Minimal Neural Recruitment from Stevens Coding and Fechner Decoding in the Brain

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ABSTRACT

The psychophysical perceptual process can be taken to occur in two steps. The first one, from sensation to the generation of the neural correlate by population coding is assumed to obey Stevens' power law, while the second one, the decoding from the neural correlate to perception is postulated to obey Fechner's logarithmic law. This is shown to lead to the Complete form of Fechner's Law (CFL) as proposed by Nutting more than a hundred years back. The Minimal Neural Recruitment (MNR) for perception is calculated to be just a pair. The phenomenon of perceptual saturation is also discussed within the proposed model.

Key Words: psychophysics, perceptual saturation, population-coding, neural correlate, Stevens's law, Fechner's law, neural recruitment

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Introduction

The true nature of the empirical psychophysical law connecting the objective physical stimulus intensity and the corresponding subjectively perceived intensity has been a matter of long-standing debate and is as yet unresolved. Beginning with Fechner's (1860) logarithmic law and Nutting's (1907) generalization of the same, it has continued vigorously through the works of Stevens (1957) who proposed a power law as the true law of psychophysics and aggressively advocated for the repeal of Fechner's law (Stevens, 1961); MacKay (1963) who sought to give a theoretical basis for both the logarithmic and the power laws; Nimh (1970) who made a caricature of all curve-fitting approaches to the psychophysical law by proposing a polynomial law which quite obviously gives excellent fits to any set of experimental data. Krueger (1989) tried to reconcile both the laws by examining their equivalence over particular ranges of the stimulus intensities for different modalities while Norwich (1993) showed that they both can be seen as limiting cases of Nutting's modification of Fechner's law.

More recently, Johnson et al (2002) on the basis of the roughness perception data for a textured surface have proposed linearity as the basic law of psychophysics, while Florentine and Epstein (2006) have proposed an inflected exponential (INEX) function as the more accurate form of the law by examining the steepness of the loudness function at the sub-decade levels in more details at the near-threshold and near-saturation regimes that were hitherto overlooked. Still more recently, Billock and Tsou (2011) have also attempted to reconcile both Stevens' and Fechner's laws while Copelli et al (2002) have shown for cellular automata models

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of neural networks that the Fechner and Stevens laws can be respectively obtained as transfer functions for excitable media as far as rate coding is concerned when the absolute and relative refractoriness of neurons are inserted as properties of individual automata alongside their excitability by external stimuli.

This knotty problem of the formulation of an empirical law for psychophysical phenomena started with Fechner when, basing upon Weber’s findings, he proposed a logarithmic relation known as the Weber-Fechner law, or simply the Fechner law:

\[ \psi = a \log \phi + b, \text{ } a \text{ and } b \text{ are constants.} \]  

(1)

Stevens, on the other hand, proposed his psychophysical law with a power function dependence of the psychical upon the physical intensity:

\[ \psi = a \phi^n; \]  

(2)

Where \( \alpha = \text{constant and } n > 0 \) is the power function exponent. Although, Stevens (Stevens 1960) realised that the above simple form of the power law cannot hold for the entire dynamic range of a modality and proposed to include \( \phi_0 \), the threshold for perception, by modifying it to \( \psi = \alpha(\phi - \phi_0)^n \), Lochner and Burger (1961) showed that the data for loudness are comparatively more accurately described by a function of the form \( \psi = \alpha(\phi^n - \phi_0^n) \).

By appealing to information theory, the Fechner logarithmic law and the Stevens power law were both shown by Norwich to be contained in a general law called the Complete form of Fechner’s law (CFL) first proposed by Nutting on the basis of visual Weber fractions and which many previous authors including Helmholtz (1924) also proposed in some form or the other and with regard to some modality or the other. The Norwich form of the CFL is given by:

\[ \psi = (k/2) \ln(1 + \gamma' \phi^n) \]  

(3)

where, \( \gamma' \text{ and } k \) are constants. Since this does not have the threshold inbuilt, Norwich and Wong (1997) proposed the modification (for loudness function):

\[ \psi = (k/2) \ln\left\{1 + \gamma(\phi / \phi_0)^n\right\} / (1 + \gamma) \]  

(4)

with \( \gamma = \text{constant.} \) This is an equivalent of Nutting’s original proposal of the CFL:

\[ \psi = K' \ln\left\{1 + \gamma''((\phi / \phi_0)^n - 1)\right\} \]  

(5)

with \( K' = k/2 \) and \( \gamma'' = \gamma / (1 + \gamma) \) new constants.

We propose here that the CFL can be obtained by first applying the Stevens power law for the formation of the neural correlate in the brain from the physical stimulus by population coding, followed by the second step, the decoding of the information thus encoded in the neural correlate to achieve perception or cognition by the Fechner logarithmic law.

The physical stimulus impinging on the senses is invariably a form of energy, mainly electromagnetic, and the stimulus intensity is proportional to the energy. According to quantum theory, this energy is proportional to the number of quanta. The number of neurons these quanta can excite to form the neural correlate will also be proportional, in general, to some power of their number, and hence to some power of the stimulus energy or intensity, depending on the various resistive and dissipative effects, channel capacity, transduction efficiency etc. associated with the neural processes such as input-coding, memory, attention and output during the transition from stimulus to perception. Once the neural correlate is formed, the perceived intensity will depend on the neural population forming the correlate. It is reasonable that the large number of neurons must then be logarithmically 'scaled down' to get the perceived intensity relative to the threshold as per the Fechner law.

We set out to find the form of the neural population \( N \) as a function of the input stimulus \( \phi \) in power units followed by the perceived intensity \( \psi \) as a function of \( N \):

\[ N = N(\phi); \text{ } \psi = \psi(N) \]  

(6)

and then, we proceed to get the subjective perceived intensity:

\[ \psi = \psi(N) = \psi[N(\phi)] \]  

(7)

The advantage of the neural correlate approach to the CFL is that the threshold appears explicitly, the phenomenon of saturation at some high value of the physical stimulus for any modality can be explained and also that the
previously proposed psychophysical laws are contained in it as special cases.

2. Population coding by Stevens’ law

From the table of exponents given by Stevens (1960) one immediately observes that that almost all the exponents are very close to unity. The exceptions like electric shock at the upper end and loudness or brightness at the lower end are such that, if the stimulus intensity is expressed in power units (i.e. energy/time), the exponent \( n \) can very generally be written as:

\[
n = 1 + m; \quad |m| \leq 3/4
\]

\( (8) \)

or, a little more generously, we may as well write, \( |m| \leq 1 \).

We note that the largest of Stevens’ exponents as tabulated by Stevens himself is \( n = 3.5 \) for electric shock and it is in terms of the current as the stimulus. When we switch to power units, the power delivered by the current will be \( P = i^2 R \), with \( R = \) resistance, as per Joule’s law and is proportional to the squared current. Hence the exponent reduces to just \( n = 1.75 \).

Experiments by Rollman and Harris (1987) for measuring the exponent for electric shock gave a median value of 1.74, with a mean value of 2.39, which in power units becomes 1.20. Similarly, at the bottom end we have \( n = 0.33 \) for brightness (for a \( 5^\circ \) target in dark) and it is also well-accommodated within the range given by eq.(8).

To appreciate the use of Stevens’ power law for population coding of the physical stimulus in the neural correlate, we note that:

- According to quantum theory the stimulus energy impinging on a sense organ is directly proportional to the number of quanta (photons for electromagnetic signals, phonons for sound signals and so on).

- There is a good deal of experimental evidence (Baylor et al., 1979; Reike and Baylor, 1998) that for visual perception the mammalian photoreceptors in the retina (rhodopsin molecules) can detect even single photons (Berntson et al., 2004) and that the eye is so sensitive that even as low as just five to eight photons hitting the retina lead to visual perception. Moreover, Field and Reike (2002) showed that nonlinearity enters at the very first stage of the transduction process itself, since each rod bipolar is connected to several (~ 15 to 20) rod photoreceptors in the retina.

- In addition to the input-coding neurons (i.e. those which receive the almost entire energy absorbed for the population coding of the stimulus input), the perception process inevitably requires the excitation of (a) other additional neurons and/or (b) multi-tasking of at least a part of the input-coding neurons for the purposes each of memory, attention, processing and possible motor output, even though such excitations may only serve the purpose of triggering the corresponding activity and the energy consumed by them may be negligible.

- The spatially extended neural correlate formed in the Brain (including the noise component) is perceived as one whole. The binding of different neuronal assemblies to form the whole is achieved by their synchrony of firing. The neural assemblies involved in the distinct tasks of input-coding, memory, processing and output may have different synchrony frequencies in general, while the noise may be spread over a larger frequency range, such that it can mask and mar each of these processes.

Therefore, as proposed by the author in an earlier work (Pradhan, 2014), we can write the set of neurons \( N \) activated at any moment, which forms the brain state or the neural correlate corresponding to an above-threshold stimulus intensity leading to perception, as the union of the sets of neurons involved in coding, processing, memory and output:

\[
N = N_{\text{noise}} \cup N_{\text{in}} \cup N_{\text{mem}} \cup N_{\text{proc}} \cup N_{\text{out}}
\]

\( (9) \)

where \( N_{\text{noise}} \) is the noise present and the other subscripts are self-explanatory. Note that the number of neurons associated with attention needed for processing is included in \( N_{\text{proc}} \). Copelli et al (2002) have shown for cellular automata models of neural networks that the Fechner and Stevens laws can be respectively obtained as transfer functions for excitable media as far as rate coding is concerned when the absolute and relative refractoriness of neurons are inserted as properties of individual automata (neurons) alongside their excitability by external stimuli. It
is reasonable to assume further on the basis of the work of Kinouchi and Copelli (2006) that the same power law behavior will also hold for population coding of stimulus intensity, since the stimulus energy absorbed $\Delta E_{abs}$ per unit time is proportional to the spike rate (synchrony frequency) $f_{in}$ of the input-coding neurons:

$$\Delta E_{abs} = P(\phi)\Delta E_{inc} = (\Delta N_{in} f_{in})\varepsilon_{in}$$  \hspace{1cm} (10)

where, $\Delta N_{in}$ is the differential increase in the input-coding neurons, $\varepsilon_{in}$ is the energy absorbed by a neuron in one spike, and $P(\phi)$ is the stimulus-dependent absorption coefficient, which is a sigmoid function having power law behavior in the dynamic range.

Thus, we are led to propose in general that when there is an increase in the stimulus intensity from $\phi$ to $\phi + \Delta \phi$, $\Delta N_{in}$ will be proportional to $\Delta \phi$, and depending on the modality, it will also be proportional to some power $m'$ of $\phi$ given by eq. (8):

$$\Delta N_{in} \propto \Delta \phi, \Delta N_{in} \propto \phi^{m'}$$  \hspace{1cm} (11)

Or, $\Delta N_{in} / \Delta \phi = K\phi^{m'}$; $K = \text{const.} \ |m'| \leq 1$  \hspace{1cm} (12)

Note that the ratio $\Delta N_{in} / \Delta \phi$ can be an increasing or decreasing function of $\phi$ depending on whether $m' > 0$ or $m' < 0$, roughly a power law behavior between direct proportionality and inverse proportionality i.e. $|m'| \leq 1$.

We move over to the ‘continuum limit’ and integrate to get:

$$N_{in} = N_0 + (K / n)(\phi^n - \phi_0^n)$$  \hspace{1cm} (13)

where $n = m' + 1$ is identified as the Stevens exponent of eq. (8) with $m = m'$ for the modality and $N_0$ is the threshold population at $\phi = \phi_0$ in the absence of noise.

It is to be noted that since we are interested only in the perceived intensity as a function of the neural population excited, the effect of the detailed neural correlations and the circuitry involved in the neural network forming the correlate are taken care of by the power function dependence in eq. (12).

### 3. Perception by decoding through Fechner's law

Now, in the second step, the information encoded in the neural correlate is to be decoded and processed with the help of the memory for perception. The perceived intensity is finally judged in terms of ratios (i.e. by comparison of numbers), which has been shown by Dehaene (2003) to be logarithmically perceived by subjects. Therefore, we propose that the decoding proceeds via the Fechner logarithmic law with the understanding that the physical stimulus in eq. (1) is now replaced by the corresponding neural population, which of course is the true physical stimulus for the perceiving subject at the mind-brain interface:

$$\Delta \psi \propto (\Delta N_{in} / N_{in})$$  \hspace{1cm} (14)

where, $\Delta \psi$ is the just noticeable difference (JND) in the Fechnerian sense and $\Delta N_{in}$ is the corresponding differential increment in neural population $\Delta N_{in}$.

In the 'continuum limit', this becomes the differential equation:

$$d\psi = K'(dN_{in} / N_{in}); \ K' = \text{prop. Const.}$$  \hspace{1cm} (15)

with the solution:

$$\psi = K'\ln(N_{in} / N_0)$$  \hspace{1cm} (16)

Using the value of $N_{in}$ from eq. (13) we get Nutting's CFL eq. (5):

$$\psi = K'\ln[1 + (K / nN_0)(\phi^n - \phi_0^n)]$$  \hspace{1cm} (17)

where $n = m + 1$ is the Stevens' exponent and the parameter $\gamma^n$ is now determined to be:

$$\gamma^n = (K\phi_0^n) / (nN_0)$$  \hspace{1cm} (18)

In the limit $(K / nN_0)(\phi^n - \phi_0^n) << 1$, by expanding the logarithm in a Taylor series and keeping the first order term only, we get,

$$\psi = K'\{K / nN_0\}(\phi^n - \phi_0^n)$$  \hspace{1cm} (19)

which is Stevens' power law with the threshold duly taken care of.
In the other extreme, when stimulus intensity is such that \( (\phi / \phi_0)^n >> 1 + (1 / \gamma^n) \), we have,

\[
\psi = K'n \ln \phi + K'\ln \gamma^n
\]  

(20)

which is Fechner’s law.

Similarly, the Norwich form of CFL eq. (3) results, when \( (\phi / \phi_0)^n >> 1 \) and with the identification: \( \gamma' = K'/(nN_0) \).

To get a feel of the parameter values involved we refer to the curve fitting of the data of Hellman and Zwislocki (1961) by Norwich and Wong (1993) of the loudness function given by eq. (4) which yields perfect fit for \( K' = k/2 = 498.7; \gamma = 1.861 \times 10^{-2} \) and \( n = 0.27 \).

Further, comparing eq. (4) and the Nutting form of the CFL eq. (5), we get \( \gamma^n = \gamma / (1 + \gamma) \approx \gamma' \).

4. Minimal Neural Recruitment

The threshold neural population \( N_0 \) can also be obtained as follows:

Using \( \gamma^n = \gamma'\phi^n \), the threshold in eq. (5) can be written as \( \psi_0 = K'\ln(1 + \gamma) \), which when compared with the corresponding threshold \( \psi_0 = K'\ln N_0 \) from eq. (16) yields the general formula:

\[
N_0 = (1 + \gamma) \geq 2
\]  

(21)

which is always above unity since \( \gamma \) has been shown (Norwich 1993) to be a small positive number in all cases. This supports the fact that at least two neurons must be excited for perception to occur since \( N_0 \) is a whole number.

Further, had we adopted Stevens’ proposed form \( \psi = \alpha (\phi - \phi_0)^n \) in place of the Lochner-Burger form, everything would have gone through fine up to eq. (20), but everywhere \( (\phi - \phi_0)^n \) would have replaced \( (\phi^n - \phi_0^n) \), and accordingly the conditions and the values of the parameters would change. Especially, they both would give identical results for \( n = 1 \) and also in the limit \( \phi >> \phi_0 \) for any value of \( n \). The Stevens and Fechner laws would also be recovered (Pradhan, 2014) in appropriate limits. However, the difference between the two would be most pronounced in the stimulus values near threshold since \( (x - 1)^n < x^n - 1 \), for \( n > 1 \), while \( (x - 1)^n > x^n - 1 \) for \( n < 1 \) where \( x = (\phi / \phi_0) > 1 \).

There is, of course, no unanimity about the form of the psycho-neural function \( \psi(N) \) although the linearity proposal of Johnson et al (2002) has gained some acceptance for some of the modalities. Further, it is not clear, with just two neurons excited by the input stimulus, what kind of bare, base-level experience about the stimulus this bi-neural perception could possibly be generating in conscious beings and is therefore a matter of future exploration.

5. Perceptual Saturation

We now discuss the phenomenon of perceptual saturation at some maximum value \( \phi_{\text{max}} \) of the applied stimulus:

For each modality, there is a particular brain area (or a set of different brain areas) allocated, with a particular total number of neurons \( N_{\text{in}}^{\text{max}} \) available for input-coding. When the input stimulus approaches this upper limit \( \phi = \phi_{\text{max}} \) given by:

\[
\phi_{\text{max}} - \phi_0^n = (n / K)(N_{\text{in}}^{\text{max}} / N_0)
\]  

(22)

the perception logarithmically saturates to a maximum \( \psi_{\text{max}} \) given by:

\[
\psi_{\text{max}} = K'\ln(N_{\text{in}}^{\text{max}} / N_0)
\]  

(23)

Thus, saturation is seen to be the result of finite ‘disk-space’ allocated to the neural coding of each modality in the brain. However, as is well known, the saturation and the near threshold behaviors are more correctly described by a sigmoid function, rather than any logarithmic form which continues to grow with the stimulus, albeit slowly. Therefore, the CFL requires a modification, with the proper sigmoid function for the absorption coefficient included to make it applicable over the entire stimulus range and it may then no longer be a logarithmic form. This requires the details of the neural network involved as well as other additional factors involved in the psycho-physical process to be
obtained from future neurophysiological research.

6. Discussion and Conclusion

We have provided a neural basis for all the known forms of the psychophysical law and at the same time have showed that the neural coding and the psychic decoding follow different laws namely, Stevens’ and Fechner’s laws respectively, to yield the complete form of the Fechner law as proposed by Nutting. We have also showed explicitly that the minimal neural recruitment for perception is just a pair.

The perceptual variable $\psi$ could in general refer to magnitude estimates, category scales or neural impulse rates, although we have mentioned only the magnitude estimates explicitly. Of particular interest for future research would be the case of duration judgement, which would directly relate to the neural firing rates rather than any kind of input-coding through any sense organ, since time is not a sensory perceived quantity, but is rather a directly perceived subjective quantity. This would require either only frequency coding or mixed coding, which we propose to take up in future work.

One unsatisfactory feature about population coding proposed here is the lack of details of the exact neural network, the neural circuitry for memory and processing and the exact location of the neural assemblies involved in the perception of a particular modality and intensity. At the same time, it is no less amazing that many of the psychophysical laws (including linearity) could be so simply and straightforwardly derived from population coding without all these details.

Finally, the formulation proposed here reduces Stevens’ power law to a mere neuro-physical coding law (transfer function) and Fechner’s law to just a psycho-neural decoding law for perception, while Nutting’s, and to some extent, Norwich’s forms of the CFL are more complete psychophysical laws.

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