

REFERENCES

- Miriyala, A., Kessler, S., Rind, F.C., and Wright, G.A. (2018). Burst firing in bee gustatory neurons prevents adaptation. *Curr. Biol.* 28, 1585–1594.
- Nikonov, A.A., and Leal, W.S. (2002). Peripheral coding of sex pheromone and a behavioral antagonist in the Japanese beetle, *Popillia japonica*. *J. Chem. Ecol.* 28, 1075–1089.
- Todd, J.L., and Baker, T.C. (1999). Function of peripheral olfactory organs. In *Insect Olfaction*, B.S. Hansson, ed. (Berlin, Heidelberg: Springer Berlin Heidelberg), pp. 67–96.
- Su, C.-Y., Menuz, K., Reisert, J., and Carlson, J.R. (2012). Non-synaptic inhibition between grouped neurons in an olfactory circuit. *Nature* 492, 66–71.
- Krahe, R., and Gabbiani, F. (2004). Burst firing in sensory systems. *Nat. Rev. Neurosci.* 5, 13–23.
- Skinner, F.K., Zhang, L., Velazquez, J.L.P., and Carlen, P.L. (1999). Bursting in inhibitory interneuronal networks: a role for gap-junctional coupling. *J. Neurophysiol.* 81, 1274–1283.
- Medvedev, G.S., and Zhuravytska, S. (2012). Shaping bursting by electrical coupling and noise. *Biol. Cybern.* 106, 67–88.
- Gupta, N., and Stopfer, M. (2014). A temporal channel for information in sparse sensory coding. *Curr. Biol.* 24, 2247–2256.
- Reiter, S., Campillo Rodriguez, C., Sun, K., and Stopfer, M. (2015). Spatiotemporal coding of individual chemicals by the gustatory system. *J. Neurosci.* 35, 12309–12321.
- Gupta, N., Singh, S.S., and Stopfer, M. (2016). Oscillatory integration windows in neurons. *Nat. Commun.* 7, 13808.
- Marsat, G., and Pollack, G.S. (2012). Bursting neurons and ultrasound avoidance in crickets. *Front. Neurosci.* 6, 1–9.
- Whitmire, C.J., Waiblinger, C., Schwarz, C., and Stanley, G.B. (2016). Information coding through adaptive gating of synchronized thalamic bursting. *Cell Rep.* 14, 795–807.
- Baker, T.C., Cossé, A.A., and Todd, J.L. (1998). Behavioral antagonism in the moth *Helicoverpa zea* in response to pheromone blends of three sympatric *Heliothinae* moth species is explained by one type of antennal neuron. *Ann. N. Y. Acad. Sci.* 855, 511–513.
- Itskov, P.M., Moreira, J.-M., Vinnik, E., Lopes, G., Safarik, S., Dickinson, M.H., and Ribeiro, C. (2014). Automated monitoring and quantitative analysis of feeding behaviour in *Drosophila*. *Nat. Commun.* 5, 4560.

Hearing: Representing the Aural Wallpaper

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Human listeners appear to represent the textures of sounds through a process of automatic time averaging that exists beyond volition. This process distils likely background sounds into their summary statistics, a computationally efficient way of dealing with complex auditory scenes.

Sweeping along the gravel driveway, your car comes to a halt under the portico. Stepping out, the doorman ushers you into the foyer, where you're met with a wash of voices, individually indistinguishable but collectively conveying a sense of heightened enjoyment. Moving through the party throng, the babble ebbs and flows until, emerging through a curtain onto the balcony beyond, voices dull to mingle with the rustle of the ash trees undulating in the breeze. You catch a stray brass note wafting from the jazz quartet in the pavilion in the garden below, against the rhythmic swash of waves setting on the pebbled beach beyond. A marbled heel-click stirs you to attention and, catching your name, you turn back towards the room to greet your caller.

Though the specifics are perhaps more common in certain social circles

than others, this everyday listening-scene poses significant challenges to the auditory brain, and raises some interesting questions. To what extent is it important to attend to every sound you hear, or to process, even unconsciously, moment-by-moment changes in those sounds? What features of sounds are critical to effective listening, and what can safely be ignored as background clutter? A new study by McWalter and McDermott [1] published in a recent issue of *Current Biology* demonstrates compelling evidence that human listeners perceive sound textures — the aural wallpaper against which many acoustic scenes unfold — through a process of time averaging. They make the case that the neural representation of these textures is of their statistical structure, *per se*, rather than the acoustic elements from which they are constructed. From an

evolutionary perspective it makes sense to process information concerning subtle changes in the environment, but, at the broadest level, does a change in the acoustic background — against which an important auditory scene might unfold — compel the same level of attention? What elements of an auditory scene can safely be unheard or, at least, represented in a more abstract manner, freeing resources to concentrate on encoding more-important foreground events?

Increasing evidence indicates that listeners parse complex scenes by means of 'statistical learning' [2,3] — sometimes called 'perceptual learning' — an automatic process of accumulating sensory information without the need for conscious storage and retrieval. Statistical learning challenges how we think about perception and the behaviours it drives. Learning, over



different time-scales — evolutionary, developmental, the life course, moment-by-moment — facilitates a diverse range of abilities from animal instinct, the acquisition of language, honing of social skills, and detection of rapid changes in complex environments. However, while a traditional view of learning might be that it requires a system of rewards and punishments to make it ‘stick’, this is not the case with statistical learning; listeners can blithely attend to an unrelated visual task, for example, ignorant of ongoing changes in the sound environment, yet their brain activity is constantly tracking changes in the sound environment and adjusting to ensure that important changes in that environment are not missed [4]. Nevertheless, even this emerging perspective — an unconscious tracking of ongoing sounds within the auditory scene — raises the question, ‘what exactly is being tracked?’ Is it individual sound elements that, together, contribute to the perceptual grouping or streaming of sounds, or is it something else, something less tangible, perhaps, but nevertheless important to our ability to process complex listening environments?

In McWalter’s and McDermott’s study [1], they hypothesized a subtly, but importantly, different perspective to the view that the auditory brain tracks individual sound elements in an unfolding acoustic scene, namely that information about these elements is, even in a task-dependent manner, inaccessible to a listener, at least in any conventional sense. Since the statistical structure of an auditory scene can really only be considered in terms of how that scene unfolds over time, the authors assessed the time course over which sensory information is averaged to determine whether it is adapted (fitted) to the time scale of the sounds being integrated. Their experimental paradigm required listeners to compare one exemplar of a sound texture comprising a fixed statistical structure, with another sound in which the statistical structure was stepped from one value to another. The range of sound textures employed was chosen by ‘morphing’ sounds along a statistical dimension, starting from a set of standard reference textures with naturalistic statistics [5]. Textural steps were relatively difficult to detect, in

order to ensure that biases in the decision process could be observed.

Having first satisfied themselves that listeners were waiting to the end of the stimulus to make their judgement as to whether a texture-step had occurred, they turned to examine the key question of how far back in time listeners average information in coming to their decision. From their assessment of the bias generated by integrating textural information before the step into their judgements, they concluded that the auditory brain processes sound textures over a relatively fixed time course, and seemingly independent of volition. Importantly, listeners were unable to overcome the ‘unconscious’ statistical learning of textural information — with its relatively long time-course into the past — even when explicitly requested to do so. This was not because listeners could not distinguish between sounds with different textures — they demonstrably were able to do so — but because they seem ‘obliged’ to integrate information over a fixed time. What’s more, this integration window is largely invariant with respect to stimulus duration; listeners appeared not to be able to adjust consciously the time course over which they averaged information. This included situations where the specific experimental design — extending the duration of the stimulus following the step change in texture — might have encouraged them to do so, suggesting, again, that the time course over which listeners integrate information is relatively fixed.

Given the multiple time scales over which sound textures might unfold, the textural density of heavy rain, for example, differs markedly from, say, the longer time-base of ocean waves [5], does integration depend upon how variable are sound textures [6]? Employing an ideal-observer model, they found no *a priori* requirement that information about textures with more or less variability in their structure be integrated over longer or shorter time courses. Nevertheless, for real listeners, the statistics of textures was a significant factor in performance; unsurprisingly, perhaps, the more variable the texture, the longer the integration time. This makes sense intuitively. More variably fluctuating textures require a longer time to generate a robust representation of

their statistics, but greater deviations from the mean might also bring other brain mechanisms into play, underpinning, perhaps, the explicit grouping of sound features based on spectral or temporal features. Consistent with this, discontinuities — discrete energy gaps — substantially reduced the influence of stimulus history on judgements of sound texture, pointing to a clear separation in the processing of potentially foreground and background sounds, although discontinuities consisting of noise bursts spectrally similar to the texture — and over which perceptual continuity of the texture exists — did not.

This new study supports a framework in which listeners are ‘deaf’ to the individual elements of an unfolding acoustic texture — they lose access to these features — but retain, or rather, represent, these features purely in terms of their statistical structure. What might be the utility of representing statistics of sounds without specific reference, then, to acoustic features? One obvious advantage lies in rapid, and learnable, separation of ‘figure’ from ‘ground’. Although not considered within such a framework, evidence from previous studies of listening in rooms indicates that the statistical structure of backgrounds is learned. Asked to transcribe an unfamiliar spoken sentence presented in different degrees of reverberation — a feature that gives rooms their ‘room-iness’ — listeners’ performance improves after recently having experienced that same environment, compared to recently experiencing a different one [7,8]. This suggests listeners might first ‘tune in’ to the background acoustic texture to improve their performance in an important foreground task. It also accords with the view that the statistics of common and rare sounds are processed in parallel, with improved performance emerging as the brain adapts to the statistics of the background sounds [9], and that listeners retain information about the acoustic background long enough for it to influence listening performance at some later time [10]. Building a representation of the statistical structure of acoustic backgrounds might be one way in which computational resources are reserved for tracking potentially

important foreground events against the aural wallpaper.

REFERENCES

1. McWalter, R., and McDermott, J.H. (2018). Adaptive and selective time averaging of auditory scenes. *Curr. Biol.* **28**, 1405–1418.e10.
2. Dean, I., Harper, N.S., and McAlpine, D. (2005). Rapid neural adaptation to sound level statistics. *Nat. Neurosci.* **8**, 1684–1689.
3. Rabinowitz, N.C., Willmore, B.D., Schnupp, J.W., and King, A.J. (2012). Spectrotemporal contrast kernels for neurons in primary auditory cortex. *J. Neurosci.* **32**, 11271–11284.
4. Barascud, N., Pearce, M.T., Griffiths, T.D., Friston, K.J., and Chait, M. (2016). Brain responses in humans reveal ideal observer-like sensitivity to complex acoustic patterns. *Proc. Natl. Acad. Sci. USA* **113**, E616–E625.
5. McDermott, J.H., and Simoncelli, E.P. (2011). Sound texture perception via statistics of the auditory periphery: evidence from sound synthesis. *Neuron* **71**, 926–940.
6. McDermott, J.H., Schemitsch, M., and Simoncelli, E.P. (2013). Summary statistics in auditory perception. *Nat. Neurosci.* **16**, 493–498.
7. Brandewie, E., and Zahorik, P. (2010). Prior listening in rooms improves speech intelligibility. *J. Acoust. Soc. Am.* **128**, 291–299.
8. Zahorik, P., and Brandewie, E.J. (2016). Speech intelligibility in rooms: effect of prior listening exposure interacts with room acoustics. *J. Acoust. Soc. Am.* **140**, 74.
9. Simpson, A.J., Harper, N.S., Reiss, J.D., and McAlpine, D. (2014). Selective adaptation to “oddball” sounds by the human auditory system. *J. Neurosci.* **34**, 1963–1969.
10. Agus, T.R., Thorpe, S.J., and Pressnitzer, D. (2010). Rapid formation of robust auditory memories: insights from noise. *Neuron* **66**, 610–618.

Chromosome Biology: The Smc–Kleisin Enzymology Finally Comes of Age

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Cohesin and condensin are Smc–kleisin complexes responsible for shaping our chromosomes. Despite extensive genetic and genomic information available on their function, their biochemistry has been hard to study. Two recent studies finally bring exciting new insights into their enzymology.

Smc–kleisins are large trimeric complexes composed of two members of the structural maintenance of chromosomes (SMC) proteins and a member of the kleisin family. They are identified as cohesin, condensin and the rather mysterious Smc5–6 complex [1]. These trimeric complexes are thought to form ‘ring’ structures of immense dimensions within which chromosomal DNA is entrapped (Figure 1A). For cohesin, this entrapment has been proven to hold the two sister chromatids together [2,3] until anaphase: it is then that the kleisin subunit of cohesin is cleaved by a dedicated enzyme [4] and the sister chromosomes can migrate towards the opposite poles of the newly formed daughter cells. Condensin, however, is dedicated to entrapping the same chromosome fibre and its action is synchronous with mitosis. Thus, condensin is mainly responsible for the axial compaction of chromatin while cohesin is responsible for keeping the

two sister chromatids attached at their centromere. It is mostly due to the combined action of these two complexes that the iconic x-shaped chromosome emerges.

How do cohesin and condensin perform these distinct roles? A central feature of all Smc–kleisins is that they are ATP hydrolysis machines; one end of their lengthy coils contains globular nucleotide-binding domains (NBDs, Figure 1A) which bear a strong resemblance (and evolutionary ancestry) to the ABC type cassettes found in membrane transporters from bacteria to mammalian cells [5]. Could it be that instead of pumping cargos across membranes, Smc–kleisins pump DNA? And could ATP hydrolysis be the key element of their DNA entrapment activity?

In a paper published recently in *Science* [6], the Haering and Dekker teams provide clear evidence that condensin ring complexes are ‘pumping’

DNA from inside their lumen, resulting in the extrusion of DNA loops. This activity is undoubtedly the core reaction required to structure chromosomes, since DNA looping is the basis of chromosome fibre formation [7]. Having previously isolated the budding yeast condensin complex, Ganji *et al.* added condensin on glass surfaces bearing fluorescently labelled DNA tethered loose (i.e. not fully stretched) to the glass at both ends. They then followed the DNA molecules using epifluorescence microscopy [8]. Under optimal conditions, the team captured single condensin rings extruding single DNA loops at a pace of ~1.5 kb/sec. Although this activity appears weak, and a rather high rate of events was observed where condensin was seen to drop off DNA, it is quite possible that multiple condensin rings cooperate inside nuclei [9]. An additional remarkable finding was that loop extrusion was unidirectional: condensin would grab DNA stably and

