Interactions between Otoliths and Vision
Revealed by the Response to Z-Axis
Linear Movements

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Compensatory eye movements evoked by linear movement in the dark are rather ineffective compared to the response to angular movements. However, the response to horizontal, linear, visual movement (Lynstam, x-axis) is enhanced if the subject is simultaneously moving. This suggests interactive effects between the visual and the otolith systems. To maintain clear vision during linear movement, compensatory eye movements have to take into account not only the physical movement itself but also the distance of regard. So it is perhaps not too surprising that the otoliths' contribution is greatest when other systems (e.g., vision) can provide the necessary distance cues. We have investigated the effect of otolith-visual interactions in the z-axis (through the top of the head) with subjects in a supine position. Linear motion along this axis is transduced primarily by the otoliths of the saccule.

Subjects lay on a sled and viewed an optokinetic stimulus during sinusoidal z-axis movement. The stimulus arrangement is shown in Figure 1. There were four stimulus conditions: vision only (in which the sled did not move), otolith only (sled movement in the dark), vision and otolith signals complementary (e.g., visual movement upwards accompanying sled motion towards the feet—as in natural vertical movements), and finally, vision and otoliths opposed (i.e., visual and physical motion in the same direction). A range of otolith/visual velocity ratios were used (Figure 1).

The vertical eye movement response to the otolith-only condition was, as expected, small. The visual velocity was chosen so that for the vision-only condition the closed-loop gain of vertical eye movements [peak slow-phase eye velocity (deg/second)/peak stimulus velocity (deg/second at zenith)] was about 0.5. When the otoliths were stimulated to complement the visual information, the gain was enhanced impressively to above 0.8 (Figure 2). Surprisingly, when the signals were opposed, the gain was not reduced below that found in the vision-only condition. There is a nice symmetry around the otolith/visual velocity ratio of unity. A ratio of unity represents the normal correspondence of otolith and visual signals.

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Otolith stimulus: 0.6 g sines @ 0.3, 0.5 & 1.0 Hz
Visual stimulus: 61 d/s sines viewed at 56 cm

Otolith/Visual velocity ratio:
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\frac{\text{Otolith peak velocity [m/s]}}{\text{Visual peak velocity [m/s]}}
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**FIGURE 1.** Methods. Subjects lay supine on a sled and looked up at a high-contrast striped pattern (84 × 84 cms, spatial frequency about 0.1 c/deg at zenith) on an endless belt suspended 56 cm above their heads. The stripe display was attached to the sled and moved with it physically. Horizontal and vertical eye movements were measured using scleral search coils. Stimuli were always sinusoidal with frequencies of 0.3, 0.5 and 1 Hz. The frequency of the visual movement was always the same as that of the sled. All visual stimuli had a peak velocity of 0.6 m/second whereas the sled had a peak acceleration of 0.6 × g. This resulted in peak sled velocities of from 0.9 to 3.1 m/second and a range of otolith/visual velocity ratios [otolith peak velocity (m/second)/visual peak velocity (m/second)].

**FIGURE 2.** Interactive effects between the otolith and visual signals in the production of vertical eye movements. The vertical axis is the peak slow-phase eye velocity (deg/second). The horizontal axis represents the degree of agreement between the otolith and visual signals as a simple ratio of the stimulus velocities in m/second. When the signals are in agreement, this produces a positive ratio; when they are in opposition it produces a negative ratio. The line is a spline interpolation through the mean data points of the five subjects. Standard deviations are also shown. Note that the response at an otolith/vision ratio of zero (the vision-alone condition) represents examples of all the frequencies that were used to generate all the other ratios: clearly the effect cannot be explained as an influence of frequency or speed.
These data add support to the emerging view that the response to physical motion cannot be regarded as a set of responses evoked from independent systems.\textsuperscript{5} The response to movement is an indicator of the integrative nature of the nervous system.

REFERENCES