of silicon chips on electrons, and numerous applications have been proposed for them.\(^5\)\(^\text{–}\)\(^7\)

Several methods\(^5\)\(^\text{–}\)\(^7\) for combining EIT and optical microresonators to obtain EIT-like resonances in integrated optical systems were proposed in 2004, and a laboratory demonstration of such an effect was published last year.\(^10\) In that experiment, EIT-like transmission spectra were observed in two interacting microresonators in the form of glass spheres approximately 400 micrometres in diameter that supported resonances of the whispering-gallery type.

Xu et al.\(^1\) take this advance a stage further. Using modern nanofabrication procedures, they manufactured a pair of micro-ring resonators coupled to parallel waveguides on a silicon-on-insulator substrate typical of an electronic chip. The refractive index of the material thus varies rapidly over a narrow frequency range, and the resulting increased dispersion can lead to ultraslow propagation of light. The narrow spike also provides a well-defined frequency marker for precision measurements.\(^1\) In a system of microresonators, studied by Xu et al.,\(^1\) EIT occurs because of destructive interference between two fields, leaving two appropriately spaced rings in the direction of the reflection port. The width of the absorption feature is determined by the overall loss of the ring resonator system (often dominated by coupling to the straight waveguide), whereas that of the transparency window is set by the internal loss of the ring resonators. (Part c adapted from ref. 1.)

whenever a whole number of wavelengths of the incident light fits into the resonator. Moreover, destructive interference occurs between light emerging from two coupled resonators.

Early microresonators were simply aerosols containing particles of varying sizes, but modern fabrication procedures produce individual resonators with highly controllable resonance frequencies.\(^3\) These resonators come in various forms: ring shapes; disks or spheres, in which the light skims across the outer surface as sound does in a ‘whispering gallery’; or less obvious forms, such as defects in an otherwise perfect photonic crystal. Their small size makes them ideally suited to perform operations on light which would be impossible at the macroscopic scale.

Figure 1: Electromagnetically induced transparency. a, In conventional EIT in an atomic system, a strong pump field \(\omega_p\) is tuned to an atomic energy transition (1–2) and creates a ‘transparency window’ for the signal field \(\omega_s\), which is tuned to a second transition (1–3). b, Destructive interference between the two absorption pathways results in a narrow spike of increased transmission within a wider absorption line. The refractive index of the material thus varies rapidly over a narrow frequency range, and the resulting increased dispersion can lead to ultraslow propagation of light. The narrow spike also provides a well-defined frequency marker for precision measurements. c, In a system of microresonators, studied by Xu et al.,\(^1\) EIT occurs because of destructive interference between two fields, leaving two appropriately spaced rings in the direction of the reflection port. The width of the absorption feature is determined by the overall loss of the ring resonator system (often dominated by coupling to the straight waveguide), whereas that of the transparency window is set by the internal loss of the ring resonators. (Part c adapted from ref. 1.)

Many of what we know about electrical signalling in the brain comes from extracellular recordings that detect when a neuron is firing action potentials. These recordings do not, however, provide continuous monitoring of the fluctuations of membrane potential, and do not capture sub-threshold changes in membrane potential such as those caused by extracellular recordings in the literature has contributed to a collective consciousness in which the action potential or ‘spike’ is viewed as an invariant, all-or-nothing stereotyped event that occurs once a threshold membrane potential is reached. This ‘digital’ signal carries information from the neuronal cell body, the soma, down the axon to presynaptic terminals,
to excite or inhibit the next neuron. In this simple framework, the spike frequency might influence the amount of transmitter release by mechanisms such as facilitation and depression\(^1\), but sub-threshold events occurring in the soma and the dendrites (the projections that receive inputs from other neurons) are thought to be too far away to influence transmitter release from the axonal terminals.

Alle and Geiger writing in *Science*, and Shu *et al.* (this issue, page 761)\(^3\) now show, however, that the release of neurotransmitter from axon terminals of certain vertebrate neurons is influenced by the somatic membrane potential. So, in terms of neuronal signalling, the axon terminals and the soma are electrically much closer than many would have assumed (Fig. 1). The salient finding in both papers, from which all of the rest of the results follow, is that the length constant, \(\lambda\), of axons is surprisingly long, at about 420–450 \(\mu m\), in two types of neuron: hippocampal mossy fibres from rats\(^2\) and layer 5 pyramidal cells from the prefrontal cortex of ferrets\(^4\). \(\lambda\) is the distance over which a voltage change imposed at one site will drop to approximately 37% of its initial value\(^5\). Although rapid changes in membrane potential are more attenuated by distance than are slow signals, when two regions of a neuron are less than \(\lambda\) apart, they are commonly considered to be electrically ‘close’. Put another way, at a distance less than \(\lambda\), changes in membrane potential at one place will appreciably alter the membrane potential at the other. In the case of the mossy fibres, \(\lambda\) was calculated using the distance between recordings made from boutons (presumably presynaptic release sites) and the soma\(^5\). In the case of the prefrontal cortical neurons, simultaneous recordings were made from the soma and axon at known distances apart\(^4\).

How surprising is it that \(\lambda\) is so long in these neurons? Some readers will undoubtedly be taken aback to discover that vertebrate neurons can be so electrically compact, at least for slow signals. But those of us who work with large neurons in invertebrates already know of cases in which somatic voltages influence the axon more than a millimetre away\(^5\). In the vertebrate hippocampal and layer 5 cortical neurons’ the consequence of \(\lambda\) being so long is that slow depolarizations (positive-going changes in membrane potential that bring the neuron closer to threshold) of the membrane at the somatic and dendritic regions are transmitted to the axon terminals, and can influence the release of transmitter.

Shu *et al.*\(^3\) show that depolarization of the soma can increase the amount of spike-mediated release of neurotransmitter from the pre-synaptic terminals by about 30% per 10 mV of somatic depolarization. Is this change likely to be important for the function of the circuits containing these neurons? This will depend on many factors, but it is fair to say that even small changes in synaptic strength can have significant effects.

In the work by Shu *et al.*\(^3\), somatic depolarization was associated with significant spike broadening, that is the return to resting potential occurred more slowly, in both the soma and the axon. Presumably this spike broadening may contribute to the enhanced transmitter release, as occurs elsewhere\(^6\). In this study\(^3\), the authors recorded ongoing barrages of synaptic potentials resulting from spontaneous network activity. The depolarizations associated with these synaptic barrages were seen in both somatic and axonal recordings, demonstrating that signals of the amplitude and time-course of normal synaptic inputs could influence axonal membrane potential.

Alle and Geiger\(^1\) saw no evidence of spike broadening in their recordings. But they did those recorded in vivo during theta oscillations (an ongoing brain rhythm) can substantially increase the amplitudes of the postsynaptic currents evoked by action potentials.

Many types of invertebrate neuron release neurotransmitter both in response to action potentials and as a graded function of membrane potential\(^1,6-11\). There is, however, an important difference between the results in the two studies highlighted here\(^1,3\) and the classic graded transmission well characterized in the retina and in many invertebrate neurons\(^12-16\).

In classic graded transmission, action potentials are not necessary for transmitter release because the threshold for transmitter release is often close to the resting potential. Therefore, synaptic release follows the analogue fluctuations of the presynaptic neuron’s membrane potential. In contrast, the results of Alle and Geiger\(^1\) and of Shu *et al.*\(^3\) show no indication that transmitter release occurs independently of action potentials, but only that the somatic membrane potential can influence how much transmitter is released by an action potential.

Over the years, I have watched the characteristics ascribed to vertebrate neurons slowly evolve to exhibit many of the attributes so clearly demonstrable in invertebrate neurons. I now find it gratifying that vertebrate neurons found in the hippocampus and cortex, brain regions well known for their importance in memory and cognition, may also avail themselves of some of the benefits of analogue processing in addition to spike-mediated release. My guess is that this work\(^3,17\) will trigger numerous studies to determine how transmitter release from spiking neurons in the vertebrate brain is influenced by slow changes in membrane potential that result from neuro-modulation and ongoing activity. In this way, we will come to understand how neural circuits produce variable outputs as a function of behavioural state and mood.

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