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 (an observers' ability to detect small changes in stimulus), as well as direct judgements of appearance or intensity. Despite their ubiquity, the relationship between these two measurements is controversial and unresolved. Here, we propose a framework in which they both arise from the properties of a common internal representation. Specifically, we assume that direct measurements of stimulus intensity (e.g., through rating scales) reflect the mean value of an internal representation, whereas measurements of discriminability reflect the ratio of the derivative of mean value to the internal noise amplitude, as captured by the measure of Fisher Information. Combination of the two measurements allows unique identification of internal representation properties. As a central example, we show that Weber's Law of perceptual discriminability can co-exist with Stevens' observations of power-law scaling of perceptual intensity ratings (for all exponents), if one assumes an internal representation with noise amplitude proportional to the mean. We extend this result by incorporating a more general physiology-inspired model for noise and a discrimination form that extends beyond Weber's range, and show that the combination allows accurate prediction of intensity ratings across a variety of sensory modalities and attributes. Our framework unifies two major perceptual measurements, and provides a potential neural interpretation for the underlying representations.

Keywords: discrimination, percept, Weber, Stevens, Fechner, Fisher information, noise variability, internal representation

As we step outdoors on a blistering summer's day, we are able to immediately sense the heat. And just as readily, we can sense the cooling relief of a soft breeze. Gauging the absolute strength of sensations and changes in sensations (discriminability) are fundamental to our daily lives. These two types of judgements have also shaped the foundations of our knowledge in sensory perception.

Our perceptual capabilities arise from the properties of internal neural representation. Measurements of discriminability of numerous stimulus attributes and sensory modalities have sculpted our understanding of underlying sensory representation. For example, in the late 1800's, Fechner proposed that our sensitivity to small stimulus changes reflected a corresponding magnitude change in some 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 representations are deterministic. In addition to stimulus discrimination, humans and animals are also able to 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 measurements of discrimination [11–14].

Consider, as a well-known example, the case of Weber's Law. For many sensory attributes, thresholds for reliable discrimination scale proportionally with stimulus intensity (i.e. sensitivity scales inversely with intensity). A simple and broadly accepted explanation, consistent with Fechner's theory, is that these attributes are internally represented on a logarithmic scale. But in the 1950s, Stevens and others found that human ratings of perceived intensity of a variety of sensory attributes 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 judgements do not arise from a common internal representation [17–20], or that the two perceptual tasks involve different nonlinear cognitive transforms [21].

Here, we develop a simple but general framework for interpreting and unifying perceptual discrimination and intensity judgements. Specifically, we use a simplified form of Fisher Information to quantify the relationship between noisy internal representation and discriminability. In the case of Weber's Law, we show that this leads to a family of internal representations with different noise properties, each consistent with Weber's Law discriminability, but only one of which is consistent with power law intensity percepts. Moreover, we demonstrate the generalizability of our framework on a set of perceptual attributes drawn from diverse sensory modalities. By incorporating a more realistic physiological noise model, our framework unifies discrimination and intensity measurements beyond the range over which Weber's Law or Stevens' power law hold.

Results

What is the relationship between measurements of perceptual discriminability and the internal representations from which they arise? Intuitively, a change in stimulus value (e.g. contrast of an image) leads to a corresponding change in an observer's internal response. Noticing a stimulus change depends on whether the internal response change is larger than that expected from stochastic variability ("noise") of those responses. 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 an enormously successful quantitative framework for analyzing and interpreting perceptual data [2, 3, 22]. Despite this success, the relationship between observers' discriminability and their corresponding internal stimulus representation is indirect. Furthermore, 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), which quantifies the precision with which a signal is represented in noisy measurements. Specifically, given the conditional probability of noisy internal responses to a stimulus, $p(r|s)$, Fisher information provides a measure of the precision (inverse variance) with which that stimulus can be recovered. Fisher information is widely used in engineering, to compute the minimum achievable error in recovering signals from measurements (known as the "Cramer-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 multimodal, discrete, and multi-dimensional responses – although only a subset of cases yield an analytic closed-form expression.

Interpreting Weber's Law using Fisher Information

Fisher Information is generally used to characterize decoding errors based on specification of an encoder, but here we are interested in the reverse: to constrain properties of an encoder (internal representation) using external measurements of perceptual discriminability. Consider the well-known case of 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 behavior? The answer is not unique, and although a complete solution is not readily expressed, a set of simple examples can be deduced and verified.

As a first example, suppose the internal representation is a nonlinear function of the stimulus, $\mu(s)$ (often referred to as a "transducer function"), contaminated by additive Gaussian noise with variance σ^2 [3, 29, 30]. In this case, the square root of FI is $\delta(s) = |\mu'(s)|/\sigma$ (see Methods). This reflects Fechner's hypothesis that sensitivity to small changes in stimulus is determined by the derivative of the transducer. If discriminability follows Weber's law, the response function can be deduced via integration as $\mu(s) \propto \log(s) + c$, with c an arbitrary constant. This logarithmic model of internal representation, due to Fechner [1, 5], is the most well-known explanation of Weber's Law.

As an alternative, a number of authors have 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]. A simple example of this is an internal representation whose mean $\mu(s)$ is proportional to the stimulus s, and contaminated by Gaussian noise with standard deviation proportional to s. Again, computing FI yields $\delta(s) \propto 1/s$, consistent with Weber's Law (see Methods). In contrast to the previous case with additive noise, for which the effect arose from the nonlinear transducer, discriminability in this case arises entirely from the inhomogeneity of the noise.

Finally, 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 these integer measurements, FI is still applicable. In this case, the variance of the noise is equal to the mean response, and Weber's Law discrimability arises from a transducer function $\mu(s) \propto [\log(s) + c]^2$ (see Methods).

These three different examples, illustrated in Fig. 1, demonstrate that the behavioral observation of Weber's Law does not uniquely specify an internal representation (see also [36, 40, 41]). In fact, they are just three members of an infinite family of possible solutions. To make this non-identifiability problem more explicit, note that for all three examples, discriminability shares a common form:

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

This expression, which we refer to as *Fisher Discriminability*, is easier to compute than FI (since it relies only on the first two moments of the response distribution), and provides a lower bound on the square-root of Fisher information [42] (see Methods). For all three of the examples above, this lower bound is exact. The Fisher Discriminability elucidates 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 $\sigma(s) = |\mu'(s)|/\delta(s)$. 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 the use of additional measurements (or assumptions) regarding the mean or variance of internal representations, or the relationship between the two. We start with the first of these, by interpreting perceptual magnitude ratings as providing a direct measurement of $\mu(s)$ [40, 43]. 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 internal

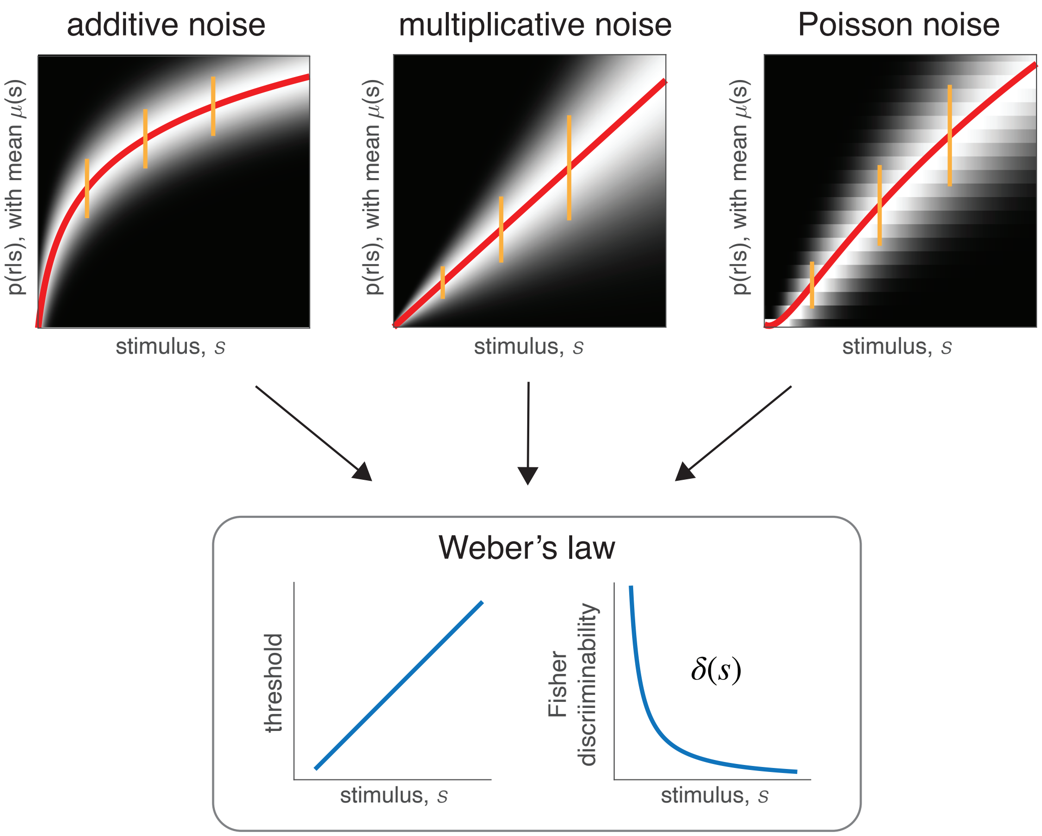

Figure 1: **Three different example internal representations, each consistent with Weber's law.** Each upper panel shows a stimulus-conditional response distribution, $p(r|s)$ (gray, brightness proportional to conditional probability), the mean response, $\mu(s)$ (red line), and three examples of response standard deviation (orange vertical lines indicate a range of 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.

response, r (up to an arbitrary scale factor that depends on the numerical scale), and that averaging over many trials provides an estimate of the mean internal representation, $\mu(s)$.

Using stimulus magnitude ratings, Stevens and others (e.g. [15, 44, 45]) found that perceived intensity of many different stimulus attributes is 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 interpreted this as direct evidence against Fechner's logarithmic transducer [11], but left the relationship between the power law ratings and Weber's Law discriminability unresolved. Over the intervening decades, magnitude rating measurements have generally been interpreted as arising from aspects of internal representation different from those underlying discriminability (e.g. [12, 17, 20, 46]), or dismissed altogether [9, 13].

The framework of Fisher Discriminability offers a potential unification of power-law intensity percepts and Weber's Law discriminability. Assuming Fisher Discriminability $\frac{|\mu'(s)|}{\sigma(s)} \propto 1/s$, and substituting a power-law for $\mu(s)$, we arrive at a simple constraint on the noise of the internal representation (Figure 2A, see Methods):

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

That is, the internal standard deviation should be proportional to the mean, and thus should grow according to the same power law. This result provides a generalization of the multiplicative noise case of the previous section (Figure 1), allowing the co-existence of Weber's Law discriminability and a power-law percept for *all* exponents α (Figure 2B). An additional prediction of this result is that the standard deviation of perceptual ratings should also grow proportionally to the mean rating, consistent with findings of a number of studies (e.g. [10, 47, 48]). 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 [47].

Connecting percept to discrimination for generalized intensity variables

The previous section provided a consistent 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. The Poisson description of neural noise implies a variance proportional to the mean spike count. Although this relationship holds for modest response levels, recent measurements in sensory cortex show substantial deviations at higher response levels. In particular, 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

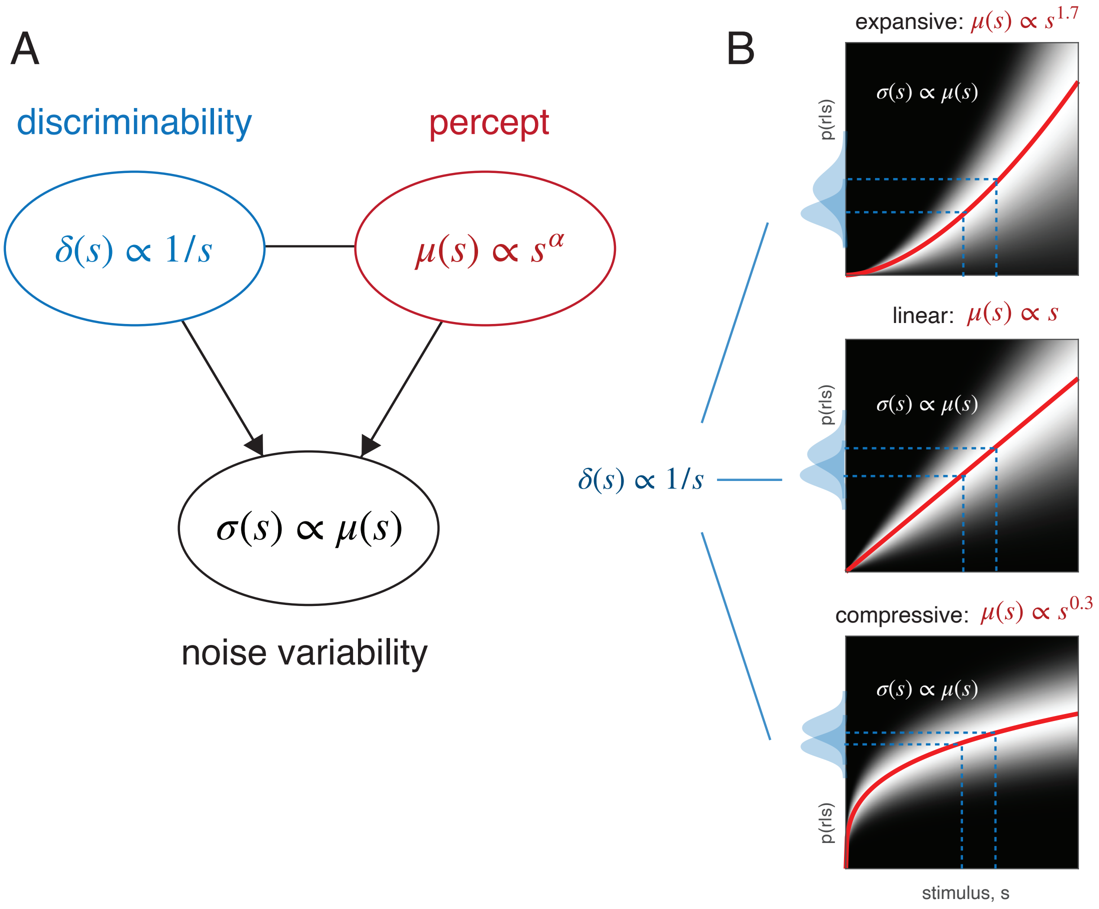

Figure 2: **Unifying perceptual measures of Weber's Law discriminability and power-law magnitude ratings. A.** Using Fisher Discriminability, perceptual sensitivity and perceptual magnitudes can be combined to constrain an internal representation. In the particular case of Weber's Law, and power-law 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 examplef 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).

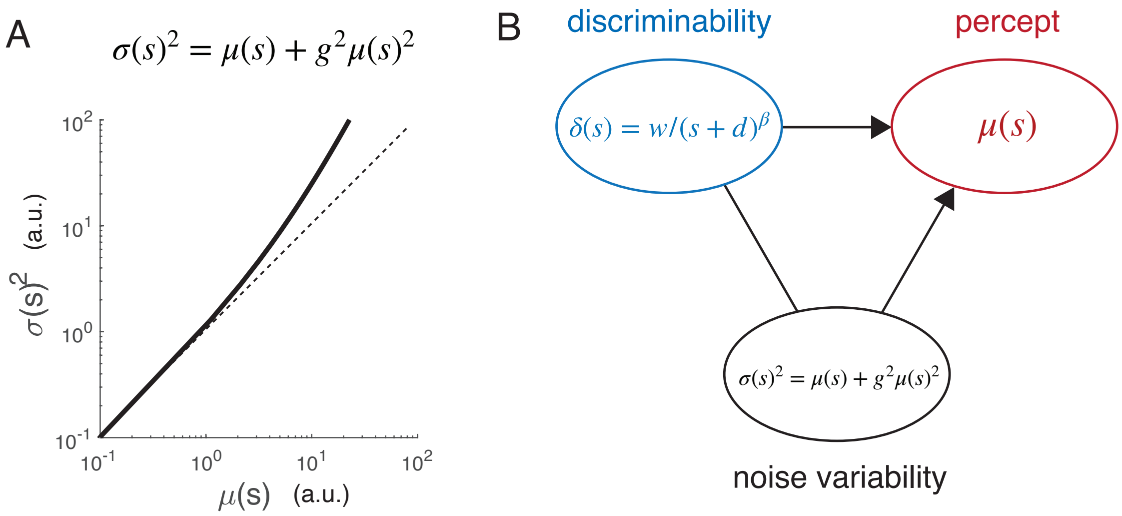

Figure 3: **Generalization beyond the Weber range. A.** Quadratic mean-variance relationship for a modulated Poisson model of sensory neurons [50, 51]. Behavior is Poisson-like at low intensities ($\sigma^2(s) \sim \mu(s)$), and super-Poisson at higher intensities ($\sigma^2(s) \sim \mu^2(s)$), with 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 $\mu(s)$.

model captures the behavior 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 sensory 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 corresponding values of the underlying individual neurons (see Supplement).

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 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 [45, 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.

Discussion

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. 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.

To develop and test this framework, 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' proposals, a number

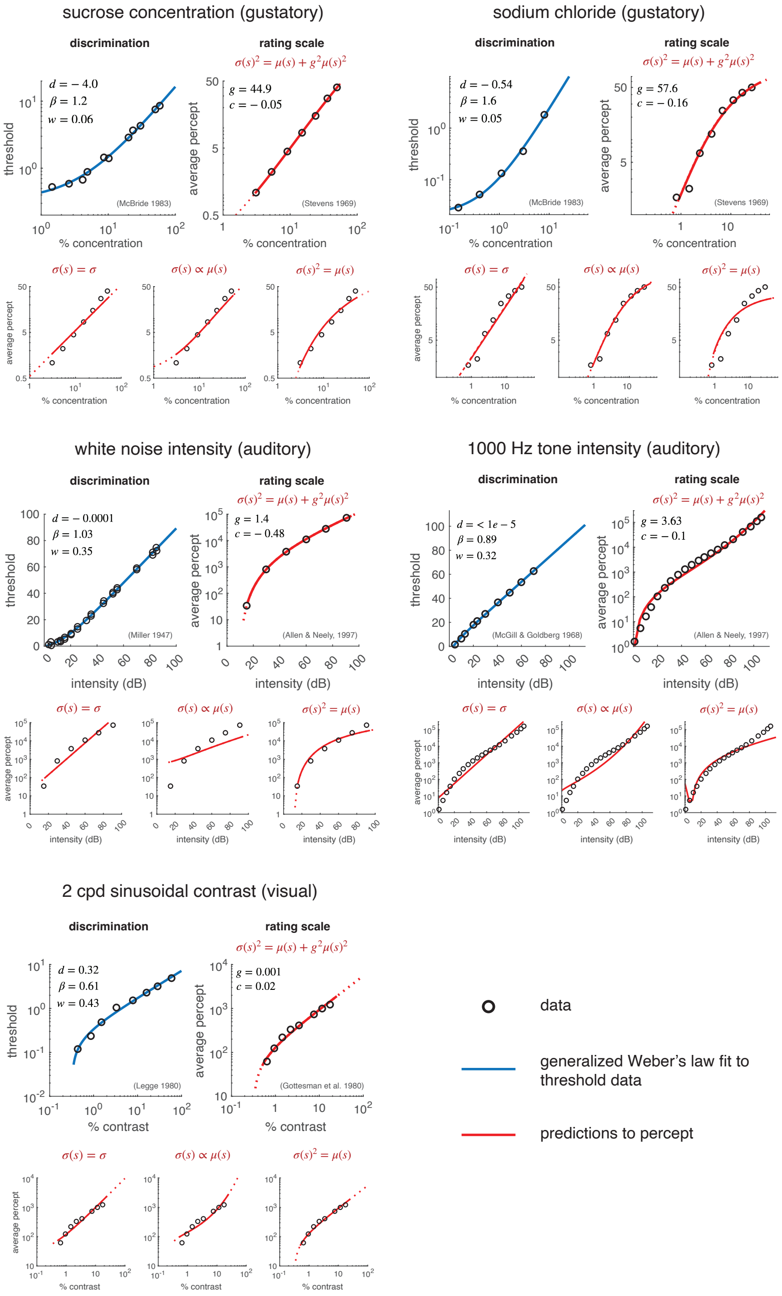

Figure 4: **Predicting perceived intensity from discriminability for five different sensory attributes.** For each attribute, we fit a three-parameter generalized form of Weber's Law (Eq. 4, blue curves, optimal parameters as indicated) to measured discrimination thresholds (black points). We set this 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 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.

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 super-threshold 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, 45, 62]) seem to reflect the mean of internal representation, which is only equal to integrated discriminability when noise variability is constant.

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 super-threshold 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.

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 proportional noise is sufficient to unify Weber's and Stevens' observations for power-law transducers, regardless of exponent.

Moreover, this form of proportional noise 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. The noise of the summed response over a population of such neurons would have the same structure (see Appendix A). 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 [64]. 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 [65].

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 [66]. In this case, an independent response noise model yields Fisher Information consistent with Weber's Law [67–71]. 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, 72, 73]). Although discrimination judgements for an attribute s 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 [74] 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 information under constraints of finite coding resources [70, 75, 76]. Exploration of these relationships provides an enticing direction for future investigation.

Acknowledgments

We thank Nikhil Parthasarathy, Mike Landy, Tony Movshon, Bill Geisler, Larry Maloney, Jacob Cheeseman and the members of the Center for Computational Neuroscience at the Flatiron Institute for helpful discussions and suggestions.

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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 Cramer-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:

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

The expression captures the relative change in measurement distribution when the stimulus 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 response density. Moreover, both s and 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 noise. Assume the internal representation has mean response $\mu(s)$, and is contaminated with additive Gaussian noise of fixed variance:

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

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 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 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:

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

Fisher discriminabiliity generalizes to a multi-dimensional response vector (eg., 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 assume an internal representation that has a mean-variance relationship consistent with a modulated Poisson distribution [10]:

$$\sigma(s)^2 = \mu(s) + g^2\mu(s)^2. \tag{9}$$

We combined this mean-variance constraint with a generalized form of Weber's Law [11]:

$$\delta(s) = \frac{w}{(s-d)^\beta}, \tag{10}$$

in which d is an additive constant that can be either positive or negative, β is a non-negative exponent, and w is a non-negative scaling factor.

We analyzed five stimulus domains in the main text and make prediction of perceptual intensities (rating measurements) in two steps. First, we fit Eq. (10), optimizing parameters $\{d, \beta, w\}$ to minimize squared error of the measured inverse discrimination (thresholds). Then, we combined the fitted discriminability model with the mean-variance relationship of Eq. (9) to generate rating predictions. In this second step, we optimize three parameters (by minimizing 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 (Fisher discriminability) for $\mu(s)$ (see below). The last parameter is a scale factor, which adjusts the predicted intensity values to the numerical range used in the associated rating experiment.

The transducer $\mu(s)$ is obtained by solving the differential equation that arises from equating the Fisher discriminability of Eq. (1) with the generalized form of Weber's law of Eq. (10):

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

The solution is a hyperbolic function:

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

Note that an overall scaling (proportionality) factor is needed to fit this functional form of $\mu(s)$ to rating data.

For comparison, we computed rating predictions from three other noise models: additive Gaussian noise, Poisson noise, and a generalized form of multiplicative noise. The fitting procedures for these three noise models 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:

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

and solve for $\mu(s)$. 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 overall scaling factor are estimated by fitting the expression for $\mu(s)$ 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 an 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. (9), fitting involves estimation of three parameters: the noise parameter g, an integration constant c, and a scaling factor.

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Appendices

A. 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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