5. Javot, H., Varma Penmetsa, R., Terzaghi, N., Cook, D.R., and Harrison, M.J. (2007). A *Medicago truncatula* phosphate transporter indispensible for the arbuscular mycorrhizal symbiosis. Proc. Natl. Acad. Sci. USA *104*, 1720–1725.

6. Floss, D.S., Gomez, S.K., Park, H.-J., MacLean, A.M., Müller, L.M., Bhattarai, K.K., Lévesque-Tremblay, V., Maldonado-Mendoza, I.E., and Harrison, M.J. (2017). A transcriptional program for arbuscule degeneration during AM symbiosis is regulated by MYB1. Curr. Biol. *27*, 1206–1212.

7. Balestrini, R., and Bonfante, P. (2005). The interface compartment in arbuscular mycorrhizae: A special type of plant cell wall? Plant Biosystems *139*, 8–15.

8. Gutjahr, C., and Parniske, M. (2013). Cell and developmental biology of the arbuscular mycorrhiza symbiosis. Annu. Rev. Cell Dev. Biol. *29*, 593–617.

9. Kobae, Y., and Hata, S. (2010). Dynamics of periarbuscular membranes visualized with a fluorescent phosphate transporter in arbuscular mycorrhizal roots of rice. Plant Cell Physiol. *51*, 341–353.

10. Alexander, T., Meier, R., Toth, R., and Weber, H. (1988). Dynamics of arbuscle development and degeneration in mycorrhizas of *Triticum aestivum* L. and *Avena sativa* L. with reference to *Zea mays* L. New Phytol. *110*, 363–370.

11. Kobae, Y., and Fujiwara, T. (2014). Earliest colonization events of *Rhizophagus irregularis* in rice roots occur preferentially in previously uncolonized cells. Plant Cell Physiol. *55*, 1497–1510.

12. Harrison, M., Dewbre, G., and Liu, J. (2002). A phosphate transporter of *Medicago truncatula* involved in the acquisition of phosphate released by arbuscular mycorrhizal fungi. Plant Cell *14*, 2413–2429.

13. Delaux, P.-M., Bécard, G., and Combier, J.-P. (2013). NSP1 is a component of the Myc signaling pathway. New Phytol. *199*, 59–65.

14. Takeda, N., Tsuzuki, S., Suzaki, T., Parniske, M., and Kawaguchi, M. (2013). *CERBERUS* and *NSP1* of *Lotus japonicus* are common symbiosis genes that modulate arbuscular mycorrhiza development. Plant Cell Physiol. *54*, 1711–1723.

15. Floss, D.S., Levy, J.G., Lévesque-Tremblay, V., Pumplin, N., and Harrison, M.J. (2013). DELLA proteins regulate arbuscule formation in arbuscular mycorrhizal symbiosis. Proc. Natl. Acad. Sci. USA *110*, E5025–E5034.

16. Pimprikar, P., Carbonnel, S., Paries, M., Katzer, K., Klingl, V., Bohmer, M., Karl, L., Floss, D., Harrison, M., Parniske, M., *et al.* (2016). A CCaMK-CYCLOPS-DELLA complex regulates transcription of *RAM1*, a central regulator of arbuscule branching. Curr. Biol. *26*, 987–998.

Neuroscience: Formation of a Percept in the Rat Cortex

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It has long been known that we subjectively experience longer stimuli as being more intense. A recent study sheds light on the neural mechanisms underlying this bias by tracking the formation of a *percept* of intensity in the rat brain.

In 1885, French physician and scientist Adolphe-Moïse Bloch asked a simple question: "Is it possible to present a luminous object sufficiently briefly so that it will not be seen?" [1,2]. To address this question, Bloch performed a visual detection task using a candle (the luminous object) and a Foucault regulator, a mechanical device of the time that allowed him to control the duration of stimulus presentation at milliseconds resolution. Bloch showed that, for short-duration stimuli, "in order to obtain the cessation of visual sensation, doubling the intensity of the light requires halving its duration", a phenomenon that was later termed Bloch's Law [2]. Today we know that, even for long stimuli, the perceived intensity of a stimulus increases with its duration [3]. This is not a quirk of vision:

rather, it seems to be a common misalignment between the Umwelt (subjective) and the physical world, as the same occurs in audition [4] and somatosensation [5]. While the physics of transduction at sensory receptors and the integrative properties of neurons in the early stages of sensory processing are likely to contribute to this phenomenon at timescales of tens of milliseconds [6], cortical mechanisms also have been speculated to play a role, especially at longer timescales [5,7]. A new study by Fassihi *et al.* [8], reported in this issue of *Current Biology*, delivers important new insight into the way physical intensity and duration are integrated in the brain to generate the *percept* of intensity.

Perception is typically studied by quantifying the subject's ability to detect a

physical stimulus (detection), or to distinguish two stimuli (discrimination) that differ along a single physical dimension, such as pitch, intensity, luminance or contrast. A popular discrimination paradigm is the delayed-comparison task, in which the two stimuli to-be-distinguished are presented sequentially, separated by a delay period.

Whisker touch is the major sensory modality that rodents use to collect information from the nearby environment. Several years ago, Fassihi *et al.* [9] developed a delayed-comparison task for rats, based on the whisker sensorimotor system. This was an important development: until that time, such delayed-comparison tasks in animals were restricted to monkeys, limiting our ability to study, and especially to interfere
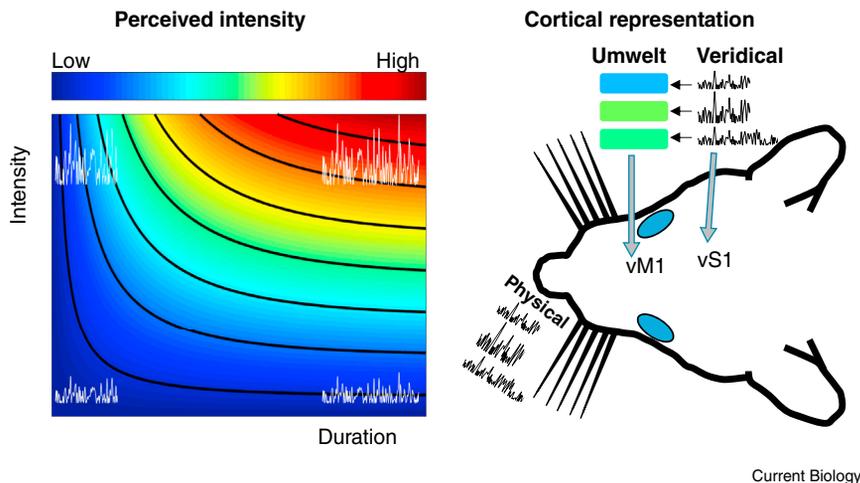
Perceived intensity

Cortical representation

Figure 1. Build-up of the intensity percept across the rat cortex.
In the study of Fassihi *et al.* [8], rats were trained to discriminate the average intensity of two noisy mechanical stimulations that were sequentially delivered to the whiskers (right). Perceived intensity depended not only on the veridical intensity of the stimuli but also on their duration: longer stimulation were perceived as being more intense (left, color coded). As a result, veridical intensity could be traded against stimulus duration so as to keep constant *perceived* intensity (left, black lines denote stimuli of equal perceived intensity). The physical signal delivered to the whiskers, despite undergoing sensory transduction and few stages of sub-cortical processing, was quite accurately represented by the neuronal activity in the vibrissal sensory cortex (vS1; right). On the other hand, activity in the vibrissal motor cortex (vM1) encoded a combination of veridical intensity and duration in a way that mirrors the perceived intensity as assessed behaviorally.

with, the neural processes underlying perception, short-term memory and decision-making. In this new paradigm, a rat is trained to hold the tip of its snout in a nose poke, such that its whiskers rest on a motor-actuated adhesive plate. The stimuli to be discriminated consist of 'noisy' movements of the plate for several hundred milliseconds and, in the new study [8], are separated by a delay of two seconds. The rat is trained to indicate which of the two stimuli had the larger *average* intensity by withdrawing and selecting one of two spouts.

Using this paradigm, Fassihi *et al.* [8] observed that stimulus duration biases rats' perception of intensity, such that longer stimuli are perceived as more intense. These results are in agreement with previous studies in monkeys [5]. To study the neural basis of this phenomenon, they used an electrode array to record the spiking activity of neurons while the animals were performing the task. They focused on two cortical regions: first, the vibrissal sensory cortex (vS1), also known as barrel cortex, which is the entry stage of whisker signals to cerebral cortex; and second, the vibrissal motor cortex (vM1), the main frontal cortex target of vS1 [10]. They

found that, during the presentation of the first stimulus, the activity of neurons in both cortical regions was modulated by the vibration mean speed. However, in vS1, but not in vM1, single-neuron activity was also modulated by the temporal fluctuations in the speed of the plate. After stimulus offset, the two cortical regions maintained information about the vibration mean speed, with two important differences. First, this memory faded away rather quickly (after several hundred milliseconds) in vS1, while it persisted throughout the inter-stimulus delay in vM1. Second, activity in vM1, unlike that in vS1, carried information about both the intensity and the duration of the first stimulus, such that the pattern of neural activity following a short-intense stimulation was similar to that generated by a longer but weaker one (Figure 1).

Taken together, these results have profound implications about the anatomical localization of the integration of duration into the percept of intensity. While the activity in vS1 encodes the physical features of the stimulus shortly after its presentation, neurons in (one of) the next cortical station, vM1, already maintain information about the *percept*, which is a combination of the intensity of

the stimulus and its duration. The Fassihi *et al.* [8] study also provides information about the *timing* of this computation — the authors demonstrate that the integration takes place already at the encoding of the intensity in vM1, and not later, for example during the retrieval of the stimulus from memory, the comparison of the stimuli or the decision-making stages.

Why is duration integrated into the percept of intensity? The rats were sensitive to stimuli durations despite the fact that they were trained to compare intensities, that is, the feedback that they received depended only on the difference between the intensities of the two stimuli. Moreover, a similar distortion in intensity perception was observed with human participants performing a similar task (vibrotactile stimulation to the finger) [8]. Clearly, humans 'understood' the task but nevertheless, they were subject to the same bias. The integration of duration into intensity is almost inevitable when considering stimuli shorter than the time-scale of neurons and synapses, several tens of milliseconds. However, this is not the case here; in fact, stimulus duration is not encoded in the activities of neurons in vS1.

It is tempting to speculate that this bias reflects a computation that may be beneficial to perception. For example, the brain may use the duration of the stimulus as a signal of its intensity, assuming that longer stimuli are typically more intense. In this framework, the incorporation of duration into the percept is a form of Bayesian inference, in which prior expectations (longer stimuli are more intense) help reduce the level of noise in the sensory input [11–13]. Indeed, Fassihi *et al.* [8] demonstrate that the intensity percept is influenced by the statistical distribution of intensities used in the task such that the intensity of the first stimulus is biased towards the center of the distribution of previously-presented stimuli. This phenomenon is also known as 'Central Tendency' or 'the contraction bias' [14–16]. The contraction bias can be explained in the Bayesian framework as the incorporation of prior expectations with noisy observations in order to improve performance [14].

Is the activity of neurons in vM1 biased by these prior expectations or is this contraction bias incorporated in the

neural activity of downstream cortical areas? Are expectations integrated during the delay period or only at a later stage, perhaps at the decision stage (as suggested in [14])? What about other biases that may affect perception as, for instance, response bias [17]? These questions remain open. However, the combination of this behavioral paradigm with the technological advances that allow us to image and manipulate the activities of large populations of neurons in the rodent brain guarantee more exciting findings to come in our journey to understanding how percepts are formed in the brain.

REFERENCES

1. Bloch, A. (1885). Experiences sur la vision. Comptes Rendus Soc. Biolog. 37, 493–495.

2. Gorea, A. (2015). A refresher of the original Bloch's Law paper (bloch, july 1885). i-Perception 6, 2041669515593043.

3. Gorea, A., and Tyler, C.W. (1986). New look at Bloch's law for contrast. JOSA A 3, 52–61.

4. Recanzone, G.H., and Sutter, M.L. (2008). The biological basis of audition. Annu. Rev. Psychol. 59, 119–142.

5. Luna, R., Hernández, A., Brody, C.D., and Romo, R. (2005). Neural codes for perceptual discrimination in primary somatosensory cortex. Nat. Neurosci. 8, 1210–1219.

6. Scharnowski, F., Hermens, F., and Herzog, M.H. (2007). Bloch's law and the dynamics of feature fusion. Vis. Res. 47, 2444–2452.

7. Duysens, J., Gulyas, B., and Maes, H. (1991). Temporal integration in cat visual cortex: A test of Bloch's law. Vis. Res. 31, 1517–1528.

8. Fassihi, A., Akrami, A., Pulecchi, F., Schönfelder, V., and Diamond, M.E. (2017). Transformation of perception from sensory to motor cortex. Curr. Biol. 27, 1585–1596.

9. Fassihi, A., Akrami, A., Esmaeili, V., and Diamond, M.E. (2014). Tactile perception and working memory in rats and humans. Proc. Natl. Acad. Sci. USA 111, 2331–2336.

10. Mao, T., Kusefoglu, D., Hooks, B.M., Huber, D., Petreanu, L., and Svoboda, K. (2011). Long-range neuronal circuits underlying the interaction between sensory and motor cortex. Neuron 72, 111–123.

11. Körding, K. (2007). Decision theory: What should the nervous system do? Science 318, 606–610.

12. Stocker, A.A., and Simoncelli, E.P. (2006). Noise characteristics and prior expectations in human visual speed perception. Nat. Neurosci. 9, 578–585.

13. Weiss, Y., Simoncelli, E.P., and Adelson, E.H. (2002). Motion illusions as optimal percepts. Nat. Neurosci. 5, 598–604.

14. Ashourian, P., and Loewenstein, Y. (2011). Bayesian inference underlies the contraction bias in delayed comparison tasks. PLoS One 6, e19551.

15. Hollingworth, H.L. (1910). The central tendency of judgment. J. Phil. Psychol. Sci. Meth. 7, 461–469.

16. Raviv, O., Ahissar, M., and Loewenstein, Y. (2012). How recent history affects perception: the normative approach and its heuristic approximation. PLoS Comput. Biol. 8, e1002731.

17. Klein, S.A. (2001). Measuring, estimating, and understanding the psychometric function: A commentary. Attent. Percep. Psychophys. 63, 1421–1455.

Evolution: Contingent Predictability in Mammalian Evolution

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Convergence of distantly related species to similar forms speaks to the predictability of evolution, but we still lack general insights into whether convergence is more common or rare than we would expect. Using a global dataset of mammalian species, Mazel and colleagues find that both convergence and divergence occur more often than expected. Convergence was especially common at broad scales that involved Australia, speaking to the extraordinary replicate mammalian communities found there.

Biologists tend to think of life on Earth as being exceptionally diverse. No matter the group, we marvel at its extraordinary diversity and at evolution's propensity for endless inventions [1]. For example, mammals include several bizarre creatures that, were they not real, would be ideal sci-fi aliens (Figure 1A).

At the same time, we are also amazed when evolution, rather than creating something new, instead reinvents [2]. As a prime example, Australia is home to many species that are strikingly similar to their counterparts in other parts of the world (for example, Figure 1B–D). It seems that, at least in some cases, entire communities of interacting species have evolved repeatedly and independently on isolated landmasses around the world [3].

But which pattern dominates? Is macroevolution dominated by divergence, with a world inhabited by species that are exceptionally divergent from one another? Or does convergence rule, so that continents fill with repeated examples of very similar species evolving over and over again? Current research is often focused on particular clades, such as Caribbean anoles, famous for convergence [4]. However, although these studies provide interesting proofs-of-concept for convergence, they do not