

SCIENTIFIC REPORTS



OPEN

Coding accuracy on the psychophysical scale

Lubomir Kostal & Petr Lansky

Received: 27 March 2015

Accepted: 15 March 2016

Published: 29 March 2016

Sensory neurons are often reported to adjust their coding accuracy to the stimulus statistics. The observed match is not always perfect and the maximal accuracy does not align with the most frequent stimuli. As an alternative to a physiological explanation we show that the match critically depends on the chosen stimulus measurement scale. More generally, we argue that if we measure the stimulus intensity on the scale which is proportional to the perception intensity, an improved adjustment in the coding accuracy is revealed. The unique feature of stimulus units based on the psychophysical scale is that the coding accuracy can be meaningfully compared for different stimuli intensities, unlike in the standard case of a metric scale.

The efficient coding hypothesis¹ states that neuronal responses are adjusted, through evolutionary and adaptive processes, to optimally encode such stimulus statistics that matches the sensory environment^{2–4}. The statistics of many natural stimuli differs, over short timescales, from the average global distribution, and typically, the limited neural coding range does not cover the wide range of possible stimuli values^{5–7}. The efficient coding hypothesis therefore predicts that neurons adapt their coding properties to the local stimulus distribution⁸. In particular, the coding accuracy should increase near the most commonly occurring stimuli in order to minimize the overall decoding error and to maintain the efficient representation of the environment. Such situation is reported in the auditory coding of the sound intensity^{5,6,9,10}, of the interaural level differences¹¹ and time differences¹², but also in the neural coding in the primary visual cortex⁷ and primary somatosensory cortex¹³. The coding accuracy is commonly evaluated by means of the stimulus-reconstruction paradigm¹⁴, that is, by answering how well may the ideal observer determine the stimulus value from the noisy neuronal response. It is assumed that the inverse of the Fisher information approximates the minimal mean squared error^{9,15–21}. Higher Fisher information reflects higher coding accuracy so that a more precise representation of stimuli is possible.

The goal of this short paper is to point out to a potentially problematic aspect of aligning the maximal coding accuracy with the most frequent stimuli. Our reasoning follows from the fact that the stimulus values are quantified by choosing some convenient, but otherwise *arbitrary*, system of measurement units. For example, the sound intensity is typically expressed as the sound pressure level in decibels (dB SPL). The same stimulus intensity can be equivalently expressed in terms of the effective pressure in Pascals (Pa)²². The seemingly arbitrary choice of stimulus scale, however, has a non-trivial and significant impact on the coding precision. As demonstrated by Kostal and Lansky²³, a non-linear relationship between different units (such as between the sound pressure and the sound level) may affect the position of maximal coding accuracy. Here we demonstrate the paradoxical consequences of the stimulus scale change on *both* the coding accuracy and the known stimulus distribution simultaneously. We show that the match between high coding accuracy regions and most frequent stimuli regions depends on the choice of the measurement unit. Second, we attempt to resolve this problem by arguing that the natural system for stimulus quantification is given by the scale linearly proportional to the perception intensity^{24,25}. As an illustration, we employ the classical Riesz's psychophysical scale for the sound intensity²⁶ to reveal the expected coding accuracy adaptation even for low pressure levels in the experimental data of Watkins and Barbour⁹.

Methods

The psychophysical scale describes the perceptual intensity, ψ , as a function of the stimulus intensity I ^{24,25}. The empirical finding known as Weber's law^{27,28} states that the smallest noticeable increment in perception, $\Delta\psi$, remains constant if the *relative* stimulus increment (also known as Weber's factor) is also constant,

$$\frac{\Delta I}{I} = \text{const.} \quad (1)$$

Institute of Physiology, Academy of Sciences of the Czech Republic, Videnska 1083, 14220 Prague 4, Czech Republic. Correspondence and requests for materials should be addressed to L.K. (email: kostal@biomed.cas.cz)

As suggested later by Fechner²⁹, Weber's law effectively sets the scale for the perceived stimulus intensity since $\Delta I/I$ is proportional to $\Delta\psi$. By integrating Eq. (1) we obtain the well known Fechner's law, stating that the perceived intensity varies as²⁸.

$$\psi = k \log \frac{I}{I_0}, \quad (2)$$

where k is a proportionality factor and I_0 some reference value.

Subsequent investigations found that Eq. (1) holds neither generally nor exactly^{24,30} across different sensory modalities. In particular, Weber's factor for human sound intensity discrimination was found to satisfy²⁶,

$$\frac{\Delta I}{I} = S_\infty + (S_0 - S_\infty)(I_0/I)^r. \quad (3)$$

Here I is the basal sound intensity in W/m^2 , ΔI is the minimum perceptible difference, S_∞ is the value $\Delta I/I$ approaches at high intensities, $S_0 > S_\infty$ is the value of $\Delta I/I$ at the threshold of hearing and r is a parameter, approximately $r = 1/2$. Weber's factor in Eq. (3) is no longer constant, but decreases rapidly to a plateau with increasing intensity I . Since the sound intensity and the sound pressure are related by the acoustic impedance $Z \doteq 400 \text{ N.s.m}^{-3} \text{ as}^{22}$

$$I = \frac{p^2}{Z}, \quad (4)$$

the following differential equation follows from Eq. (3)

$$\frac{d\psi}{dp} = \frac{2/p}{S_\infty + (S_0 - S_\infty)(p_0/p)}, \quad (5)$$

provided that the derivative $d\psi/dp$ is a good approximation to $\Delta\psi/\Delta p$. The solution to Eq. (5) is

$$\psi = \frac{2 \log[(S_0 - S_\infty)p_0 + S_\infty p]}{S_\infty} + C, \quad (6)$$

which is proportional to $\log(c + p)$. Setting the values²⁶ $S_\infty = 0.2$, $S_0 = 1$ and arbitrary $p_0 = 20 \mu\text{Pa}$ (the actual reference level is of little importance here) we obtain

$$\psi = 10 \log(0.00008 + p) + c, \quad (7)$$

where $c \doteq 94.3$ so that $p = 0 \text{ Pa}$ yields $\psi = 0$ for convenience. Equation (7) determines Riesz's scale (in arbitrary units) of sound pressure values, correcting the inadequate Fechner's law in Eq. (2) for small sound intensities (pressures). In other words, the value of ψ can be used to measure the sound intensity on the scale which is linearly related to the perception intensity. The standard sound pressure level scale L (given in dB SPL) is essentially equivalent to Fechner's law, since due to Eq. (4) it holds²²

$$L = 20 \log_{10} \frac{p}{p_0}. \quad (8)$$

The Eqs (7) and (8) are approximately proportional to each other for sufficiently high pressure levels (Fig. 1).

Results

The coding accuracy as a function of the stimulus intensity is significantly affected by the choice of the measurement scale²³. The question is whether the coding accuracy adaptation to the stimulus distribution (as observed, e.g., in the experiments^{5,6,9}), is preserved under the change of stimulus units.

The Fisher information $I_F(p)$ as a function of the sound pressure, and the Fisher information $I_F(\psi)$ for the sound intensity measured on Riesz's scale from Eq. (7), are related as

$$I_F(p) = \left(\frac{d\psi}{dp} \right)^2 I_F(\psi). \quad (9)$$

Similarly, one may additionally use Eq. (8) to relate, e.g., $I_F(\psi)$ and $I_F(L)$. The transformation rule in Eq. (9) is well known and can be derived directly from the definition of the Fisher information by using the chain rule for derivatives¹⁵. Similarly, the stimulus probability density function $f(\cdot)$ satisfies³¹

$$f(p) = \left| \frac{d\psi}{dp} \right| f(\psi). \quad (10)$$

Therefore it follows that any visual alignment between the values of the coding accuracy and the stimulus distribution depends crucially on the choice of units. Even though the square root of the Fisher information transforms analogously to Eq. (10), the potential match between the peaks of $\sqrt{I_F}$ and f is *not preserved* under the stimulus scale change because $\sqrt{I_F}$ and f are often related non-linearly. In fact, it can be shown rigorously that also

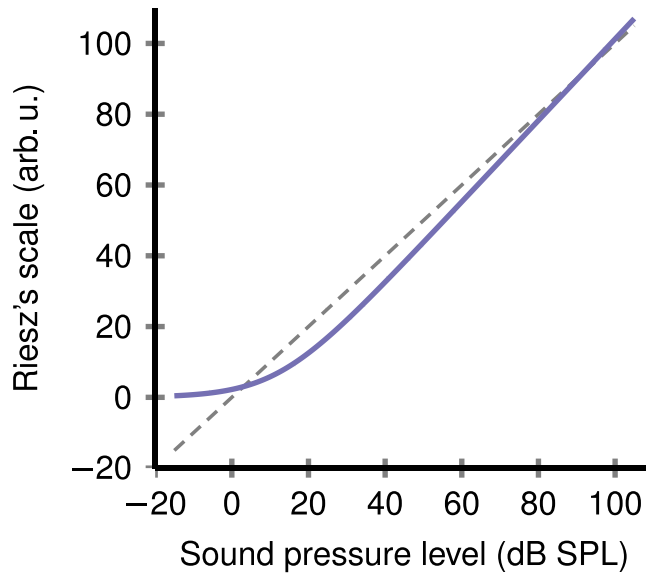


Figure 1. Relationship between two possible measurement scales for the sound intensity. The psychophysical scale by Riesz as a function of the sound pressure level (solid) is significantly non-linear only for low sound intensities. The identity function is shown for comparison (dashed).

the global match between the profiles of $\sqrt{I_F}$ and f is *not preserved* under the stimulus scale change³², unless the stimulus probability density function is *exactly* proportional to the square root of the Fisher information (known as the Jeffreys prior³³).

We illustrate how a specific choice of the stimulus units improves the experimentally observed adaptation of the coding accuracy to the stimulus distribution. We argue that the stimulus scale proportional to the actual perception intensity (the psychophysical scale) is the natural reference frame under which the coding accuracy should be evaluated.

Neurons in the auditory system are reported to adjust their rate-intensity functions in order to improve coding accuracy over high-probability stimulus regions^{5,9,10}. The match is not perfect for low sound intensities and a positive bias of maximal coding accuracy towards higher intensities is reported. For example, in the experiment of Watkins and Barbour⁹, the sound level distribution was set to be uniform over -15 dB SPL to 105 dB SPL, with an added 20 dB-wide plateau of high-probability stimulus region (Fig. 2A, filled area). At every 100 ms during the experiment a new sample was drawn from the distribution to set the amplitude of a pure tone, with its frequency matching the characteristic frequency of the studied neuron (primary auditory cortex of marmoset monkey). The dynamic rate-level function was measured and the coding accuracy (the Fisher information) was calculated (Fig. 2A, solid line), see Watkins and Barbour⁹ for more details. The coding accuracy adaptation was determined for four different positions of the plateau, centered at 5, 25, 45 and 65 dB SPL respectively (Fig. 2A–D). The peak coding accuracy does not align with frequently occurring low sound intensities (Fig. 2A).

The same experimental data evaluated on Riesz's scale yield far better alignment of coding accuracy with stimuli statistics, especially for low intensities (Fig. 2E). On the other hand, the existing match for high levels (Fig. 2C,D) is preserved (Fig. 2G,H) due to the similarity of both scales for high intensities (Fig. 1). The match between the stimulus statistics and the coding accuracy can be quantified by the ratio of the maximal Fisher information in the high-probability region to the global maximum of the Fisher information. For the four examined cases of the plateau centered at (5, 25, 45, 65) dB SPL we obtain the following values of this ratio: (0.46, 0.96, 1, 1) on the pressure level scale, and (1, 1, 1, 1) on Riesz's scale. Note that the non-uniform shape of the high-probability regions results from the transformation rule for the probability density function.

Discussion

The described adaptation of neural coding precision to the local stimulus distribution results in a more efficient representation of the environment^{5,9}. However, the investigation of coding strategy should also take the actual perception intensity into the account¹¹. In all likelihood, coding precision expressed by employing the psychophysical scale (such as Riesz's scale) is more useful and natural than when evaluated in the standard metric system (such as dB SPL). The reasoning is that Riesz's scale is linear in the true perception intensity as described in the Methods section. Consequently, the smallest noticeable increment in perception $\Delta\psi$ is proportional to a fixed value on Riesz's scale, and this value is constant for all stimulus intensities. Hence the unique feature of a stimulus unit based on the psychophysical scale is that the coding accuracy evaluated in such units can be meaningfully compared for different stimuli intensities – unlike the metric scale case. Even if coding precision varies with the stimulus intensity on the metric scale substantially, these variations might be immaterial provided that the actual difference in sensation falls within the smallest noticeable increment.

Note that if Weber's law was valid for the sound intensity perception, the dB SPL scale would correspond to the exact psychophysical scale. From this point of view the shifted-logarithm in Eq. (7) represents a seemingly

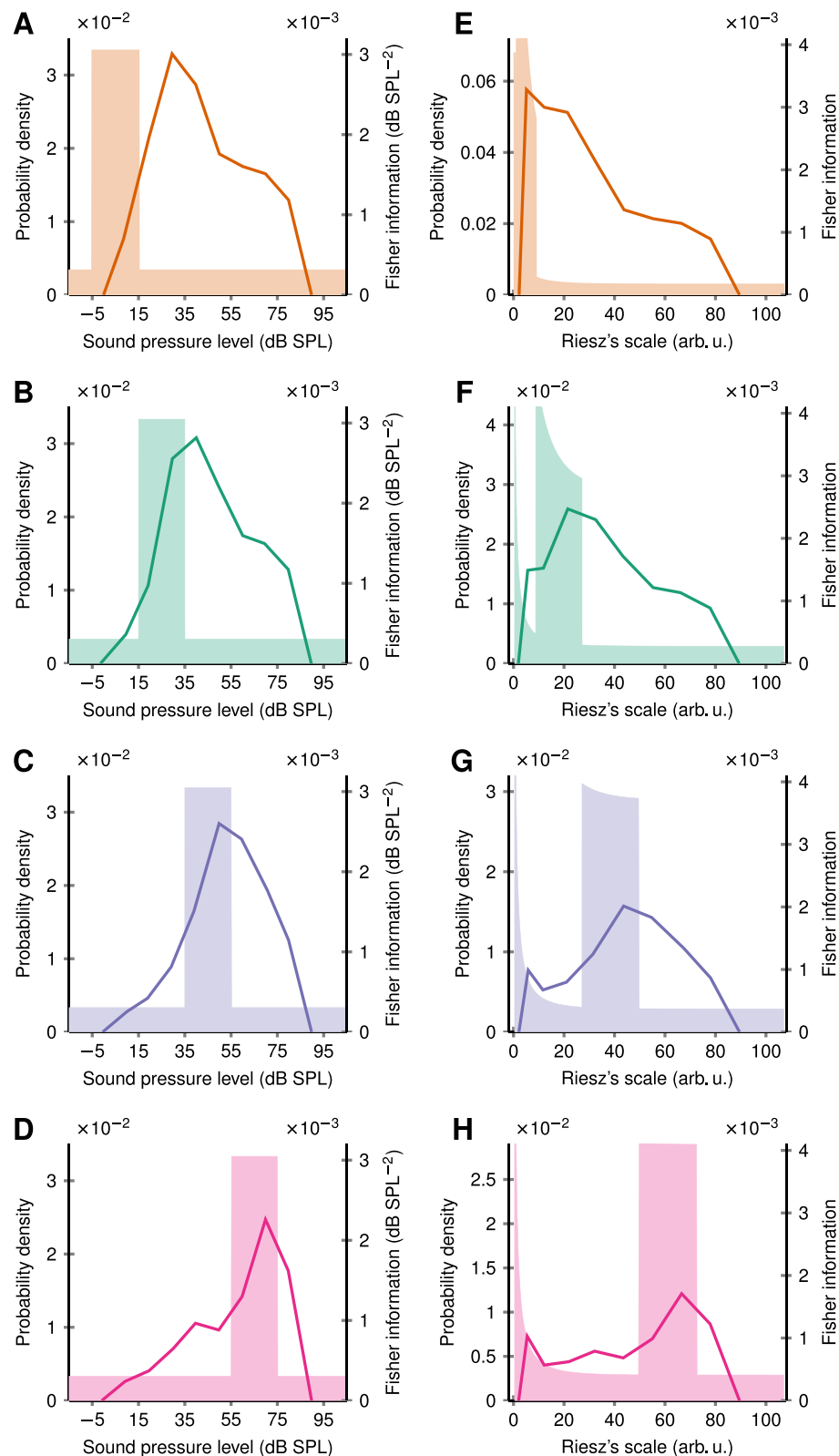


Figure 2. Maximal coding accuracy aligns with stimulus statistics only on the proper stimulus measurement scale. Colored area indicates the stimulus probability density function, solid line is the coding accuracy (Fisher information). (A–D) Original data reconstructed from Watkins and Barbour⁹ show weak adaptation of the coding accuracy to frequent low-intensity sounds (A) on the sound level scale (dB SPL). The alignment improves as the high-probability stimulus region moves towards higher sound intensities (B,C). (E–H) The same data plotted on Riesz's scale of sound intensities (in arbitrary units) reveal that the coding accuracy is actually perfectly adjusted for all four stimulus distributions.

negligible correction. We have shown, however, that the difference between Riesz's and sound pressure level scales affects the coding accuracy adjustment substantially. Riesz's correction, $\psi \propto \log(const. + I)$, to the purely logarithmic Fechner's law in Eq. (2) has a long history and is more fundamental and general, going beyond the case of the sound intensity perception. See^{34–36} for a detailed account. For example, the equation for Riesz's scale as a function of the sound pressure in Eq. (7) is formally identical to the psychophysical mel scale³⁷, which describes the perception intensity for sound frequency. Both the mel and Riesz's psychophysical scales thus follow Weber's law for large stimuli values only.

Our message, however, reaches beyond the topic of psychophysical scales and auditory neuroscience. We argue that the coding accuracy is generally a relative quantity, with respect to chosen units, a fact whose consequences seem to have been neglected in the experimental research. The expected matching of stimulus statistics with the coding accuracy is thus not absolute and does not hold in different unit systems. The coding accuracy reflects the spread of estimated stimulus values, which is affected not only by the stochastic nature of neural responses but also by the arbitrarily chosen unit system for stimulus quantification. In addition, we believe that coding accuracy should generally be evaluated on the scale which is linearly proportional to the internal representation of the stimulus, i.e., proportional to the actual perception intensity.

Finally, it is worth noting that different ways to assess the neural coding efficiency were developed over the decades. A substantial part of the literature employs Shannon's measure of information³⁸ to determine the absolute scale on neuronal performance³⁹. By treating the neuronal system as an information channel, and by maximizing the mutual information between stimuli and responses, one obtains the optimal stimulus distribution, as for example in^{40–44}. Under the assumption of vanishing response variability, the optimal stimulus distribution is proportional to $\sqrt{I_F}$ ^{45–51}, which is known to be invariant under coordinate transformations³³. Heuristically, one may view this result as providing support for the idea of high coding precision matching high probability stimulus regions⁴⁰. Unlike the local method of Fisher information described in this paper, however, the information theory determines the complete (global) form of the stimulus distribution.

References

- Barlow, H. B. Possible principles underlying the transformation of sensory messages. In Rosenblith, W. (ed.) *Sensory Communication*, 217–234 (MIT Press, Cambridge, 1961).
- Simoncelli, E. P. & Olshausen, B. A. Natural image statistics and neural representation. *Annu. Rev. Neurosci.* **24**, 1193–1216 (2001).
- Lewicki, M. S. Efficient coding of natural sounds. *Nat. Neurosci.* **5**, 356–363 (2002).
- Kostal, L., Lansky, P. & Rospars, J.-P. Efficient olfactory coding in the pheromone receptor neuron of a moth. *PLoS Comput. Biol.* **4**, e1000053 (2008).
- Dean, I., Harper, N. S. & McAlpine, D. Neural population coding of sound level adapts to stimulus statistics. *Nat. Neurosci.* **8**, 1684–1689 (2005).
- Wen, B., Wang, G. I., Dean, I. & Delgutte, B. Dynamic range adaptation to sound level statistics in the auditory nerve. *J. Neurosci.* **29**, 13797–13808 (2009).
- Durant, S., Clifford, C. W. G., Crowder, N. A., Price, N. S. C. & Ibbotson, M. R. Characterizing contrast adaptation in a population of cat primary visual cortical neurons using Fisher information. *J. Opt. Soc. Am. A* **24**, 1529–1537 (2007).
- Wark, B., Lundstrom, B. N. & Fairhall, A. Sensory adaptation. *Curr. Opin. Neurobiol.* **17**, 423–429 (2007).
- Watkins, P. V. & Barbour, D. L. Specialized neuronal adaptation for preserving input sensitivity. *Nat. Neurosci.* **11**, 1259–1261 (2008).
- Watkins, P. V. & Barbour, D. L. Level-tuned neurons in primary auditory cortex adapt differently to loud versus soft sounds. *Cereb. Cortex* **21**, 178–190 (2011).
- Dahmen, J. C., Keating, P., Nodal, F. R., Schulz, A. L. & King, A. J. Adaptation to stimulus statistics in the perception and neural representation of auditory space. *Neuron* **66**, 937–948 (2010).
- Maier, J. K. *et al.* Adaptive coding is constrained to midline locations in a spatial listening task. *J. Neurophysiol.* **108**, 1856–1868 (2012).
- Garcia-Lazaro, J. A., Ho, S. S. M., Nair, A. & Schnupp, J. W. H. Shifting and scaling adaptation to dynamic stimuli in somatosensory cortex. *Eur. J. Neurosci.* **26**, 2359–2368 (2007).
- Berens, P., Ecker, A. S., Gerwin, S., Tolias, A. S. & Bethge, M. Reassessing optimal neural population codes with neurometric functions. *Proc. Natl. Acad. Sci. USA* **108**, 4423–4428 (2011).
- Lehmann, E. L. & Casella, G. *Theory of point estimation*, Ch. 2, 115–117 (Springer Verlag, New York, 1998).
- Seung, H. S. & Sompolinsky, H. Simple models for reading neuronal population codes. *Proc. Natl. Acad. Sci. USA* **90**, 749–753 (1993).
- Dayan, P. & Abbott, L. F. The Effect of Correlated Variability on the Accuracy of a Population Code. *Neural Comput.* **11**, 91–101 (1999).
- Seriès, P., Latham, P. E. & Pouget, A. Tuning curve sharpening for orientation selectivity: coding efficiency and the impact of correlations. *Nat. Neurosci.* **7**, 1129–1135 (2004).
- Zhang, K., Ginzburg, I., McNaughton, B. L. & Sejnowski, T. J. Interpreting neuronal population activity by reconstruction: unified framework with application to hippocampal place cells. *J. Neurophysiol.* **79**, 1017–1044 (1998).
- Harper, N. S. & McAlpine, D. Optimal neural population coding of an auditory spatial cue. *Nature* **430**, 682–686 (2004).
- Sreenivasan, S. & Fiete, I. Grid cells generate an analog error-correcting code for singularly precise neural computation. *Nat. Neurosci.* **14**, 1330–1337 (2011).
- Raichel, D. R. *The Science and Applications of Acoustics* (Springer, New York, 2006).
- Kostal, L. & Lansky, P. Coding accuracy is not fully determined by the neuronal model. *Neural Comput.* **27**, 1051–1057 (2015).
- Gescheider, G. A. *Psychophysics: The fundamentals* (Lawrence Erlbaum Associates, Mahwah, New Jersey, 1997).
- Sun, J. Z., Wang, G. I., Goyal, V. K. & Varshney, L. R. A framework for Bayesian optimality of psychophysical laws. *J. Math. Psychol.* **56**, 495–501 (2012).
- Riesz, R. Differential intensity sensitivity of the ear for pure tones. *Phys. Rev.* **31**, 867–875 (1928).
- Weber, E. H. *De pulsione, resorptione, auditu et tactu. Annotationes anatomicae et physiologicae* (Koehler, Leipzig, 1834).
- Dayan, P. & Abbott, L. F. *Theoretical Neuroscience: Computational and Mathematical Modeling of Neural Systems* (MIT Press, 2001).
- Fechner, G. T. *Elemente der Psychophysik* (Breitkopf und Härtel, Leipzig, 1860).
- Masin, S. C. The (Weber's) law that never was. In Elliot, M. A. *et al.* (eds) *Proceedings of the twenty-fifth annual meeting of the International Society for Psychophysics*, 441–446 (International Society for Psychophysics, Galway, Ireland, 2009).
- Papoulis, A. *Probability, random variables, and stochastic processes*, Ch. 5, 92–94 (McGraw-Hill, New York, 1991).
- Kostal, L. Stimulus reference frame and neural coding precision. *J. Math. Psychol.* in press (2016).
- Jeffreys, H. An invariant form for the prior probability in estimation problems. *Proc. Roy. Soc. A* 453–461 (1946).

34. Hecht, S. The visual discrimination of intensity and the Weber-Fechner law. *J. Gen. Physiol.* **7**, 235–267 (1924).
35. Norwich, K. H. & Wong, W. Unification of psychophysical phenomena: The complete form of Fechner's law. *Percept. Psychophys.* **59**, 929–940 (1997).
36. Dzhafarov, E. N. & Colonius, H. The Fechnerian Idea. *Am. J. Psychol.* **124**, 127–140 (2011).
37. Stevens, S. S., Volkman, J. & Newman, E. B. A scale for the measurement of the psychological magnitude pitch. *J. Acoustic. Soc. Am.* **8**, 185–190 (1937).
38. Shannon, C. E. Communication in the presence of noise. *Proc. IRE* **37**, 10–21 (1949).
39. Rieke, F., de Ruyter van Steveninck, R., Warland, D. & Bialek, W. *Spikes: Exploring the Neural Code* (MIT Press, Cambridge, 1997).
40. Laughlin, S. B. A simple coding procedure enhances a neuron's information capacity. *Z. Naturforsch.* **36**, 910–912 (1981).
41. de Ruyter van Steveninck, R. R. & Laughlin, S. B. The rate of information transfer at graded-potential synapses. *Nature* **379**, 642–644 (1996).
42. Ikeda, S. & Manton, J. H. Capacity of a single spiking neuron channel. *Neural Comput.* **21**, 1714–1748 (2009).
43. Suksompong, P. & Berger, T. Capacity analysis for integrate-and-fire neurons with descending action potential thresholds. *IEEE Trans. Inf. Theory* **56**, 838–851 (2010).
44. Kostal, L. & Kobayashi, R. Optimal decoding and information transmission in Hodgkin-Huxley neurons under metabolic cost constraints. *Biosystems* **136**, 3–10 (2015).
45. Bernardo, J. M. Reference posterior distributions for Bayesian inference. *J. Roy. Stat. Soc. B* **41**, 113–147 (1979).
46. Brunel, N. & Nadal, J.-P. Mutual information, Fisher information, and population coding. *Neural Comput.* **10**, 1731–1757 (1998).
47. McDonnell, M. D. & Stocks, N. G. Maximally informative stimuli and tuning curves for sigmoidal rate-coding neurons and populations. *Phys. Rev. Lett.* **101**, 058103 (2008).
48. Ganguli, D. & Simoncelli, E. P. Implicit encoding of prior probabilities in optimal neural populations. In Lafferty, J., Williams, C., Shawe-Taylor, J., Zemel, R. S. & Culotta, A. (eds) *Advances in Neural Information Processing Systems (NIPS)*, vol. 23, 658–666 (MIT Press, Cambridge, Massachusetts, 2010).
49. Yarrow, S., Challis, E. & Seriès, P. Fisher and Shannon information in finite neural populations. *Neural Comput.* **24**, 1740–1780 (2012).
50. Kostal, L., Lansky, P. & McDonnell, M. D. Metabolic cost of neuronal information in an empirical stimulus-response model. *Biol. Cybern.* **107**, 355–365 (2013).
51. Wei, X. & Stocker, A. A Bayesian observer model constrained by efficient coding can explain 'anti-bayesian' percepts. *Nat. Neurosci.* **18**, 1509–1517 (2015).

Acknowledgements

We are grateful to Dennis Barbour for helpful discussion and to Ehtibar Dzhafarov for pointing us to the relevant literature. We also thank two anonymous referees for their comments, which helped to improve the manuscript significantly. This work was supported by the Institute of Physiology RVO:67985823 and by the Czech Science Foundation project GA15-08066S.

Author Contributions

L.K. and P.L. prepared the manuscript. All authors reviewed the manuscript.

Additional Information

Competing financial interests: The authors declare no competing financial interests.

How to cite this article: Kostal, L. and Lansky, P. Coding accuracy on the psychophysical scale. *Sci. Rep.* **6**, 23810; doi: 10.1038/srep23810 (2016).



This work is licensed under a Creative Commons Attribution 4.0 International License. The images or other third party material in this article are included in the article's Creative Commons license, unless indicated otherwise in the credit line; if the material is not included under the Creative Commons license, users will need to obtain permission from the license holder to reproduce the material. To view a copy of this license, visit <http://creativecommons.org/licenses/by/4.0/>