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The conjugacy of the vestibulo-ocular reflex evoked by single labyrinth stimulation in awake monkeys

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Abstract

It is well known that the vestibulo-ocular reflex (VOR) is conjugate when measured in the dark with minimal vergence. But the neural basis of the VOR conjugacy remains to be identified. In the present study, we measured the VOR conjugacy during single labyrinth stimulation to examine whether the VOR conjugacy depends on reciprocal stimulation of the two labyrinths. There are conflicting views on this issue. First, since the vestibular signals carried by the ascending tract of Deiters' are distributed exclusively to the motoneurons of the ipsilateral eye, the neural innervations after single labyrinth stimulation are not symmetrical for the two eyes. Thus, single labyrinth stimulation may generate disjunctive VOR responses. Second, the only published study on this issue was an electrooculography (EOG) study that reported disjunctive VOR responses during unilateral caloric irrigation (Wolfe in *Ann Otol* 88:79–85, 1979). Third, the VOR during unilateral caloric stimulation performed in clinical vestibular tests is routinely perceived to be conjugate. To resolve these conflicting views, the present study examined the VOR conjugacy

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during single labyrinth stimulation by recording binocular eye position signals in awake monkeys with a search coil technique. In contradiction to the previous EOG study and the prediction based on the asymmetry of the unilateral brainstem VOR circuits, we found that the VOR during unilateral caloric irrigation was conjugate over a wide range of conditions. We conclude that the net neural innervations received by the two eyes are symmetrical after single labyrinth stimulation, despite the apparent asymmetry in the unilateral VOR pathways. A novel role for the ascending tract of Deiters' in the VOR conjugacy is proposed.

Keywords

VOR pathway; Conjugacy; Single labyrinth stimulation; Unilateral caloric stimulation

Introduction

The vestibulo-ocular reflex (VOR) produces smooth compensatory eye movement to stabilize gaze against head rotation (Vilis and Tweed 1988). When vergence is minimal, the VOR response is conjugate, i.e., the two eyes move in the same direction and at the same speed. In the past several decades, neurophysiological and anatomical studies have revealed the bilateral organization of the brainstem neural circuits for the angular VOR (AVOR). During natural head rotation, the two labyrinths are reciprocally stimulated and a push-pull pattern of neural innervation for each eye is produced via the three-neuron arc (Lorente De No 1933; Scudder and Fuchs 1992). This bilateral organization not only enables the VOR to operate over a much wider linear range than would be predicted from its components (Tomlinson and Bahra 1986; Lauritis and Robinson 1986; Smith and Galiana 1991; Galiana and Outerbridge 1984; Vilis and Tweed 1988) but also may be critical to the VOR conjugacy.

The goal of the present study was to determine whether the VOR conjugacy depends on the reciprocal stimulation of the bilateral labyrinths. There are conflicting views on this issue. First, it has been shown that the neural innervation of the two eyes from a single labyrinth is not symmetrical (Fig. 1). For example, during activation of the left horizontal canal, the ipsilateral eye is driven by neural innervations from three sources: excitatory innervation from the ascending tract of Deiters' (ATD), excitatory innervation from the contralateral abducens internuclear neurons (medial rectus) and inhibitory innervation from the ipsilateral vestibular nuclei (lateral rectus) (Scudder and Fuchs 1992; Highstein and Baker 1978; Baker and Highstein 1978). The contralateral eye, however, is driven by neural innervation from only two sources: an excitatory innervation from the contralateral vestibular nuclei (lateral rectus) and an inhibitory innervation from the ipsilateral abducens internuclear neurons (medial rectus). The asymmetry is compensated when the two labyrinths are reciprocally stimulated during head rotation. During unilateral stimulation, however, the extra excitatory input from the ATD received by the ipsilateral eye may produce disjunctive VOR response. Second, an early EOG study examined this issue and reported that unilateral caloric irrigation generated disjunctive slow phase (Wolfe 1979). Third, while clinicians may routinely observe conjugate VOR during unilateral caloric irrigation, there are no published studies that support this claim.

To resolve these conflicting views, the present study measured the VOR conjugacy during unilateral caloric stimulation using a search coil technique in awake monkeys. The results do not support the early EOG study but are consistent with observations in clinical vestibular testing. We further analyzed the implications of the VOR conjugacy during single labyrinth stimulation and suggest a novel role for the ATD in generating conjugate VOR.

Materials and methods

Experiments and surgical procedures were performed in accordance with the National Institutes of Health *Guide for the Care and Use of Laboratory Animals* and were approved by the University of Mississippi Medical Center's Institutional Animal Care and Use Committee.

Animal preparation for recording binocular eye movements

Three *Macaca mulatta* monkeys (Monkey W, R and H) were prepared for the chronic recording of binocular eye movements. Search coils were surgically implanted in both eyes to record binocular eye movements with an accuracy of 0.01° (Robinson 1963). During experiments, monkeys were comfortably seated in a custom-fabricated chair, with head upright and stabilized with respect to the electromagnetic field of the eye coil system by a stainless steel rod attached to the head holder. Monkeys could be tilted along the horizontal axis ($\pm 30^\circ$). Each eye coil was calibrated at the start of each experimental day by requiring the monkey to fixate on known target positions ($\pm 20^\circ$, every 5°).

Unilateral caloric irrigation

Caloric irrigation is widely used to test the functional integrity of the horizontal semicircular canals. In the present study, we recorded binocular eye movements induced by unilateral caloric stimulation at different temperatures (cold temperature: 22, 27, 32°C ; warm temperature: 42, 47°C). During irrigation, monkeys were in total darkness to prevent visual inhibition of the nystagmus. Caloric irrigation was delivered to one ear canal using the open-loop GN Otometrics NCI-480 Water Caloric Stimulator at a rate of 300 cc/min. We employed two protocols to deliver the caloric stimulation. In the first protocol, we employed caloric stimulation in a manner similar to that used in a clinical situation. Monkeys were given continuous caloric stimulation for 5 min, while they were upright or tilted 30° backward from the vertical plane. The power spectrum of the traditional caloric stimulation has been estimated to be equivalent to a very low-frequency value of about 0.003 Hz (Hamid et al. 1987). In the second protocol, caloric step stimulation was rapidly created by moving the head (and the torso en bloc) rapidly to a semi-reclining position, which places the horizontal canal in a vertical plane where it is maximally stimulated (Formby and Robinson 2000). In the first part of the caloric step protocol, monkeys were given a 2-min caloric stimulation with head in a nose-down position (20°), making the horizontal canal insensitive to ongoing caloric stimulation. This established a steady-state thermal gradient across the horizontal canal and effectively eliminated the potentially confounding effects of dynamic thermal transmission. In the second phase of this protocol, the monkeys were rapidly (~ 0.5 –1 s) tilted backward so that their heads were in a position that was about 30° past the upright position (nose up) (Fig. 3a, thick black line in the lower panel). This position, maintained for 2 min, places the horizontal canal in a vertical plane with respect to gravity. In the third phase of the protocol, the monkeys were rapidly returned to the neutral position and maintained in this position for the final 2 min of irrigation. The power spectrum of the caloric step stimulation has been estimated to consist of high spectra components up to 2 Hz (Formby and Robinson 2000).

Data acquisition and analysis

A master PC running specialized software controlled the experiments, and a CED Power 1401 system (Cambridge Electronics Devices, Cambridge, UK) was used for data acquisition. Signals representing horizontal and vertical eye positions of each eye were sampled at 2 kHz with 16 bits resolution and stored on a hard disk for off-line analyses. Eye movement responses were analyzed using Spike2 (Cambridge Electronics Devices, Cambridge, UK). Raw eye position data were filtered and differentiated with a bandpass of

DC to 100 Hz to measure eye velocity. To quantitatively assess the conjugacy of the slow phase of caloric stimulation-induced nystagmus, we performed a linear regression analysis of the contralateral and ipsilateral eye velocities during unilateral stimulation. The linear regression yielded a slope and a correlation coefficient R . The slope that measured the ratio of the two eyes' velocities is defined as the conjugacy index. A slope of 1 indicates the two eyes move in the same direction with the same amplitude. The square of the correlation coefficient (R^2) indicates how much variance of the data can be explained by the correlation. Both the slope and R^2 are essential to assess the strength of the conjugacy. Perfect conjugacy requires that both the slope and the R^2 are 1.

Results

Figure 2a shows an example of binocular eye position signals of the nystagmus induced by caloric stimulation (Monkey W: left ear irrigation with cold water 22°C, gray for the ipsilateral and black for the contralateral eye). The slow-phase eye velocity signals of the two eyes are displayed in Fig. 2b (gray for the ipsilateral and black for the contralateral eye). The traces of the two eyes overlap, indicating that the slow phase of caloric-induced nystagmus is conjugate. To quantitatively assess the conjugacy of the slow phase, we plotted the contralateral eye slow-phase velocity against the ipsilateral eye slow-phase velocity (Fig. 2c) and computed the slope of the regression line (i.e., conjugacy index of the slow phase), which is 0.969 ± 0.001 ($R^2 = 0.991$). Table 1 summarizes the conjugacy indexes measured in various conditions for three monkeys. For a total of 20 measurements, the average conjugacy index is 1.004 ± 0.005 ($R^2 = 0.988 \pm 0.001$). We also measured the vertical conjugacy indexes on the seven caloric irrigations with vertical slow-phase velocity larger than 30 degree/s. The average vertical conjugacy index was 0.974 ± 0.03 ($R^2 = 0.950 \pm 0.009$). These results indicate that the VOR evoked by unilateral caloric stimulation is 98.8% and 95% conjugate for horizontal and vertical eye movement, respectively.

Figure 3a shows the binocular eye position signals of the nystagmus induced by the caloric step stimulation (Monkey W: right ear irrigation with warm water (47°C), gray for the ipsilateral and black for the contralateral eye). Caloric stimulation evoked minimal nystagmus in both eyes when the monkey's head was in the neutral position (Fig. 3a, lower panel, before the rapid head tilt). After reorienting the head position, nystagmus developed rapidly and reached a peak within 20 s (Fig. 3a, b). The conjugacy index in this condition is 1.034 ± 0.001 ($R^2 = 0.992$). Table 2 summarizes the conjugacy index data from three monkeys for both cold and warm water irrigation. For a total of 8 measurements using caloric step stimulation, the average conjugacy index was 1.010 ± 0.007 ($R^2 = 0.989 \pm 0.002$). These results indicate that the VOR evoked by unilateral caloric step stimulation is nearly 99% conjugate.

Discussion

The main finding of the present study was that the VOR response during single labyrinth stimulation was perfectly conjugate. This finding does not agree with an earlier EOG study that reported disjunctive VOR during unilateral caloric irrigation in humans (Wolfe 1979). We suggest that the differences in these findings are due to the different methods employed to measure binocular eye position signals. In the earlier study, binocular eye position signals were measured by the EOG. Without a rigorous treatment of the EOG signals, it would be difficult to overcome its limitations (nonlinearity and baseline drifts) in order to provide an accurate assessment of the VOR conjugacy (Schlag et al. 1983; Khojasteh and Galiana 2009). In the present study, binocular eye position signals were measured using a search coil technique that has high spatial/temporal resolution, and excellent linearity and stability (Robinson 1963). Our quantitative findings are consistent with the observations in routine

clinical vestibular testing. Thus, we conclude that the VOR induced by single labyrinth stimulation is conjugate, rather than disconjugate as previously reported. We further suggest that the VOR conjugacy does not depend on the reciprocal stimulation of the two labyrinths. Instead, it is an intrinsic feature of the unilateral VOR pathway.

Since VOR response during single labyrinth stimulation is conjugate, the net neural innervations originating from a single labyrinth must be balanced for the two eyes, i.e.,

$$V_{ATD} + K_{INT} * V_C + K_M * V_I = K_M * V_C + K_{INT} * V_I$$

where V_{ATD} , V_C and V_I are the neural inputs to the ipsilateral oculomotor nucleus, the contralateral abducens nucleus and the ipsilateral abducens nucleus, respectively; K_{INT} and K_M are the percentages of the neural inputs that are distributed to the internuclear pathway and the motoneuron pathway in the two abducens nuclei, respectively. Caloric stimulation activates the VOR pathways by directly activating the peripheral vestibular afferents as well as activating the central velocity storage mechanisms (Arai et al. 2002; Peterka et al. 2004). Because of the commissural pathways, single labyrinth stimulation activates not only neurons in the ipsilateral vestibular nuclei but also neurons in the contralateral vestibular nuclei. However, the neural innervation patterns after single labyrinth stimulation remain asymmetric for the two eyes because of the unilateral nature of the ascending tract of deiters' (Fig. 1). Although Fig. 1 only shows the direct VOR pathways, V_{ATD} , V_C and V_I are the summed neural innervations received by motoneurons from both the direct and indirect VOR pathways. Since the above equation describes the net neural innervations received by motoneurons, it accounts for the effects of single labyrinth stimulation on both the ipsilateral and contralateral vestibular nuclei. The above equation was used to explore the role of the ATD in generating conjugate VOR during single labyrinth stimulation. After rearranging the components in the above equation, V_{ATD} is expressed as a function of the other inputs to the abducens nuclei, i.e.,

$$V_{ATD} = (K_M - K_{INT}) * (V_C - V_I)$$

Consider the case described in Fig. 1 when only the left horizontal canal is activated. Because the ATD neurons are modulated during the VOR (Scudder and Fuchs 1992; Lisberger et al. 1994; Chen-Huang and McCrea 1998; Nguyen et al. 1999; Reisine et al. 1981; Evinger et al. 1977; Fuchs et al. 1988; McCrea et al. 1987; King et al. 1976) and vestibular nuclei make stronger projection to the contralateral abducens nucleus than to the ipsilateral abducens nucleus (Scudder and Fuchs 1992), both V_{ATD} and $V_C - V_I$ are larger than zero. Thus, $K_M - K_{INT}$ must be larger than zero, i.e., the abducens motoneuron pathways receive more inputs than the abducens internuclear pathway.

The VOR conjugacy during unilateral stimulation not only justifies monocular recording in clinical vestibular tests but also has three implications regarding the neural organization of the VOR pathways. First, the VOR conjugacy is an intrinsic feature of unilateral VOR pathways. It does not depend on the reciprocal stimulation of the two labyrinths. Second, we propose that the ATD pathway plays an important role in achieving the VOR conjugacy by providing the required neural innervations to compensate for the different inputs received by the two abducens nucleus ($V_C - V_I$) and by the abducens internuclear and motoneuron pathways ($K_M - K_{INT}$). If there is a change in $K_M - K_{INT}$ (e.g., oculomotor nerve lesion) or $V_C - V_I$ (e.g., brainstem lesion), the ATD pathway may be adjusted to keep the VOR conjugate. Third, if unilateral labyrinth stimulation evokes a disjunctive VOR response, it is likely that the vestibular end organs other than the canals are activated. For example, Zhou et al. (2004) showed that acoustic clicks evoked horizontal disjunctive eye movements in monkeys. Since the unilateral angular VOR is conjugate, this disjunctive component should result from acoustic activation of the otolith end organs. Indeed, recent studies found that

acoustic clicks activate both the canal and otolith VOR pathways (Zhou et al. 2007; Xu et al. 2009).

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Fig. 1.

Schematic illustration of the direct angular VOR pathways that are activated during unilateral caloric stimulation. *Blue line* is vestibular afferent, *red line* is excitatory VOR interneuron projection, *green line* is inhibitory ipsilateral VOR interneuron projection, and *black line* is motoneuron or internuclear neuron projection. For simplicity, this figure only draws the direct VOR pathways. However, V_{ATD} , V_C and V_I are the summed neural innervations received by motoneurons from both the direct and indirect VOR pathways. K_{INT} and K_M are the percentages of the abducens inputs that are distributed to the internuclear and motoneuron pathways, respectively. For simplicity, we assume the same K_{INT} and K_M are shared by the two abducens nuclei. The ipsilateral eye is driven by the neural innervations from three sources: an excitatory innervation from the ascending tract of Deiters' (V_{ATD} , *red line*), an excitatory innervation from the contralateral abducens internuclear neurons ($K_{INT} \cdot V_C$) and an inhibitory innervation from the ipsilateral vestibular nuclei ($K_M \cdot V_I$). The contralateral eye is driven by the neural innervations from two sources: an excitatory innervation from the contralateral vestibular nuclei ($K_M \cdot V_C$) and an inhibitory innervation from the ipsilateral abducens internuclear neurons ($K_{INT} \cdot V_I$).

Fig. 2.

The conjugacy of the slow phase of the nystagmus induced by the traditional (low frequency) caloric stimulation in Monkey W (cold water irrigation in the left ear). **a** Binocular eye position signals. *Black line* is for the contralateral eye and *gray line* for the ipsilateral eye. The two eye position traces overlay very closely, indicating conjugate horizontal eye movement. **b** Binocular eye velocity signals. *Black line* is for the contralateral eye and *gray line* for the ipsilateral eye. The two eye velocity traces overlay very closely, indicating conjugate horizontal eye movement. **c** The conjugacy index of the slow phase, defined as the slope of the regression line of the contralateral eye velocity plotted against the ipsilateral eye velocity, is 0.969. R^2 is 0.991. Time zero is the onset of caloric irrigation

Fig. 3.

The conjugacy of the slow phase of the nystagmus induced by the caloric step stimulation in Monkey W (warm water irrigation in the right ear). **a** Binocular eye position signals. *Black line* is for the right eye and *gray line* for the left eye. Head orientation with respect to gravity is displayed by the *thick black line* in the *lower panel*. The step in head orientation indicates a rapid 30° backward head tilt. The two eye position traces overlay very closely, indicating conjugate horizontal eye movement. **b** Binocular eye velocity signals. *Black line* is for the right eye and *gray line* for the left eye. The two eye velocity traces overlay very closely, indicating conjugate horizontal eye movement. **c** The conjugacy index of the slow phase, defined as the slope of the regression line of the right eye velocity plotted against the left eye velocity, is 0.960. R^2 is 0.992. Time zero is the onset of the head tilt that is delivered after a 2-min continuous caloric irrigation. For details, see “Methods”

Table 1

Summary of conjugacy indexes: traditional caloric stimulation

		Caloric water temperature	Peak slow-phase velocity (deg/s)	Conjugacy index	R ²
Monkey W	Left ear	Warm 47°C	112	1.005	0.997
		Warm 42°C	27	0.993	0.981
		Cold 30°C	-67	0.962	0.975
		Cold 22°C	-97	0.969	0.991
	Right ear	Warm 47°C	-116	1.042	0.992
		Warm 42°C	-43	1.012	0.978
		Cold 32°C	64	1.013	0.989
		Cold 27°C	97	1.015	0.992
		Cold 22°C	163	1.038	0.991
		Warm 47°C	78	0.984	0.989
Monkey R	Left ear	Cold 22°C	-138	0.991	0.991
		Warm 47°C	-179	1.017	0.990
	Right ear	Warm 42°C	-38	1.033	0.972
		Cold 27°C	106	0.974	0.990
		Cold 22°C	163	1.038	0.991
		Warm 47°C	160	0.994	0.993
	Left ear	Cold 27°C	-105	0.991	0.988
		Cold 22°C	-141	1.004	0.991
	Right ear	Warm 47°C	-180	0.994	0.985
		Cold 22°C	140	1.007	0.993
Monkey H	Left ear	Warm 47°C	160	0.994	0.993
		Cold 27°C	-105	0.991	0.988
		Cold 22°C	-141	1.004	0.991
		Warm 47°C	-180	0.994	0.985
		Cold 22°C	140	1.007	0.993
	Left ear	Warm 47°C	160	0.994	0.993
		Cold 27°C	-105	0.991	0.988
	Right ear	Cold 22°C	-141	1.004	0.991
		Warm 47°C	-180	0.994	0.985
		Cold 22°C	140	1.007	0.993

Table 2**Summary of conjugacy indexes: caloric step stimulation**

		Caloric water temperature	Peak slow-phase velocity (deg/s)	Conjugacy index	R^2
Monkey W	Right ear	Warm 47 °C	-168	1.042	0.992
		Cold 24°C	125	1.029	0.993
	Left ear	Warm 47 °C	101	1.023	0.986
		Cold 22°C	-104	0.988	0.984
Monkey R	Right ear	Warm 47 °C	-185	0.993	0.992
		Cold 22°C	123	0.983	0.990
Monkey H	Right ear	Warm 47 °C	-218	1.015	0.994
		Cold 23 °C	113	1.006	0.980