Acta Otolaryngol (Stockh) 1991; Suppl. 481: 266–268

The Effect of Canal/Visual and Canal/Otolith Conflict on Type I Vestibular Nucleus Neurones

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Second-order horizontal semicircular cells in the vestibular nucleus are a site of convergence of information related to movements of the head. Signals not only from the semicircular canals but also from the otoliths, the visual system and probably other sources of information about movements of the head combine on these neurones (1). Each of these signals has its own inadequacies (for example the cupula of the semicircular canals has a time constant of only about 5 s) but together they normally provide an accurate description of what is happening to the head. In the absence of evidence of change, the vestibular system acts as a flywheel to buffer this best estimate. Thus the time constant of the vestibulo-ocular reflex far exceeds that of its sensory input (about 16s in the cat) and optokinetic nystagmus is insensitive to brief periods of darkness, such as might accompany an eye blink (2). Already at the level of the second-order vestibular nucleus neurones, the time constant of the response to rotation is longer than the end-organ's, suggestive of velocity storage (3) operating at this early stage.

When the senses do not provide complementary information but instead conflict, maintaining the status quo can no longer be the optimum strategy. Under such conditions, measurement of eye movements indicate that the velocity store is in fact discharged (2). But this discharge represents a paradox: since information from the different senses converges onto second-order vestibular nucleus cells, information on the output side of these cells cannot be distinguished as originating from any particular source (e.g. otoliths, canal or vision). So conflict must be detected in some different, parallel system.

Previous experiments using visual suppression of the vestibulo-ocular reflex (an extreme form of conflict) in the monkey have suggested some attenuation of vestibular nucleus activity and a decoupling of neuronal activity from eye movements (2). The present experiments were designed to see whether the store on vestibular nucleus neurones was discharged during a less extreme type of inter-sensory conflict in which eye movements are still required. This would reflect the discharge of the store seen in the eye movements during otolith/canal conflicts (4).

Cats were prepared for chronic recording of eye movements and single cell activity (4). The activity of single cells were recorded through a stereotaxically placed Trent-Wells chamber. Canal/visual conflict was obtained by rotating at constant velocity around an earth-vertical axis in the light until the canals' response had declined to zero and then suddenly slowing. Canal/otolith conflict was obtained by rotation about an off-vertical axis before the sudden slowing. At the point of slowing, the canals, since they respond to the acceleration, indicate rotation commencing in the opposite direction whereas vision or otolith signals are veridical. By adjusting the initial and final velocities, a greater or lesser degree of conflict can be achieved. The extent of the conflict can be described as a ratio between the presumed canal signal (change in angular velocity) and the rate of rotation (presumed to be veridically signalled by the visual or otolith systems). This technique has been described in a paper in which the eye movement reponses to canal/otolith conflict were examined in detail (4).

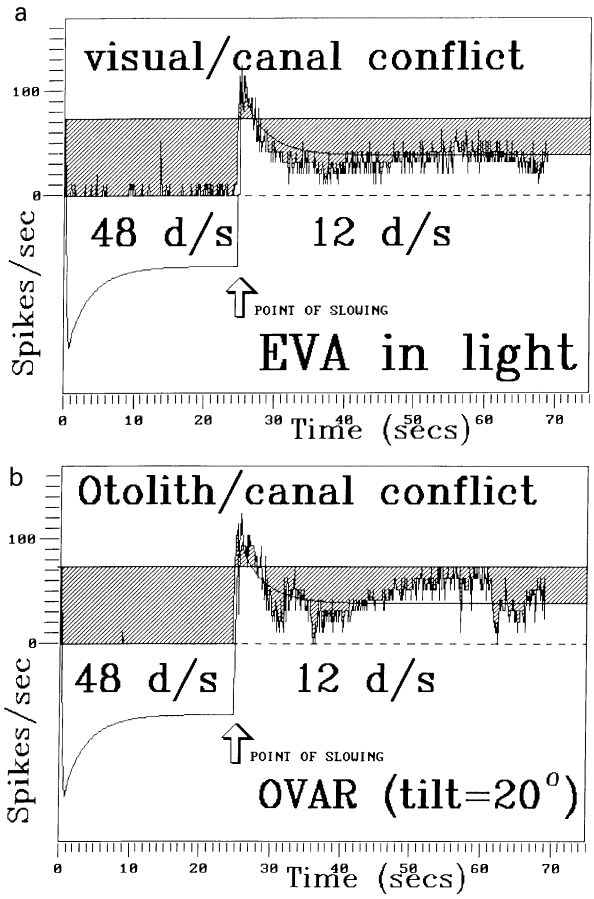

Fig. 1. A typical response profile for a type I vestibular nucleus neurone recorded during visual/canal conflict (*a*) or otolith/canal conflict (*b*). In both cases the conflict was achieved by altering rotation (in the inhibitory direction of the neurone, i.e. contralaterally) from 48°/s to 12°/s. Visual/canal conflict was achieved by rotation about an earth-vertical axis (EVA) in the light, whereas otolith/canal conflict was achieved by off-earth-vertical axis rotation (OVAR; tilt = 20°) in the dark. The canal/otolith and canal/vision ratios were −3. Deviation of the cell's firing rate from the spontaneous level (73 spikes/s) is shown by diagonal-shaded area. The cell was fully inhibited in the initial part of the record; in the latter half (during conflict) the cell's response is well fitted by the output of Robinson's model (although no attempt has been made to fit the modulation in the OVAR response).

The activity of 66 vestibular nucleus type I cells was recorded from 7 cats during patterns of rotations designed to produce conflicts. All the cells' responses were fitted well by the outputs of either the Robinson (5) or the Raphan & Cohen (3) model of visual-vestibular interactions. The outputs of these models were scaled and displaced to best fit (by eye) the cell's responses during non-conflict vestibuloocular reflex and optokinetic nystagmus. These values were then used in simulating the response to changes of speed (conflict). A typical response is shown in Fig. 1. during contralateral (inhibitory) rotation with a canal/otolith or canal/vision ratio of −3. The simulation lines shown in Fig. 1*a* and 1*b* are the same, obtained by using the visual-vestibular interaction model of Robinson (5). No attempt has been made here to simulate the working of the otoliths. This is because the visual and otolith influences probably occur at the same point in the processing of information (see Fig. 3, Harris 1988). In any case, the fit of the model to the cells' response is quite good. However, simultaneous recording of the eye movements confirmed my previous findings that the nystagmus recorded during otolith/canal conflict was much reduced (4). Instead of the normal 0.73 gain produced by OVAR rotation (corresponding to a mean eye velocity of 9°/s recorded in the absence of conflict), the gain was 0.2±0.15 (corresponding to a mean eye velocity of only about 2°/s in the example illustrated). Surprisingly, no such reduction was seen in the cell's response whose activity deviates from baseline by even more than the model at several points in the illustrated record. No

reduction in the eye movement gain could be seen in the closed-loop optokinetic nystagmus accompanying conflicts.

The velocity of compensatory eye movements showed attenuation during conflicts between canals and otolith signals which was not seen in the simultaneous activity of vestibular nucleus cells. No such mismatch was seen during canal/visual conflicts (examined on the same cells). I suggested (4) that the site of optokinetic and otolith input convergence was also the site of the so-called dumping facility in which the store is "dumped" when signals are judged incompatible. Such a signal might arise in the nodulus (6). The effect of dumping can be simulated in the Raphan & Cohen model by closing a discharging loop around the velocity store. This does make the simulation a better fit to the eye movements but not to the vestibular nucleus activity. The present study therefore suggests that convergence of canals, otoliths and vision takes place at a different site to the discharging effect of conflict detection. The vestibular nucleus holds a memory of the head movement. The rest of the system can "forget it" (for example during attentional changes) or "suppress it" (by the nodulus during conflict). However, the memory remains and can be seen by a microelectrode and "recalled" by the system when the conditions are right.

ACKNOWLEDGEMENT

This work was supported by MRC (UK) grant no: G8601355N to LRH.

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