

Vestibular Adaptation in the Laboratory: review of VOR adaptation

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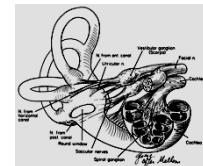
With slides contributed by David Zee, Scott Eggers.

Why the need for VOR adaptation?

Abnormal VOR allows unwanted image motion (slip) on the retina during head motion, degrading vision. The brain must compensate.



Examples:
magnifying or minifying effects of corrective spectacles, or loss of labyrinthine function.



Definitions

Vestibulo-ocular reflex (VOR) adaptation: the process by which VOR parameters are calibrated on the basis of performance errors to ensure accurate eye movements and clear vision.

- Typically we think of adaptation of the **GAIN** of the VOR.
- **Gain=(eye velocity)/(head velocity)**
[there are other definitions]
- **Gain=1.0 is normal**

Example: reversing prism goggles

- I Kohler (1962) Experiments with goggles. *Sci Am* 206:62-72.
 - Subjects wore prism goggles that reversed right and left.
 - Could engage in near-normal activities after 4-8 weeks.
 - Presumably the VOR had changed – this requires a change in the direction of the VOR (phase change from 0° to 180°).
- A Gonshor, G Melvill Jones (1976) Extreme vestibulo-ocular adaptation induced by prolonged optical reversal of vision. *J Physiol* 256:381-414.
 - 28 days exposure.
 - Gain ~0.3, Phase ~-120.
 - Impressive but not very realistic for normal biology.

Example: magnifying and minimizing lenses

- FA Miles, BB Eighmy (1980) Long-term adaptive changes in primate vestibuloocular reflex. I. Behavioral observations. J Neurophysiol. 43:1406-1425.
- Several days of wearing x2, x0.5, or x0 spectacles.
- Rhesus monkeys.
- Tested with sinusoidal oscillations, 0.1-1.0 Hz.

Time course of VOR adaptation

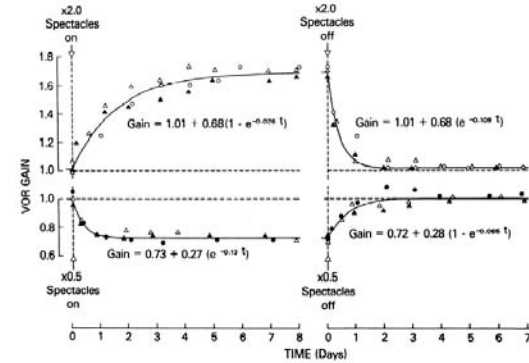


FIG. 2. Time-course of the VOR gain changes associated with $\times 2$ (above) and $\times 0.5$ (below) telescopic spectacles. Data were taken from four different animals, each represented by a different symbol. 0.2 Hz , $\pm 20^\circ$ oscillations were used, each data point being the mean of at least 20 determinations. Curves were determined using an exponential fitting procedure, forcing through the mean initial and final gain values. Note that in the equations, time t is in hours.

Effect of repeated adaptation

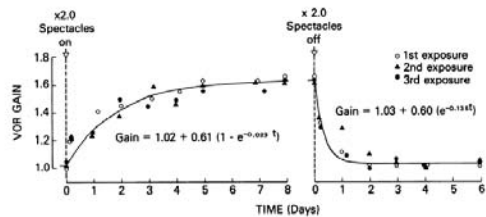
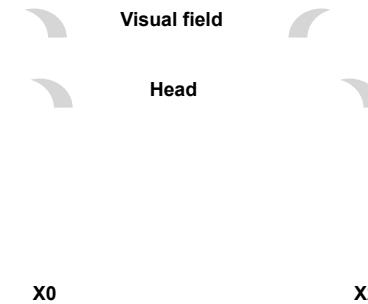
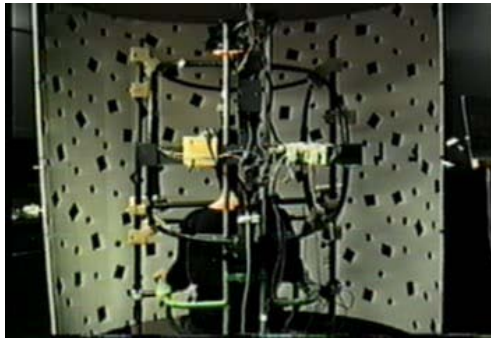


FIG. 5. VOR gain changes associated with repeated exposures to $\times 2$ spectacles (one animal). Spectacles were worn for periods of 8 days interspersed with 8 days of recovery. Note the time constant τ in the gain equations is in hours. RMS error for the least-squares best-fit exponential was 0.06 for both the acquisition and recovery data.

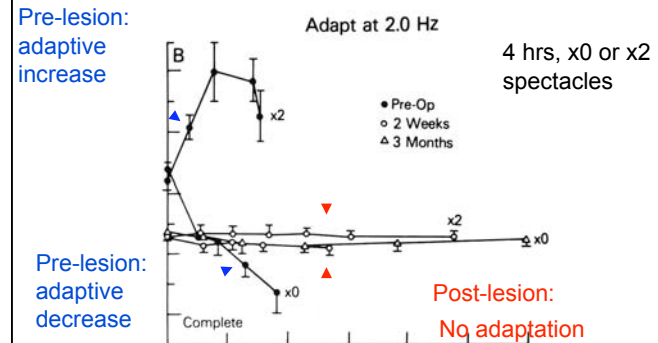
Example: visual-vestibular mismatch



Method



Loss of VOR gain adaptation after cerebellar lesions (flocculus/paraflocculus)



What is the site of VOR adaptation?

- **It involves the cerebellum:**
 - cerebellum is necessary for VOR adaptation
 - Purkinje cells change their responses after adaptation

BUT there are competing hypotheses:

- **Ito (1972, 1982): cerebellar Purkinje cells**
- **Miles & Lisberger (1981): brainstem (vestibular nuclei)**

Where are the modifiable synapses?

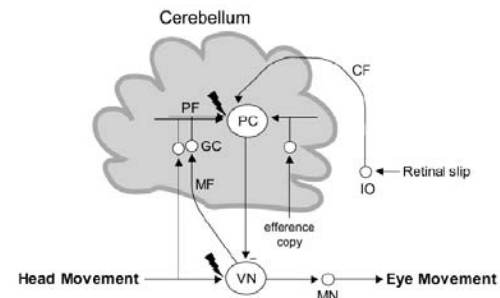


Figure 3 Proposed sites of plasticity in the circuit for the VOR (indicated by lightning bolts). CF, climbing fibers; GC, granule cells; IO, inferior olive; MF, mossy fibers; MN, oculomotor nuclei; PC, Purkinje cells; PF, parallel fibers; VN, vestibular nuclei.

Boyden et al. (2004) Cerebellum-dependent learning: the role of multiple plasticity mechanisms. *Ann Rev Neurosci* 27:581-609.

Ito (1972, 1982): Cerebellar Purkinje cells – parallel fibers

- LTD in Purkinje cell - parallel fiber synapses
- climbing fibers carry retinal slip (error signal)
- parallel fibers carry head velocity
- adaptation is stored in the cerebellum
- confirming evidence: disruption of LTD pathways impairs adaptation

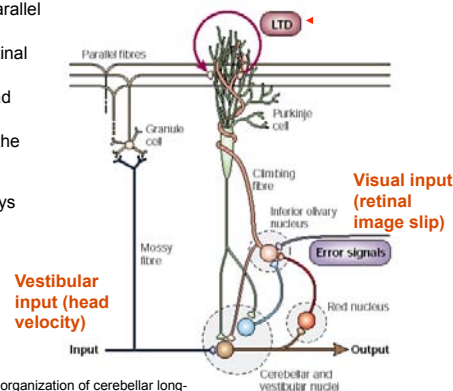


Figure: M Ito (2002) The molecular organization of cerebellar long-term depression. Nat Rev Neurosci 3:896-902.

Miles & Lisberger (1981): Flocculus Target Neurons

- cerebellum processes error signal, adaptation is implemented via Purkinje cell synapses onto flocculus target neurons (FTN) in the vestibular nuclei
- altered Purkinje cell responses after adaptation attributed to altered eye movement command (efference copy) carried by mossy fibers
- confirming evidence: short latency of adaptive response, inactivation of cerebellum leaves adaptation intact

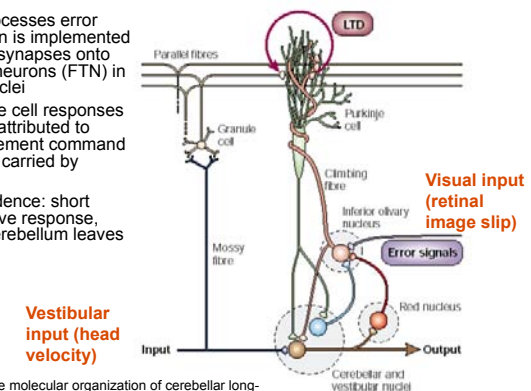


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What are the error signals that drive adaptation?

- Typically, we think of VOR adaptation as accomplished by detection of an error signal (retinal slip) during head motion, with a subsequent adaptive readjustment of the slow-phase response.

However:

- Prior work by many others has shown that:
 - Error signals other than retinal slip can drive adaptation (visual-vestibular conflict in strobe light, after-image tracking, position errors).
 - Saccades (typically driven by position errors) can be an important component of the adaptive response.
 - For clear vision not only overall image slip but also foveation needs to be accomplished by the VOR, and this need may be reflected in the error signals that can drive adaptation.

Retinal Slip as an error signal

Consider an experiment where subject tracks a counter-rotating visual surround during sinusoidal rotation.

- Asks for increase in VOR gain
- High retinal slip would not be tolerated for an hour or more
- Hypothesis: Subject augments deficient VOR with smooth pursuit
- Retinal slip is low throughout adaptation paradigm
- If retinal slip is the *only* error signal, no adaptation will occur! But it does.

So, what really is the error signal?

Is retinal slip *necessary*?

After-Image Tracking

Tracking a retinal after-image increases VOR gain – WHY?

- Corollary discharge: internal copy of command to move the eyes.
 - Maintains visual constancy by canceling effects of visual motion due to eye movements
 - World appears stable when eyes move
 - World appears to move if eye is moved passively

- Perceived target motion = retinal motion + corollary discharge
- If corollary discharge gain $K \neq 1$, perceived target motion is not 0 even though retinal motion is zero
- Pursuit is activated to overcome perceived target motion
- Additional pursuit increases apparent VOR gain

Perceived Visual Motion as Effective Stimulus to Pursuit Eye Movement System. S Yasui, LR Young (1975) Science 190:906-8.

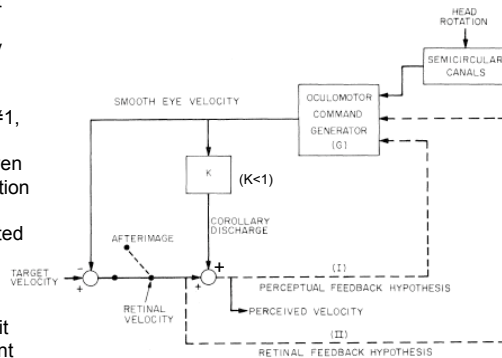
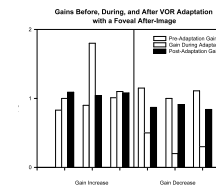
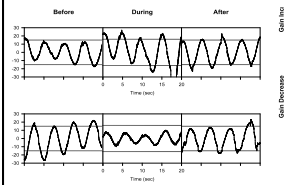


Fig. 1. Compensation by corollary discharge for the eye movement effect on the retinal image motion. In this experiment the input is from head rotation. Tracking a foveal afterimage rather than an external target opens the retinal feedback loop and activates only the internal positive feedback loop that results from connecting the corollary discharge with the postulated perceptual feedback path; G , open loop gain of vestibulo-ocular reflex arc; K , gain of corollary discharge path.

After-image Tracking Experiment

- Track after-image
- 30 minutes
- 0.2 Hz, 20 deg/sec peak velocity
- Refresh after-image as needed
- Measure VOR before and after adaptation in darkness
- To INCREASE gain: “follow the after-image”
- To DECREASE gain: “keep the after-image in one place so that it does not move”

VOR Adaptation with a Foveal After-image

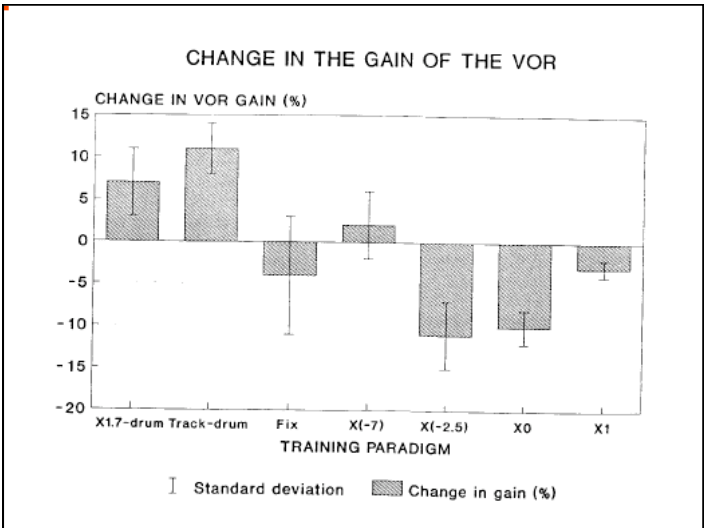


Can VOR gain be adapted *without head movement* ?

- **Wide-field visual motion stimulates vestibular nucleus just as does head movements**
 - This visual-vestibular interaction (VVI) works synergistically during extended head movements in the light: OKN augments VOR
- Can “virtual” head motion induced by visual motion be used to “trick” the brain into adapting the VOR?

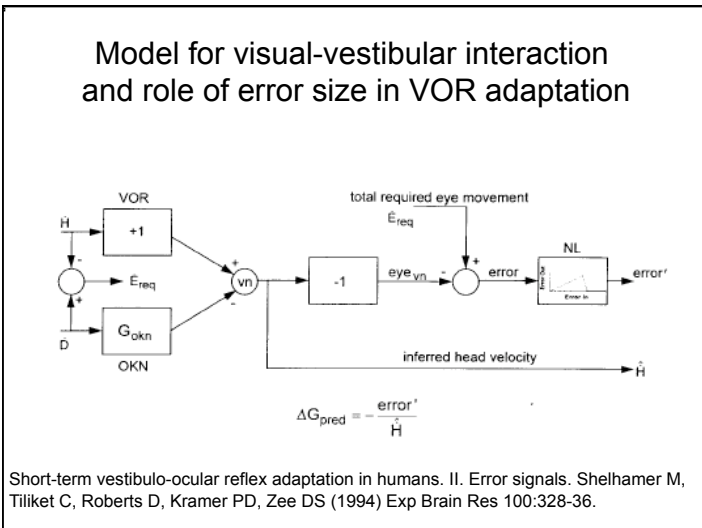
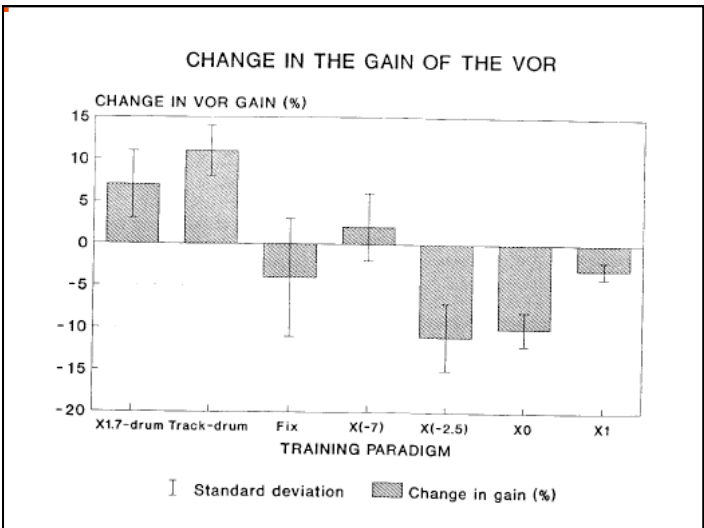
Can VOR gain be adapted *without head movement* ?

- Stationary subject
- Motion of surrounding visual field *only*
- 1 hour
- 0.2 Hz, 50 deg/sec peak velocity
- OKN is induced to track the visual motion
- OKN gain is <1
- Smooth pursuit makes up the difference
- Pursuit also indicates that VOR gain is too low (error signal for VOR adaptation)
- Wide-field motion indicates to brainstem that head is moving, so it is appropriate to have a VOR



How large an adaptive demand can system respond to?

- **1 hr sinusoidal rotation**
- **-2.5 gain adaptation**
 - Chair 20 deg/seg
 - Drum 70 deg/sec
 - Rotation in same direction
- **-7 gain adaptation**
 - Chair 7 deg/sec
 - Drum 56 deg/sec
 - Rotation in same direction



Short-term vestibulo-ocular reflex adaptation in humans. II. Error signals. Shelhamer M, Tiliket C, Roberts D, Kramer PD, Zee DS (1994) Exp Brain Res 100:328-36.

How about the converse – is it better to ask for many small changes?

- Steps of head rotation
- 300 trials, 10 blocks of 30
- Target moves during head motion
- Self-generated (active) movements during adaptation
- Passive and active testing before and after adaptation
- Conventional x2 adaptation
 - Constant X2 gain demand (100% increase)
- Incremental adaptation
 - 10% increase, incremented by 10% in each block

