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Faculty of Computer Science, Dalhousie University, 6050 University Avenue PO Box 15000, Halifax, Nova Scotia, Canada, B3H 4R2.
E-mail: beiko@cs.dal.ca

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Binocular Vision: The Eyes Add and Subtract

Our two eyes' views of the outside world are slightly different, providing the basis for stereopsis. A new study has found evidence that the human visual system has separately adaptable channels for adding and subtracting the neural signals from the two eyes, supporting an unconventional view of the initial stages of stereopsis.

Frederick A.A. Kingdom

Two forward looking eyes confer upon their owner stereoscopic, or 'three-dimensional' vision. The two eyes view the world from a slightly different angle, and the resulting small differences between the images in the two eyes is exploited for stereopsis. Figure 1 shows an example stereo-pair — readers who can free-fuse the top two images will see a scene in three-dimensions. Underneath are shown the images produced by adding (left) or subtracting (right) the two stereo-half-images. If there were no difference between the two stereo-halves in the upper figure, the lower right image would be blank, so this image reveals the disparities between the two stereo-halves; it is these disparities that are detected by the brain and used to construct the three-dimensional view. Traditionally it was thought that stereopsis was achieved by combining signals from neurons that simultaneously detected objects in disparate parts of the two eyes' images [1], as illustrated in Figure 2A. An alternative view [2], however, suggests that binocular neurons that encode the sum and the difference between the two stereo-halves, shown in Figure 1, are used for stereopsis; this view is illustrated in Figure 2B. While there has been a history of speculation about the possibility of binocular-summing and binocular-differencing channels in human vision [2–4], an ingenious study by May *et al.* [5] reported in this issue of *Current Biology* has finally produced convincing evidence that such channels exist.

May *et al.* [5] focused on a defining feature of Li and Atick's [2] theory about

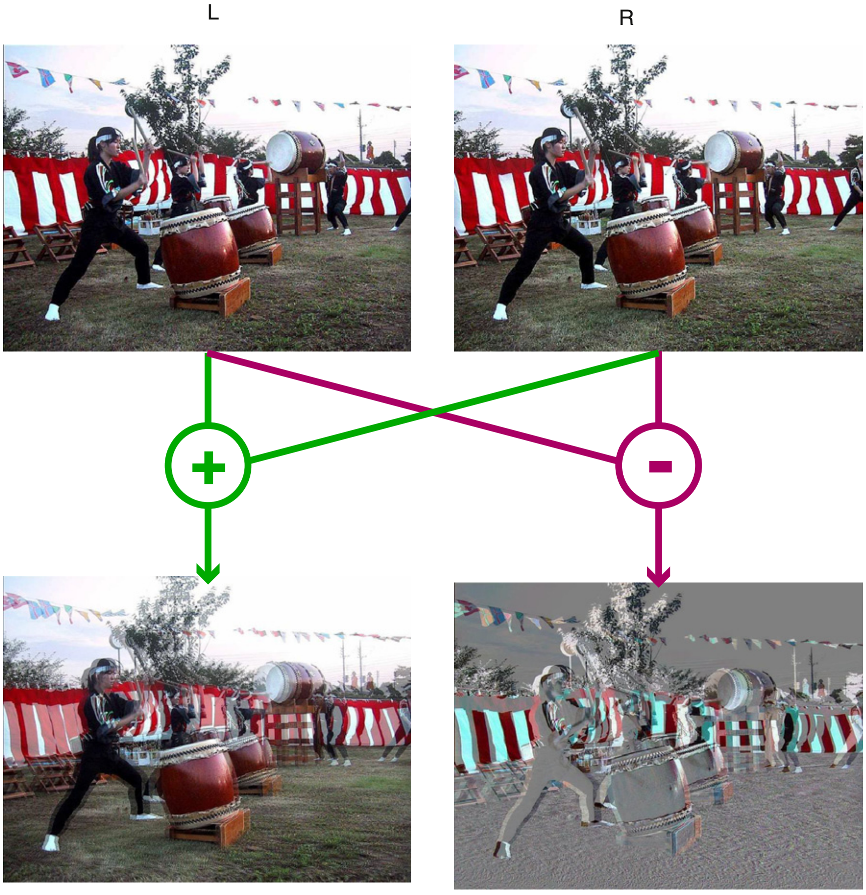

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Figure 1. Stereopsis. Fusion of the left (L) and right (R) stereo-half images reveals an image in three-dimensions.

The bottom left image shows the sum and the bottom right image the difference between the two stereo-halves. Although the difference image is weaker than the sum image, it reveals the disparities that are critical for stereopsis.

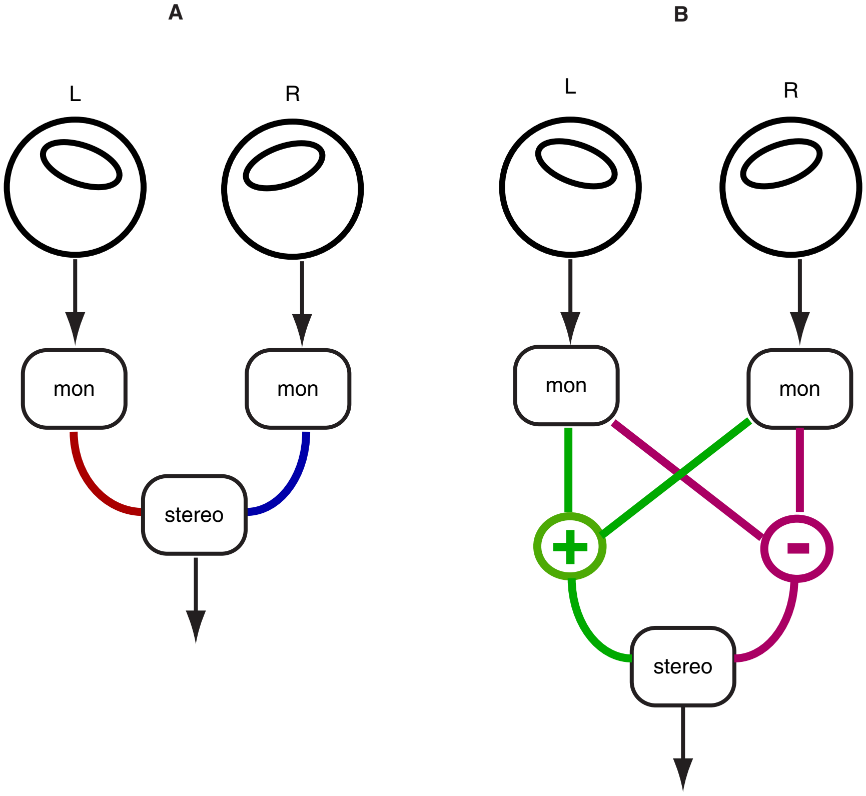

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Figure 2. Two views on the initial stages of stereopsis.

(A) Left (L) and right (R) eye monocular (mon) neurons sensitive to objects at particular disparities feed their responses into disparity-sensitive neurons that signal depth. (B) Responses from monocular neurons are added and subtracted in the process of being mapped onto disparity-sensitive neurons.

stereopsis, namely that the gains, or response strengths, of the hypothesized binocular-summing and binocular-differencing channels — call these *B*+ and *B*– channels — are independently adjustable. One of the most effective ways of adjusting the gain of a visual channel is by adaptation, achieved by prolonged viewing of a stimulus pattern to which the channel is sensitive. Adaptation has the effect of reducing sensitivity, that is, reducing gain, causing predictable changes in the appearance of subsequently presented stimuli. May *et al.* [5] designed an elegant method for selectively adapting the hypothesized *B*+ and *B*– channels in order to see if the adaptation caused the changes in stimulus appearance that would be predicted.

Two of the adaptation conditions in their experiment suffice to get the general idea. To selectively adapt the hypothesized *B*– channel, test observers were repeatedly presented with pairs of images of natural scenes in which one eye received the photographic negative of the other. Call the two images I and $-I$. Because the *B*– channel takes the difference between the two eyes' images, its response to the image pair would be $I - (-I) = 2I$, a strong response, whereas the response of the *B*+ channel to the same image pair would be $I + (-I) = 0$, no response. On the other hand, to stimulate the *B*+ channel, identical images of natural scenes were presented to the two eyes. Now we have $I + (+I) = 2I$ for the *B*+ channel and $I - (+I) = 0$ for the *B*– channel. The test stimuli that were viewed after adaptation were flickering patterns that were offset spatially as well as in the phase of their flicker in the two eyes' views [6]. The test stimuli had the important property that the sum of the two patterns moved in one direction and the difference between the two patterns moved in the other direction. May *et al.* [5] found that if their subjects adapted to the opposite-image pair (which would be expected to de-sensitize the *B*– channel), the test pattern appeared to move in the 'summing' direction, whereas if they adapted to the same-image pair (which would be expected to de-sensitize the *B*+ channel), the pattern appeared to move in the 'differencing' direction. The conclusion: there must be separately adaptable channels for summing and differencing the images in the two eyes.

May *et al.*'s [5] result is remarkable in itself, because the adaptation patterns were purely *static*, yet they had a profound effect on the perceived direction of a *moving* stimulus. But what new light does the existence of these two channels shed on how we see the world stereoscopically? Li and Atick [2] suggest that the key to

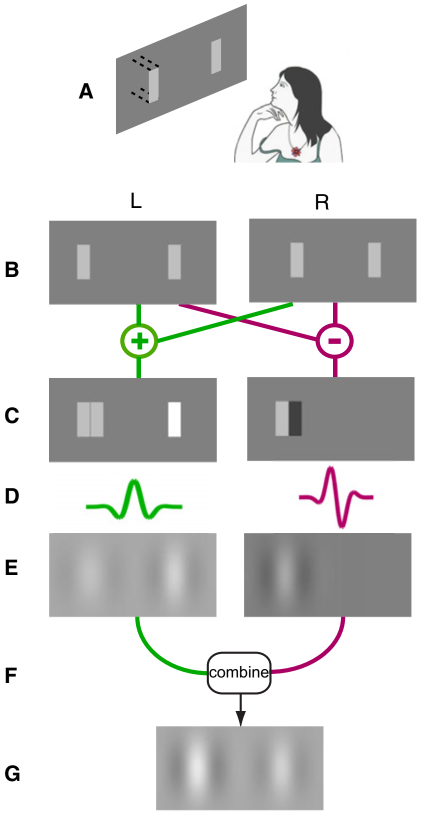

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Figure 3. Detecting disparity using *B*+ and *B*– channels.

(A) Observer viewing a pattern with two bars, one of which is out in front. (B) Left (L) and right (R) views — note the disparity of the left bar. (C) Sum and difference of two views. (D) *B*+ neurons with even-symmetric and *B*– neurons with odd-symmetric receptive-fields process, respectively, the sum and difference images, and (E) their responses. Note that the disparate bar produces similar responses in the two neurons. (F,G) Responses are combined. The disparate bar produces the bigger response.

understanding their role in stereopsis is that the *B*+ and *B*– channels have different receptive field shapes. The receptive field of a visual neuron describes the pattern of its response to light, and receptive fields of visual neurons typically have alternating excitatory (response increased by light) and inhibitory (response decreased by light) sub-regions, with a particular phase of alternation.

Figure 3 illustrates how in principle two neurons whose receptive fields have ‘even-symmetric’and ‘odd-symmetric’ phases are able to capture the disparity of a simple bar positioned in depth, via their respective responses to the sum and difference signals from the two stereo-halves. The *B*+ and *B*– neurons are shown to respond to the already-summed and already-differenced images, but in practice both neurons would respond to each stereo-half and their responses would be summed and differenced, but the result is the same and is shown the other way round for convenience. What the figure demonstrates is that the responses of an even-symmetric neuron to the sum, and an odd-symmetric neuron to the difference of the two stereo-halves, are stronger to the disparate bar compared to the bar with zero disparity. Hence a neuron that combines the *B*+ and *B*– responses is selective to disparity.

Why this arrangement? Li and Atick [2] argue that there is a two-fold advantage to basing stereopsis on a mechanism that sums and differences the two eyes’ signals. Because the left and right images of the stereo-pair in Figure 1 are very similar, in other words highly correlated, there is a lot of redundancy in the responses of the visual neurons that encode them. One way to reduce the redundancy is to convert the responses into sums and differences, as these are uncorrelated. A similar process occurs with colour vision. There are three receptors termed ‘cones’ in the eye that are active in daylight vision. They are differentially sensitive to short (*S*), medium (*M*) and long (*L*) wavelengths of light. Nevertheless, their responses to natural scenes are very similar, that is, they are highly correlated. By taking the sum of the cone signals to produce a luminance-sensitive channel, and the differences between cone signals to produce colour-sensitive channels, the visual system ‘decorrelates’ the cone signals. The result is improved efficiency of information transmission along the visual pathway and the means to distinguish luminance (or brightness) from colour [7].

The other advantage of having *B*+ and *B*– channels is precisely what May *et al.* [5] have revealed in their study: the ability of the visual system to independently adjust the gains, or response strengths, of the two channels. This enables vision to compensate for the relatively weak *B*– signal found in images of natural scenes — compare the bottom right and bottom left images in Figure 1 — resulting also in improved coding efficiency.

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McGill Vision Research, Department of Ophthalmology, 687 Pine Av. W. Rm. H4-14, Montreal, Quebec, H3A 1A1, Canada.
E-mail: fred.kingdom@mcgill.ca

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Brain Organization: Wiring Economy Works for the Large and Small

The highest-resolution test to date of the wire minimization hypothesis has found that this principle works well for brain regions with a volume just over 400 μm^3. What is the wire minimization hypothesis, and why should anyone care about it?

Charles F. Stevens

Axons and dendrites count as ‘wire’ and everything else in the brain is ‘non-wire’. The idea is that axons and dendrites carry information over long distances and so are analogous to wire in, for example, a telephone system. Extracellular space, synapses, and glia carry information at most over short distances so they are not-wire. The wire-minimization hypothesis holds that neural components should be arranged in a way to make the volume of wire in the brain as small as possible. Wire volume should be minimized so that as much room as possible is left over for the computational elements that carry out the brain’s main job. This idea, like so many others, can be traced to Cajal, but in modern times it was first used by Mitchison [1] and by Cherniak [2] about twenty years ago. According to Rivera-Alba *et al*. [3] in work published recently in *Current Biology*, the hypothesis has passed the highest-resolution test it has been put to so far.

Wire minimization has been found to explain many structural features of brain organization, such as why the cortex is divided up into distinct functional areas, why there are ocular dominance columns, why brain areas in the mammalian cortex and ganglia in the worm are arranged as they are (see references in Rivera-Alba *et al*. [3]). This principle is important, then, because it provides a simple explanation for many aspects of brain structure. Perhaps more importantly, though, when wire minimization is violated it means that some feature of brain structure is unexpected and demands a special explanation.

Although the literature contains many papers on wire minimization (64×10^3 hits in Google Scholar), almost all deal with large-scale features