Directional preponderance in human optokinetic nystagmus

M. Ohmi, I.P. Howard, and B. Eveleigh*

Department of Psychology, York University, Toronto, Ontario M3J 1P3, Canada

Summary. In afoveate animals, and in neonatal or cortically deficient foveate animals, monocular optokinetic nystagmus (OKN) is controlled by directly innervated subcortical nuclei and occurs only in response to temporonasal motion. In higher mammals, the subcortical nuclei receive direct inputs predominantly from the nasal hemiretinae and indirect inputs from the visual cortex. These indirect inputs counterbalance the directional asymmetry of the primitive mechanism. These facts lead to the prediction that the velocity of the slow phase of OKN in the normal human adult should be higher for stimuli moving centripetally rather than centrifugally in each monocular and binocular hemifield. The predicted patterns of directional preponderance were found in both monocular and binocular hemifields. Directional asymmetries were still present in monocular hemifields when the central retina was occluded and were reduced when the stimulus was confined to a narrow central strip of the visual field. These results are discussed in terms of the contributions of the central and peripheral retina to directional preponderance.

Key words: Optokinetic nystagmus – Directional preponderance – Visual pursuit

Introduction

In afoveate mammals, such as the guinea pig and rabbit, optokinetic nystagmus (OKN) induced when only one eye is open (monocular OKN) occurs only in response to a stimulus moving in the temporonal direction. When the two eyes are open, the response in both is controlled by whichever eye is stimulated by temporonasal movement. This is known as directional preponderance of OKN. It allows compensatory pursuit eye movements to occur in response to image motions accompanying rotation of the head, because one or other eye receives a temporonasal stimulus. However, as an animal with laterally placed eyes moves forward in a visual environment consisting of stationary objects at various distances, a rotation of the eyes cannot compensate for the parallactic motion of the whole scene. The absence of a nystagmic response to nasotemporal motion ensures that under these circumstances ineffective eye movements do not occur and that the images of objects directly ahead of the animal are not destabilized (see Howard 1982 for a general review of OKN).

In the rabbit the nucleus of the optic tract (NOT) in the pretectum and the dorsal terminal nucleus (DTN) of the accessory optic tract on each side of the brain receive direct inputs wholly or predominantly from the contralateral eye (Scalia 1972; Klooster et al. 1983; Collewijn and Holstege 1984) and contains movement-sensitive cells all of which respond to movements of the distal stimulus only in the temporonal direction (Collewijn 1975). Outputs from these nuclei relay through the nucleus reticularis tegmenti pontis and vestibular nucleus before impinging on the oculomotor nuclei (Cazin et al. 1980). This is believed to be the mechanism of directional preponderance.

Higher mammals, such as primates possess foveae, and have frontal vision with vergence control and stereopsis. When such animals move forward they are able to attend to objects in a particular depth plane and pursue them visually so as to stabilize their retinal images while ignoring image motions produced by objects in other directions or at other
distances (Howard and Gonzalez 1985). Since these animals can cope with conflicting motion signals they no longer need directional preponderance.

Several lines of evidence suggest that the visual cortex of higher mammals is responsible for converting asymmetrical monocular OKN into a symmetrical response (Tauber and Atkin 1968). For instance, monkeys and humans show directional preponderance of OKN during the first few months of life, probably because the visual cortex takes time to develop its control over the subcortical centers (Atkinson 1979; Naegle and Held 1982). This asymmetry persists into adult life in cats reared with one eye sutured for some weeks after birth (Van Hof-Van Duin 1978) and in adult humans who have had abnormal binocular visual inputs in early life (Schor and Levi 1980; Westall and Schor 1985). It seems that normal binocularly-driven cells in the visual cortex are required for OKN symmetry. Hoffmann (1979) recorded from cells in the NOT of the adult cat and found that 60% of them responded only to temporonasal movement in the contralateral eye while 40% responded to stimulus movement in a given direction in either eye. Monocular deprivation in kittens was found to abolish the response of the binocularly-driven cells of the NOT leaving only the response of the monocularly driven cells. The binocularly driven cells of the NOT are thus thought to receive only an indirect visual input through cortical binocular cells and the monocularly driven cells only a direct input from W cells of the contralateral eye (Hoffmann and Stone 1985; Montarolo et al. 1981). Until recently evidence regarding inputs to the NOT of primates was equivocal (Giolli and Tigges 1970; Benevento et al. 1977; Hendrickson et al. 1970). However, Hoffmann and Distler (1986) have now recorded from cells in the NOT and DTN of the monkey which respond to moving stimuli in the contralateral eye. In the monkey, these cells have much weaker direct visual inputs and respond to much small stimuli than corresponding cells in the cat.

Abolition of the direct input to the subcortical nuclei in the cat by sectioning of the optic chiasma leads to a nasotemporal preponderance (Harris et al. 1980; Precht et al. 1980). This suggests that OKN driven from the temporal hemiretina through the indirect cortical route has a nasotemporal preponderance which, in the intact animal, balances the temporonasal preponderance of the directly-driven subcortical response. Patients with damage to the occipital cortex have been found to show a strong temporonasal preponderance of monocular OKN presumably because of the release of the subcortical mechanism from cortical control (Mehdorn 1982).

The following set of predictions can be derived for primates if we assume that the neural connections are similar to those in cats. In animals with hemidecussation of the visual inputs, stimuli confined to the nasal retina of one eye should elicit OKN with a temporonasal preponderance because the pretectum gets most of its direct inputs from the nasal retinae. On the other hand, stimuli confined to the temporal retina of one eye should elicit OKN with a nasotemporal preponderance because inputs from this half of each eye reach the pretectum only by the indirect cortical route.

A stimulus moving in a temporonal direction and stimulating only the nasal retina of one eye has a centripetal motion in the sense that it moves towards the fixation point. A stimulus moving nasotemporally and confined to a temporal hemiretina also has a centrifugal motion. Thus, there should be a centripetal preponderance in each monocular hemifield. It follows that there should be a centripetal preponderance in each binocular hemifield.

Van Die and Collewijn (1982), Howard and Ohmi (1984a) and more recently Westall and Schor (1985) have reported the expected centripetal preponderance in each monocular hemifield. In Experiment I we sought to confirm centripetal monocular preponderance and investigate the question of preponderance in binocular hemifields.

Van Die and Collewijn found no evidence of centripetal preponderance when the occluded region extended a few degrees over the vertical midline of the retina and concluded that directional preponderance is not a feature of OKN induced solely by the peripheral retina. This is not what they expected, nor is it what one would expect from the evidence reviewed above. A slight centrifugal preponderance which they found when the stimulus was confined to a vertical strip far to one side of the fovea was probably due to the reflex tendency of the eyes to move towards an eccentrically placed object (Dubois and Collewijn 1979). We suggest that Van Die and Collewijn did not find centripetal preponderance when the fovea was occluded because this occlusion, combined with the presence of the vertical edge of the occluder, severely reduced the gain of the response. This reduction in gain is very evident in their records. We have found a way to occlude the central retina without reducing the gain of OKN and in Experiment II we use this procedure to reinvestigate the roles of the central and peripheral retina in directional preponderance.

**Experiment I**

This experiment was designed to confirm centripetal preponderance of OKN in monocular hemiretinae.