Figure 1. Plane and circularly polarised light.

(A) A plane polarised light wave with a vertical electric vector. (B) The same as A, but with the vertical vector resolved into two vectors at 45°. The wave remains plane polarised with a vertical resultant vector. (C) When a 90° phase difference is introduced between the two vectors in B, the resultant vector is no longer in a single plane, but rotates in a spiral around the direction of travel of the beam. Seen end-on it describes a circle, and the beam is said to be circularly polarised. (D) The effect of a birefringent quarter-wave plate. The two vectors in B are retarded by different amounts by the plate, so that they emerge with a 90° (quarter-wavelength) phase difference. The vectors are shown in the same plane, but are actually perpendicular to each other, as in B.

polarised light into plane polarised light, which the underlying seven receptors are then able to detect. Interestingly, the eighth cell microvilli are orthogonal to each other in the two ommatidial rows, meaning that they introduce orthogonal retardations into circularly polarised beams. Referring back to Figure 1C, this means that one will produce plane polarised light from a right-hand helix, and the other from a left-hand helix. This accounts for the animals' ability to distinguish right-hand and left-hand polarised light.

In scarab beetles, the highly coloured left-hand circularly polarised light reflected from the elytra is a consequence of the helicoidal structure of the chitin making up the outer region of the exocuticle. [2]. Stacked layers of parallel fibrils, each making a small angle with the next, induce form optical rotation in the reflected light. The overall repeat period of these layers corresponds to half a wavelength of light, and with the optical rotation this results in interference colours that are also circularly polarised. The tails of stomatopods also show highly coloured circularly polarised reflections, and it is likely that these will have a similar microstructural basis, although this has yet to be shown. It also remains to be seen whether the remarkable optical feat of both producing and detecting circularly polarised light is confined to this one group of crustaceans.

References
1. von Frisch, K. (1949). Die Polarisation des Himmelslichtes als orientierender Faktor bei den Tänzen der Bienen. Experientia 5, 142–148.
2. Neville, A.C., and Caveney, S. (1969). Scarabeid beetle exocuticle as an analogue of cholesteric liquid crystals. Biol. Rev. 44, 531–562.
3. Chiou, T.-H., Kleinlogel, S., Cronin, T., Caldwell, R., Loeffler, B., Siddiqi, A., Goldizen, A., and Marshall, J. (2008). Circular polarisation vision in a stomatopod crustacean. Curr. Biol. 18, 429–434.
4. Horváth, G., and Varjú, D. (2004). Polarised Light in Animal Vision (New York: Springer).
5. Moody, M.F., and Parriss, J.R. (1961). The discrimination of polarized light by Octopus: a behavioural and morphological study. Z. vergl. Physiol. 44, 268–291.
6. Rossel, S., and Wehner, R. (1986). Polarization vision in bees. Nature 323, 128–131.
7. Schwind, R. (1991). Polarization vision in water insects and insects living on a moist substrate. J. Comp. Physiol. A 169, 531–540.
8. Shashar, N., Hagan, R., Boal, J.G., and Hanlon, R.T. (2000). Cuttlefish use polarization sensitivity in predation on silvery fish. Vision Res. 40, 71–75.
9. Marshall, N.J., Land, M.F., King, C.A., and Cronin, T.W. (1991). The compound eyes of mantis shrimps (Crustacea, Hoplocarida, Stomatopoda). I. Compound eye structure: the detection of polarised light. Phil. Trans. R. Soc. Lond. B 334, 33–56.
10. Marshall, N.J., and Oberwinkler, J. (1999). The colourful world of the mantis shrimp. Nature 401, 874.

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Phase Coding: Spikes Get a Boost from Local Fields

The brain exhibits coherent, long-range oscillations, and it now appears that these oscillations play a substantial role in neural coding: they can boost the information contained in action potentials by as much as 50%.

Peter E. Latham[1] and Máté Lengyel[2]

Our brains produce on the order of 100 billion action potentials, or 'spikes', each second, and these spikes tell us everything we know — about both the outside world and our own inner thoughts and feelings. Or almost
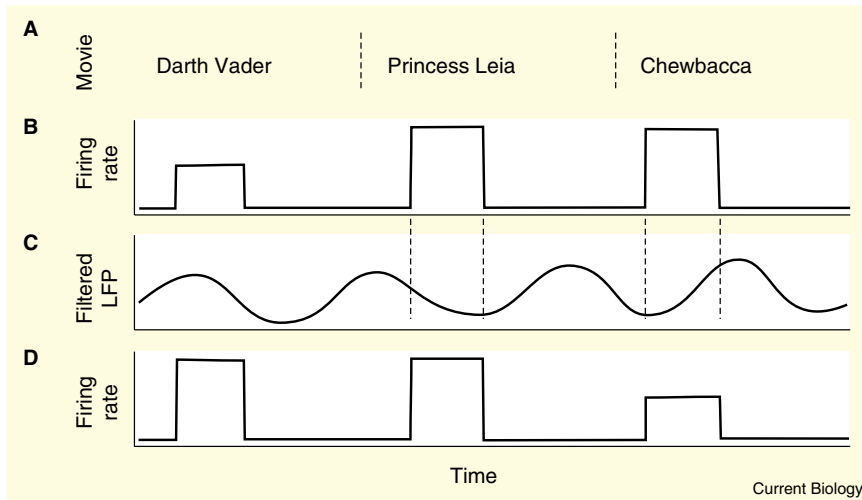
Figure 1. An illustration of Montemurro *et al.*'s [6] experiment.

(A) A portion of the movie Star Wars II showing scenes containing Darth Vader, Princess Leia, and Chewbacca. (B) The response of a hypothetical neuron to these scenes. This neuron can distinguish Darth Vader from both Princess Leia and Chewbacca, but can not tell Princess Leia and Chewbacca apart. (C) The local field potential — or at least a bandpassed and averaged version of it — can disambiguate Princess Leia from Chewbacca, because they occur at different phases. (D) A second neuron can also disambiguate Princess Leia from Chewbacca. Indeed, by looking at the neurons in panels B and D, one could distinguish all three characters. It is not known whether the local field potential adds information to populations of neurons (as it would if no neuron like the one in panel D existed), or if it adds only redundant information (meaning there are always neurons like the one shown in panel D).

everything. There is, it turns out, another signal in the brain: the local field potential, or LFP. The LFP is a relatively long-range and low frequency potential, extending several millimeters and operating at frequencies between 1 and 300 Hz. It is also locked to stimuli in the outside world, at least in sensory cortices [1–4]. These observations place the LFP in a prime position to influence neural coding: but it has been hard to determine whether it really does have such influence, or if it is just another epiphenomenon, the sole purpose of which is to distract neuroscientists from interesting problems [5]. As they recently reported in *Current Biology*, Montemurro *et al.* [6] performed a set of experiments designed to address this issue. And what they found argues for a role in neural coding: the LFP increases the information carried by spikes by up to 50%. This is a large effect, and it will become particularly interesting if it can be extended in two important ways. First, a similar gain in information needs to be shown for populations of neurons. Second, the computational role played by an LFP-coupled spiking code — beyond the general-purpose encoding of stimuli — needs to be worked out.

So how, exactly, does the LFP boost the information in the spikes? To answer this, we need to take a look at the experiment of Montemurro *et al.* [6]. What they did was show movies to anesthetized macaque monkeys — 'Star Wars II' and 'The Last Samurai' — while recording both spikes and the LFP in visual area V1. They then asked how much information the spikes alone provided, and compared that to how much the spikes provided when combined with the LFP. Their main finding is illustrated schematically in Figure 1: panel A of this figure shows a segment of Star Wars II in which first Darth Vader is present, then Princess Leia, and finally Chewbacca; panel B shows the response of a hypothetical neuron to this segment of the movie. The neuron fires at medium rate for Darth Vader, and at high rate for both Princess Leia and Chewbacca. Consequently, it can distinguish Darth Vader from Princess Leia and Chewbacca, but by its firing rate alone it cannot distinguish Princess Leia from Chewbacca. With the help of the LFP, though, it can — at least in principle. To see how, we show in panel C a hypothetical bandpassed and averaged LFP. The key feature of this LFP is that, in the region where the neuron fires (between the dashed lines), its phase is different when Princess Leia

appears than when Chewbacca appears. Consequently, by looking at both spikes and LFP, one could distinguish between Princess Leia and Chewbacca, something one could not do by looking only at spikes.

Figure 1 shows only average traces, and so hides an important caveat: the brain does not have the luxury of averaging signals over trials. Thus, the trial-averaged firing rates and the filtered and averaged LFP tell only part of the story; the other part is contained in the fluctuations around the averages. Fortunately, there is a well developed formalism, information theory [7,8], that can address this issue. This theory tells us that the mutual information between stimuli (scenes from the movie) and responses (spikes or spikes plus LFP) provides a measure of how much the responses tell us about the stimuli *on single trials*. What Montemurro *et al.* [6] found is that spikes plus bandpassed LFP carried far more information than spikes alone: an average of nine bits per second versus six bits per second, at least in the low frequency LFP bands (1–4 Hz). Furthermore, through a clever application of information theory, the authors were able to show that, as in Figure 1, the LFP truly carries extra information — information that is simply not contained in firing rate alone. And it wasn't only the bandpassed LFP that boosted the information; when effectively the whole LFP was used (bandpassed between 1 and 250 Hz), spikes plus LFP provided more than eight bits per second, on average — still about 40% more than spikes alone. Thus, the LFP really does provide a large boost to the information carried by single neurons.

The study of Montemurro *et al.* [6] was partially anticipated by previous work in several other areas of the brain. In the hippocampus, the timing of action potentials relative to the LFP phase has been shown to provide information about position, above and beyond that contained in firing rate [9,10]. But the LFP in hippocampus has a very different character than that in visual or motor cortex: while its amplitude and frequency are determined at least partially by the state of the animal, it is mainly generated internally, and so does not provide much information about the outside world [11]. In motor cortex, the LFP does carry information about planned actions [12–14], but it is carried

primarily in the amplitude of the LFP in high frequency bands, rather than the phase in low frequency bands, as in V1. And in visual cortex, there have been intriguing hints that the LFP boosts the information in the spikes [3], but it was not clear that the LFP carried extra information, as found by Montemurro et al. [6], or simply enhanced the information already carried by the firing rate.

The finding that the LFP adds truly extra information in visual cortex is, then, a new and exciting result. There is, though, at least one important caveat: the LFP was shown to enhance the information only in single neurons (or, more accurately, small groups of neurons, as the study focused primarily, although not exclusively, on multi-unit activity). Whether this enhancement extends to populations is not clear. For example, the neuron in Figure 1 needed the help of the LFP to distinguish between Princess Leia and Chewbacca. But it could just as easily have received help from other neurons in the population, like the hypothetical one shown in panel D: by looking at the activity of the neurons in panels B and D, one could distinguish between Darth Vader, Princess Leia, and Chewbacca without having to resort to the LFP. Fortunately, whether or not Montemurro et al.'s [6] results extend to populations is testable using multi-electrode recording.

This caveat aside, these results fill an important gap in our knowledge: we now know that, in visual cortex, the LFP adds information to spiking activity — information that is at least partially independent of that contained in firing rate. This independence is reminiscent of a proposal in the context of memory retrieval in the hippocampus [15]. In that proposal, phase carries information about the retrieved memory and firing rate codes for the degree of certainty. Thus, epochs with high firing rates tend to produce more reliable firing phases than those with low firing rates — exactly what Montemurro et al. [6] found. It will be exciting to see future experiments testing this, and other [16], theories about the computational role of phase coding.

References
1. Victor, J.D., Purpura, K., Katz, E., and Mao, B. (1994). Population encoding of spatial frequency, orientation, and color in macaque V1. J. Neurophysiol. 72, 2151–2166.
2. Temereanca, S., and Simons, D.J. (2003). Local field potentials and the encoding of whisker deflections by population firing synchrony in thalamic barreloids. J. Neurophysiol. 89, 2137–2145.
3. Lee, H., Simpson, G.V., Logothetis, N.K., and Rainer, G. (2005). Phase locking of single neuron activity to theta oscillations during working memory in monkey extrastriate visual cortex. Neuron 45, 147–156.
4. Liu, J., and Newsome, W.T. (2006). Local field potential in cortical area MT: stimulus tuning and behavioral correlations. J. Neurosci. 26, 7779–7790.
5. Buzsáki, G. (2006). Rhythms of the Brain (USA: Oxford University Press).
6. Montemurro, M.A., Rasch, M.J., Murayama, Y., Logothetis, N.K., and Panzeri, S. (2008). Phase-of-firing coding of natural visual stimuli in primary visual cortex. Curr. Biol. 18, 375–380.
7. Shannon, C., and Weaver, W. (1949). The Mathematical Theory of Communication (Urbana, Illinois: University of Illinois Press).
8. Cover, T., and Thomas, J. (1991). Elements of Information Theory (New York: John Wiley & Sons).
9. Huxter, J., Burgess, N., and O'Keefe, J. (2003). Independent rate and temporal coding in hippocampal pyramidal cells. Nature 425, 828–832.
10. Shapiro, M.L., and Ferbinteanu, J. (2006). Relative spike timing in pairs of hippocampal neurons distinguishes the beginning and end of journeys. Proc. Natl. Acad. Sci. USA 103, 4287–4292.
11. Buzsáki, G. (2005). Theta rhythm of navigation: link between path integration and landmark navigation, episodic and semantic memory. Hippocampus 15, 827–840.
12. Murthy, V.N., and Fetz, E.E. (1996). Oscillatory activity in sensorimotor cortex of awake monkeys: synchronization of local field potentials and relation to behavior. J. Neurophysiol. 76, 3949–3967.
13. Pesaran, B., Pezaris, J.S., Sahani, M., Mitra, P.P., and Andersen, R.A. (2002). Temporal structure in neuronal activity during working memory in macaque parietal cortex. Nat. Neurosci. 5, 805–811.
14. Mehring, C., Rickert, J., Vaadia, E., Cardosa de Oliveira, S., Aertsen, A., and Rotter, S. (2003). Inference of hand movements from local field potentials in monkey motor cortex. Nat. Neurosci. 6, 1253–1254.
15. Lengyel, M., and Dayan, P. (2007). Uncertainty, phase and oscillatory hippocampal recall. In Advances in Neural Information Processing Systems 19, B. Schölkopf, J. Platt, and T. Hoffman, eds. (Cambridge, MA: MIT Press), pp. 833–840.
16. Hopfield, J. (2004). Encoding for computation: recognizing brief dynamical patterns by exploiting effects of weak rhythms on action-potential timing. Proc. Natl. Acad. Sci. USA 101, 6255–6260.

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Metabolic Gradients: A New System for Old Questions

Metabolic gradients are likely to be crucial to normal and abnormal development of cells and tissues. As shown by a new study, a *Xenopus* egg model system has great promise to illuminate quantitative measures of metabolic gradients in living cytoplasm.

Neil W. Blackstone

One of the canonical features of life is obtaining energy from the environment (e.g., food, light) and converting this energy into forms that are more useful to cells. Hence it is no surprise that cells and organisms have developed many mechanisms to detect and respond to molecules used in energy metabolism. A study published in this issue of *Current Biology* by Niethammer et al. [1] pioneers *Xenopus* egg cytoplasm as a useful model to investigate these metabolic signaling mechanisms. This model system will help to answer questions that have intrigued biologists for some time. For example, C.M. Child in 1941 wrote: "That quantitative metabolic differences seem to be the most conspicuous features in early stages of many forms and that they are essential factors in development is a justifiable conclusion from the data…. Undoubtedly, there is interaction between nucleus and cytoplasm, and…different genes become activated or in some way come to play a part in determining the differences in different cells; but…differences in gene effect must be based on conditions in the cytoplasm" [2].

At that time, further tests of Child's hypothesis were thwarted by both technological and theoretical obstacles. With regard to the former,