unaffected in the same allelic combination, but they may not have sought the subtle effect reported by Landsberg et al. [2]). As additional evidence that the cortical cytoskeleton, myosin II in particular, influences cell bond tension, it appears that myosin II and F-actin are both significantly, albeit moderately, increased along the anterior–posterior compartment boundary. Although myosin II is superficially expected to affect only cortical tension, it could also indirectly affect cell adhesion, e.g. by modulating the trafficking of adherens junction components [17]. A possible contribution of cell adhesion to cell bond tension and hence to the boundary, cannot therefore, be currently excluded. Further analysis will require these two contributions to be modelled separately; distinguishing between these two contributions experimentally still remains a substantial challenge.

Myosin-dependent tension may be of general significance as it has been implicated in other morphogenetic events, such as cell sorting during zebrafish gastrulation [18] and axis elongation in the *Drosophila* embryo [16,19]. Interestingly, Fernandez-Gonzalez et al. [19] have demonstrated that, in the *Drosophila* embryo, positive feedback enhances the localization of myosin II at regions of high tension. Such self-reinforcement leads to the formation of actomyosin 'cables' that span multiple adjacent cell bonds. It will be of great interest to see whether this feature is observable at the anterior–posterior boundary of wing imaginal discs, and whether, in simulation, it would lead to further straightening of the boundaries.

Any cell behaviour that maintains the boundary is expected to be regulated by Hedgehog signalling. As described above, one such behaviour is the alignment of cell interfaces parallel to the boundary. Using a clever genetic trick, Landsberg et al. [2] generated artificial interfaces between cells that activate Hedgehog signalling and cells that do not. Cell bonds tend to align parallel to these interfaces, suggesting that Hedgehog may indeed trigger a change in junctional behaviour. One must note, however, that a rigorous demonstration awaits measurements of cell bond tension around the clones. This would require clones to be recognised in live discs, which

is feasible though painstaking with current technology. How do we expect Hedgehog to modulate cell bond tension? It is likely that one or several target genes are involved. Since increased tension is not seen in all the cells that are within Hedgehog's influence, such target genes are only expected to affect tension at the interface between Hedgehog signalling and non-signalling cells. The present study suggests that the relevant target genes are likely to regulate myosin II activity, although other means of modulating the cortical cytoskeleton could be at work. While identification of the relevant target genes remains a challenge for the future, the study by Landsberg et al. [2] lays the foundation for a rigorous assessment of candidate target genes and widens the class of molecules that should be considered.

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Visual Perception: Adapting to a Loss

The visual system is built to be highly adaptable, but the nature and purpose of this adaptation remains poorly understood. A new study opens the door to exploring visual plasticity in entirely new ways.

Michael A. Webster

Stare at a waterfall or expanding spiral for a moment, and afterward objects will briefly appear to move in the opposite direction. Hypnotists sometimes use the spiral illusion as a trick to convince audiences of their powers of mind control, but what is really controlling your mind is the stimulus, for your vision rapidly recalibrates whenever the image before you changes. The aftereffects of these response changes are often

dramatic, and are widely used as a tool for dissecting visual processes. Yet the processes of adaptation itself remain an enigma, for we still know little about how they are manifest in reality — as observers actively interact with their world. A report in this issue by Zhang and colleagues [1] provides a new paradigm for bridging this gap, by measuring how observers adapt when they interact with worlds altered through virtual reality.

Research into the natural states of adaptation has seen a surge of activity in the last decade. One approach has been to draw on techniques and principles that were developed with simple stimuli represented at early visual stages, and apply them to explore how we adapt to high-level and more ecologically relevant properties of the world. For example, motion aftereffects have now been found for the patterns of relative movement that define different styles of walking [2,3], while form aftereffects occur for shapes as complex as a human face [4,5]. Recent studies have also shown that adaptation affects not only the color of a surface but its perceived material — for example, whether it appears glossy or matte [6] — and can also affect perceived properties of scenes such as how cluttered or panoramic they appear [7].

Such results show that adaptation probably plays an important role in shaping all visual experience, but to further understand this role it is important to explore adaptation when the viewing conditions are themselves natural. The vast majority of studies have instead been limited to passively viewing highly restricted sets of images. Zhang et al. [1] circumvented this limitation by having subjects view the world through a head-mounted display that allowed the visual input to be filtered in real time. Thus, the observer could explore and freely move about while their visual diet was altered.

This more natural approach to adapting the observer builds on a tradition of examining how perception changes when observers experience the world through modified optics such as prisms that displace or even invert the image on the retina [8]. A closer precursor was a study [9] that

Figure 1. In the new study by Zhang et al. [1] observers viewed the world through a virtual reality display that removed the energy only at certain orientations.

reversed bright and dark while the observer walked about looking through a video camera. Yet the technological breakthrough of the new study [1] is that the scenes can be manipulated in arbitrary ways, providing seemingly limitless possibilities for probing how and what we can adapt to.

For example, most natural images — even a garish one like Figure 1 — have substantial energy at all orientations. Zhang et al. [1] filtered the images to remove the energy at particular orientations from the video, but even for this manipulation many interesting variants seem realizable. One would be to include information on head tilt to remove what is vertical in the scene rather than in the retinal image, to examine plasticity at more object-centered than viewer-centered levels [10]. Another would be to keep all orientations but pair them with other attributes, for instance so that verticals are red while horizontals are green. In simple patterns, this pairing leads to a contingent aftereffect known as the McCollough effect, in which opposite color afterimages are seen in vertical and horizontal grids [11]. The McCollough effect is one of the most widely studied aftereffects in vision, yet we know little about how it might behave in natural viewing.

What happens when we are deprived for a time of a particular orientation? Selectivity for orientation is one of the clearest properties to emerge in the receptive fields of cells in primary visual cortex. Classic studies of 'stripe-rearing' in animals showed that deprivation during development leads to a permanent loss of cells tuned for the missing orientation [12,13]. This makes sense, as

there is no point in developing a neuron that has little prospect to be active. But what happens to cortical cells in the mature visual system that are suddenly confronted with a loss? Zhang et al. [1] found that observers became more sensitive to the missing information. This also makes sense, because one of the presumed functions of adaptation is to match neurons' response ranges to the range of available stimuli [14,15]. Just as we must increase or decrease sensitivity to light as we move to darker or brighter worlds — an adjustment that occurs largely in the photoreceptors —so also may neurons at later stages in the visual pathway adjust to center their operating ranges relative to the average level of the signals they encode.

The new results [1] may help to resolve the paradox that adaptation in theory should improve vision, but in practice more often seems to impair it [14]. That is, sensitivity to patterns almost always declines after adapting. However, these declines are typically assessed by comparing performance to a 'pre-adapt' state where observers are given time to adjust to a blank field. This baseline is a highly unnatural stimulus that we rarely experience while awake. The new results reinforce the idea that a more appropriate baseline is the world we are normally in, which is full of texture and pattern. Importantly, the results also suggest that this world is something we are always adapted to [16] — that the notion of 'pre-adapted' is in fact meaningless. If visual sensitivity is already 'desensitized' to match the natural variation in scenes, then it becomes apparent that sensitivity should increase when this variance is reduced.

Another recent study [17] similarly found increases in contrast sensitivity when observers were exposed to a low contrast world (by wearing contrast-reducing goggles). The implications of these studies reach beyond adaptation to how we should understand visual coding. Many of the standards for characterizing normal vision — such as the contrast sensitivity function — have been based on nonstandard states of adaptation, and should be revisited under more representative viewing conditions.

A second intriguing property of the improvements in orientation and contrast sensitivity was that they persisted for hours. This is much longer than observed in typical experimental protocols, where the adaptation is for a few minutes and the aftereffects last only a few seconds. If the orientation changes were instead tracking the aftereffects to a lifetime of exposures, then these aftereffects are perhaps more remarkable for how rapidly they begin to emerge. Much work suggests that adaptation can operate over multiple timescales [15,18] — the brief aftereffects that are typically reported ride atop a sea of much longer 'memories' of the history of stimulation, and whether these reflect distinct processes and how they interact to determine neural responses is something vision scientists are only beginning to consider.

Measurements of sensitivity provide just a hint of the possible consequences of adaptation. Instead of asking how well we can see, another question is what the world looks like. For example, orientation adaptation is also famous for inducing 'tilt' aftereffects [19]. The relationships between sensitivity and appearance depend fundamentally on adaptation. Individuals with an astigmatic lens have poorer acuity for some orientations, yet gratings at these orientations do not always look weaker to them because adaptation compensates appearance for the sensitivity deficit [20]. In fact, the perceptual balance of color and shape that seems to characterize the world is probably a consequence of adaptive processes that

discount non-uniformities in the environment and in the sensitivity limits of the perceiver. Such adjustments are likely to play a critical role in maintaining perceptual constancy as either the world or the observer varies. Including measures of both performance and appearance will further enrich the power of this new virtual reality technique to penetrate the mysteries of adaptation.

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Mitosis: Too Much of a Good Thing (Can Be Bad)

Recent studies reveal that the precise regulation of microtubule dynamics is essential for an error-free mitosis. Kinetochore microtubule attachments that are too stable increase the rate of chromosome mis-segregation, a leading cause of chromosomal instability in tumors.

**Alexey Khodjakov
and Conly L. Rieder**

The scholars of mitosis will soon have a reason to celebrate: November of 2009 marks the 25th anniversary of the discovery that microtubules are dynamically unstable, commonly referred to as microtubule dynamic instability [1]. The revelation that microtubule plus ends undergo periodic transitions between phases of growth and shrinkage rapidly led to the 'search-and-capture' hypothesis [2], which remains the prevailing guiding principle of mitotic spindle assembly.

According to this hypothesis, the attachment of kinetochores to the spindle occurs stochastically in that kinetochores simply capture microtubules as they grow into their