Orissa Journal of Physics
ISSN 0974-8202

Vol. 21, No.1
February 2014
pp. 65-72

Population Coding of Neural Correlates and the Generalized Fechner Law

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Received: 7.12.2013 ; Revised: 31.12.2013 ; Accepted: 15.1.2014

Abstract : It is proposed that Fechner's and Stevens' laws can be viewed as special cases of a Generalized Fechner law (GFL) if the psychophysical process occurs in two steps, namely, the neuro-physical transduction by Stevens' law followed by the psycho-neural decoding by Fechner law for perception. It is argued that the physical stimulus impinging on any sense organ is invariably a form of energy, mostly electromagnetic, and the stimulus intensity is proportional to the incident energy density, a portion of which is absorbed by the sense organ and is relayed to the brain for the formation of the neural correlate. Once the neural correlate is formed, the perceived intensity which is coded by the population of neurons in the correlate will then depend on the number of neurons 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. The phenomena of sensory adaptation and saturation are explained.

PACS: 43.80.-n, 87.16.Xa, 87.19.La, 87.19.Bb

Keywords: psychophysics, perception, sensory adaptation, saturation, population coding, neural correlate, Stevens' law, Fechner's law.

1. Introduction

There has been an ongoing debate [1-5] on the true nature of the empirical psychophysical law connecting the objective physical stimulus intensity ϕ and the corresponding subjectively perceived psychical intensity ψ. Fechner [6] basing upon Weber's findings proposed a logarithmic relation known as the Fechner law or the Weber-Fechner law:

$$\psi = \alpha \log(\phi/\phi_0): \quad \alpha = \text{constant} : \phi_0 = \text{threshold} \tag{1}$$

Stevens [7] on the other hand proposed his psychophysical law with a power function dependence of the psychical upon the physical intensity:

$$\psi = \alpha(\phi - \phi_0)^n \quad ; \quad \alpha = \text{constant} \tag{2}$$

where n is the power function exponent having values in the open interval (0, 2).

Recently, by appealing to information theory, these two laws were shown by Norwich [8] to be contained in a general law called the Complete form of Fechner's law (CFL) first proposed by Nutting [9], upon which many previous authors including Helmholtz [10] have also stumbled time and again in some form or the other and with regard to some modality or the other [11]. We show here that the CFL can be obtained by first applying the Stevens power law to the neuro-physical transduction from the physical stimulus to the brain for the population coding during the formation of the neural correlate, followed by the second step, the decoding of the information thus encoded in the neural correlate to achieve perception or cognition by the Weber-Fechner logarithmic law.

According to quantum theory, this energy is proportional to the number of photons. The number of neurons these photons can excite to form the neural correlate will also be proportional, in general, to some power of the photon number, and hence to some power of the stimulus energy or intensity, depending of course, on the various resistive, dissipative and other associated memory and processing related neural excitations occurring during the transition from sensation to perception.

Therefore, We set out to find the form of the neural population N as a function of the input stimulus ϕ in power units, followed by the perceived intensity ψ as a function of N, and then, we proceed to get the psychophysical law. This is shown to result in a Generalized Fechner Law (GFL) somewhat similar in form to the CFL proposed by Nutting [9]. The advantages of the GFL over the Norwich form of the psychophysical law proposed are that the threshold appears explicitly, and that the issue of saturation at some high value of the physical stimulus for any modality can be incorporated. The phenomenon of sensory adaptation to continued application of a constant stimulus is also explained.

2. Power Law Population coding

The psychophysical exponents tabulated by Stevens [12] are such that most of the exponents are pretty close to unity and 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), we can write the exponent 'n' very generally as:

$$n = 1 + m\ ;\ \ |m| \leq 1 \tag{3}$$

Note that the largest of Stevens' exponents, n = 3:5 occurs for electric shock and it is in terms of the current as the stimulus. In power units, Joule's law tells us that the power delivered by the current I is:

$$P = I^2R,\ R = \text{resistance}, \tag{4}$$

It reduces the exponent to n = 1.75. Experiments by Rollman and Harris [13] for the exponent for electric shock yielded a median value of 1.74 and a mean value of 2.39, which in power units becomes 1.20. Similarly, the lowest value 0.33 for the exponent n for brightness (for 50^0 target in dark) and is also in the range specified by eq(3) above. To motivate the use of Stevens' power law for population coding in the brain, 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 absorption of such quanta follows the all-or-nothing rule. For the modality of visual perception, Baylor et al [14] and Reike and Baylor [15] showed that mammalian photoreceptors in the retina (rhodopsin molecules) can detect even single photons and that the eye is so sensitive that even as low as just five to eight photons hitting the retina lead to visual perception.
- In reality, the direct proportionality implied by quantum theory does not hold strictly, because the perception, in addition to the input-coding neurons (i.e. those corresponding directly to population coding of the stimulus input), inevitably requires the excitation of either other additional neurons or multiple-tasking of at least a part of the input-coding neurons for the purposes of memory, attention, processing and possible motor output.
- The perceiver perceives simultaneously the neural correlate formed in the Brain (including the noise) as one whole, the binding of different neuronal assemblies to form the whole being achieved by their synchrony of firing.

We can write the neural population that encodes an above-threshold stimulus intensity leading to perception as the cardinality of the union of sets of neurons involved in coding, processing, memory and output:

$$\mathcal{N} = | \mathcal{N}_0 \cup \mathcal{N}_{in} \cup \mathcal{N}_{mem} \cup \mathcal{N}_{proc} \cup \mathcal{N}_{out} | \quad (5)$$

where, N_0 is base level neural population corresponding to the noise present at the threshold value of the stimulus. Further, N_{in} will be the major component while others must be negligible as far as the coding of the input stimulus intensity is concerned. The subscripts are self-explanatory and N_{proc} includes those neurons associated with attention needed for processing.

Thus, we are led to propose in general that the differential increase ΔN in the neural population N forming the neural correlate when there is an increase in the stimulus intensity from ϕ to $(\phi + \Delta\phi)$ will be proportional to $\Delta\phi$, and depending on the modality it will also be proportional to some power *m* of $(\phi - \phi_0)$ as per Stevens' law i.e.

$$\Delta\mathcal{N} \,\alpha\, \Delta\phi \;; \quad \text{and,} \quad \Delta\mathcal{N} \propto (\phi - \phi_0)^m \quad (6)$$

Since perceptions usually involve large number of quanta and hence large number of neurons, we move over to the 'continuum limit' to get the differential equation:

$$d\mathcal{N} / d\phi = K(\phi - \phi_0)^m ; \quad K = \text{prop. Const.} \quad (7)$$

which yields the solution:

$$\mathcal{N} = \mathcal{N}_0 + \{K/(m+1)\}(\phi - \phi_0)^{m+1} \quad (8)$$

where, $\mathcal{N}_0$ is the 'neural noise' at threshold.

3. Logarithmic Decoding of Neural Correlates

Now, in the second step, the information thus encoded in the neural correlate is decoded and processed with the help of the memory for perception and this proceeds via the Weber-Fechner law:

$$\Delta\psi = \Delta\mathcal{N} / \mathcal{N} \quad (9)$$

where, $\Delta\psi$ is the just noticeable difference (JND) in the Fechnerian sense and $\Delta\mathcal{N}$ is the corresponding differential increment in neural population. In the 'continuum limit', this becomes the differential equation:

$$d\psi = K' (d\mathcal{N}/\mathcal{N}), \quad K' = \text{prop. Const.} \quad (10)$$

with the solution:

$$\psi = K' \, ln \; (\mathcal{N}/\mathcal{N}_0) \quad (11)$$

Using the value of $\mathcal{N}$ from eq (8) we get the Generalized Fechner Law (GFL):

$$\psi = K' \, ln[1+\gamma(\phi-\phi_0)^n] \quad (12)$$

with $\gamma = K/(n\ \mathcal{N}_0)$ and n = m + 1 is the Stevens' exponent.

In the low intensity limit, when ϕ is not much above ϕ_0, and $\gamma(\phi-\phi_0)^n << 1$, by expanding the logarithm in a Taylor series and keeping the first order term only, we get,

$$\psi = K' \gamma(\phi-\phi_0)^n \quad (13)$$

which is Stevens' power law [eq.(2)] with the identification $\alpha = K'\gamma$.

In the other extreme, when stimulus intensity is far above the threshold, $\phi >> \phi_0$ and $\gamma(\phi-\phi_0)^n >> 1$, we have

$$\alpha = K' n \, ln \phi + K' \, ln \gamma$$

which is Fechner's law [eq.(1)] with the identification $\gamma = (\phi_0)^{-n} = K/(n\ \mathcal{N}_0)$, $K' n = \alpha$.

Thus, the Fechner limit of the $GFL\, \gamma(\phi-\phi_0)^n >> 1$, becomes, simply the higher stimulus values $\phi >> \phi_0$, Stevens law is more valid nearer to the threshold. At larger values of the stimulus intensity, deviations from the power law behavior will be more pronounced while nearer to the threshold deviations from the logarithmic behavior will be more pronounced. Therefore, the Fechner and Stevens' laws are contained in the GFL as special cases [8].

4. Adaptation and Saturation

It is well known that when a steady stimulus is continuously applied to a sense organ, the phenomenon of sensory adaptation occurs and it leads to a gradual diminishing of the subjectively perceived intensity. In the neural correlate based approach proposed here, this can be understood as follows: The perceiver's attention is primarily directed to sense any changes in the perception since that is essential for survival. Thus a constant stimulus would require progressively less attention and hence less memory neurons once it has been perceived. Although the input-coding neural population remains the same, the neural population allocated for memory and processing and output coding gradually decreases with time. This leads to a decrease in the total neural population with time. Norwich [8] has proposed on the basis of information-based analysis that the psychophysical law in this time-dependent form will be:

$$\psi = K' ln[1+(\beta / t)\phi^n] \; ; (\beta = \text{const}) \quad (15)$$

This can be derived by introducing an additional time-dependence of $\Delta\mathcal{N}$ in eq (6) of the form:

$$\Delta\mathcal{N} \;\; \psi = K' \propto t^{\delta} \; : \; (\delta > 0) \quad (16)$$

For constant stimulus , ϕ so that eq (8) becomes:

$$\mathcal{N} = \mathcal{N}_0 + (K / nt^{\delta})(\phi - \phi_0)^n \quad (17)$$

and γ gets changed to $\gamma' = \gamma / t^{\delta}$ in eq.(12) which now reads:

$$\psi = K' ln[1+(\gamma / t^{\delta}) \; (\phi - \phi_0)^n] \quad (18)$$

Note that it is not necessary that the time-dependence be an inverse power law type. In general it could be any decreasing function of the time consistent with the experimental data. In Norwich's formulation $\delta = 1$, while it may very well be conjectured that δ will be some way related to the Stevens' exponent '*n*'.

Similarly, another aspect which Norwich's formulation fails to tackle is that of perceptual saturation at some maximum value $\phi_{\max}$ of the applied stimulus, since the Norwich form of the psychophysical law does not have the threshold inbuilt. In the present approach, however, saturation can be understood as follows:

For each modality, there is a particular brain area (or a combination of different brain areas) allocated with a particular total number of neurons $\mathcal{N}_{\max}$ as per eq (5), and when the stimulus approaches the upper limit $\phi_{\max}$ given by:

$$(\phi_{\max} - \phi_0)^n = (n / K) \; (\mathcal{N}_{\max} - \mathcal{N}_0) \quad (19)$$

the perceived intensity "logarithmically" saturates to a maximum max given by:

$$\psi_{\max} = K' ln \; (\mathcal{N}_{\max} - \mathcal{N}_0) \quad (20)$$

Thus, saturation is seen to be the result of finite “disk-space" allocated to the neural coding of each modality in the brain. Of course, the logarithmic function will continue to grow, slowly though, and the truncation $\mathcal{N}_{max}$ has to be put in by hand unless, the sigmoid nature of the psychophysical functions is explained on the basis of more detailed investigation of the coding and decoding of the neural networks.

5. Discussion and Conclusion

We have provided a neural basis for all the three 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 a Generalized Fechner law (GFL) for psychophysical phenomena..

As far as intensity coding is concerned, the GFL is sufficient. For different modalities which are encoded differently as distinct neural correlates, the population coding proposed above is clearly insufficient. Further neurobiological and psychophysical research is necessary to have detailed pictures of such distinct neural correlates corresponding to different modalities. The perceptual variable could in general refer to magnitude estimates, category scales or neural impulse rates, although we have mentioned only the magnitude estimates explicitly. Duration judgement, however, would directly relate to the neural firing rates rather than any kind of input-coding through any sense organ, since time is not a sensorily perceived quantity, but is rather a directly perceived subjective quantity and it remains to be seen in future research along the lines proposed here, which form of the psychophysical law holds. This would inevitably require the population coding of the neural correlate to be replaced by frequency coding or mixed coding.

Finally, in the population coding proposed here the details of the exact neural network, the neural pathways and the exact location of the neural assemblies involved in the perception of a particular modality and intensity are not involved. At the same time, it is no less amazing that all the proposed psychophysical laws could be so easily derived from population coding (without details). The formulation proposed here reduces Stevens' power law to a coding law for neuro-physical transduction and Fechner's law to a psycho-neural decoding law for perception.

Acknowledgments

The author thankfully acknowledges the discussions with Prof. L.P. Singh and also to thank the Institute of Physics, Bhubaneswar for computer and library facilities.

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