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Visual Perception: A Novel Difference Channel in Binocular Vision

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A recent study provides compelling evidence that binocular vision uses two separate channels; one channel adds the images from the two eyes, and the other subtracts them.

We look out on the world through two separate eyes, but perceive it as a unified whole. Our brains combine the images from the left and right eyes into a single fused percept, while using the small differences between the two images to deduce information about depth. Much previous work has shown that the fused image is dominated by the sum of left and right images [1–4]. In this issue of *Current Biology*, however, May and Zhaoping [5] report an ingenious experiment which adds to emerging evidence that, in addition to the binocular summation channel, there is also a channel that takes the binocular difference — that is, subtracts one image from the other. Separate summation and difference channels may help the brain to encode binocular information in a statistically optimal fashion, though we argue that further work is needed to demonstrate

that the brain really exploits this possibility.

A Tilt After-effect without Tilt Adaptation?

May and Zhaoping [5] employ a classic technique for demonstrating visual channels: adaptation [6–9]. Adaptation is responsible for many familiar visual illusions: for example, after gazing at a waterfall for some seconds, we experience a motion after-effect such that static objects appear to move upwards. Similarly, in the tilt after-effect, after adapting to left-tilted stripes, vertical stripes are seen as tilted to the right. To probe the question of whether there are separate binocular channels in the brain, May and Zhaoping [5] made use of the fact that stimuli can be constructed where the left and right images will give different percepts depending on whether they are added or subtracted. This is illustrated in

Figure 1: adding the two patterns shown in the top panel will result in bars that appear to be tilted downwards to the right (L + R); but if we subtract one pattern from the other, we obtain bars that are tilted downwards to the left (R − L). So if the brain sums the images, people should see right-tilted bars, whereas if the brain subtracts the images, people should see left-tilted bars. Importantly, in these stimuli there is no information from the images of either eye about the direction of tilt; the tilt emerges only when the left and right images are combined.

May and Zhaoping [5] found that adaptation can alter observers' tendency to report the tilt consistent with the binocular summation or difference percept. In their experiments, observers first spent some seconds observing either correlated stimuli (identical in both eyes, so that the binocular difference was zero), or anticorrelated stimuli (one

eye's image was the photographic negative of the other, so that the binocular sum was zero). Viewing anticorrelated images — that is, adapting to large binocular differences, and thus adapting the difference mechanism — biased observers towards reporting the summation percept. Conversely, viewing correlated images — that is, adapting to large binocular sums and adapting the summation mechanism — made observers more likely to report the difference percept. This agrees with previous research by the same group [4] using flickering gratings which yield upward or downward motion depending on whether one adds or subtracts the binocular images.

In the classic tilt after-effect, adaptation to anticlockwise orientations biases observers towards perceiving clockwise orientations, reflecting changes in orientation-selective neurons. Here [5], as oriented bars were never presented to the observers as adaptors, the adaptation took place in the binocular summation and difference channels. Thus, this illusion is not really a 'tilt after-effect', because it doesn't occur after adaptation to tilt; really, it is a 'binocular correlation after-effect', and is strong confirmation that distinct sum and difference channels exist and can be adapted.

Binocular Vision and Neuronal Correlates
In general, depending on the images seen by left and right eyes, binocular vision can operate in several different 'modes'. If the left and right images are completely incompatible, we experience binocular rivalry, our perception alternating between left or right images. Otherwise, we fuse left and right into a single percept, usually close to the sum of left and right images. If the images are locally similar apart from a horizontal displacement, we additionally perceive stereoscopic depth consistent with the disparity. Disparity is not the same as the difference signal investigated by May and Zhaoping [5]; it is the offset between corresponding regions which are highly correlated with each other. Nevertheless, disparity inevitably creates differences between the left and right images at a given position.

Neurons in primary visual cortex, V1, perform the initial stage of the disparity computation, and also contribute to

Left (L) **Right (R)**

Sum (L + R) **Difference (R − L)**
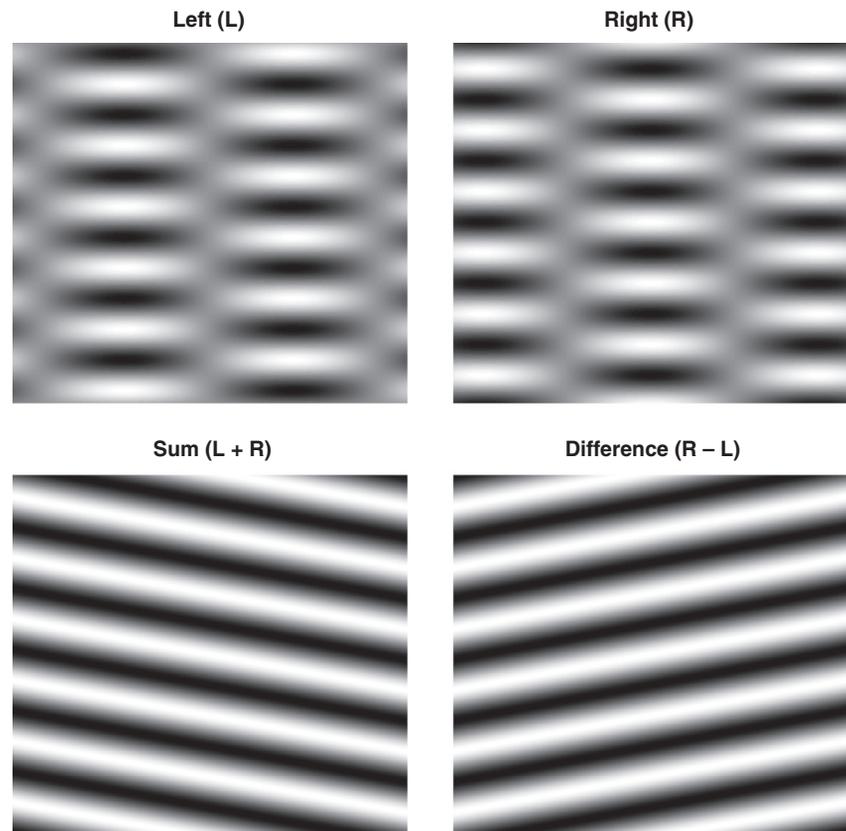
Current Biology

**Figure 1. Horizontal test image from May and Zhaoping [5].**
The top panel shows the *monocular* images presented to the left and right eyes. The bottom panel shows the *binocular* images obtained by either summing or subtracting the two images (denoted by L + R and L − R, respectively).

binocular fusion. May and Zhaoping [5] state that "signals from the summation and differencing channels are multiplexed so that each V1 neuron receives a weighted sum of the signals in these two channels". This puts it rather back-to-front. The input channels to V1 are the left and right eyes, and these are multiplexed so that each V1 neuron receives a weighted combination of the signals from the two eyes, which can equally be expressed as a weighted combination of summation and difference signals.

Neuronal models of stereopsis already contain features such as 'tuned excitatory' and 'tuned inhibitory' neurons, which have been identified with the summation and difference channels [10,11]. Thus, the finding that one can be adapted to perceive the difference signal in vertical stimuli is consistent with current models of stereopsis. However, May and Zhaoping [5] now show clear

evidence for a difference channel even when both adaptor and test are horizontal and the task involves binocular fusion rather than stereopsis. This implies that a difference channel contributes to fusion, something which future models of fusion should take into account.

Previous work with test images containing only near-horizontal orientations (as, for example, in Figure 1) has found that, in the absence of adaptation, observers are more likely to perceive the summation image [1–4]. This may reflect the predominance of tuned-excitatory binocular neurons in V1 [12]: cells which (roughly speaking) begin by summing the left and right eye signals are much more common than cells which subtract them. However, for vertical test images, May and Zhaoping [5] found less bias towards the summation percept. This could occur if neurons tuned to vertical orientations are distributed more evenly between tuned-excitatory and
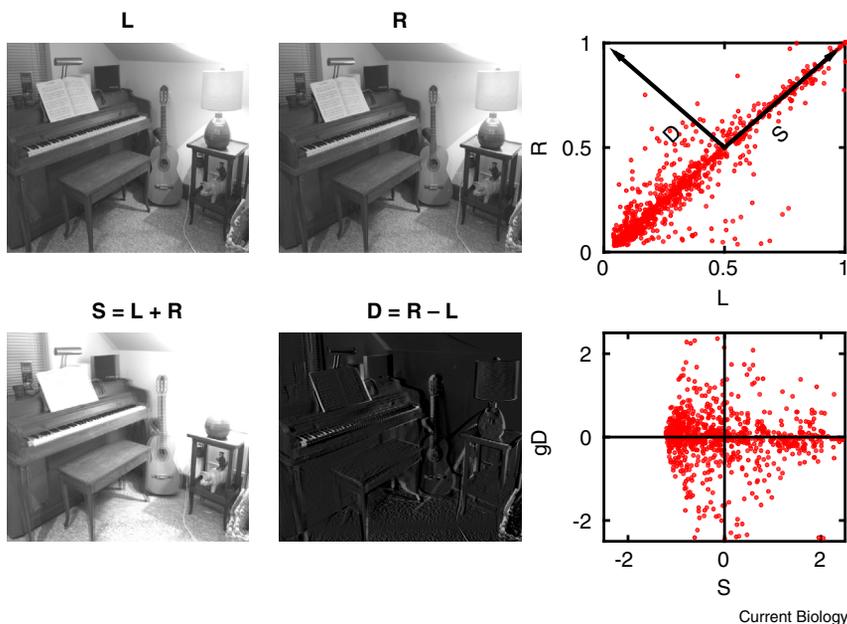
Figure 2. Stereopairs and pixel-by-pixel relationships.
Top row shows two images seen by the left (L) and right (R) eyes, and a scatterplot showing the contrast of each pixel in the right image (R) plotted against the luminance of the pixel at the same position in the left image. The left and right images are highly correlated, so a more efficient representation can be achieved if we rotate the axis so that the L and R values are expressed in terms of the sum and difference ($S = R + L$ and $D = R - L$, respectively). The bottom row shows the summed and differenced images, and the pixel-by-pixel relationship between S and D, following a scaling g applied to D such that S and D have the same variance. Due to the axis rotation in the top panel, S and D are now uncorrelated. Importantly, it is the scaling which achieves the efficiency gain. An axis rotation alone would not achieve this. Stereopair is 'piano' from the 2014 Middlebury dataset [14].

tuned-inhibitory disparity tuning, with the overall predominance of tuned-excitatory tuning driven mainly by horizontal orientations. As far as we know, no one has examined this. If true, it would be an impressive physiological prediction of May and Zhaoping's [5] psychophysical work.

Efficient Stereo Coding
Indeed, the binocular difference channel is itself a prediction of Li Zhaoping's theory of efficient stereo encoding [10,11]. Zhaoping points out that, in natural images, the differences between left and right eye contrasts at a given location are generally much smaller than their sum (Figure 2). Thus, to encode the two eyes' images efficiently, it makes sense to re-express them as their sum and difference, and apply a larger gain to the difference. This theory motivated the present psychophysical experiments.

Although the demonstration of the predicted difference channel is impressive, other key components of the efficient encoding theory remain to be demonstrated. The theory's distinctive

feature is not just the existence of binocular summation and difference channels, but the larger gain applied to the difference channel. May and Zhaoping's [5] experiments cannot address this because they do not discuss the normal value of gain, only how it is changed by adaptation. The effect of adaptation is not distinctive for summation/difference axes; for example, in binocular rivalry, adapting the left eye also biases perception away from the left eye's test image [13]. Indeed, one assumes it would be possible to adapt to arbitrary combinations of the two eyes' images.

Thus, the new results [5], while suggestive, cannot be regarded as confirming efficient stereo encoding. More generally, efficiently coding and transmitting retinal signals is clearly beneficial when passing large amounts of information down the bottleneck of the optic nerve, but may not be the most helpful framework for binocular fusion and stereopsis. For example, in Figure 2 (top right), many of the points

with large differences between left and right images represent positions where the left and right images are near-identical after an appropriate offset. It is not clear to us how the axis rotation and gain change helps the visual system figure out what the appropriate offset (the disparity) is at each location.

Thus, while we agree that the new results [5] are consistent with the theory, we are less convinced that it is strong evidence for it. The critical feature for efficient encoding is not the axis rotation, but the higher gain applied to the difference channel, and this has not been demonstrated.

Gender Differences in Visual Perception
A secondary, unexpected feature of May and Zhaoping's [5] data are gender differences in psychophysical performance. In their initial work, they found to their surprise that males were much more affected by the adaptation than females. Following up on this, the authors gathered data from a further 25 subjects and again found that males were significantly more affected by adaptation than females, though the size of the effect was now smaller. This is surprising because the authors studied very low-level psychophysical phenomena in healthy subjects whose age and experience with psychophysical experiments did not differ. We know of no other reports of sex differences in comparably low-level visual processing. At present, speculation on the source of these differences seems premature, but it certainly merits further investigation.

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Innate Immune Memory: Activation of Macrophage Killing Ability by Developmental Duties

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Innate immune systems in many taxa exhibit hallmarks of memory in response to previous microbial exposure. A new study demonstrates that innate immune memory in *Drosophila* embryonic macrophages can also be induced by the successful engulfment of apoptotic cells, highlighting the importance of early exposure events for developing responsive immune systems.

The observation that immune systems have memory has been around for centuries; for example, B- and T-cell-mediated adaptive immune memory provides us with robust protection against pathogens that we've encountered previously. We've made practical use of that sort of immune memory in vaccination since the time of Jenner. Although we've known about this type of immune memory for a long time, somehow we are still surprised when other aspects of the immune response show memory. Perhaps the problem is that, as we've uncovered the molecular mechanisms governing this response, we've equated these particular memory mechanisms with the system property of memory, yet the two are not equal. Clearly there are many sorts of memory mechanisms: we can remember things in our brains and our foam pillows can remember the shapes of our heads, yet neither of these involve recombination of genes to produce functional antibodies

as in adaptive immune memory. To discuss the potentially diverse types of immune memory, we need to define what we mean by 'memory'. At its most basic, the reactions of a system with memory are influenced by past experiences. Systems that have memory exhibit the property of hysteresis, where the past and current state of the system must be known in order to predict future states (Figure 1A). In a new study published recently in *Cell*, Weavers *et al.* [1] have shown that macrophages of *Drosophila* embryos can engulf microbes only if the macrophages have previously participated in the important developmental role of engulfing dead cells that the embryo no longer needs. Thus, these macrophages exhibit the property of memory. Although previous work has reported that invertebrate immune cells show memory of interactions with microbes [2,3], this new study provides the first demonstration that these cells can

remember interactions with self and that this in turn affects interactions with non-self.

Memory in innate immune systems appears to be a general phenomenon spanning many taxa. A wide variety of insects, from bees to beetles to moths [4], are able to mount a more protective immune response against microbes that they've previously encountered. Mouse macrophages, firmly part of the innate immune system, undergo a shift in metabolic physiology after exposure to components of microbes [5] that allows for increased and longer-lasting resistance to infection. It makes sense that memory would be a general property of immune systems; after all, parasites constantly come and go in host populations, rising in epidemics and disappearing after everyone has suffered infection. Maintaining levels of immunity that could ward off all potential parasites, whatever their actual abundances, would

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