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- Friday, July 10, 1998
Cone Combinations

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Kathy Mullen

5.0 Kathy Mullen gave a talk on cones and colour vision (approved by Kathy)

5.1 Old world primates are the only mammals to have three cone types. These three cones types are distinguished by having slightly different photopigments with slightly different spectral absorptions and are known by the relative wavelengths that they absorb best: long (corresponding to the red part of the spectrum), medium (green) and short (blue). The exquisite colour vision that this imparts is very helpful to survival by enhancing the ability to detect, identify and discriminate important objects like food. Mullen convincingly demonstrated this by comparing some black and white and colour photographs.

5.2 Parvocellular lateral geniculate cells the ones relevant to colour vision, the X cells of old) have antagonistic regions which arise from these cone types arranged such they come in six flavours:

the so called red/green system

- (i) long wave length cones exciting, medium inhibiting
- (ii) long wave length cones inhibiting, medium exciting

the blue/yellow system

- (iii) long and medium inhibiting, short exciting
- (iv) long and medium exciting, short inhibiting

the achromatic system

- (v) all excitatory
- (vi) all inhibitory

5.3.1 Mullen, in collaboration with Marcel Sankeralli, has developed an innovative method for analyzing the performance of these systems called "chromatic noise analysis".

5.3.2 Central to this method is the use of a particular way of thinking of colours. Mullen uses a three dimensional representation in which each of the three axes represents the contrast of the stimulus as responded to by each of the three cone types. Contrast here is defined as the change in cone response produced by the stimulus divided by the cone response to the adapting background. For example, the contrast in this space of an edge between two areas with spectral content and intensities chosen so that both sides stimulated the short wavelength cones equally and both sides stimulated the medium cones equally, would have a contrast exactly along the long cones axis.

5.3.3 In practice stimuli are generated on a computer screen where only the intensities of the three guns in the cathode ray tube are varied. The spectral content of each gun and phosphor is thoroughly documented and so the position of a given stimulus can be calculated in this space from the known absorption properties of the three photopigments.

5.4.1 Now a masking experiment is done in which a stimulus, carefully defined in this cone-contrast space, is detected in the presence of noise. The logic is that when the noise maximally stimulates an underlying neural mechanism, it will maximally mask a nearby stimulus. Therefore, by finding the location in cone-contrast space of noise that is most effective, the properties of the neural mechanisms can be revealed.

5.4.2 The stimuli are gratings which vary sinusoidally in cone contrast across the screen. In cone-contrast space these stimuli move towards and away from the origin. The stimuli are detected first on their own to determine their threshold contrast and then in the presence of noise. The noise is a variation in contrast along a different vector in cone contrast space. The noise is also distinguished from the stimulus in its spatial distribution. Instead of a single sinewave across the screen, there are multiple sinewaves of different spatial frequencies (different number of cycles across the screen) all mixed together. The position of the noise is varied systematically in cone-contrast space.

5.5.1 In each of the examples given the stimulus was detected by one underlying neural mechanism. When the noise was well matched to this mechanism it produced maximal masking of the stimulus. When the noise had no match to the mechanism (ie was orthogonal to it in the cone contrast space) no masking was found. The positions of maximal and minimal (or null) masking were used to determine (via a cosine curve fit) the location (in the cone-contrast space) of the underlying neural mechanism that is detecting the test stimulus.

5.5.2 These experiments were repeated to sample the whole of cone contrast space. Only three mechanisms were found and the cone weights to each were defined. These were:

1. a red-green mechanism which differences L and M cones with equal weights.
2. a blue-yellow mechanism which differences S with L and M cones, with an approximately equal proportion of L and M cones in the 'yellow arm' of the mechanism.
3. A luminance mechanism which sums the L and M cone outputs. The L to M ratio is variable between subjects, but the S cones seem to be excluded from the mechanism.

5.5.3 These experiments provide psychophysical support for perceptual mechanisms which appear somewhat similar to the physiologically characterized colour opponent mechanisms characterized by Hering in the nineteenth century. However these mechanisms are not the same and are working over much larger spatial areas.

5.6.1 Another set of experiments investigated how many of these higher-order, psychophysically defined mechanisms there are. There are two distinct red/green type LGN cell types, for example, (see 5.2) but this does not mean that there must be two higher order mechanisms. The two cone types could be combined to form a single higher-order mechanism.

5.6.2 Experiments took place along the line in cone contrast space in which $M = \text{minus } L$. A stimulus was chosen with M positive and L negative and the effectiveness of masks all along the line were assessed (separating the stimulus and mask in time to avoid physical interference between the stimulus and mask).

5.6.3 If there was only one mechanism then masking should have been symmetrical with +M and -L being as effective as -M and +L. But this was not the case: a +L-M stimulus was only effectively masked by +L-M masks and -L+M masks were ineffective.

5.6.4 This, when taken together with similar experiments along other lines, suggests that there are six higher-order psychophysically-defined mechanisms. This implies a rectification of the two cone opponent mechanisms (red-green, blue-yellow) and the cone additive luminance mechanism (black-white) into six mechanisms overall (red, green, blue, yellow, black & white).

Kathy Mullen