basal chordate lineage. As discussed above, there is now substantial molecular support for the idea that ctenophores branch most basally within the animal kingdom, implying that sponges are secondarily simple. The case for a morphologically complex common bilaterian ancestor (Urbilateria) has been eloquently made by de Robertis [18] and others, but these recent large-scale studies imply that this also holds for Urmetazoa and Urchordata. Hence, not only is genetic complexity ancestral [19,20], but the same may be true for morphological complexity as well.

Outstanding Questions

As outlined above, these are interesting times for students of evolutionary genomics, with genome sequencing in progress for representatives of several missing key phyla. It is to be hoped that decreasing costs permit the determination of whole genome sequences for more representatives of each phylum in the near future, as gene losses in individual lineages obscure general patterns, and many animal phyla are very diverse.

With so much sequence data now available for *Trichoplax*, it will be fascinating to see where and when the homologs of many of the key development regulators are expressed. Very few expression patterns are yet available, but these imply much greater cell diversity than does morphology alone. It is possible, however, that many of these genes are not expressed in the presently known life form. Notwithstanding the importance of the forthcoming whole genome sequence for the sponge *Amphimedon*, the most intriguing question of all at the moment is where the ctenophores

fit — more sequence data from ctenophores are urgently required. Other outstanding questions include how placozoans have maintained large and complex mitochondrial genomes, and whether sponges are monophyletic or paraphyletic. Although sponges are classically lumped together, there is an emerging view that the phylum Porifera is a paraphyletic group, homoscleromorph sponges (such as *Oscarella*) being most closely related to the Eumetazoa. We live in interesting times indeed.

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Visual Neuroscience: Retinotopy Meets Percept-otopy?

In the mammalian brain, the primary visual cortex forms a systematic spatial map of the visual field. A new study suggests that the representations on this map are affected by visual illusions that alter perceived size. Spatial patterns of activity may thus reflect perceived size.

Alexander C. Huk

Retinotopic organization is a fundamental organizational element in visual neuroscience. In the early visual cortices of many animals (including monkeys and humans), nearby neurons respond to adjacent parts of the visual field. This 'topographic' relationship maintains a systematic structure on a large scale, so that each half of the visual field is mapped onto the contralateral hemisphere [1]. Figure 1 shows that, when a human observer views a high-contrast checkerboard ring, a corresponding ring-like swath of activity is generated upon the cortical surface. This isomorphic relationship is typically assumed to be inherited: so long as the wiring that connects the retina to the cortex is not
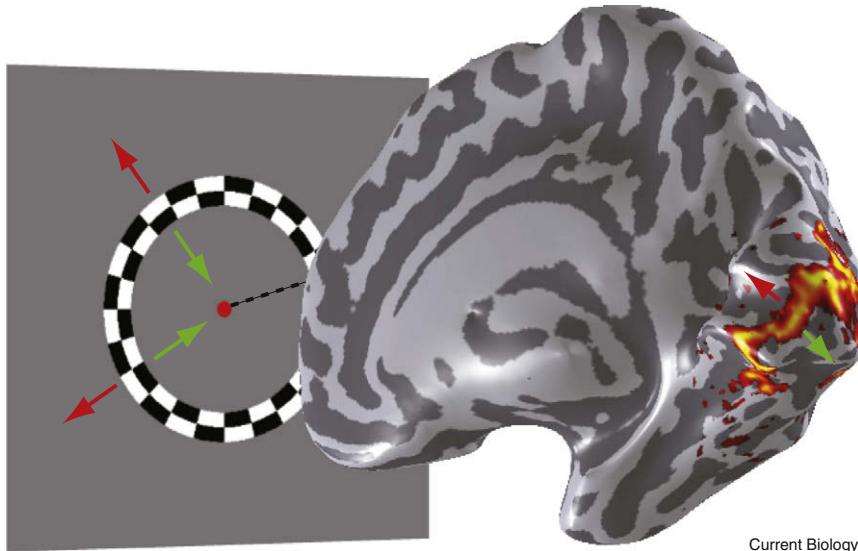
Figure 1. Retinotopic representation of a simple ring pattern in human visual cortex.

Viewing a ring elicits a ring-like pattern of activity across the retinotopic map in visual cortex. As the ring becomes larger — as it moves outward from the red fixation point — the ring of activity would move away from the occipital pole (red arrows). As the ring becomes smaller, the ring of activity would shrink inwards (green arrows). (Figure panels courtesy of S. Dumoulin.)

scrambled, the cortical recipient of retinal inputs will express a retinotopic map. A new study by Fang *et al.* [2] in this issue of *Current Biology* suggests that such 'retinotopic' representations may reflect more than just retinal inputs, carrying top-down signals related to perceived location and size.

Visual information processing occurs on each point within the retinotopic map. Each point on the map is conceived of as a *hypercolumn*, a module of independent processing units that each extract different types of information about the same portion of the visual field [3]. For example, each hypercolumn in primary visual cortex receives inputs from corresponding parts of both retinas, and contains a full set of neural subpopulations that process the range of orientations within the image. Other key features such as spatial and temporal frequency, and perhaps direction and binocular disparity, are likely also represented within points on maps.

Although retinotopic maps are crucial pieces of information in identifying visual areas and circuits [4], the retinotopic map itself is not commonly appealed to when considering neural computation *per se*. Rather, maps are typically relegated to serving as experimental

conveniences for neurophysiologists. One simply puts a visual stimulus somewhere in the visual field, and then exploits the retinotopic map to target the responsive part of the visual cortex. The neural computations are studied *within* the map, and not typically *upon* it.

The new study by Fang *et al.* [2] may motivate amendments to this simple view of retinotopic representations. The study shows that the size of retinotopic representations is modulated, not just by the physical size of retinal stimulation, but by changes in perceived size affected by visual illusions. This relation between perceived and retinotopic sizes was found to be dependent on the observer directing attention to the object. Together, these results imply that the retinotopic map may contribute to a 'space code' for perceived size. The underlying computations may be performed downstream, and show up in primary visual cortex as top-down modulations arising through attentional feedback circuits.

These implications derive from an elegant series of parallel human psychophysical and neuroimaging experiments. Fang *et al.* [2] began by demonstrating that two physically-identical rings can be perceived as relatively larger or smaller based on the simulated

three-dimensional context in which they appear. A ring rendered as being located farther from the observer is perceived as being larger than an identical one drawn as if it were closer to the observer (compare top and bottom rings in Figure 2, left). This is the result of the visual system making an inference: if both rings subtend the same amount of the retina, the one that is farther away must actually be bigger to compensate for its distance [5]. Fang *et al.* [2] began their study by making a series of careful behavioral measurements to quantitatively characterize this illusion using simple ring stimuli. These measurements indicated that the far ring was perceived as approximately one-sixth larger than the near ring.

In parallel experiments, cortical activity was measured in humans using functional magnetic resonance imaging (fMRI). Observers viewed the pair of rings described above, and the same size illusion was induced. When subjects fixated the center of the far ring (which appeared larger), the spatial distribution of fMRI response was shifted outwards, towards more eccentric parts of the visual field (Figure 2, right, red activation). This is a cortical representation that corresponds to a larger ring. Likewise, when subjects fixated the center of the near ring which appeared smaller, the cortical representation was shifted inwards, consistent with the representation of a smaller object (Figure 2, right, green activation).

These results show that the spatial distribution of activity was determined not just by the size and location of the rings as they were drawn on the screen — and as they landed on the retinas — but by the *perceived* size of the rings. Interestingly, this relationship was greatly degraded when subjects were instructed to divert their attention from the rings. This implies that the perceptually-congruent signals originate in later parts of the visual system that integrate multiple sources of information with prior knowledge of the structure of the three-dimensional world, extrapolating beyond the size of the rings on the retina to infer the size of the rings as they would occur in a real three-dimensional environment.

The study is also notable in providing a series of elegant controls that should satisfy many aficionados. The use of relatively high spatial resolution fMRI,
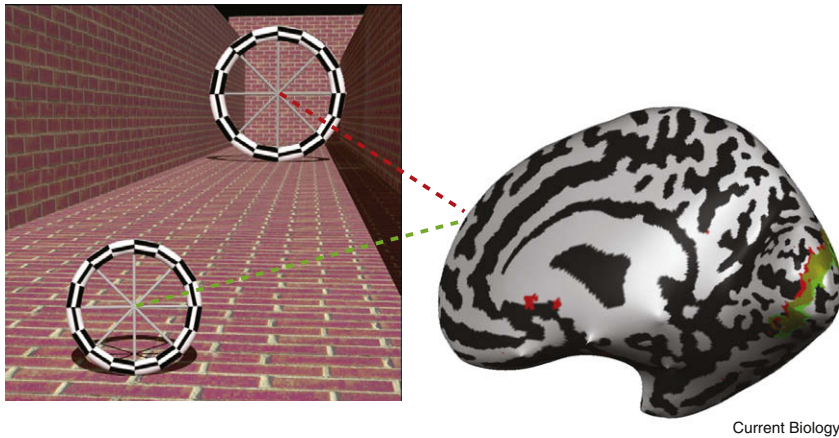
Figure 2. Perceived size of rings affects retinotopic representations.
Viewing the ring at the back (/front) of the three-dimensional scene (left) yields an illusory percept that it is slightly larger (/smaller) than the other ring. The ring-like retinotopic representation (right) shifts outward (/inward), consistent with the perceived size (red and green, respectively). (Figure panels courtesy of F. Fang and S. Murray.)

How do the top-down signals that define perceptual experience interact with bottom-up activity in the retinotopic map? Are there other conditions where retinally-driven and perceptually-influenced topographic representations would be expected to differ? The perceived size of retinotopy's contribution to neural computation may itself change as these questions are answered.

combined with ring stimuli, provide compelling evidence that the changes in retinotopic representation are truly changes in represented locations of the inner and outer edges of the rings, instead of simply a larger response intensity to less precisely-defined patterns that has been blurred and thresholded. The authors also provide a generous set of behavioral and neurophysiological controls that mitigate concerns about possible biases in eye position or the allocation of spatial attention providing hidden links between perceived size and cortical representation.

Although retinotopic representation remains bedrock, these new results may motivate future work investigating the perceptual relevance of retinotopy.

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Animal Migration: Seasonal Reversals of Migrant Moths

A recent study has found that, as migrating silver Y moths pass high overhead above central England in the spring, their headings were generally aimed towards north — a reversal of direction relative to that of autumn migrants. The silver Y must detect its direction of movement, likely by a magnetic sense which must reverse with the season.

Ring T. Cardé

Long-distance migration to a seasonally favourable habitat is well known in insects [1,2]. One of the most thoroughly studied migrants is the silver Y moth, *Autographa gamma*: in the autumn, it migrates from northern Europe to North Africa and the Mediterranean basin; in spring, its descendents re-migrate northward where they exploit a temporarily favourable habitat, but one unsuitable for overwintering. Visual observations from the ground of low-flying silver Y moths in England conducted between 1933 and 1964 documented that the trajectory of night-time flight was predominantly downwind, but whether moths contributed to their displacement by also heading downwind was not resolved [3].

In a recent report in *Current Biology* [4], the vertical-looking radar (VLR) technique [5] and meteorological data were coupled to show how long-distance migration is accomplished in autumn. VLR permits measurement of the body orientation of individual moths as they pass overhead. VLR tracking of the directions of numerous individual moths on many evenings, and the analysis of wind direction at relevant altitudes, showed that migratory flights occurred on those nights when the wind direction was favourable and, furthermore, moths were concentrated at those altitudes providing maximum nightly displacement. Events of mass migration were not correlated with changes in ground level temperature, humidity, wind speed, wind direction or barometric pressure — in other words, such cues did not forecast a favourable wind above. In contrast to a widely held assumption, in autumn the wind direction at migratory height was randomly distributed. The question of whether the spring migration of silver Y moths involved a similar directional sense, but with a reversal of direction, remained unresolved [6].