Control and modulation of canal driven vestibulo-ocular reflex

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Abstract It has been well known that the canal driven vestibulo-ocular reflex (VOR) is controlled and modulated through the central nervous system by external sensory information (e.g., visual, otolithic and somatosensory inputs) and by mental conditions. Because the origin of retinal image motion exists both in the subjects (eye, head and body motions) and in the external world (object motion), the head motion should be canceled and/or the object should be followed by smooth eye movements. Human has developed a lot of central nervous mechanisms for smooth eye movements (e.g., VOR, optokinetic reflex and smooth pursuit eye movements). These mechanisms are thought to work for the purpose of better seeing. Distinct mechanism will work in appropriate self motion and/or object motion. As the results, whole mechanisms are controlled in a purpose-directed manner. This can be achieved by a self-organizing holistic system. Holistic system is very useful for understanding human oculomotor behavior.

Key words: vestibulo-ocular reflex, semicircular canal, otolith, optokinetic reflex, smooth pursuit eye movements, human oculomotor behavior, holistic system.

Introduction

The vestibulo-ocular reflex (VOR) stabilizes a visual world in human. VOR is one of the important functions generated by semicircular canals. It has been well known that the canal driven VOR is controlled and modulated through the central nervous system by external sensory information (e.g., visual (Barnes & Edge 1983, Koenig et al. 1986), otolithic (Gresty et al. 1987) and somatosensory (Bles et al. 1985) inputs) and by mental conditions (Barr et al. 1976, Barnes & Eason 1988, McKinley & Peterson 1985). The purpose of this paper was to review the behavioral studies related to the control and modulation of the canal driven VOR in human.

Vision is degraded by image motion on the retina when the retinal image velocity goes over only 2 to 3 degrees per second. In order to maintain clear vision, it is required to diminish the image motion on the retina which goes not more than one degree per second. Because the origin of retinal image motion exists both in the subjects (eye, head and body motions) and in the external world (object motion), the head motion should be canceled and/or the object should be followed by smooth eye movements. The VOR, the optokinetic reflex (OKR) and the smooth pursuit (SP) system work together for the purpose of generating smooth eye movements in human. In addition, these eye movements must have an appropriate velocity to maintain clear vision.

Canal-otolith interaction

The term “VOR” is often used for the canal driven response of the eyes. However, VOR means the combination of ocular response to the angular motion of the head (AVOR; Canal driven VOR) and that to the translation motion of the head (TVOR; Otolith driven VOR). In general, TVOR has been thought to be small compared with AVOR. In fact, when we employ the head translation stimulus, minimal response is observed in darkness (Hashiba et al., 1988). However it has been demonstrated that TVOR can be modified by visual information and by mental conditions. TVOR is suppressed by gazing a target fixed on head (Hashiba et al., 1997). Moreover TVOR gain increases in imaging a target fixed on the earth and decreases in imaging a target fixed on head (Hashiba et al., 1995). When a subject is imaging a target fixed on the earth, the TVOR gain is the variable depending on the distance of the imaginary gaze point (Skipper & Barnes, 1989; Paige 1989). Otolith inputs are able to evoke powerful eye movements in a certain situation.
In the natural condition, there must be canal-otolith interaction during head motion combined with rotation and translation, showing off-centered rotation around vertical axis (eccentric rotation). Gresty et al. (1987) reported the effects of otolithic inputs on AVOR. Eye movements were evoked by angular oscillation in the dark about a vertical axis with the head displaced 30 cm eccentrically from the axis. Subjects were either given no instructions or were told to imagine fixating on targets at 60 cm or 5 m distance. Eye movements of significantly higher velocity were evoked in the eccentric position, particularly at the higher frequencies when subjects imagined near targets.

On the other hand, the otolith organ responds to gravitational force change as well as linear head movements. Thus the canal-otolith interaction can be expected (Fig.1). However, the action of TVOR seems to be useless for compensatory eye movements, because AVOR works to compensate head rotation. There has been no report for the canal-otolith interactions during head rotation around off vertical axis. We investigated the relation between TVOR elicited by periodic lateral linear acceleration and subjects’ head position (Hashiba et al., 1991; Hashiba et al., 1997). It was found that TVOR was larger in nose-down position than in nose-up position. This suggested that the theoretical canal-otolith conflict of off-vertical axis rotation during the nose-up to nose-down phases might be able to be avoided.

Other type of the canal-otolith interaction has been investigated. The post-rotational nystagmus is modulated by head tilts (Benson & Bodin 1966). The reason for this is thought to be that static otolith inputs affect the AVOR outputs via the velocity storage mechanism (VSM) (Raphan et al., 1979). The semicircular canals are effective at transferring high frequency head motion so that eye velocities match head velocity, but they are ineffective at very low head frequencies (below about 0.02 Hz) and the vestibular response dies away after constant velocity rotation for several seconds. This low frequency limitation of the semicircular canal response is compensated, in part, by VSM. VSM uses the peripheral labyrinthine signal and through the process of signal integration in the mathematical sense, increases the VOR response threefold for semicircular canal to function during low frequency head motion.

To investigate the canal-otolith interaction, we observed the effects of periodic linear acceleration on caloric nystagmus (Watanabe et al., 1987). Subjects were mounted on a sled type linear accelerator with supine position. After the caloric stimulus, subjects were oscillated in the right-left direction. The caloric nystagmus was modulated by the sled oscillation. The degree of modulation was larger than that expected from the sum of TVOR elicited by the same sled oscillation. Because of the characteristics of very low frequency, the caloric response could be nearly the outputs of VSM. Thus dynamic as well as static otolith inputs could modulate AVOR via VSM.

**Visual-Vestibular interaction**

Since the role of VOR is to stabilize the image on the retina during head movements, VOR cooperates with the visual driven smooth eye movements, OKR and SP. OKR is composed of 2 components: one is slow-rise and the other is rapid-rise component. The slow-rise OKR is thought to be the output of VSM and the rapid-rise OKR is recognized to be nearly equal to the smooth pursuit eye movements (SPEM) (Morrow & Sharpe, 1993).

There are 2 different interactions between VOR and the visual driven smooth eye movements: one is direct interaction and the other is indirect one through VSM (Fig. 2). AVOR and the slow-rise OKR are mediated by the common VSM (Cohen et al., 1977, Cohen et al., 1981). Therefore, there is a difference in the post-rotational nystagmus between in darkness and in the light. After unidirectional constant velocity rotation, a long-lasting post-rotational nystagmus is observed in darkness. However, in the light condition, optokinetic after-nystagmus (OKAN) and post-rotational nystagmus cancel each other out, and no after-nystagmus appears.

VOR is suppressed by visual information. This has been investigated in both VOR induced by rotatory stimuli (Barnes & Edge, 1983) and caloric response (Takemori & Cohen, 1974). The SP system has several properties in
common with visual modulation of VOR. However, SP does not account entirely for VOR modulation.

Voluntary control of VOR

Barr et al. (1976) reported that VOR can be modified by mental effort in darkness, where there is no visual stimulus to drive SP. We investigated voluntary suppression of caloric nystagmus in normal subjects under the following 3 conditions; 1) with visible, earth-fixed target in the dark (“visual”), 2) with imaginary target in the dark (“imaginary”) and 3) after-image on the fovea in the dark (“after-image”) (Watabe et al. 1996). The after-image did not move with eye movements. Since there was no visual feedback information, this condition was open-loop condition. The suppression rate under “imaginary” condition was approximately 14%, which was much lower than that obtained using rotational stimuli in the report of Barr et al. (1976). SP system played a major role in visual suppression during caloric nystagmus. The voluntary control might be less effective for extremely low frequency range of VOR although it still works.

There are a number of differences between the imaginary gaze effect on AVOR and the SP system. Imaginary gaze effects on VOR do not have the same phase or gain characteristics as SP (Barnes & Eason 1988). In addition, in contrast to SP, it is unaffected by stimulus predictability (McKinley & Peterson 1985).

To explain the imaginary gaze effects on VOR, Viirre et al. (1986) propose a model called the target locator network (Fig. 3). The target locator network updates the target location continuously on the basis of current vestibular input as well as adjusting VOR correctly. The concept of the target locator network is similar to the internal percept of self-rotation proposed by Bloomberg et al. (1988). Theoretically, such a target location signal can be used by a variety of motor systems to stabilize the head, body, and arm in space. Furthermore, the target locator can be updated by proprioceptive input or efference copies of the motor command as well as by vestibular input (Vilis 1993).

It is reported that imaginary gaze effects on VOR, in contrast to SP, is unaffected by stimulus predictability. However, effects of prediction on the compensatory eye movements during head rotation has been reported. A subject without any vestibular function at all after bilateral vestibular deafferentation can still produce normal gain (0.6), and 100-degree, phase-advanced, compensatory smooth eye movements in response to en bloc rotation in darkness, but only if the rotation is sinusoidal, the maximal acceleration does not exceed 100 degrees/sec² and the maximal frequency does not exceed 0.25 Hz (Halmagyi & Curthoys 1987). In response to rapid unpredictable head impulses, this subject is unable to generate any compensatory eye movements at all in less than about 120 msec (Halmagyi et al. 1990). In the case of this patient, extravestibular information that may be proprioceptive information generates compensatory eye movements.

We investigated eye movements elicited by extravestibular information, a moving sound source was compared with the linear acceleration as sensory information generating eye movements (Hashiba et al. 1995). The eye movement responded to both stimuli had a considerable variability among individual subjects. However, in the individual subject, there was a good correlation in response between linear acceleration stimulus and acoustic stimulus.
It is generally believed that the stimulation of SPEM requires a smoothly moving visual target. However, image motion on the retina is not the only stimulus capable of eliciting SPEM. There have been several reports about non-visual induced SPEM (Steinbach & Held 1968, Lackner & Evanoff 1977, Brandt et al., 1977, Zambbarbieri et al., 1981). We investigated non-visual induced SPEM quantitatively (Hashiba et al. 1996). Targets were subjects’ fingertip movements as somatosensory stimulus and a moving sound source as acoustic stimulus. Horizontal sinusoidal target movements were provided at an amplitude of 15 degrees and frequencies of 0.2, 0.4 and 0.8 Hz. The servo-controlled swing arm was driven sinusoidally in the horizontal plane. The perceptual targets of a red LED, a fingertip and a small loudspeaker were attached to the distal end of the mechanical arm device as a visual target, a somatosensory cue, and an acoustic target, respectively. In comparison to conventional visual SPEM, low gains and phase lead at high frequency were indicated. There was considerable inter-individual variability in the non-visual SPEM performance. The positive correlation between the gains of somatosensory and acoustic SPEM in each subject was observed. We supposed that a common system integrating these non-visual SPEM gains of somatosensory and acoustic SPEM in each subject was observed. We supposed that a common system integrating these non-visual SPEM performance. The positive correlation between the gains of somatosensory and acoustic SPEM in each subject was observed. We supposed that a common system including the predictive control might involve the non-visual SPEM, and the visual SPEM in part.

Our experimental results suggested that any perceptual information, which represented the target motion, could potentially elicit the corresponding SPEM. During self-motion, ongoing vestibular information contributed to the perception of target movement. In the case of a space-fixed imaginary target, the vestibular information represented the main source for target perception. Therefore non-visualy induced SP system could be driven by the vestibular information and could account for effects of imaginary target on VOR, only in low frequency range and in predictable vestibular stimuli (Fig. 4) (Hashiba et al., 1995).

Holistic concept

Human has developed a lot of central nervous mechanisms for smooth eye movements, AVOR, TVOR, slow-rise OKR, visual SP, non-visual SP and target locator network. These mechanisms are thought to work for the purpose of better seeing. Distinct mechanism will work in appropriate self motion and/or object motion. As the results, whole mechanisms are controlled in a purpose-directed manner. This can be achieved by a self-organizing holistic system. Recently such system is proposed to understand the eye movement response (Fig. 5) (Collewijn 1989) and locomotion (Takahashi et al., 1991). The three-neuron arc VOR is only a part of the holistic eye movements system. It can be recognized that the semicircular canal driven VOR is modified by many properties. Holistic system is very useful for understanding human oculomotor behavior.

References


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**Fig. 4** Interaction between TVOR and Non-visual SPEM. Non-visual SPEM can be induced by otolith information during a space-fixed imaginary target condition.

**Fig. 5** Diagram of a holistic concept of oculomotor control. This is a drawing of a holistic concept of oculomotor control proposed by Collewijn (1989).


