teases two *super-threshold* perceptual measurements apart – rating scales and super-threshold perceptual distance, which were thought to measure the same perceptual aspect, and generated decades of mixed experimental results in the literature.

Keywords: discrimination, percept, Weber, Stevens, Fechner, Fisher information, stochastic representation, stimulus representation

Significance Statement

Perceptual measurements of stimulus sensitivity (discriminability) and stimulus appearance (intensity) are ubiquitous in the study of perception. However, the relationship between these two seemingly disparate measurements remains unclear. Existing proposals have been made since 60 years ago, but generally lack support from perceptual or physiological measurements, and at the same time, new theories have still been proposed each year. This problem is central to perceptual studies, and lacking understanding of which have resulted in many other conundrums in the literature remain unresolved. Here, we provide a simple and elegant framework with which to interpret and unify perceptual discrimination and intensity measurements, and the framework gained empirical support from data in multiple perceptual domains.

Introduction

As we step outdoors on a blistering summer's day, we can immediately sense the heat. And just as readily, we can sense the cooling relief of a soft breeze. Gauging the absolute strength of our sensations, as well as changes in their strength, are ubiquitous and automatic perceptual behaviors. Importantly, these two judgements have also shaped the foundations of our knowledge in sensory perception.

Perceptual capabilities arise from our internal representations of sensory inputs. Measurements of the ability to discriminate between two similar sensory inputs have sculpted the understanding of sensory representations across different domains. For example, in the late 1800's, Fechner proposed that discrimination between similar sensory inputs was proportional to the change in their corresponding internal representation [1]. By the 1950s, signal detection theory was formulated to capture stochastic internal representations (e.g. [2, 3]), as an extension to Fechner's implicit assumption that each stimulus is represented deterministically. In addition to stimulus discrimination, humans and animals can also make absolute judgements of stimulus intensities [4–8]. But the experimental methods by which this can be quantified are more controversial [9, 10], and the resulting measurements have proven difficult to link to discrimination measurements [11–14].

Consider the well-known example of Weber's law, which states that percpetual thresholds for reliable discrimination scale proportionally with stimulus intensity (and thus, discriminability scales inversely with intensity). Weber's law holds for an impressive variety of stimulus attributes. Fechner's broadly accepted explanation of Weber's law is that internally, these attributes are represented logarithmically. But in the 1950s, Stevens and others found that human ratings of perceived intensity of a variety of sensory attributes (proposed as an alternative measure of internal representation) follows a power law, with exponents ranging from strongly compressive to strongly expansive [15, 16]. Stevens presented this as a direct refutation of Fechner's logarithmic hypothesis [11], but offered no means of reconciling the two. Subsequent explanations have generally proposed either that intensity and discrimination judgementsarise from different percpeptual representations [17–20], or that the two perceptual tasks involve different nonlinear cognitive transforms [21].

Here, we develop a simple but general framework to interpret and unify perceptual discrimination and intensity judgements. Specifically, we use a simplified form of Fisher Information to quantify the relationship between perceptual discriminability and noisy internal representations. In the particular case of Weber's Law, we show that, a family of internal representations with dramatically different noise properties are all consistent with Weber's law, but only one of these is also consistent with power law intensity percepts. Moreover, we show that our framework generalizes to a set of perceptual attributes drawn from diverse sensory modalities. Finally, by incorporating a noise model that is compatible with physiology, we demonstrate that the framework can unify discrimination and intensity measurements beyond the range over which Weber's Law or Stevens' power law hold.

Results

What is the relationship between perceptual discriminability, and the internal representations from which it arises? Intuitively, a change in stimulus value (e.g. contrast of an image) leads to a change in our internal responses. When stimulus-induced internal response change is larger than variability of those responses (or "noise"), we notice the stimulus change. This conceptualization, based on Fechner's original proposals [1] and formalized in the development of Signal Detection Theory in the middle of the 20th century, has provided a successful quantitative framework to analyze and interpret perceptual data [2, 3, 22]. Despite this success, signal detection theory does not emphasize how internal representations transform stimuli, and most uses of signal detection theory have been restricted to assuming internal responses are corrupted by noise that is additive, independent and Gaussian.

A more explicit relationship between discriminability and internal representation may be expressed using Fisher Information (FI). Fisher information quantifies the precision with which a signal is represented by noisy measurements. Specifically, the noisy internal responses (r) to a stimulus (s) are described by a conditional probability $p(r|s)$, and Fisher information measures the precision (inverse variance) with which the stimulus can be recovered from $p(r|s)$. Fisher information is a widely used statistical tool. In engineering, it is used to compute the minimum achievable error in recovering signals from measurements (known as the "Cramér-Rao" bound). In perceptual neuroscience, it has been used to describe the precision of sensory attributes represented by noisy neural responses [23–25], and as a bound on discrimination thresholds [26–28]. Fisher Information is quite general – it can be used with any type of measurement distribution, including multi-modal, discrete, and multi-dimensional responses – although only a subset of cases yield an analytic closed-form expression.

Interpreting Weber's Law using Fisher Information

Typically, Fisher Information is used to characterize decoding errors based on specification of an encoder. Here, we are interested in the reverse: we want to use measurements of perceptual discriminability (decoder errors) to constrain properties of an internal representation (an encoder).

Consider Weber's Law, in which discriminability of a stimulus attribute is inversely proportional to the value of the attribute: $\delta(s) \propto 1/s$. What internal representation, $p(r|s)$, underlies this observation? The answer is not unique. Although a complete solution is not readily expressed, we can deduce and verify a set of three illustrative examples.

In the first example, Weber's law can arise from non-linear internal representational mean $\mu(s)$, which is also referred to as a "transducer function." Assuming that $\mu(s)$ is contaminated by additive Gaussian noise with variance σ^2 [3, 29, 30]: $p(r|s) \sim \mathcal{N}[\mu(s), \sigma]$. Discriminability $\delta(s)$ can be accordingly quantified using square-root of FI, expressed as $\delta(s) = |\mu'(s)|/\sigma$ (see Methods). This expression reflects Fechner's hypothesis that discrim-

inability in small stimulus changes is determined by the derivative of the transducer. When discriminability follows Weber's law, the transducer can be deduced as $\mu(s) \propto \log(s) + c$, and c is an arbitrary constant (Fig. 1A). This logarithmic model of internal representation, due to Fechner [1, 5], is the most well-known explanation of Weber's Law.

Alternatively, a number of authors proposed that Weber's Law arises from representations in which noise amplitude grows in proportion to stimulus strength (sometimes called "multiplicative noise") [3, 31–36]. Suppose representational mean $\mu(s)$ is proportional to stimulus strength (s), and is contaminated by Gaussian noise with standard deviation also proportional to s: $p(r|s) \sim \mathcal{N}[s, s^2]$. Again, the square root of FI for this representation yields $\delta(s) \propto 1/s$, consistent with Weber's Law (see Methods). In contrast to the previous case in which Weber's law arose from the nonlinear transducer, discriminability in this case arises entirely from the inhomogeneity of the noise (Fig. 1B).

Now consider a third case, inspired by neurobiology. The variability in neural spike counts is often approximated as Poisson-distributed (e.g. [37–39]). Despite the discrete nature of the integer (spike count) measurements, FI is still applicable. In this case, noise variance is equal to the mean response, and Weber's Law discrimability arises from both a transducer function $\mu(s) \propto [\log(s) + c]^2$, and the noise variability $\sigma(s)^2 = \mu(s)$ (see Methods and Fig. 1C).

These three different examples, illustrated in Fig. 1, demonstrate that the Weber's law discriminability does not uniquely specify an internal representation (see also [40–43]). In fact, these are three members of an infinite family of solutions. To make this non-identifiability problem more explicit, note that for all three examples, discriminability shares a common form:

$$\delta(s) = \frac{|\mu'(s)|}{\sigma(s)}. \tag{1}$$

We refer to this expression as *Fisher Discriminability*. FI can be difficult to compute for a general distribution, but Fisher discriminability relies only on the first two moments of the response distribution, and provides a lower bound to the square-root of FI [44] (see Methods). For all three of the examples above, this lower bound is exact – Fisher discriminability is identical to the square-root of FI. Fisher Discriminability offers a direct and intuitive understanding of the identifiability problem: To explain any measured pattern of discriminability $\delta(s)$, one can choose an arbitrary mean internal response $\mu(s)$ that increases monotonically and continuously, and pair it with an internal noise variability $\sigma(s) = |\mu'(s)|/\delta(s)$. So there are infinitely many pairs of $\mu(s)$ and $\sigma(s)$ that explain Weber's law for discriminability. How can we resolve this ambiguity?

A unified interpretation of power-law intensity percepts and Weber's Law

The ambiguity introduced in the previous section can be resolved through additional measurements (or assumptions) of the mean or variance of internal representations, or the relationship between the two. We start by introducing an additional experimental measure

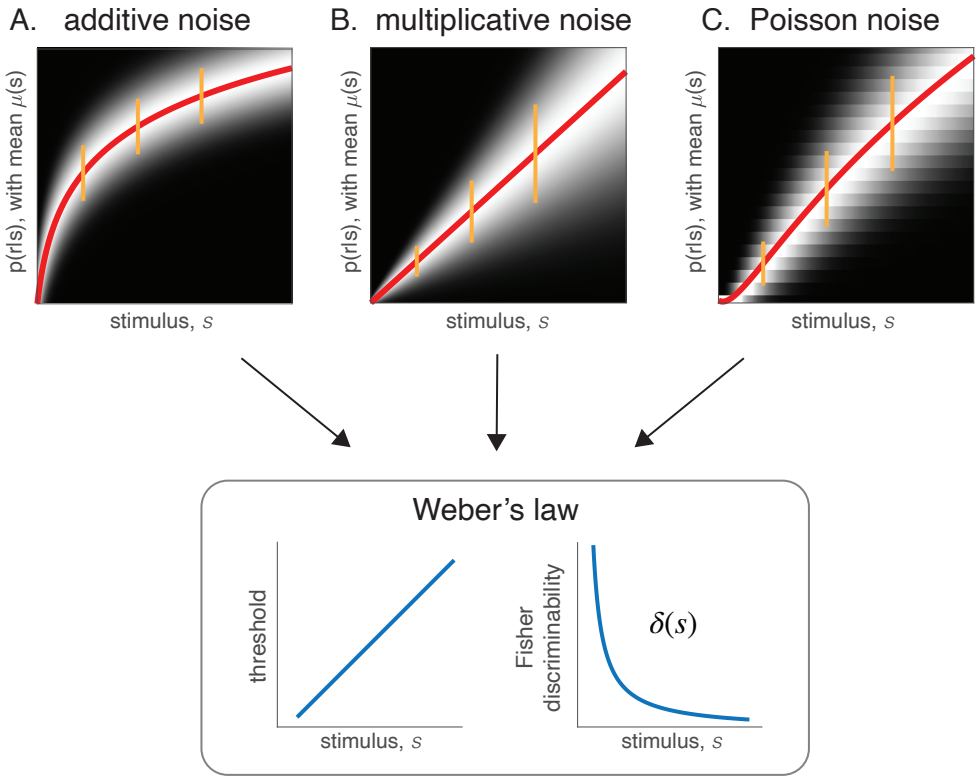

Figure 1: **Three different example internal representations, each consistent with Weber's law.** Each upper panel shows a stimulus-conditional response distribution, $p(r|s)$ (gray, brightness proportional to conditional probability), the mean response, $\mu(s)$ (red line), and three examples of response standard deviation (orange vertical lines indicate a range of $\pm$ one standard deviation around the mean). **A** Mean response proportional to $\log(s) + c$, contaminated with additive Gaussian noise. **B** Mean response proportional to s, with "multiplicative" Gaussian noise (standard deviation proportional to s). **C** Mean response proportional to $\log^2(s + c)$, with Poisson (integer) response distribution. The bottom panel indicates the discrimination threshold (left) and the sensitivity (right), that arise from the calculation of Fisher Information for all three representations.

of representational means, by interpreting perceptual magnitude ratings as providing a direct measurement of $\mu(s)$ [40, 45]. In a rating experiment, observers are asked to report perceived stimulus intensities by selecting a number from a rating scale (e.g. [7, 15, 16]). Suppose that these ratings reflect the observers' internal response r (up to an arbitrary scale factor that depends on the numerical scale), and that averaging over many trials of r (drawn from $p(r|s)$) provides an estimate of the mean internal representation, $\mu(s)$.

Using magnitude ratings, Stevens and others (e.g. [15, 46, 47]) found that perceived intensity of many stimulus attributes can be well-approximated by a power law, $\mu(s) \propto s^{\alpha}$. The exponent α was found to vary widely across stimulus attributes ranging from strongly compressive (e.g., $\alpha = 0.33$ for brightness of a small visual target) to strongly expansive (e.g., $\alpha = 3.5$ for electric shock to fingertips). For stimulus attributes obeying Weber's Law, Stevens' power law measure was used as direct evidence against Fechner's hypothesis of logarithmic transducers [11]. But the relationship of power law ratings to Weber's Law discriminability was left unresolved. Over the intervening decades, magnitude rating measurements have generally been interpreted as arising from aspects of internal representation that are different from those underlying discriminability (e.g. [12, 17, 20, 48]), or sometimes, measurements of magnitude ratings were dismissed altogether [9, 13].

Fisher Discriminability offers a potential unification of power-law intensity percepts and Weber's Law discriminability. Weber's law can be expressed using Fisher Discriminability: $\frac{|\mu'(s)|}{\sigma(s)} \propto 1/s$. We can substitute a power function for $\mu(s)$, which leads to a simple constraint on the internal noise (Figure 2A, see Methods):

$$\sigma(s) \propto \mu(s). \tag{2}$$

That is, the standard deviation of the internal representation is proportional to the mean. Because the mean takes a power form s^{α}, standard deviation grows with stimulus according to the same power law s^{α}. This result does not assume Gaussian internal representations, thus provides a generalization of the multiplicative noise case from the previous section (Figure 1). In particular, this noise form allows Weber's Law discriminability to co-exist with a power-law percept for *all* powers α (Figure 2B).

Connecting percept to discrimination for generalized intensity variables

Previous section provided a unification of three relationships: Weber's Law for discriminability, a power-law behavior for intensity ratings, and proportionality of mean and standard deviation in internal noise. In this section, we consider deviations from these relationships, and show that these deviations remain consistent under our framework.

Consider first the internal noise. Poisson neural noise implies a variance proportional to the mean spike count, and this relationship holds for relatively low response levels [cite]. At modest to high firing rates, spiking variance in individual neurons is generally super-Poisson, growing approximately as the square of mean response [49–51], consistent with the proportional noise assumption of the previous section. A quadratic model can capture how

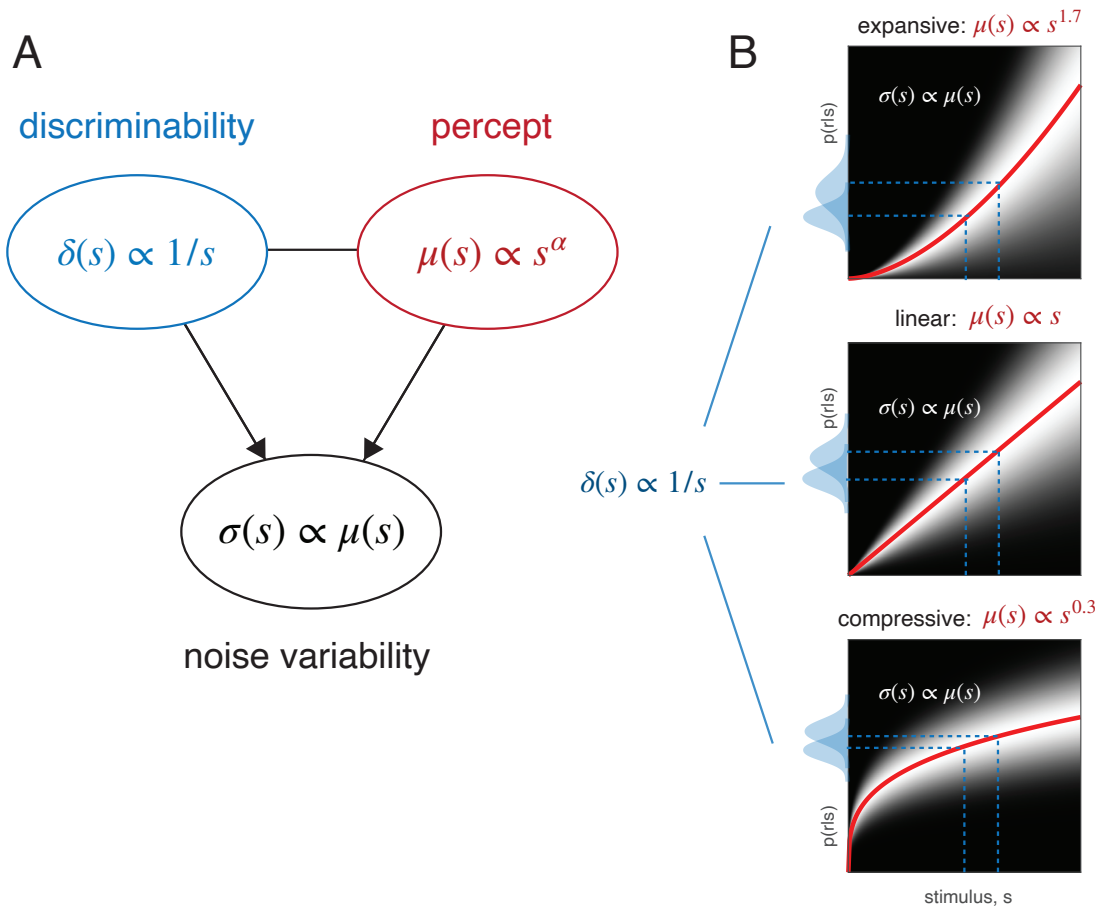

Figure 2: **Unifying perceptual measures of Weber's Law discriminability and power-law magnitude ratings. A.** Using Fisher Discriminability, perceptual sensitivity and perceptual magnitudes can be combined to constrain an internal representation. In the particular case of Weber's Law, and power-law intensity ratings, this yields an internal representation with noise variance proportional to squared mean. **B.** This pattern of proportional internal noise serves to unify Weber's Law and power-law magnitudes for any exponent α, allowing for transducer functions that are expansive ($\alpha > 1$, upper panel), linear ($\alpha = 1$, middle), or compressive ($\alpha < 1$, lower). Blue dashed lines indicate an example pair of stimuli that are equally discriminable in all three cases, as can be seen qualitatively from the overlap of their corresponding measurement distributions (shown along left vertical edge of each plot, in shaded blue).

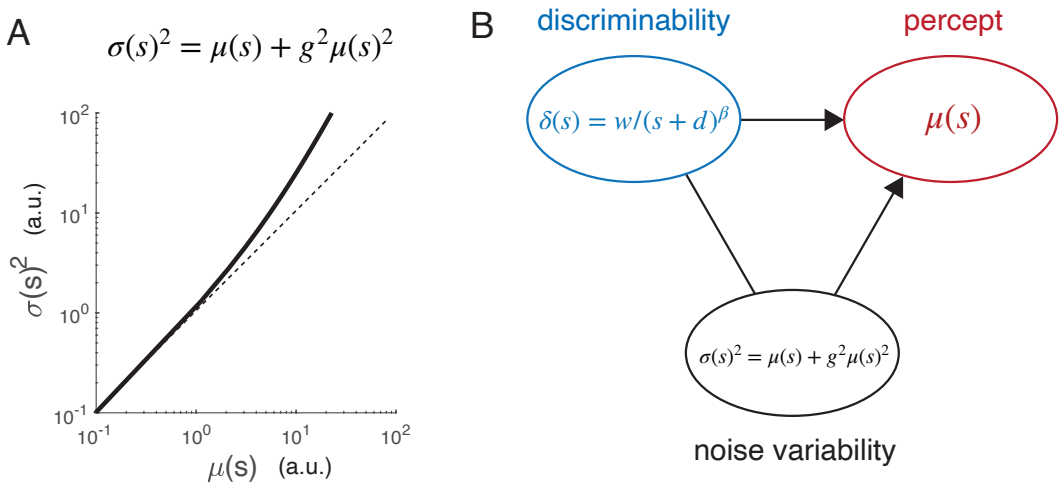

Figure 3: **Generalization beyond the Weber range. A.** Quadratic mean-variance relationship for a modulated Poisson model of sensory neurons [50, 51]. Behavior is Poisson-like at low intensities ($\sigma^2(s) \sim \mu(s)$), and super-Poisson at higher intensities ($\sigma^2(s) \sim \mu^2(s)$), with parameter g determining the response level of the transition between the two. **B.** Using Fisher Discriminability, we can combine a generalized form of Weber sensitivity with the mean-variance relationship in panel A to generate numerical predictions of perceived stimulus intensity $\mu(s)$.

neuronal spiking variance relates to the mean over the extended range [49, 50]:

$$\sigma(s)^2 = \mu(s) + g^2\mu(s)^2, \tag{3}$$

with g^2 a non-negative constant that governs the transition from the Poisson range (smaller μ) to the super-Poisson range (larger μ). For stimulus attributes that are represented with the combined activity of many such neurons, the sum of their responses also has a variance that is quadratic in the mean, and the effective g may be derived from the values of the underlying individual neurons (see Appendix).

Perceptually, both Weber's Law for discrimination and the power-law for perceptual magnitudes have been found to fail, especially at low intensities (e.g. [7, 52]). A generalized form of Weber's Law has been proposed to capture discrimination data over broader intensity ranges:

$$\delta(s) = w/(s+d)^\beta, \tag{4}$$

where d is an additive constant that governs discriminability at low intensities, the exponent β determines how discrimination deviates from Weber's law at high intensities, and w is a non-negative scaling factor. Weber's Law corresponds to the special case of $d = 0$ and $\beta = 1$.

To test the generalization of our unified framework, we combined the modulated Poisson noise model (Eq. 3) with fitted versions of this generalized form of Weber's Law (Eq. 4), and

used Fisher Discriminability to generate predictions of $\mu(s)$ (Figure 3B). We then compared these predictions to averaged perceptual intensity ratings. These predictions rely on the choice of three parameters: g that determines the transition from Poisson to super-Poisson noise, an integration constant c (see Methods), and a final scale factor that adjusts the predictions to the rating scale range.

We examined predictions for five different stimulus attributes, for which both discrimination and rating scale data (averaged across trials) are available over a large range of stimulus intensities. Figure 4 shows results for: 1) sucrose concentration (or "sweetness" perception, [53, 54]); 2) sodium chloride concentrarion (or "saltiness" perception, [53, 54]); 3) intensity of auditory white noise [55, 56]; 4) intensity of 1000 Hz pure tone (auditory loudness, [56, 57]); and 5) sinusoidal visual contrast [47, 58].

The discrimination curves vary substantially across these stimulus attributes, but all are well-fit by the generalized Weber functional form (blue curves, Figure 4). In all cases, the rating scale data are well-predicted by combining the discriminability fit with the noise model of Eq. (3) (red curves). Moreover, we find that reducing to simpler noise models (additive, multiplicative, or Poisson) yields substantially worse predictions for most cases. Note that the latter two models are special cases of Eq. (3), corresponding to the limit of large g and zero g, respectively.

Absolute judgement and discriminability are amongst the most important and widely assessed characteristics of perception [59, 60], but the relationship between the two has proven elusive. In this paper, we've proposed a framework that relates these characteristics to two fundamental properties of internal representation – a nonlinear "transducer" mapping and the strength of internal noise. Our proposal is simple, and relies on two primary assumptions: 1) discriminability reflects the ratio of the derivative of the transducer and the internal noise standard deviation (Eq. 1), a simplified form (and lower bound) of Fisher information; and 2) absolute judgements (specifically, those obtained through average ratings of stimulus intensity) reflect the value of the transducer. This combination allows a unified interpretation in which percept and discriminability reflect a single underlying representation, providing a potential link to physiology.

Discussion

To develop and test our framework, in this paper, we've focused on attributes that obey Weber's Law, and its modest generalizations. Despite its ubiquity, the relationship between Weber's Law and underlying representation has been contentious. In the late 19th century, Fechner proposed that perceptual intensities correspond to integrated discriminability [1], and in particular predicted that Weber's Law discriminability implied a logarithmic internal representation. Using rating scales as a form of measurement, Stevens instead reported that many sensory variables appeared to obey a power-law, with exponents differing substantially for different attributes [11]. Stevens interpreted this as a refutation of Fechner's logarithmic transducer. In order to explain the discrepancy between Fechner and Stevens'

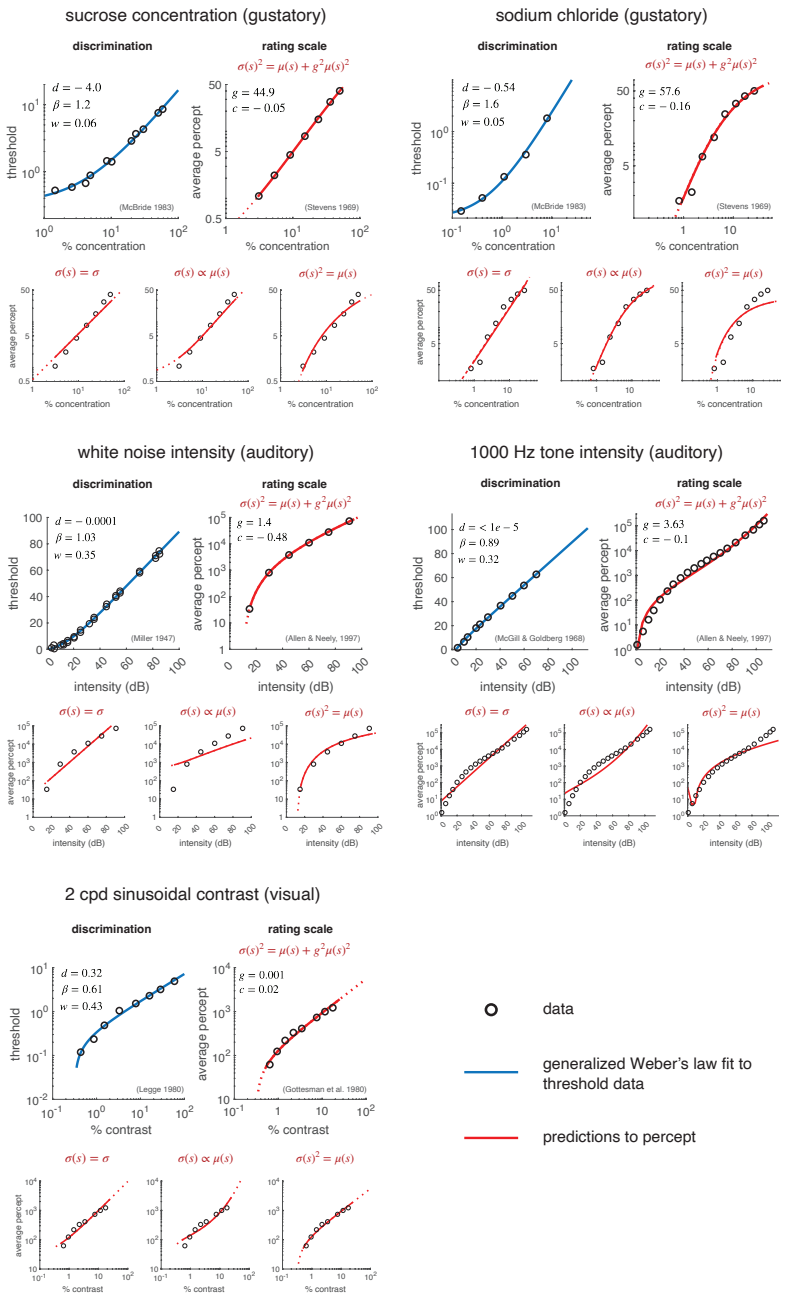

Figure 4: **Predicting perceived intensity from discriminability for five different sensory attributes.** For each attribute, we fit a three-parameter generalized form of Weber's Law (Eq. 4, blue curves, optimal parameters as indicated) to measured discrimination thresholds (black points). We set this equal to the Fisher Discriminability relationship of Eq. (1), and combined this with the mean-variance relationship of the modulated Poisson noise model (Eq. 3) in order to generate predictions of $\mu(s)$. The predictions (red curves) depend on the choice of g in the noise model, as well as an additive integration constant and overall multiplicative scale factor, all three of which are adjusted to best fit average perceptual rating scale measurements (black points). The three smaller graphs at the bottom of each panel depict predictions of $\mu(s)$ for alternative noise models: constant standard deviation, standard deviation proportional to mean, and variance proportional to mean.

proposals, a number of authors suggest that perceptual intensities and discrimination reflect different stages of processing, bridged by an additional nonlinear transform. Specifically, [17] proposes a type of sensory adaptation, [18] reflects additional sensory processing, and [21] incorporates an additional cognitive process. Our framework offers a parsimonious resolution of these discrepancies, by postulating that perceptual intensity and discriminability arise from different combinations of the mean and variance of a common representation.

It is worth noting that while Fechner's integration hypothesis is inconsistent with Stevens' power law measurements, it appears to be consistent with many types of suprathreshold comparison of stimulus differences. Specifically, experimental procedures involving many suprathreshold comparative judgements (e.g. maximum likelihood difference scaling, categorical scales and bisection [16, 36, 53, 61]) seem to reflect integration of local discriminability, whereas experimental procedures that require absolute judgements (e.g. rating scales [16, 47, 62]) seem to reflect the mean of internal representation, which is only equal to integrated discriminability when noise variability is constant (Figure 5).

This subtle distinction between comparative and absolute judgement is at the heart of multiple debates in perceptual literature. For example, it arises in discussions of whether perceptual noise is additive or multiplicative in visual contrast (e.g. [36, 40, 63]). We have proposed that mean and variance of internal representations can be identified through the combination of absolute and discriminative judgements, because the two measurements reflect different aspects of the representation. On the other hand, if suprathreshold comparative judgements reflect integrated local discriminability, they do not provide additional constraints on internal representation, and combining such measurements does not resolve the identifiability issue. This gives, for example, a consistent interpretation of the analysis in [36], which shares the logic of our approach in seeking an additional measurement to resolve non-identifiability of discrimination measurements, but reaches a different conclusion regarding consistency of additive noise. Several other theoretical or experimental constraints have been proposed to resolve the identifiability issue, including imposing a common criterion between two discrimination tasks [63], connecting the response accuracy for the first and the second response in a four-alternative choice [28], and connecting discrimination to an identification task [43]. An open question is whether our framework can be extended to account for these more diverse perceptual scenarios.

Our examination of the particular combination of Weber's Law discriminability with power-law intensity percepts led to the conclusion that the amplitude of internal noise in these cases should vary in proportion to the mean response. While such "multiplicative noise" has been proposed previously as an explanation for Weber's Law [3, 31–33], it has generally been proposed in the context of a linear transducer (as in Fig. 1). In our framework, we find that this form of noise (standard deviation proportional to the mean) is sufficient to unify Weber's and Stevens' observations for the complete family of power-law transducers, regardless of exponent. An additional prediction of our model is that the standard deviation of perceptual ratings should also grow proportionally to the mean rating. This is consistent with findings of a number of previous studies (e.g. [10, 64, 65]). Greene and Luce, for example, showed that when observers were asked to rate 1000 Hz tone loudness, their

coefficient of variations (standard deviation divided by the mean) in the ratings are near-constant for a large range of intensities [64].

The proportionality of the mean and standard deviation of a stimulus representation offers a potential interpretation in terms of underlying physiology of neural responses. We considered, in particular, recently proposed "modulated Poisson" models for neural response which yields noise whose variance grows as a second-order polynomial of the mean response [50, 66]. The noise of the summed response over a population of such neurons would have the same structure (see Appendix). At high levels of response, this allows a unification of Weber's Law and Stevens' power law. At lower levels, it produces systematic deviations that lead to consistent predictions of ratings for a number of examples (Fig. 4). Recent generalizations of the modulated Poisson model may allow further refinement of the perceptual predictions [67]. For example, at very low levels of response, sensory neurons exhibit spontaneous levels of activity that are independent of stimulus drive [30], suggesting that inclusion of an additive constant in Eq. 3 could provide predictions of perceptual detection thresholds [68].

We've restricted our examples to perceptual intensity attributes that obey Weber's Law, but the proposed framework is more general. In particular, the bound on Fisher information holds for any noisy representation, and has, for example, been applied to representation of sensory variables in the responses of populations of tuned neurons [23, 25, 26]. In some cases, these attributes exhibit Weber's Law behavior, which may be attributed to heterogeneous arrangements of neural tuning curves rather than noise properties of individual neurons. For example, neurons in area MT that are selective for different speeds have tuning curves that are (approximately) shifted on a logarithmic speed axis [69]. In this case, an independent response noise model yields Fisher Information consistent with Weber's Law [70–74]. More generally, changes in a stimulus attribute may cause changes in both the amplitude and the pattern of neuronal responses, which, when coupled with properties of internal noise, yield predictions of discriminability through Fisher Information. Specifically, the abstract internal representation that we have assumed for each perceptual attribute corresponds to the projection of high-dimensional noisy neuronal responses onto a decision axis for perceptual judgements (e.g. [49, 75, 76]). Although discrimination judgements for a stimulus attribute are generally insufficient to uniquely constrain underlying high-dimensional neuronal responses, the one-dimensional projection of these responses provides an abstract but useful form for unifying the perceptual measurements.

Our framework enables the unification of two fundamental forms of perceptual measurement – absolute judgement and discrimination – with respect to a common internal representation. However, the study of perception is diverse and mature, with numerous additional perceptual measurements [77] whose connection to this framework might be explored. The descriptive framework outlined here also raises fundamental questions about the origin of this relationship between internal representation mean and noise. The forms of both noise and transducer may well be constrained by their construction from biological elements, but may also be adapted to satisfy normative goals of efficient transmission of environmental

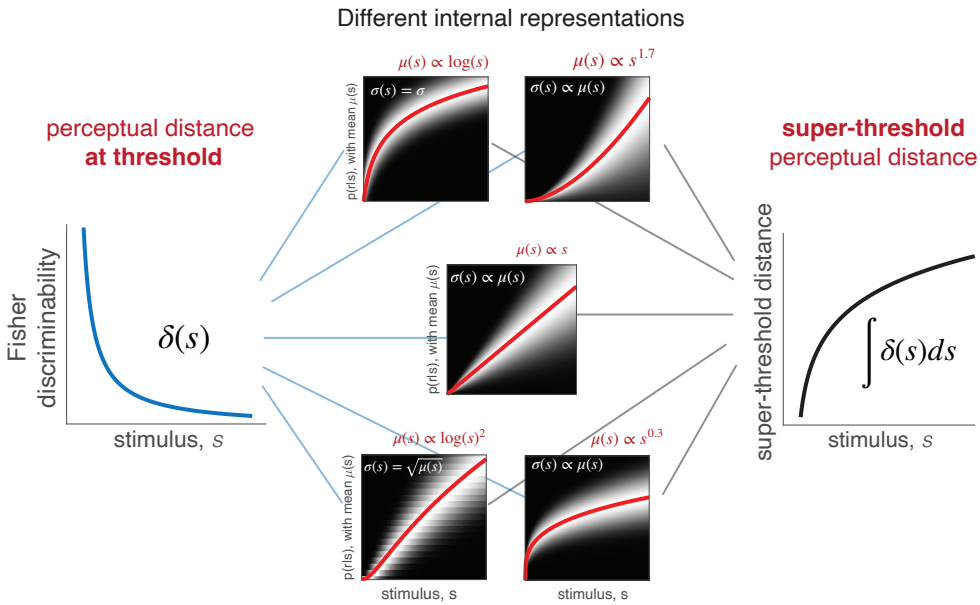

Figure 5: **Super-threshold perceptual distance and internal representations.** More general than Fechner's original proposal, many different shapes of internal representational mean (logarithmic shape being only one of them) once paired with appropriate noise can give rise to Weber's law. One proposal closely resembles Fechner's original one is that all these representations that are consistent with Weber's law discriminability ($1/s$) predict logarithmic super-threshold perceptual distance ($\int 1/s\, ds$), which can potentially be measured using super-threshold comparative judgements. We revealed that two distinct aspects of the internal representations can possibly be revealed using two types of *super-threshold perceptual judgements* – rating scales (which measures the mean of the internal representations) and super-threshold perceptual distance (which measures the integrated perceptual discriminability). The two aspects of the internal representations are generally different, but coincide when the internal noise is additive Gaussian ($\sigma(s) = \sigma$).

information under constraints of finite coding resources [73, 78, 79]. Exploration of these relationships provides an enticing direction for future investigation.

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Methods

Fisher information

Fisher Information provides a measure of the precision with which stimuli are encoded in noisy measurements [1]. In statistics and engineering communities, it is often used in the context of the Cramér-Rao bound, which states an upper bound on the precision (inverse variance) attainable by an unbiased estimator [2]. It was first proposed as a means of quantifying perceptual discrimination by Paradiso [3], and further elaborated for neural populations by Seung and Sompolinsky [4]. In this context, the square root of Fisher information provides a bound on perceptual precision (discriminability) [5], and may be viewed as a generalization of "d-prime", the traditional metric of signal detection used in psychophysical studies [6].

For a stimulus attribute s, the Fisher Information is derived from a stochastic model of responses, $p(r|s)$, and the Fisher bound on discriminability may be written as:

$$\delta(s) = \sqrt{\mathbb{E}\left[\left(\frac{\partial \log p(r|s)}{\partial s}\right)^2 \Big| s\right]}. \tag{5}$$

The expression captures the relative change in measurement distribution $p(r|s)$ when the stimulus s is perturbed. This definition relies only on the differentiability of the measurement distribution with respect to s and some modest regularity conditions [2], but does not make assumptions regarding the form of the measurement distribution. Either s and/or r can be vector-valued, but for our purposes in this article, we assume a one-dimensional stimulus attribute, and thus the internal representation r that is relevant to the discrimination experiment is also effectively one-dimensional.

The three examples shown in Figure 1 are each consistent with Weber's Law discriminability, but differ markedly in their response distributions: a fixed-variance Gaussian density ("additive noise"), a variable-variance Gaussian density ("multiplicative noise"), and a discrete Poisson distribution. Below, we derive each of these.

Additive Gaussian noise. Assume the internal representation has mean response $\mu(s)$, and is contaminated with additive Gaussian noise of variance σ:

$$p(r|s) = (\sqrt{2\pi}\,\sigma)^{-1} \exp[-(r-\mu(s))^2/(2\sigma^2)].$$

Substituting into Eq. (5) and simplifying yields $\delta(s) = |\mu'(s)|/\sigma$. Weber's Law states that $\delta(s) \propto 1/s$, and thus we require a transducer such that $|\mu'(s)| \propto 1/s$. If we assume monotonicity, the transducer is uniquely determined (up to a proportionality factor) via integration: $\mu(s) \propto \log(s) + c$.

"Multiplicative" Gaussian noise. Assume a representation with identity transducer $\mu(s) = s$ and Gaussian noise such that the amplitude scales with the mean, $\sigma(s) = \sqrt{a}s$:

$$p(r|s) = (\sqrt{2\pi a}\, s)^{-1} \exp[-(r - \mu(s))^2/(2as^2)].$$

Substituting into Eq. (5) and simplifying again yields Weber's Law: $\delta(s) = (\sqrt{2 + 1/a})/s$.

Poisson noise. Assume the internal response r is an (integer) spike count, drawn from an inhomogeneous Poisson process with rate $\mu(s)$, a widely-used statistical description of neuronal spiking variability. Then

$$p(r|s) = \frac{\mu(s)^r \exp[-\mu(s)]}{r!}.$$

In this case, $\delta(s) = |\mu'(s)/|\sqrt{\mu(s)}$. If $\delta(s)$ follows Weber's law, we can again derive the form of the transducer: $\mu(s) \propto [\log(s) + c]^2$ for some constant c.

Fisher discriminability

In general, Fisher information for arbitrary distributions can be difficult to compute and often cannot be expressed in closed form. But for arbitrary distributions, a lower bound for the square-root of Fisher information, which we term "Fisher discriminability", is readily computed and interpreted, because it depends only on the mean and variance of the distribution. Specifically, we define Fisher discriminability as $\delta(s) \equiv |\mu'(s)|/\sigma(s)$. Its role as a lower bound can be derived using a modified form of Cauchy-Schwartz inequality:

$$\int f(y)^2 p_y(y)dy \geq \frac{\left[\int\int g(x)f(y)p_{xy}(x,y)dxdy\right]^2}{\int g(x)^2 p_x(x)dx}. \tag{6}$$

We then make the following substitutions:

$$\begin{aligned} \int f(y)^2 p_y(y)dy &= \int \left\{\frac{\partial \log p(r|s)}{\partial s}\right\}^2 p(r|s)dr \\ \int g(x)^2 p_x(x)dx &= \int [r - \mu(s)]^2\, p(r|s)dr. \end{aligned} \tag{7}$$

The left-hand side of Eq. (6) is the Fisher information, and the bound arises after simplification of the right-hand side:

$$
\begin{aligned}
I_F(s) &\geq \frac{\left\{\int [r-\mu(s)] \frac{\partial \log p(r|s)}{\partial s} p(r|s) dr\right\}^2}{\int [r-\mu(s)]^2 p(r|s) dr} \\
&= \frac{\left\{\int [r-\mu(s)] \frac{\partial p(r|s)}{\partial s} dr\right\}^2}{\sigma(s)^2} \\
&= \frac{\left\{\frac{\partial}{\partial s} \int r p(r|s) dr - \mu(s) \frac{\partial}{\partial s} \int p(r|s) dr\right\}^2}{\sigma(s)^2} \\
&= \frac{\mu'(s)^2}{\sigma(s)^2}.
\end{aligned}
\tag{8}
$$

Fisher discriminabiliity generalizes to a multi-dimensional response vector (e.g., a neural population), by replacing the inverse variance with the Fisher information matrix, and projecting this onto the gradient of the log likelihood [7]. The derivation of the full bound for the multi-dimensional case (both stimuli and responses) may be found in [8].

In the three examples of Fig. 1, the lower bound is exact: Fisher discriminability is equal to the square-root of Fisher information. An equivalent expression for Fisher discriminability has also been obtained by assuming a minimal-variance unbiased linear decoder [9]. Compared to our interpretion as a lower bound, this interpretation has the advantage of being an exact expression, but the disadvantage of relying on restrictive assumptions about decoding.

Internal representations consistent with Weber's law and Stevens' Power law

Using Fisher discriminability and assuming monotonicity of $\mu(s)$, Weber's law can be expressed as: $\frac{\mu'(s)}{\sigma(s)} \propto \frac{1}{s}$. Because both $\mu(s)$ and $\sigma(s)$ are functions of s, neither is uniquely constrained by the discriminability. To identify $\mu(s)$ and $\sigma(s)$, we must combine Weber's law with some other measurement that constrains $\mu(s)$, $\sigma(s)$, or some other combination of the two. In this paper, we analyzed one example measurement – magnitude ratings – which we assume provides a direct measurement of $\mu(s)$. For many intensity variables, magnitude ratings follow a power-law s^α. Assuming $\mu(s) \propto s^\alpha$, we can substitute the derivative of the power-form $\mu(s)$ into Eq. (1), which yields $\sigma(s) \propto s^\alpha$. That is, Weber's Law results when both $\mu(s)$ and $\sigma(s)$ follow a power law with the same exponent, α. Note that this result holds for all exponents.

Data Fitting

To examine the validity of our framework beyond Weber's range, we analyzed five different sensory attributes (Fig. 4). For each, we first fit a generalized form of Weber's Law [10] to

perceptual discrimination data:

$$\delta(s) = \frac{w}{(s-d)^{\beta}}, \tag{9}$$

in which d is an unrestricted additive constant, β is a non-negative exponent, and w is a non-negative scaling factor. These three parameters were optimized to minimize squared error of the measured inverse discrimination (thresholds).

Next, we combined the fitted discrimiability model with a model of internal noise to generate a prediction for the mean percept, $\mu(s)$, which was then compared with rating measurements. Our primary predictions assume a mean-variance relationship consistent with a modulated Poisson distribution [11]:

$$\sigma(s)^2 = \mu(s) + g^2\mu(s)^2. \tag{10}$$

The transducer $\mu(s)$ is obtained by solving the differential equation that arises by substituting this variance expression into the Fisher discriminability of Eq. (1), and equating this with the generalized form of Weber's law (Eq. 9):

$$\frac{\mu'(s)}{\sqrt{\mu(s) + g^2\mu(s)^2}} = \frac{w}{(s-d)^{\beta}} \tag{11}$$

The solution may be expressed in closed form:

$$\mu(s) = \sinh^2\left(\frac{g(s-d)^{-\beta}[w(d-s) + c(s-d)^{\beta}]}{2(\beta-1)}\right) \Big/ g^2. \tag{12}$$

The parameters $\{d, \beta, w\}$ were held at values obtained when fitting the discrimination data, but the function has three additional free parameters that we adjusted to minimize squared error with the log-transformed rating data. The first is g, which governs the transition from Poisson to super-Poisson noise behavior (large g indicates an early transition). The second parameter is c, an integration constant that arises from solving the differential equation for $\mu(s)$. The last parameter is a scale factor, which rescaled the predicted intensity values to the numerical range used in the associated rating experiment.

For comparison, we computed rating predictions from three other noise models: additive Gaussian noise, Poisson noise, and a generalized form of multiplicative noise. The derivation of the corresponding transducers are detailed below.

Additive Gaussian noise. As for modulated Poisson model, we first fit the generalized Weber's law to discrimination data, and lock the parameters $\{d, \beta, w\}$. Then we solve a differential equation arising from equating Fisher discriminability with the generalized Weber's Law:

$$\frac{\mu'(s)}{\sigma} = \frac{w}{(s-d)^{\beta}}. \tag{13}$$

The solution for $\mu(s)$ in this case also has a closed form:

$$\mu(s) = \frac{w\sigma(s-d)^{1-\beta}}{1-\beta} + c \tag{14}$$

The integration constant c and an overall scaling factor are adjusted to fit $\mu(s)$ to the rating data (minimizing the squared error between logarithmically transformed rating data and the function).

Poisson noise. Following a similar procedure for the case of additive Gaussian noise, we find a closed-form solution for $\mu(s)$ using Poisson noise and Fisher discriminability:

$$\mu(s) = \frac{(s-d)^{-2\beta}[w(d-s) + (\beta-1)c(s-d)^{\beta}]^2}{4(\beta-1)^2} \tag{15}$$

Again, the integration constant c and overall scaling factor are optimized to fit the rating data.

Generalized multiplicative noise. Here, we assume a noise mean-variance relationship $\sigma(s)^2 = g^2\mu(s)^2$, which is the choice that enables the co-existance of Weber's law and Stevens' power law. As in previous cases, we plug this into the expression for Fisher discriminability to obtain a prediction for $\mu(s)$:

$$\mu(s) = \exp\left[\frac{gw(s-d)^{(1-\beta)}}{1-\beta}\right] c. \tag{16}$$

Note that, as for the full noise model of Eq. (10), fitting involves estimation of three parameters: the noise parameter g, an integration constant c, and a scaling factor.

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Appendices

Connecting noise parameters estimated for perception and for neuronal responses

In this section, we analyze how parameter g of the modulated Poisson noise model, when estimated from perceptual data, can be related to noise properties of underlying individual neurons.

In the modulated Poisson model [1], each neuron's response is captured by a Poisson distribution parameterized by $\mu_i(s)$:

$$p(r_i|s) = \frac{\mu_i(s)^{r_i} e^{-\mu_i(s)}}{r_i!} \tag{S.1}$$

Unlike a standard Poisson model, $\mu_i(s)$ is also a random variable that is constructed as a product of two components: $\mu_i(s) = f_i(s)G$. The function $f_i(s)$ captures the stimulus-dependent input drive, and G is a random variable, with mean $\mathbb{E}(G) = 1$ that represents a multiplicative modulator, that capture the combined effects of noisy feedback or recurrent inputs.

Because neuronal responses fluctuate due to both the modulator and the Poisson spiking process, they are more variable than those arising from a Poisson model. Indeed, we can partition response variance into two additive components, one from the input-drive, which follows a Poisson description (variance proportional to the mean), and the other from the modulator:

$$\sigma(r_i|s)^2 = \mu_i(s) + \sigma_G^2 \mu_i(s)^2 \tag{S.2}$$

For further analysis, we assume the modulator distribution is the same for all neurons. Conditioning on a single modulator G, all neurons share a single modulator variance, σ_G^2. This assumption is reasonably consistent with data analyzed from neuronal population in LGN, V1, V2, and MT [1].

The relationship between mean and variance in a single modulated-Poisson spiking neuron may be tied to the assumed mean-variance relationship for intensity perception in the main text. For simplicity of analysis, we assume independent responses so that the variance of a population is the sum of variance in individual cells:

$$\sum_i^N \sigma(r_i|s)^2 = \sum_i^N \mu_i(s) + \sigma_G^2 \sum_i^N \mu_i(s)^2. \tag{S.3}$$

We further assume that perception is the consequence of summing this set of neuronal responses. Because the population is assumed independent, percept, $\mu_p(s)$, corresponds to the sum of individual mean response rate: $\mu_p(s) = \sum_i^N \mu_i(s)$. Perceptual variance, σ_P^2, is the sum of individual response variance $\sum_i^N \sigma(r_i|s)^2$. So we can re-write the mean-variance relationship assumed for perceptual noise in the main text as:

$$\sum_i \sigma(r_i|s)^2 = \sum_i \mu_i(s) + g^2 \left[\sum_i \mu_i(s) \right]^2. \tag{S.4}$$

Now we can find a connection between perceptual noise parameter g (in equ. S.4), and the noise parameter in individual neurons σ_G (in equ. S.3). These two parameters are generally different, because summing the squared mean responses is generally different from the square of the sum (right hand side of equ. S.3 and equ. S.4).

Suppose perception is the consequence of a homogeneous neuronal population's response. Within this population, each neuron shares the same response to a stimulus s, and $\mu_i(s) = \mu(s)$. When the population has N number of neurons, $\sum_i^N \mu_i(s)^2 = N\mu(s)^2$. For perceptual noise, $(\sum_i^N \mu_s)^2 = N^2\mu(s)^2$. As a consequence, the perceptual noise parameter g relates to the neuronal noise parameter σ_G via $g = \sigma_G/\sqrt{N}$.

In general, when neuronal responses are assumed independent, the perceptually estimated noise parameter g is a lower bound for neuronal noise parameter σ_G. The perceptual noise parameter exactly matches the neuronal parameter when perception is the consequence of a single neuron's response. In general, the lower bound is tighter when the neuronal population sparsely responds to a stimulus, i.e. most neurons do not respond to the stimulus.

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