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Visual attention modifies spectral sensitivity of nystagmic eye movements

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Abstract

If we look out of the window of a travelling train our eyes move rapidly back and forth (saccadic movement). With no attention to individual objects, gaze velocity is low but nystagmic frequency is high (stare nystagmus). If we are interested in individual objects, the angular velocity of gaze is high and the nystagmic frequency low (look nystagmus) (Ter Braak, J.W.G. (1936). Untersuchungen ueber optokinetischen Nystagmus. Archives Néerlandaises de Physiologie de L'homme et des Animaux, 21, 309–376) We show that the spectral sensitivities of the two types of nystagmus differ and that the short-wavelength-sensitive cones significantly contribute only to look nystagmus. © 1999 Elsevier Science Ltd. All rights reserved.

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Parallel processing is a fundamental feature of our visual system. Incoming information is distributed among various channels at an early stage, in the retina. The pathways running from here to the visual cortex are anatomically and functionally distinguishable, the best known being the magnocellular and parvocellular tracts (Livingstone & Hubel, 1988; Kaplan, Lee & Shapley, 1990). There are also two anatomically distinct, parallel pathways for the control of eye movements: 'stare' nystagmus is mainly, but not exclusively, mediated by subcortical nuclei in the so-called accessory optical system (Fuchs & Mustari, 1993), whereas a cortical pathway contributes to 'look' nystagmus (Ilg & Hoffmann, 1993). We have studied the spectral sensitivity in humans of both kinds of nystagmus, in order to learn whether the signals entering the two parallel pathways derive from the same population of photoreceptors or different populations.

1. Methods

1.1. Subjects

All experiments were carried out with four subjects, three measurements/subject. The subjects' colour vision was normal as determined by the Farnsworth-Munsell 100-Hue Test.

1.2. Stimulus

The left eye viewed a tangential back-projection screen (distance from the eye 25 cm) showing a homogeneously illuminated area (60×60 cm^2, in the horizontal 100°) upon which was superimposed a circular field (diameter 75 cm, angular subtense 113°) with a horizontally moving vertical square-wave grating (pattern wavelength 5 cm, gives 11.4° in the centre and 10.1° at 20° distance to the centre; velocity 20°/s, corresponding to a temporal frequency of 1.7 Hz). A stationary horizontal black bar ran across the screen (2.2 cm in height, corresponding to 5° in the centre). This bar reduces a contribution of the fovea to the response and suppresses vertical eye movements. The grating was moved to the left for 16 s, stopped for 4 s and then moved for 16 s rightwards. The intensity and wavelength of the light bars of the grating were changed (monochromatic light of half bandwidth 10–20 nm).

1.3. Adaptation

During the 1 min preadaptation, applied before a stimulus was presented, the moving grating was illumi

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nated with 270 cd/m^2 xenon white light (mean intensity 315 cd/m^2; for chromatic adaptation: 233 cd/m^2 OG495-light, mean 280 cd/m^2), ensuring photopic adaptation. The homogeneous area was illuminated with white light (180 cd/m^2), or for chromatic adaptation, with wavelength-restricted light (filter OG495 from Schott, Mainz, Germany) (162 cd/m^2).

1.4. Gaze measurement

A camera was directed to the right eye via a mirror. IR-LEDs close to the camera illuminated the eye. The direction of the gaze was determined by the relative position of the corneal reflex in the pupil by a computer 25 times/s. A sigmoid curve was fitted to the calculated gain at different light intensities. The reciprocal of the intensity at half maximum gain is given as sensitivity in Fig. 2.

1.5. Two instructions

The subjects had to follow one of two instructions.

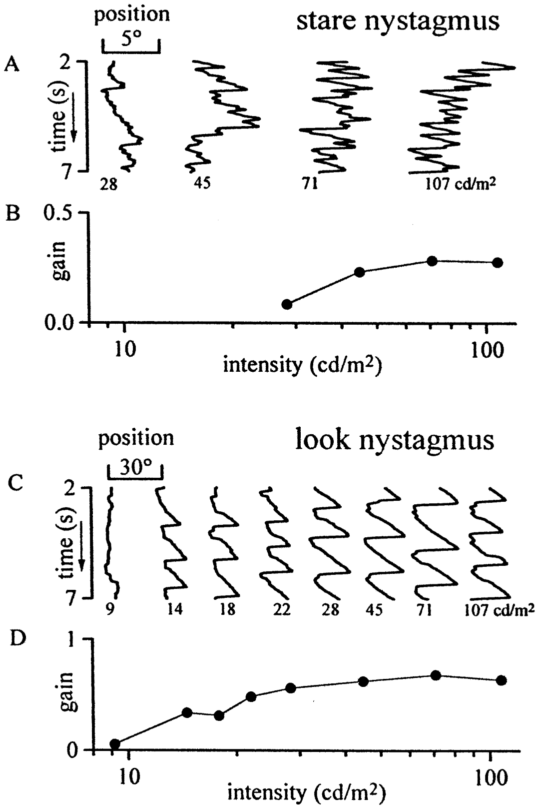

Fig. 1. Samples of stare (A) and look nystagmus (C) measured in our setup. In both cases the gain (B, D) of the eye movements increases with the intensity of the bright stripes in the moving pattern. The gain is a measure of the mean following velocity of the eye as a fraction of the stimulus velocity. The numbers under the position traces indicate the difference in brightness between the dark and light stripes in the pattern. The brightness of the dark stripes was always 180 cpd/m^2.

The stare instruction was intended to produce subcortical stare nystagmus: 'stare straight ahead. Hold your eyes on the horizontal black bar. Don't try to follow the moving grating, but don't prevent your eyes from doing so'.

The look instruction: 'hold your eyes on the horizontal black bar and follow the grating's motion. When you reach the mark switch to the next bar on the other side'. (Two marks—13.5° left and right of the centre—were provided during the looking condition, to reduce the amplitude of the movement).

The instructions led to the respective kind of nystagmus (Fig. 1).

2. Results and discussion

The spectral sensitivity curves of stare and look nystagmus are shown in Fig. 2. The stare instruction results in a curve with a clear single maximum near the wavelength 540 nm. The look instruction results in a broader spectral sensitivity curve with a maximum near 555 nm and with a secondary maximum in the short-wavelength range (near 440 nm). Instead of preadaptation with white light, chromatic adaptation to wavelengths longer than 495 nm was used to strengthen the contribution of short-wavelength receptors. Significant changes in spectral sensitivity were found only under the look instruction: following chromatic adaptation, the sensitivity in the short-wavelength range rises and becomes even higher than the former maximum.

The change in curve shape brought about by chromatic adaptation demonstrates a contribution of short-wavelength cones to look nystagmus. Such a change was not evoked under the stare instruction. If there is any short-wavelength cone contribution to stare nystagmus at all, it is too small to be shown by our technique.

The spectral sensitivity of stare nystagmus seems to be well described by the relative luminous efficiency function $V(\lambda)$ (Wyszecki & Stiles, 1967) (a weighted sum of the spectral sensitivities of long- and middle-wavelengths cones). Closer inspection shows, however, that the stare spectral sensitivity is significantly higher in the short-wavelength range. There are two explanations for this obvious difference: We consider this heightened sensitivity in the short-wavelength range as a sign for shift to the look mode for brief, unnoticed periods. If the short-wavelength cones would make a small contribution to the response, this contribution should be more obvious under chromatic adaptation.

The spectral sensitivity of look nystagmus, in its breadth and double peaks, resembles the spectral sensitivity curves produced by increment threshold proce-

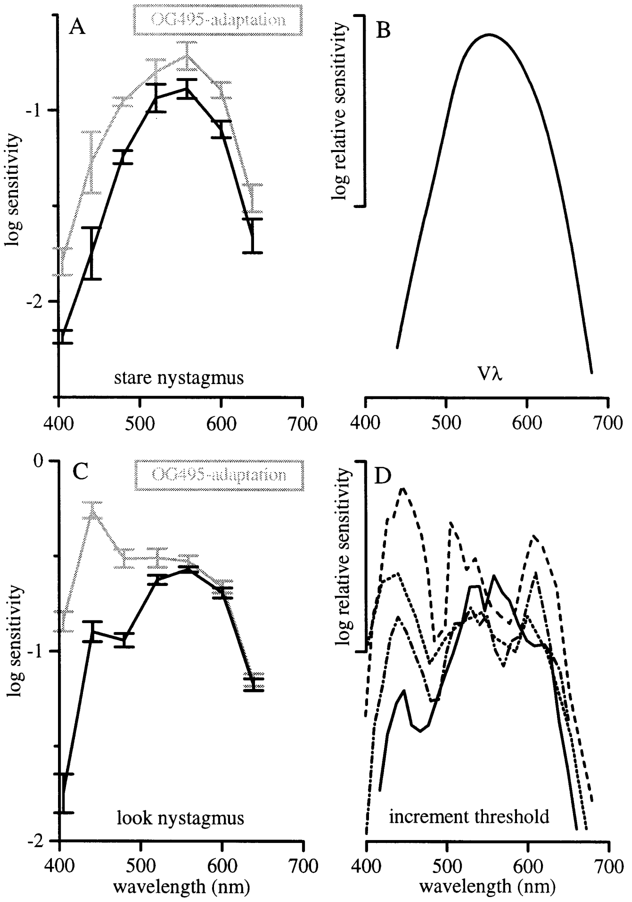

Fig. 2. Spectral sensitivity of stare (A, black line) and look nystagmus (C, black line). Chromatic adaptation produces no change in shape of the stare curve (A, grey line) but changes the shape of the look curve (C, grey line) considerably. This result indicates that the short-wavelength cones feed into the two systems differently. The stare curve—while somewhat broader—is similar to the $V(\lambda)$ curve (B, Wyszecki & Stiles, 1967). The look curve, in contrast, resembles the spectral sensitivity curves determined with an increment threshold procedure (D: dashed (Krastel, Jaeger & Braun, 1984), dotted (King-Smith & Carden, 1976), dash-dotted (Zrenner, 1983), continuos line (Stiles & Crawford, 1933)). The relatively great width of the curve and its multiplicity of peaks are understood as a reflection of colour opponent signals. The length of the box 'OG495-Adaptation' gives the spectral range of the light used for chromatic adaptation. The error bars denote the S.E.M. The sensitivity in A and C is given in $1/(\mathrm{cm}^2 * \mathrm{SR} * 10^{12}$ quanta/s). The bar in B and D gives 1 log unit.

dures (Stiles & Crawford, 1933; King-Smith & Carden, 1976; Zrenner, 1983; Krastel, Jaeger & Braun, 1984). The exact curve form of this type of spectral sensitivity curve depends on the experimental conditions, but is always broader than the $V(\lambda)$ curve and has more than one peak. The eldest of these curves is the most similar one, having only two peaks. The multiple peaks reflect the input by the three cones and are assumed to be indicators of the colour opponent signals in the responsible neuronal pathway.

Retinal ganglion cells differ in their cone input and in their projections to the central nervous system. Attention determines which parts of the brain are used to accomplish a given task. We have demonstrated here that attention by that determines which cone types are used.

Our findings are supported by the finding that patterns, whose spectral composition has been selected in such a way that only one of the chromatic mechanisms can contribute to a reaction, hardly elicit stare nystagmus, but to a higher degree look nystagmus (Crognale & Schor, 1996). Mainly middle- and long-wavelength cones contribute to the stare nystagmus, but hardly short-wavelength cones. All three cones contribute to look nystagmus.

In all the animal species so far examined (several species of butterflies and one species each of fly, bee, goldfish, and turtle) short-wavelength photoreceptors have been found not to be involved in the optomotor response, i.e. in stare nystagmus; indeed, usually only one type of receptor contributes to this response (Kaiser, 1968; Kaiser & Liske, 1974; Horridge, Marcolja & Jahnke, 1984; Schaerer & Neumeyer, 1996). Here we have shown that also in humans short wavelength-sensitive cones do not contribute to stare nystagmus and insofar also follow this rule. There are good reasons to think that movement detectors ought to be colour blind, in order to provide a reliable movement signal (Srinivasan, 1985). A priori, however, there is no apparent advantage in using only photoreceptors sensitive in the long-wavelength spectral region for movement detection. The rule that only long-wavelength photoreceptors contribute to the stare optomotor response applies from the arthropods to the primates, spanning very diverse phyla. It is therefore less likely that the rule is a consequence of homologous evolution than (assuming it is not merely a matter of chance) that convergent evolution in response to similar environment has been operating here. The possibility has been raised that this development is an adaptation to 'life in the green', useful for animals ordinarily surrounded by leaves and grass; in such a habitat, long-wavelength light dominates, so that receptors sensitive to long-wavelengths could be advantageous (Srinivasan, 1985).

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