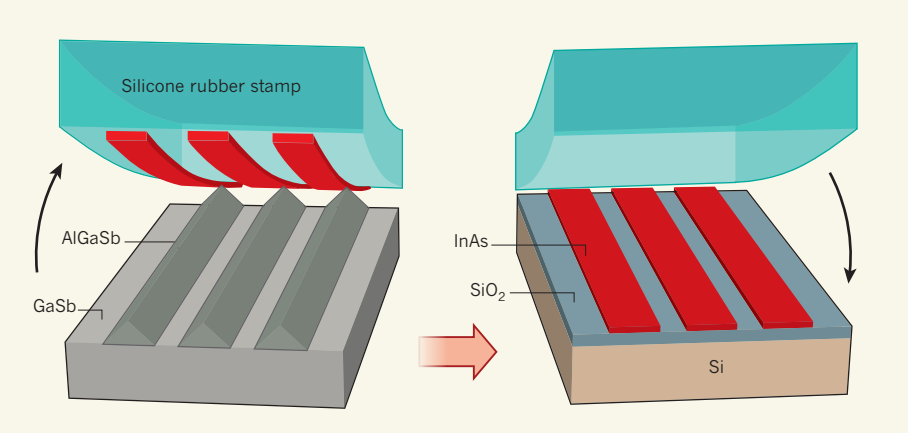

Figure 1 | Heterogeneous electronics by printing. Ko and colleagues' printing technique[3] for making heterogeneous structures for electronic applications uses a silicone rubber stamp to lift nanoscale-thickness indium arsenide (InAs) ribbons from a gallium antimonide (GaSb) wafer coated with a layer of aluminium gallium antimonide (AlGaSb). The nanoribbons are then delivered to a silicon dioxide/silicon (SiO_2/Si) substrate in a process in which the InAs acts as the ink.

and photovoltaic modules[8]. In many of these examples, viscoelastic effects[4] and/or specialized relief structures[10] on the stamps enable printing of pristine, unaltered material onto bare substrate surfaces, even without any separate adhesive layers. Yields approaching 99.99% are now possible with highly developed tools that also offer micrometre-scale precision in the positions of the printed parts, and throughputs corresponding to millions of printed structures per hour, or more[8].

These printing methods are presently in use for the pre-commercial manufacture of photovoltaic modules that incorporate sparse arrays of thin compound-semiconductor solar cells and micro-optics for focusing incident sunlight[11]. Although the same methods have been suggested for integrating compound semiconductors with silicon[4,5,12], Ko and colleagues[3] achieve by far the most impressive results in this context, accomplished by using semiconductor-material layers at exceptionally small thicknesses, down to just a few nanometres.

With remarkably clean, adhesiveless interfaces and high-quality, thermally grown oxides, these ultrathin semiconductor layers yield transistors that can be switched on and off much more effectively than their conventional, bulk counterparts. The authors[3] describe systematic experimental studies that capture the essential physics of operation of one such type of device, in which an interesting and gradual transition from three- to two-dimensional electronic transport occurs as the thickness decreases from 50 nm to less than 10 nm. Device simulations not only quantitatively capture these trends, but also explain related improvements in switching properties. This match between theory and experiment provides further evidence of the defect-free, predictable nature of the printed material stacks from which the devices are made.

The transistor's performance parameters are highly promising, with electron mobilities that significantly exceed those of silicon transistors of similar design. The behaviour of the device at high switching speeds, however, must be evaluated to determine the potential for enhancing the performance of state-of-the-art silicon platforms. Exploring aspects of operation in this regime and demonstrating interconnected operation with silicon transistors represent directions for future work. Research of this type is appealing because it advances knowledge in both science and engineering, in the context of potential solutions to problems of practical importance. The increasingly ubiquitous nature of electronics in modern society suggests that successful outcomes will have widespread, positive implications. ■

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NEUROSCIENCE

The split view of motion

In both fruitflies and vertebrates, signals from photoreceptor cells are immediately split into two opposing channels in the downstream neurons. This might facilitate the computation of visual motion. SEE LETTER P.300

CHI-HON LEE

Nearly a century ago, the great Spanish neuroanatomist Santiago Ramón y Cajal compared[1] the vertebrate retina with the fly's compound eye and noted similarities in their neural circuits (Fig. 1). He redrew the cell bodies of the fly's monopolar cells, transforming them to vertebrate retinal bipolar neurons. Ultrastructural studies have since revealed that, indeed, both sets of neurons receive inputs from photoreceptor cells at structurally unique junctions called ribbon synapses in their first visual neuropiles, or neural switchboards — namely the fly's lamina and the retina's outer plexiform layer[2]. On page 300 of this issue, Joesch *et al.*[3] further extend the analogy, reporting that, like their vertebrate bipolar-neuron counterparts, fly monopolar cells split photoreceptor signals into ON and OFF channels to encode brightness increment and decrement, respectively.

Two main types of fly monopolar cell — L1 and L2 — receive a similar number of synaptic inputs from the type of photoreceptors that mediate motion detection. Using genetic methods to manipulate the activity of specific neurons, behavioural studies[4,5] have suggested that L1 and L2 have overlapping but differentiable roles in detecting visual motion.

By recording electrical activity from downstream motion-sensitive neurons, Joesch *et al.* provide a physiological basis for the behavioural observations. They find that blocking L1 eliminates the response to a moving bright edge (ON), whereas blocking L2 abolishes responses to a moving dark edge (OFF). In a separate paper[6], the same group directly examines the activity of L2 neurons by calcium-imaging techniques and confirms that L2 encodes the OFF signals. Thus, as for vertebrate photoreceptors, the fly photoreceptor signal is split into ON and OFF channels at the first synapse.

Joesch and colleagues[3] further unexpectedly find that L1 and L2 are electrically coupled through gap junctions — specialized complexes that connect the cytoplasm of

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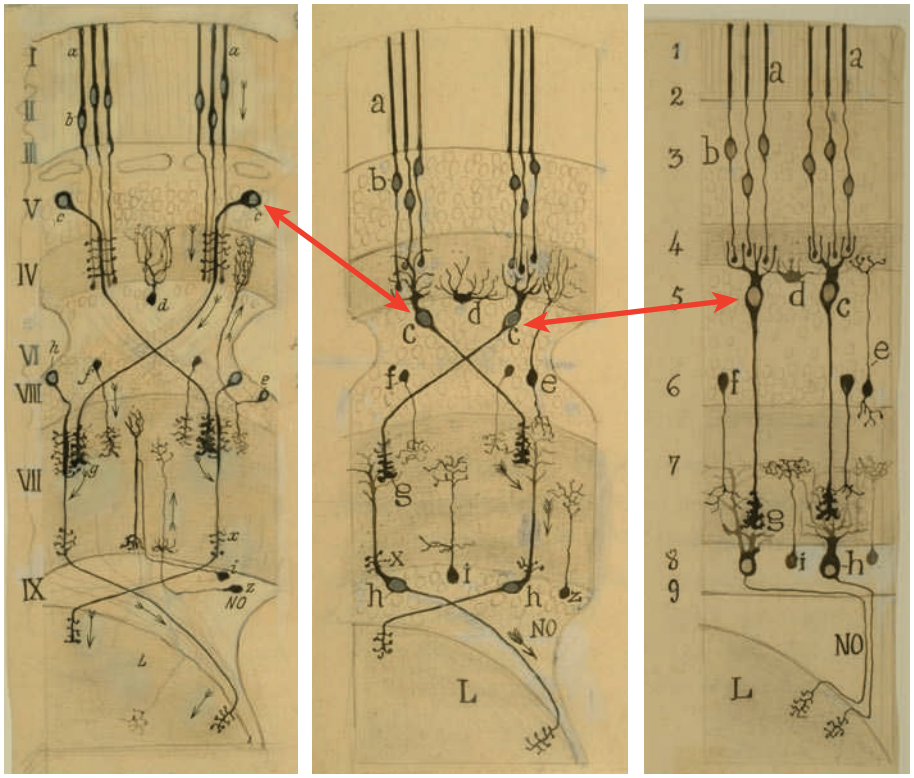
two adjacent cells. This observation reconciles a conundrum of previous behavioural observations[4,5]: reconstituting photoreceptor input to either L1 or L2 is sufficient to generate a near-normal response to motion stimuli, whereas blocking the output of either L1 or L2 diminishes that response.

Why split photoreceptor signals into ON and OFF channels? It has been suggested[7] that this coding mechanism satisfies both information and metabolic constraints: to keep the downstream retinal ganglion neurons at a high level of basal neural activity costs energy; to inhibit them below a certain basal level conveys little information. But why do only those fly photoreceptors that mediate motion detection split their signals into ON/OFF channels in the lamina? The other photoreceptors, which mediate colour vision, do not. Joesch *et al.* argue that splitting facilitates the computation of visual motion, and to do so they invoke the original Hassenstein–Reichardt model for motion detection.

The Hassenstein–Reichardt model was developed[8] in the 1950s to explain behavioural experiments on the beetle *Chlorophanus*. Despite these humble origins, in its abstract form this model has arguably been the most influential theory of visual motion detection[9]. It explains how motion can be computed from local luminance changes — the fundamental form of visual motion. And it makes several counterintuitive predictions that match well with electrophysiological and behavioural data from many species, including humans.

The core computation of the Hassenstein–Reichardt model is based on a delay-and-compare mechanism: the signal from one photoreceptor is delayed and then compared, by multiplication, with the instantaneous signal derived from a neighbouring photoreceptor. Despite its simple construction, the multiplication stage is actually difficult to implement by known synaptic mechanisms, because this seemingly simple mathematical operation needs to be carried out in a way that respects the 'sign' of the signal — that is, multiplying two negative signals should generate a positive signal.

Joesch *et al.*[3] point out that the 'original' Hassenstein–Reichardt model (reported in German and consequently lost to most of the English-speaking world) offers a solution to this problem. In that model, photoreceptor signals are first split into ON and OFF channels, which carry positive and negative components, respectively. Four separate multiplications for the two neighbouring signals are then added or subtracted to correct the sign and generate a direction-specific motion signal. In a way, the sign of the signal is 'remembered' by the signal paths, and the outcome is identical to a sign-corrected multiplication. Electrical engineers in the 1960s devised a similar solution called the four-quadrant (Gilbert) multiplier, which is still used in analog circuits today.



CAJAL LEGACY, INSTITUTO CAJAL (CSIC), MADRID

Figure 1 | Similarity between fly and vertebrate visual systems. Santiago Ramón y Cajal[1] compared the monopolar cells in the fly visual system (left panel) with the bipolar cells in the vertebrate retina (right panel). He redrew the cell bodies of the former to take on the bipolar form (middle panel) (as shown by the added red arrows). The 'mysterious' black arrows (left panel), which appear in many of Cajal's drawings, correctly indicate the flow of visual information, from the photoreceptors (a, b) to the monopolar cells (c) and to the downstream neurons (h).

An advantage of the Hassenstein–Reichardt model is its robustness: inactivating either the ON or OFF channel reduces but does not abolish the motion response, consistent with both behavioural and electrophysiological data. Over time, however, several motion-detection models have been proposed, including the energy model[10], which generates output identical to that of the Hassenstein–Reichardt model but has a very different internal structure. To determine which of these various models explains the behaviour of neurons mediating visual motion, direct access to the actual neural circuits is required.

As one cost of its abstract nature, the Hassenstein–Reichardt model is anatomically inexplicit and only hints at the actual neural implementation. To carry out four-quadrant multiplication, each elementary motion detector requires four separate pathways feeding ON and OFF channels into four multipliers, each of which converges on the wide-field motion-sensitive neurons from which Joesch *et al.*[3] recorded. Previous anatomical and electrophysiological studies[11,12] have revealed a number of candidate neurons for visual motion dectection. More are anticipated from ongoing ultrastructural projects to reconstruct these circuits *in toto*, especially those at the Janelia Farm campus of the Howard Hughes Medical Institute in Ashburn, Virginia. The recent convergence of anatomical, behavioural and electrophysiological investigations — all aided by powerful fly genetics — provides renewed hope that the neural mechanism of motion detection might finally be resolved in the near future. ■

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