

REVIEW

GETTING AHEAD OF ONESELF: ANTICIPATION AND THE VESTIBULO-OCULAR REFLEX

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Abstract—Compensatory counter-rotations of the eyes provoked by head turns are commonly attributed to the vestibulo-ocular reflex (VOR). A recent study in guinea pigs demonstrates, however, that this assumption is not always valid. During voluntary head turns, guinea pigs make highly accurate compensatory eye movements that occur with zero or even negative latencies with respect to the onset of the provoking head movements. Furthermore, the anticipatory eye movements occur in animals with bilateral peripheral vestibular lesions, thus confirming that they have an extra vestibular origin. This discovery suggests the possibility that anticipatory responses might also occur in other species including humans and non-human primates, but have been overlooked and mistakenly identified as being produced by the VOR. This review will compare primate and guinea pig vestibular physiology in light of these new findings. A unified model of vestibular and cerebellar pathways will be presented that is consistent with current data in primates and guinea pigs. The model is capable of accurately simulating compensatory eye movements to active head turns (anticipatory responses) and to passive head perturbations (VOR induced eye movements) in guinea pigs and in human subjects who use coordinated eye and head movements to shift gaze direction in space. Anticipatory responses provide new evidence and opportunities to study the role of extra vestibular signals in motor control and sensory–motor transformations. Exercises that employ voluntary head turns are frequently used to improve visual stability in patients with vestibular hypofunction. Thus, a deeper understanding of the origin and physiology of anticipatory responses could suggest new translational approaches to rehabilitative training of patients with bilateral vestibular loss. © 2013 Published by Elsevier Ltd. on behalf of IBRO.

Key words: vestibulo-ocular reflex, VOR, efference copy, motor control, sensory–motor transformations, cerebellum.

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Abbreviations: ES, eye movement sensitivity; EH, eye–head; FTN, flocculus target neurons; P-cells, Purkinje cells; PVP, position-vestibular-pause; TVOR, translational vestibulo-ocular reflex; VO, vestibular only; VOR, vestibulo-ocular reflex; HIS, head in space; EIS, eye in space; EIH, eye in head; EMG, electromyograph.

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INTRODUCTION

Walls (1962) wrote, “the ancient and original function of the eye muscles was not really to move the eye but rather to hold it still with respect to the environment”. He added “if the original control of the eye muscles was from the labyrinths, then one may say that the resulting movements of the globes must have been the very *raison d’être* of the muscles themselves ... to impart appropriate movements of the eyes as dictated by head movements”. Ironically, according to his viewpoint, the goal of eye movements is to hold the globes, and hence the retinas, stationary in space during head movements.

The purpose of maintaining retinal stability in man, as achieved by the vestibulo-ocular reflex (VOR), is the prevention of a motion-provoked visual blur, which is commonly experienced by patients with vestibular hypofunction (Leigh and Zee, 2006). A physician, John Crawford, experienced an acute ototoxic lesion of his vestibular system and, with his head stabilized in bed, described how “. . . the pulse beat in my head became a perceptible motion, disturbing my equilibrium” (Crawford, 1952). This interpretation is clearly valid for primates that have high visual acuity created by a dense concentration of photoreceptors in the fovea (Mollon, 1982). However, many other species such as guinea pigs have fewer photoreceptors spread across their retinas and poorer visual acuity than primates (Buttery et al., 1991). For these species, Land (1999) argued that visual blur caused by motion would be less of a problem because the lower density of photoreceptors would restrict blur to higher speeds of head movement. Instead of preserving acuity, Land suggested that retinal stability is essential to an afoveate animal’s ability to detect motion. Indeed, if image stability were perfect,

then the visual scene would dissolve and only that which moves would be seen: “It simplifies the world enormously if the ‘AC-coupled’ nature of the early visual process can be used to restrict what can be detected to just those things that are of vital importance: those that move” (Land, 1999). An important corollary to this idea is that an animal must stabilize its eyes in space during voluntary head movements in order to distinguish image motion that is not produced by self-motion (Walls, 1962).

This review compares the VOR in man and non-human primates to that of an afoveate mammal, the guinea pig. Although the functional aspects and physiology may appear to be quite different in these two species, this review will argue that the underlying anatomy and neural signal processing is fundamentally similar and that understanding how the guinea pig stabilizes its eyes in space has significant value for understanding human vestibular physiology and for treatment of patients with profound vestibular loss such as that experienced by John Crawford.

VESTIBULO-OCULAR REFLEX (VOR)

The VOR has been studied intensively in multiple species. The basic pathway underlying the reflex is remarkably simple: a 3-neuron arc that links receptors and primary neurons located in the inner ear to the extraocular muscles of the eye (Lorente de No, 1933). Numerous studies over the past 50 years have characterized the connectivity and discharge properties of the peripheral neurons in the inner ear (Goldberg and Fernandez, 1971a,b,c); secondary vestibular neurons in the vestibular nuclei (Precht and Shimazu, 1965; Precht and Baker, 1972; Fuchs and Kimm, 1975; Buttner and Waespe, 1981; Tomlinson and Robinson, 1984; McCrea et al., 1987; Scudder and Fuchs, 1992; Stahl and Simpson, 1995; Ris et al., 1995; Phillips et al., 1996; Serafin et al., 1999; Gdowski and McCrea, 1999; Roy and Cullen, 2001, 2004; Cullen and Roy, 2004; Beraneck and Cullen, 2007), and plasticity and motor learning within the VOR pathways (Gonshor and Jones, 1976; Miles and Lisberger, 1981; Lisberger et al., 1994; Lisberger, 1994; Sadeghi et al., 2010, 2011). Measurement of eye movements produced by the VOR is an essential component of contemporary clinical tests of vestibular function, largely based on methods established by Barany for which he received the Nobel Prize in 1914 (for an example of Barany’s teachings translated into English, see Ibershoff and Copeland, 1910; for a review of clinical applications, see Baloh and Halmagyi, 1996; Leigh and Zee, 2006). Eye and head movement exercises that provoke the VOR are basic techniques that can improve retinal stability in patients with vestibular hypofunction (Herdman et al., 2007; Schubert et al., 2008; Scherer et al., 2008; Boyer et al., 2008).

More recently, neurophysiological studies of the VOR have focused on the possible roles played by efference copy or proprioceptive signals in producing or modulating ocular responses to head movements. Efference copy, as originally described by von Holst and

Mittelstaedt (1950) and the concept that the brain uses internal models of sensory organs are essential features of many motor control hypotheses (Merfeld et al., 1999; Angelaki et al., 2004; Shadmehr et al., 2010; Laurens and Angelaki, 2011). Sadeghi et al. (2011) have described the influence of proprioceptive inputs from neck receptors onto secondary vestibular neurons in the VOR pathway in animals recovering from acute unilateral vestibular loss. Cullen and her colleagues have also described vestibular neurons whose discharge patterns may reflect cancellation of reafferent signals resulting from active head movements by internal signals based on efference copy or proprioception (Cullen et al., 1991; Roy and Cullen, 2001, 2002, 2004; Cullen and Roy, 2004; Cullen et al., 2011). Roy and Cullen described the modulation of secondary vestibular neuron activity that apparently was related to efference copy in a task that excluded neck proprioception (Roy and Cullen, 2001, 2002). In guinea pigs, compensatory eye movements have been reported, which anticipate voluntary head movements and which are likely to be produced either by proprioception originating in the neck or an efference copy of voluntary head movement (Shanidze et al., 2010a; King and Shanidze, 2011).

EYE/HEAD COORDINATION IN GUINEA PIGS

Guinea pigs do not have a fovea and experience relatively poor visual acuity (at a maximum, 2.7 cycles/deg along the visual streak, Buttery et al., 1991). They make very few, if any, voluntary saccades (Escudero et al., 1993; Shanidze et al., 2010b). They do, however, exhibit a typical pattern of voluntary gaze shifts that closely resemble the predictive gaze shifts described by Bizzi et al. in non-human primates (1972). Fig. 1 illustrates a typical voluntary gaze shift made by a guinea pig (modified from Fig. 2 in King and Shanidze, 2011). Typically, the head (gray arrow, trace labeled HIS) initiates the gaze shift. Eye position in space (EIS) during the head movement is stabilized by compensatory counter-rotations of the eyes within the orbits (EIH). About 75 ms after the onset of the head movement, the animal makes a rapid eye movement in the same direction as the head movement (black arrow, anti-compensatory), which is followed by further ocular counter-rotation. It was initially assumed the compensatory eye movements were caused by the VOR, but in three animals careful measurements of latencies with respect to the head movements using cross-correlation showed that the compensatory eye movements occurred with a mean latency of -0.2 ± 0.27 ms (in the example of Fig. 1, the latency was -1.0 ms, King and Shanidze, 2011). For comparison, the mean latency of the passively evoked VOR in these animals was 6.9 ms (Shanidze et al., 2010b). The negative or zero latency of the compensatory eye movements strongly suggests that they have an extra vestibular origin. Further evidence for this hypothesis was obtained from guinea pigs with chemically induced bilateral lesions of the labyrinth that

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