

Modification of the Balance and Gain of the Vestibulo-ocular Reflex in the Cat*

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Summary. The characteristics of the vestibulo-ocular reflex (VOR) of a normal cat can be modified in response to visual demands. Two aspects of the VOR are modifiable independently by a normal cat: the gain and the balance. An imbalance results in a spontaneous nystagmus and an asymmetric VOR. Neither the gain nor the balance of a dark-reared cat's VOR is susceptible to visual modification. A cat whose crossed visual pathways are severed at the level of the optic chiasm is able to modify the gain of the VOR but not its balance. Both dark-reared and split-chiasm cats have only very short-lasting optokinetic after-nystagmus.

Key words: Vestibulo-ocular reflex – Modification – Plasticity – Optokinetic after-nystagmus – Dark rearing

The maintenance of acute vision during head and body movements requires that the visual world be kept reasonably stationary on the retina. Normally this is achieved by the harmonious operation of two compensatory eye movement reflexes, the vestibulo-ocular reflex (VOR) and the optokinetic reflex. Each of these reflexes operates with limitations. For short sharp head movements the long latency of the visual system simply does not allow time for compensation to occur. Moreover, with high frequencies of sinusoidal stimulation (above 1.0 Hz) the efficacy of visual pursuit systems declines. The vestibular system is, on

the other hand, well suited to generate compensatory eye movements at high frequencies. Its short latency (under 10 ms) and the ability to respond to high frequency stimulation (over 7 Hz: Donaghy 1980) allow the vestibulo-ocular reflex to provide image stabilisation when visual reflexes become ineffective. While the VOR is the prime mover of the compensatory eye movement system with high frequency stimulation, its performance declines at low frequencies (Landers and Taylor 1975).

Recently it has become evident that the vestibular and visual systems cooperate in the process of image stabilisation on a more long-term basis. The optokinetic reflex (optokinetic nystagmus: OKN) operates as a closed-loop negative feedback system, in which the velocity of the retinal image (retinal slip velocity) evokes the corrective reflex. The VOR, however, operates as an open-loop system: the vestibular organ has no direct measure of the effectiveness of its compensatory efforts. Open-loop control systems in general require accurate calibration and it appears that one role of the optokinetic system is to provide this calibration of the vestibulo-ocular reflex.

There are two aspects of the VOR that need to be adjusted. The gain of the reflex can be modified by vision to cope with, as Robinson (1976) suggests, cell loss due to trauma, disease and ageing. The gain of the VOR of man and other mammals has recently been shown to be extremely adaptable and able to compensate for enormous artificial dysmetrias, for example that induced by reversing prisms (Gonshor and Melvill Jones 1971, 1976a, b, man; Melvill Jones and Davies 1976, cat; Ito et al. 1974, Collewyn and Kleinschmidt 1975, rabbit). The other aspect of the VOR that can be adjusted is the balance of the signals coming from the two sets of labyrinths (Robinson 1975). The spontaneous resting activity in the VIIIth nerves from the two stationary semicircu-

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lar canals is normally balanced centrally. An imbalance (such as results from the extreme case of unilateral hemilabyrinthectomy) causes a spontaneous nystagmus (Magnus 1924; Kornhuber 1966) but this is normally removed by a subsequent compensation of the system (Precht et al. 1966; Courjon et al. 1977). In the adult cat the gain and balance of the vestibulo-ocular reflex are each modifiable separately. And some evidence indicates that different neural mechanisms are involved in the two compensation processes (Haddad and Robinson 1977).

In this paper, we report investigations of the modifiability of balance and gain of the VOR in three groups of animals. These are normal cats, cats reared in darkness, and normally reared adult cats in which the optic chiasm has been surgically sectioned. Initially we were concerned with the modifiability of the VOR by vision in the dark-reared animals. Subsequently our findings indicating that the dark-reared cat uses exclusively crossed visual pathways for the optokinetic reflex (Harris et al. 1980) led us to study the capacity for VOR modification in animals which use exclusively uncrossed visual pathways (the split chiasm cats).

Methods

Surgical Preparation of the Animals

Nine cats were used in this study. Four were normal, three were dark-reared and two were normally-reared cats in which the optic chiasm was sectioned in adulthood. Chiasm section was performed with the aid of a dissecting microscope using a transbuccal (ventral) approach. All three classes of cat were implanted, as adults, with an eye-coil for the measurement of eye position (Robinson 1963; Fuchs and Robinson 1966) and a head-holder by means of which the animals could be restrained. Details of eye movement recording and calibration are described in the previous paper (Harris and Cynader 1981).

Method for Speedy Modification of the Balance of the Vestibulo-ocular Reflex

The balance of the vestibulo-ocular reflex (VOR) has been investigated up until now by assessing the ability of an animal to correct for the drastic effects of unilateral labyrinthectomy (see for example Courjon et al. 1977). Here we describe a speedy method for reversible modification of the balance of the cat's vestibulo-ocular reflex.

The animal was mounted in the apparatus by means of the implanted tubes and was rotated sinusoidally. Simultaneously an optokinetic drum was rotated continuously around him. The speed of the drum was chosen to match the peak velocity of the sinusoidally oscillating table. When the table and drum were moving in the *same* direction the movement of the drum had the effect of approximately cancelling the visual slip that would be caused by movement of the table alone in the light. In this circumstance it was appropriate for the vestibulo-ocular reflex to be suppressed; that is the gain of the VOR should be reduced to

zero in this direction. However, during the other half of the table's cycle, the table and drum were moving in *opposite* directions and the visual slip was thus twice that due to the movement of the table alone. The appropriate change in the VOR was now to *increase* the gain to two. The VOR had therefore two simultaneous demands put on it. The gain should increase in one direction and simultaneously decrease in the other. The average gain was asked to remain constant: the balance was asked to change.

Method for Modification of the Gain of the Vestibulo-ocular Reflex

We used forced rotation to induce substantial changes in the gain of the VOR of the normal cat within a short period. By attaching the optokinetic drum to the moving table on which the cat was riding we created a partial suppression of the normal cat's VOR (see Fig. 10) within 2 h. Since the VOR of the dark-reared cat has a low gain (Harris and Cynader 1979a, 1981) we were able to try not only to reduce the gain by this method but also to increase the gain by the simple expedient of rotating the cat with the room lights on and the optokinetic drum stationary (unattached to the table).

Results

Part 1

Modification of the Balance of the Vestibulo-ocular Reflex

Normal Cat. The cat was positioned on a sinusoidally rotating table with an optokinetic drum moving continuously in one direction around him. The table oscillated at 0.2 Hz with a peak-to-peak amplitude of 10° (peak velocity = 6.3 deg/s). The drum rotated at 6.3 deg/s thus cancelling the visual slip that would otherwise be produced by the movement of the table in one direction and doubling it in the other direction (see methods). This treatment was prolonged for one hour while the animal was maintained in an alert state by a series of loud and varied noises produced by the experimenters. The effect of this stimulus regime is displayed in Fig. 1. The vestibulo-ocular reflex (VOR) measured in the dark before the adaptation procedure is shown by the traces on the left of the figure. The top trace shows the horizontal eye position signal, the next the movement of the table and the next the cumulative slow-phase of the horizontal eye movements. The cumulative trace was produced by hand, extracting the fast saccadic phases and lining up the remaining slow phases by eye. The lower trace shows an instantaneous measure of eye velocity. The solid horizontal line through the velocity trace corresponds to zero velocity. The saccades, because they are so much faster than the slow-phase in these examples, tend to saturate the chart recorder. The sinusoidal velocity trace is initially (left hand

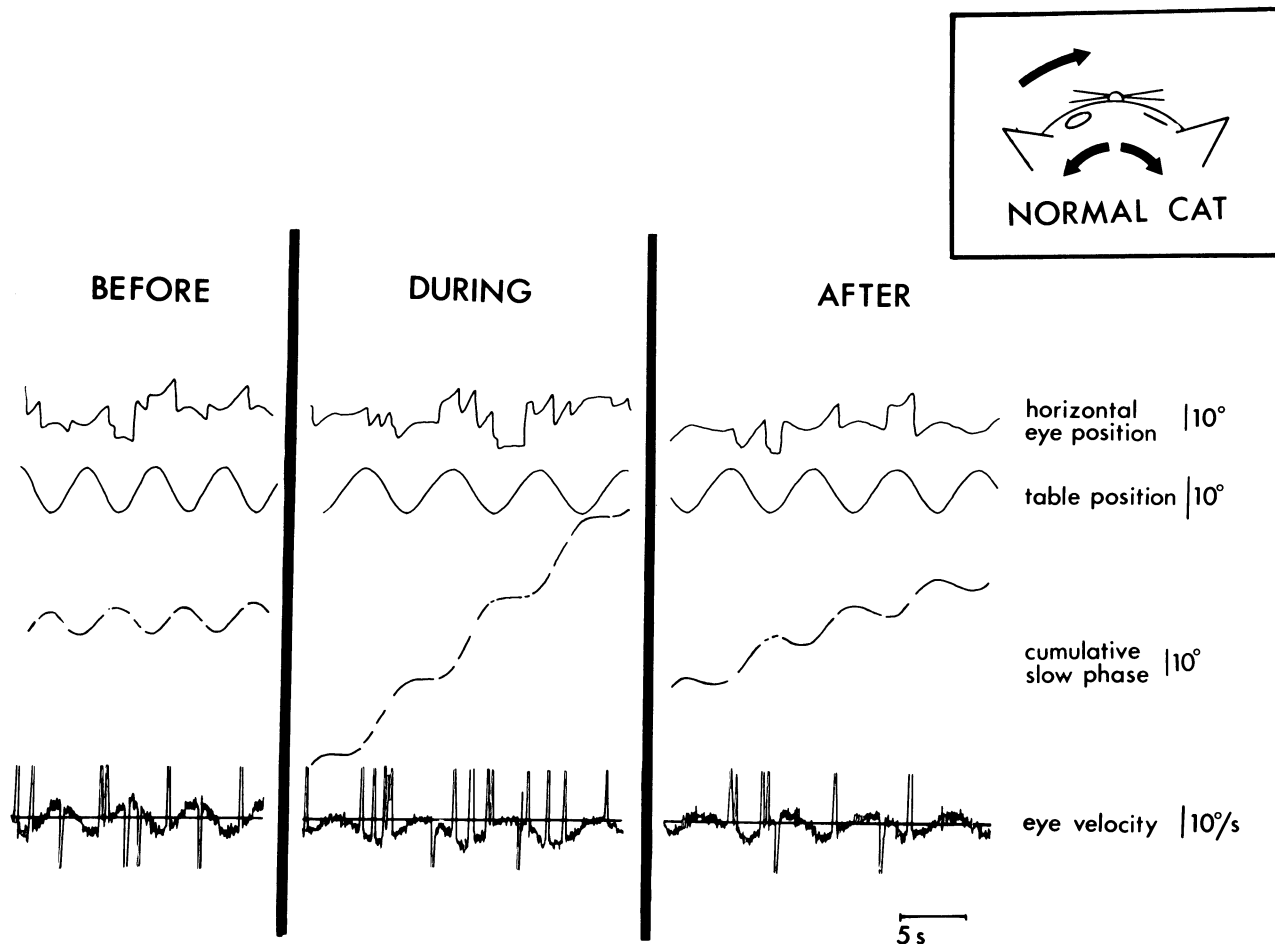


Fig. 1. The modification of the balance of the vestibulo-ocular reflex (VOR) of a normal cat. The VOR before modification is shown by the set of traces on the left. The central traces show the combination of optokinetic and vestibular information during the modification procedure. The right hand set of traces was obtained 30 min after the end of the adaptation stimulus and still retains many of the features of the central set of records. Note the amplitude scales on the right and the time scale on the lower right. The adaptation procedure was done monocularly, viewing through the monitored eye. The optokinetic stimulus direction was medial

traces) centred around zero indicating that the cat had a well-balanced vestibulo-ocular response.

The central set of traces in Fig. 1 shows the same set of data obtained *during* the adaptation procedure. The visual response is summed with the vestibular response to give the pattern of eye movements seen in the top trace. In the velocity trace (lower trace) it can be seen very clearly that the slow-phase response has two major components: a sinusoidal response, due to the table's movement and a constant velocity component, corresponding to the visually induced optokinetic nystagmus which appears on the velocity trace as a displacement of the whole trace with respect to zero.

After 1 h of adaptation the lights were turned off and the VOR once again measured in complete darkness. A set of traces obtained 30 min after the

lights were extinguished is shown on the right of Fig. 1. There was still a large DC component to the velocity trace which now corresponds to eye movements in response to vestibular stimulation alone. The amplitude of the sine wave component remained unaltered by our manipulation indicating that the *gain* of the VOR remained constant, but the DC component in the signal shows that the sinusoidal response is superimposed on a constant drift to one side. The *balance* of the VOR has been selectively altered by the exposure conditions of our experiment.

These VOR balance adaptation experiments were always done with the adapting frequency at about 0.2 Hz. The effect of modification of the *gain* of the VOR at one frequency extends to frequencies far removed from the adapting one (see Part 2). To

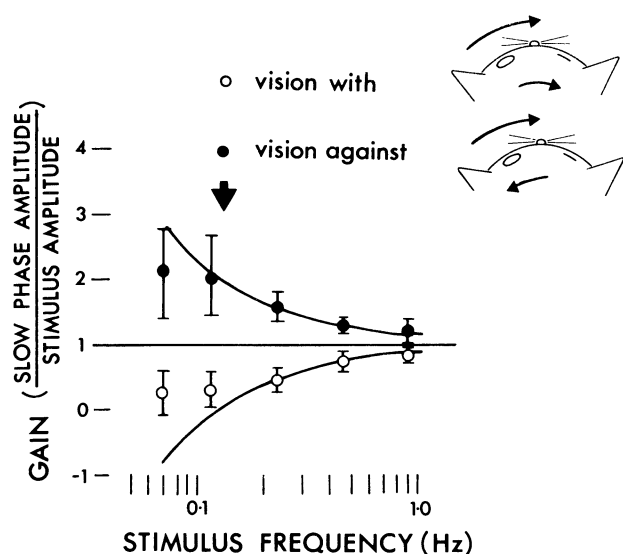


Fig. 2. The positional gain in each direction after adaptation is plotted over the frequency range tested. The gain of the response in the direction in which visual information suppressed the vestibular response (*open circles*, vision with, see inset) is very much lower than in the direction which vision enhanced (*filled circles*, vision against, see inset). The solid lines show the arithmetic sum of a constant velocity (that of the drum) and a sinusoidal response of unity gain. The arrow indicates the adapting frequency

see whether this was the case for modification of the balance of the reflex we measured the post-adaptation VOR at several different frequencies. Different frequencies were randomly interleaved to control for systematic changes over time of the induced balance change. In Fig. 2 the amplitudes of the cumulative slow-phase in response to movements of the table in each direction have been plotted separately as functions of the frequency of vestibular stimulation. The amplitudes in each direction clearly varied with frequency. The solid curves show the arithmetic result of adding a constant velocity to a sinusoid of varying frequency. Because the peak velocity of the sinusoidal response increases with frequency (the amplitude was held constant at 10° peak-to-peak) the relative effect on the expected gain of adding a constant velocity decreases with increasing frequency (and thus peak velocity).

A characteristic feature of imbalance in the VOR as induced by unilateral labyrinthectomy is the existence, in the dark, of a spontaneous horizontal nystagmus whose slow phase is towards the damaged side. Our animals in which the balance of the VOR was altered by visual stimulation, also exhibited a spontaneous nystagmus in the dark following adaptation. The slow phase of this spontaneous nystagmus was in the direction of drum movement and thus

towards the side of the brain whose labyrinthine input had been suppressed by vision. The velocity of the slow phase of this nystagmus diminished over time (see Fig. 9) and the velocity offset from zero of the sinusoid of Fig. 1 was roughly similar to the velocity of the spontaneous nystagmus.

Dark-reared Cat. The vestibulo-ocular reflex of the dark-reared cat demonstrates several anomalies which we have described in detail elsewhere (Harris and Cynader 1979a, 1981). Briefly the gain is only about 0.3 (compared to the normal gain of close to unity) over the frequency range 0.05–1.2 Hz, the gain is rather variable over time and we have observed a frequency-dependent phase relation (see Figs. 3, 10B, and Fig. 4 of Harris and Cynader 1981). Three dark-reared cats were exposed to the adaptation procedure described above for the normal cat. Typical results are presented in Fig. 3 which shows the eye movements obtained before, during and after treatment. The layout of this figure is the same as for Fig. 1. The original gain was much less than a normal cat (0.3 in the section of record shown on the left of Fig. 3) and there was a phase lead of about 180° at this frequency. When the animal was rotated sinusoidally inside a continuously rotating optokinetic drum, several immediate alterations to the pattern of eye movements induced by vestibular stimulation alone were seen. First the gain of the sinusoidal component of the response had a gain close to unity (measured under these conditions in the light); second the optokinetic stimulus was effective in adding a constant velocity component to the response (appearing as an offset in the differentiated record); third the characteristic phase relation (evident on the left; 180° phase lead) was corrected resulting in an effective compensatory eye movement; and finally there appeared a characteristic pendular nystagmus (Harris and Cynader 1981). The first three changes make the central records of Fig. 3 similar to those of Fig. 1 despite the abnormalities both in the optokinetic and vestibular systems of a dark-reared cat (see Harris and Cynader 1981, for a full description of these abnormalities). While the visual stimulus was actually present the anomalies of the vestibulo-ocular reflex were corrected by the visual system: the balance and the gain of the VOR of the dark-reared cat were, in fact, temporarily altered. After 1 h of the combination of visual and vestibular information (with the continuous response shown in Fig. 3) the lights were extinguished and the vestibulo-ocular reflex again measured in total darkness. An example of the records obtained 10 min after the lights went out is shown on the right of Fig. 3. There was no difference between the VOR measured before (left

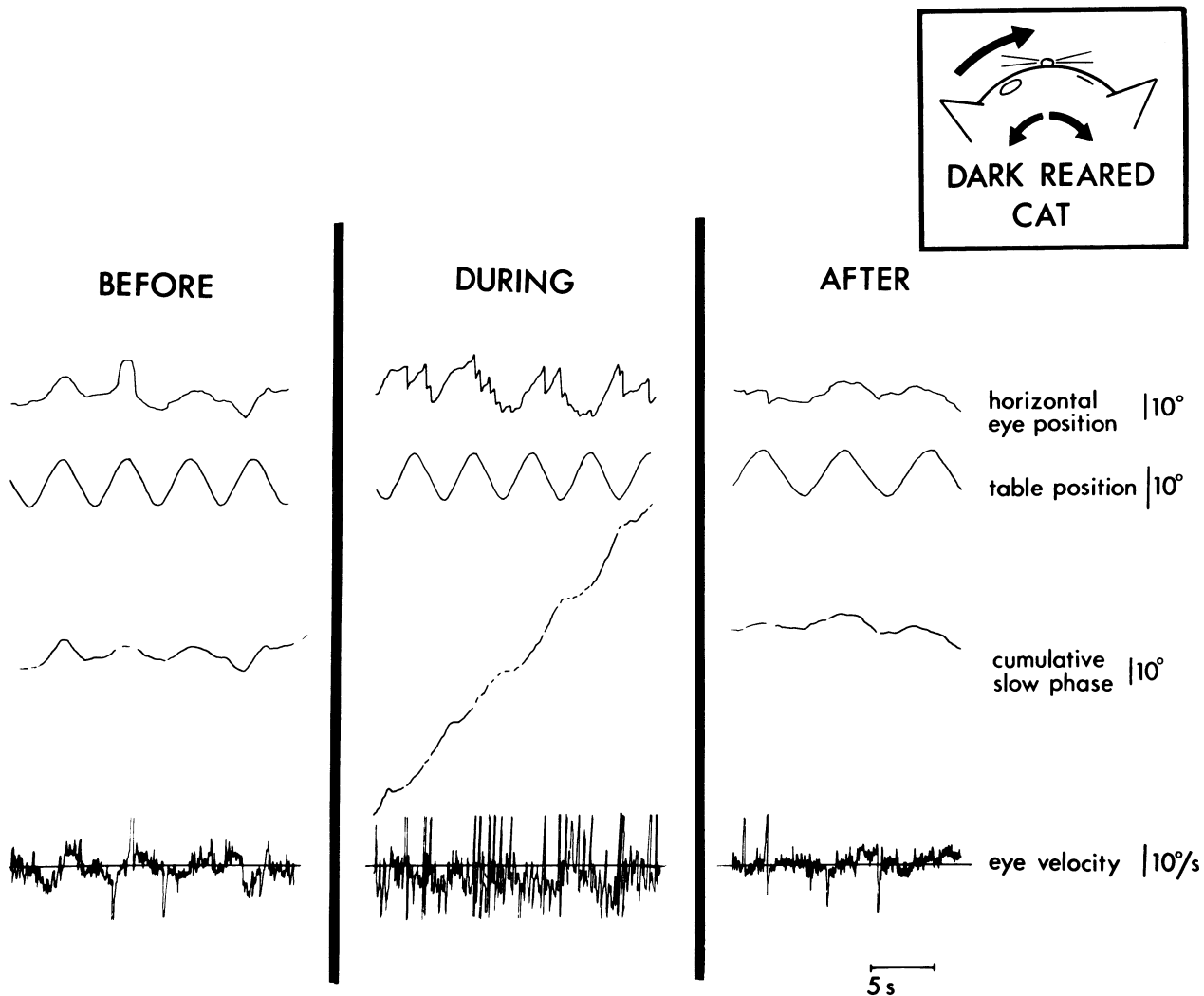


Fig. 3. An attempt to modify the balance of the VOR of the dark reared cat. The format for this figure is just as for Fig. 1. Although during the adaptation procedure (central traces) the optokinetic and vestibular cues combined to produce an appropriate compensatory response there was no effect on the VOR measured afterwards in the dark (right hand traces obtained 10 min after adaptation). Visual stimulation was again monocular through the monitored eye with medial movement of the drum

of Fig. 3) and after (right of Fig. 3) the experience. The results thus show that there was no modification of the balance (or the gain) of the VOR of the dark-reared cat by our experimental procedure.

This lack of modification is further shown in Fig. 4 in which the gains of the two directions of the VOR measured at several frequencies after adaptation are plotted. The format of this figure is the same as for Fig. 2. The theoretical changes in gain in the two directions which would be caused by the addition of a constant unidirectional eye velocity are shown as solid lines. Their location on the graph differs from Fig. 2 because of the low starting value of the dark-reared cat's VOR gain.

Thus the results indicate that the dark-reared cat appears unable to modify the balance of his vestibulo-ocular reflex in response to a stimulus that shows itself to be a very powerful modifier in the normal cat. This absence of plasticity is not due to any inadequacy of the visual stimulus in modifying the response while it is actually present.

Split-chiasm Cat. The procedure outlined above for the modification of the balance of the VOR of normal cats was also applied to two cats that had been subjected to surgical section of their optic chiasm. This operation deprived them of the visual pathways from the nasal hemi-retinae, since these are

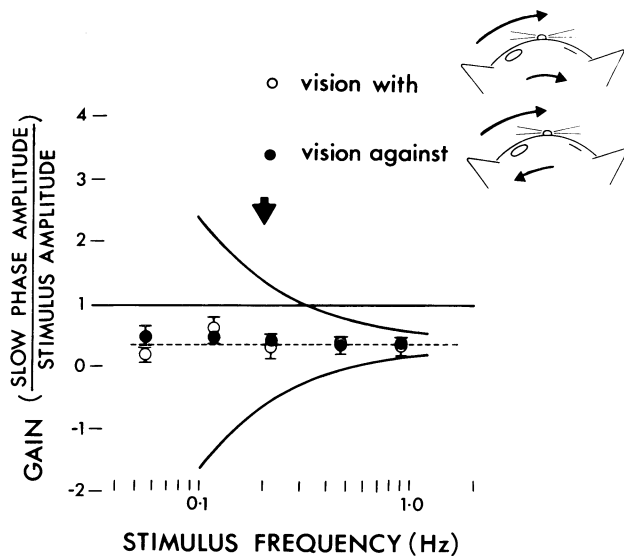


Fig. 4. The positional gain in each direction after the adaptation procedure had been applied to dark-reared cats. The format is the same as Fig. 2. The solid lines show the arithmetic sum of a constant velocity (that of the drum) and a sinusoidal response of a constant gain (the initial gain, 0.3). The arrow indicates the adapting frequency

completely crossed in the cat (Stone 1966), while leaving the uncrossed visual pathways intact. The results are summarized in Figs. 5 and 6. These figures have the same formats as Figs. 1 and 2. The VOR measured before the adaptation of both the split-chiasm animals was of a slightly lower gain than generally found in normal cats. The gains were, however, within the normal range (see for example, Robinson 1976). The central traces of Fig. 5 show that, while the adapting stimulus was presented, the balance of the VOR could be temporarily changed. However, when, after 1 h of the treatment, the VOR was measured in the dark, the balance remained unaltered by the visual experience. This is illustrated by the traces on the right of Fig. 5. These data were obtained after 20 min of darkness following the adaptation stimulus. Figure 6 confirms that there has

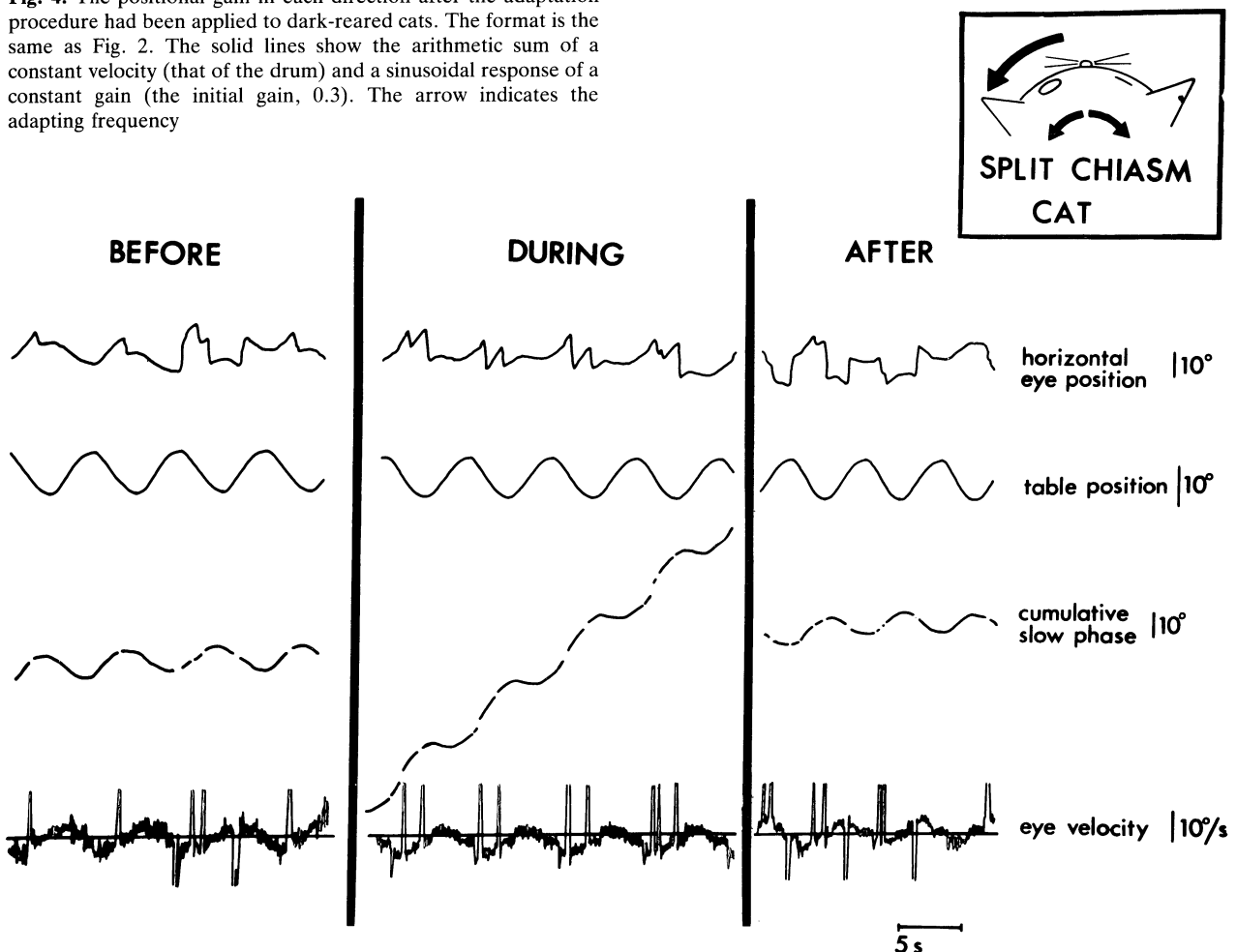


Fig. 5. An attempt to modify the balance of the VOR of the split-chiasm cat. The format of this figure is just as Fig. 1. As for the dark-reared there was a satisfactory summation of visual and vestibular information during the adaptation procedure, but there was no effect on the VOR measured afterwards in the dark (right hand traces, obtained 20 min after adaptation). The visual stimulation was again monocular but the visual stimulus used in this example moved laterally (away from the nose). Both lateral and medial movement failed to alter the balance of the VOR of the split-chiasm cat

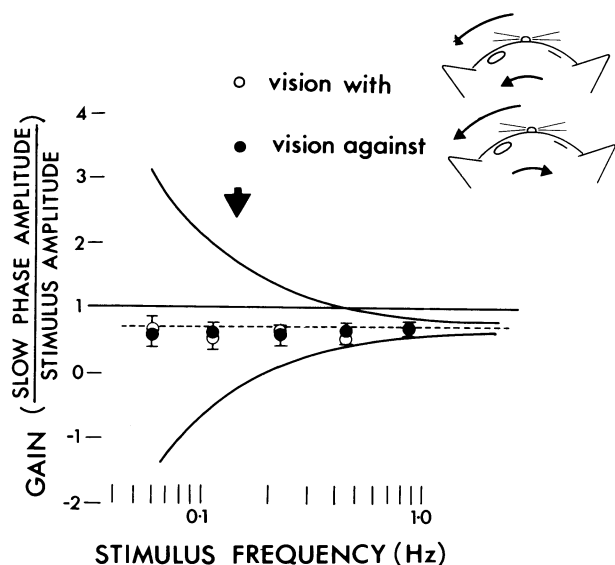


Fig. 6. The positional gain in each direction after the adaptation procedure had been applied to split-chiasm cats. The format is the same as Fig. 2. The solid lines show the arithmetic sum of a constant velocity (that of the drum) and a sinusoidal response of constant gain (the initial gain, 0.8). The arrow indicates the adapting frequency

been no effect of the experience either at the adapting frequency or at any point along the measured range of VOR frequencies.

The split-chiasm cat, like the dark-reared cat, cannot change the balance of his VOR in response to vision; at least not using a stimulus regime that is quite adequate to alter the balance of the VOR in a normal cat.

Comparison of a Split-chiasm Cat with a Normal Cat with his Peripheral Field Occluded. It was possible that the failure of the split-chiasm cat to modify the balance of his VOR was due to the contribution of the nasal hemi-retina (peripheral hemi-field) to this ability of a normal cat. This part of the retina was, of course, prevented from making connexions with the brain by the chiasm section. We therefore subjected one *normal* cat to the VOR balance modification procedure exactly as described above except that the peripheral field was masked. This is shown in the inset in Fig. 7. One eye was completely patched; a mask extended from the straight ahead position of the open eye covering the entire temporal field. Movements of the viewing eye nasally, therefore did allow some vision in the nasal hemi-retina but only up to the range of eye movement (maximum of 20–25°). The peripheral field past this, however, was patched throughout the exposure, regardless of eye deviation. The results of this experiment are sum-

marized in Fig. 7. The balance of the VOR was changed just as if the patch had not been there (right hand traces of Fig. 7). The modification extended over the entire measured frequency range, just as shown in Fig. 2 for the normal cat in which the peripheral field was not occluded.

The reason that the split-chiasm cat was unable to modify to balance of his VOR appears not to be simply the restriction of the peripheral field of vision. The loss of vision in the temporal visual field within 20° of the area centralis, however, cannot be ruled out as a possible explanation.

Modification of the Balance of the Vestibulo-ocular Reflex and Optokinetic After-Nystagmus. Our animals were exposed to two simultaneous stimuli during the modification of the balance of their vestibulo-ocular reflex. The table and animal were rotated sinusoidally providing vestibular stimulation and, at the same time, the optokinetic drum was rotated providing optokinetic stimulation. We have no evidence that the sinusoidal vestibular stimulation by itself had any after effects. Following optokinetic stimulation, however, several workers have described after effects. The first of these is optokinetic after-nystagmus (OKAN) in which the eyes continue to execute a nystagmus in the same direction as the preceding OKN. The OKAN gradually declines to zero velocity and eventually gives way to a nystagmus of the *opposite* polarity: secondary optokinetic after-nystagmus. Little attention has been paid to the effects of *prolonged* visual exposure to an optokinetic stimulus. It has generally been assumed that, once time has been allowed for OKN to reach a steady state, the duration of the preceding OKN is irrelevant to the resulting after-nystagmus. In order to examine the possible role of optokinetic after-nystagmus in the modification of the VOR balance, we rotated the optokinetic drum continuously around the animals exactly as before for 1 h but *without the table movement* and hence without direct vestibular stimulation.

Figure 8 shows that, surprisingly, the effects on the VOR of a normal cat were exactly as for the condition in which both the table and the drum moved. The gain of the VOR after the experience remained unaltered, but the *balance* between the two sides was upset (right hand traces). The spontaneous nystagmus, described earlier, which followed the exposure to the original modifying stimulus was once again observed but in this case may be considered to be an extremely prolonged form of optokinetic after-nystagmus (OKAN). The nystagmus persisted for nearly 1 h (the period of adaptation) and its superimposition upon a vestibular response appears sufficient

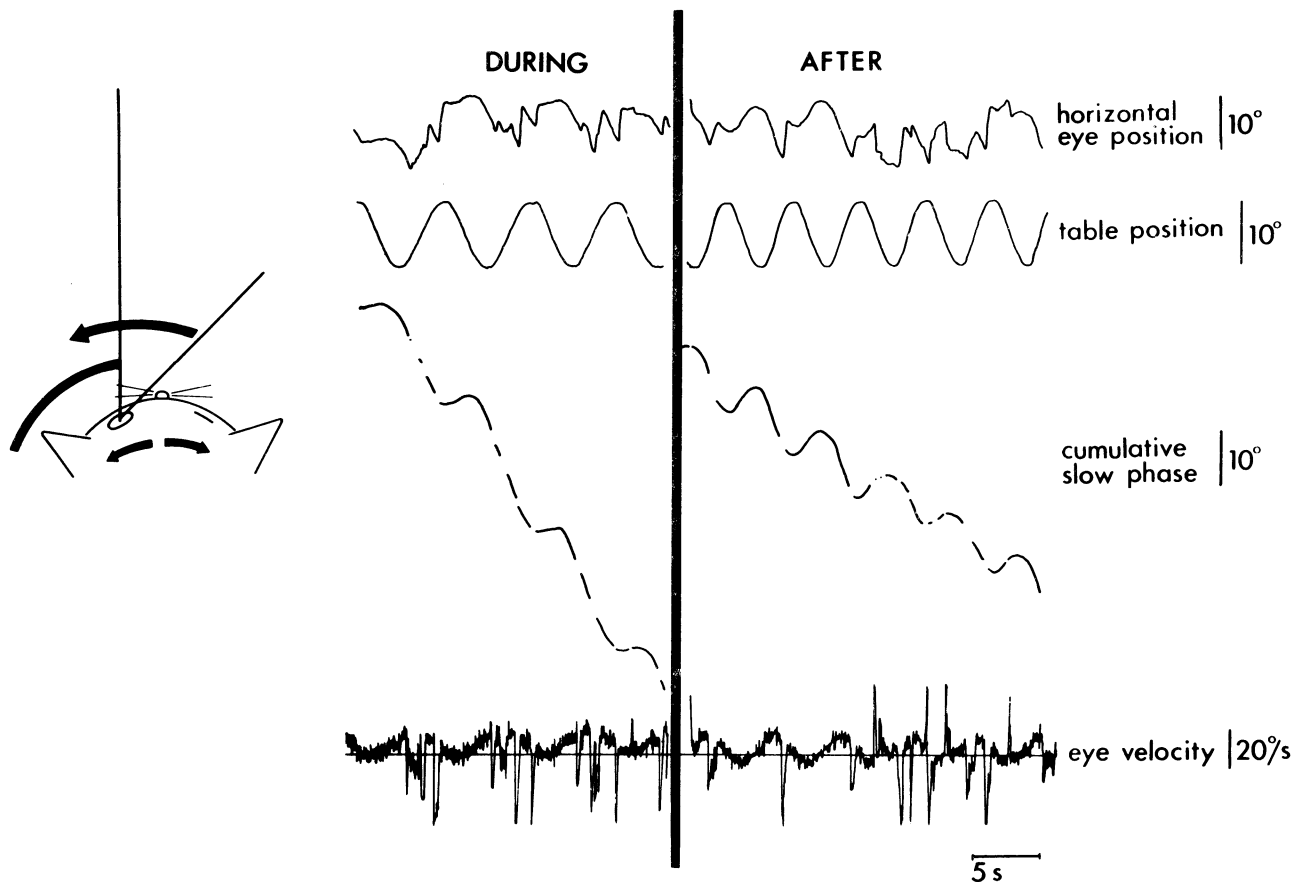


Fig. 7. Modification of the balance of the VOR of a normal cat with the peripheral field occluded (*inset*). Visual stimulus movement was lateral. The VOR measured in the dark after the adaptation (*right-hand traces*; after 20 min) showed considerable balance alteration and resembled the response during the procedure (*left-hand traces*)

to account for a good deal of the balance alteration of the normal cat illustrated by Figs. 1 and 2. The time course of the nystagmus is shown in Fig. 9. In this figure the duration of after-nystagmus resulting from 1 h of drum rotation alone is shown for the three classes of cat (normal, dark-reared and split chiasm). Clearly the after-nystagmus was very much longer lasting for the normal cat. The after-nystagmus of the split-chiasm cat declined very much faster and resembled more that of the dark-reared cat in this respect (Fig. 9). The split-chiasm cat differed from the dark-reared, however, in producing a very pronounced secondary optokinetic after-nystagmus although even this lasted much less time than the after-nystagmus of the normal cat. The secondary after-nystagmus was, on occasion, faster than the original OKN (but in the opposite direction). When the vestibular response to sinusoidal oscillation of the animals was measured in the dark during this relatively short-lived oppositely-directed nystagmus, a balance change in the *opposite direction* (compared to the normal cat) was apparent.

This is shown by the two traces that form the lower part of Fig. 9. These traces show the horizontal eye movements of a split chiasm cat during the first few minutes of darkness after the full adaptation procedure (i.e., drum and table moving). The OKAN lasted only about a minute and was then replaced by the oppositely-directed secondary OKAN. When the response to sinusoidal rotation was measured (right hand part of trace) a balance change was found (DC component to velocity trace) in the *opposite direction* to the temporary balance change induced during and for a few seconds following stimulus presentation (left hand part of trace). This observation closely links the visual generation of after-nystagmus to the mechanisms underlying modification of the balance of the vestibulo-ocular reflex.

A further intriguing finding concerning the OKAN of a normal cat is shown in Fig. 9. The OKN induced by the movement of the optokinetic drum was initially of an appropriate gain (unity gain at this speed of drum rotation, 6.3°/s). However, after 1 h of

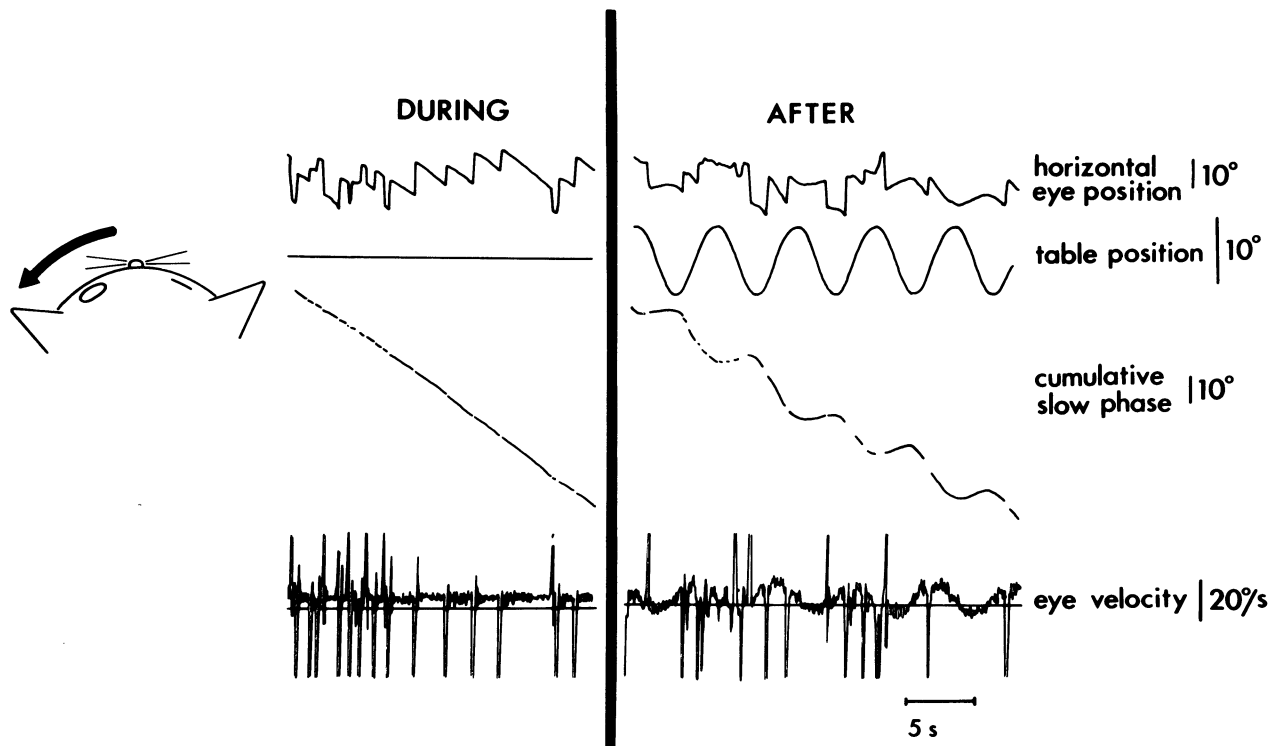


Fig. 8. Modification of the balance of the VOR of a normal cat by vision alone. The format of this figure is as Fig. 7. During the adaptation procedure the drum was rotated continuously (as in the original case, see Fig. 1) but the table (*second trace down*) remained stationary. The VOR measured in the dark after the adaptation (*right-hand traces*, after 30 min) showed considerable balance alteration. The examples shown here were obtained with monocular lateral stimulation; medial stimulation produced similar results

continuous presentation of the moving drum (and the optokinetic response) the gain of the reflex (defined as eye velocity divided by stimulus velocity) had risen to about 1.3; that is the eyes were rotating *faster* than the drum itself. This observation could not be an artefact of eye movement calibration; the speed of the drum was monitored continuously throughout the experiments. All three normal animals showed this phenomenon and in both directions of drum movement. It is unlikely that fatigue of eye muscles or the peripheral motor control is responsible for this increase in gain above unity since the split-chiasm animals showed no such increase despite the equally prolonged performance of OKN.

A second method adopted for presenting the visual modifying stimulation without concurrent vestibular stimulation was to reverse the normal roles of the table and drum: the table rotated continuously and the drum oscillated sinusoidally about the spinning animal. Under these conditions the vestibular system (sensitive only to acceleration) soon ceased to provide movement information and yet the visual stimulation remained the same as in the original paradigm. This treatment produced results identical to those produced by the original stimuli combina-

tion. The balance of the VOR can clearly be modified by optokinetic stimuli alone, in the absence of direct vestibular stimulation.

Part 2

The Modification of the Gain of the Vestibulo-ocular Reflex

Normal Cat. In order to modify the gain of the vestibulo-ocular reflex (VOR) of a normal cat the animal was held in the centre of an optokinetic drum that filled the visual field and moved with him while he was rotated sinusoidally. The visual scene was therefore stationary with respect to the moving cat and the visual information (no movement) was in conflict with the vestibular information (movement).

The normal animals were subjected to this visual-vestibular conflict for 2 h at the end of which time the lights were switched off and the VOR measured over the full range of frequencies available. The results are shown in Fig. 10A and demonstrate that the gain of the VOR was substantially decreased over a large part of the frequency range (open circles). When the animal was released into his normally-lit home col-

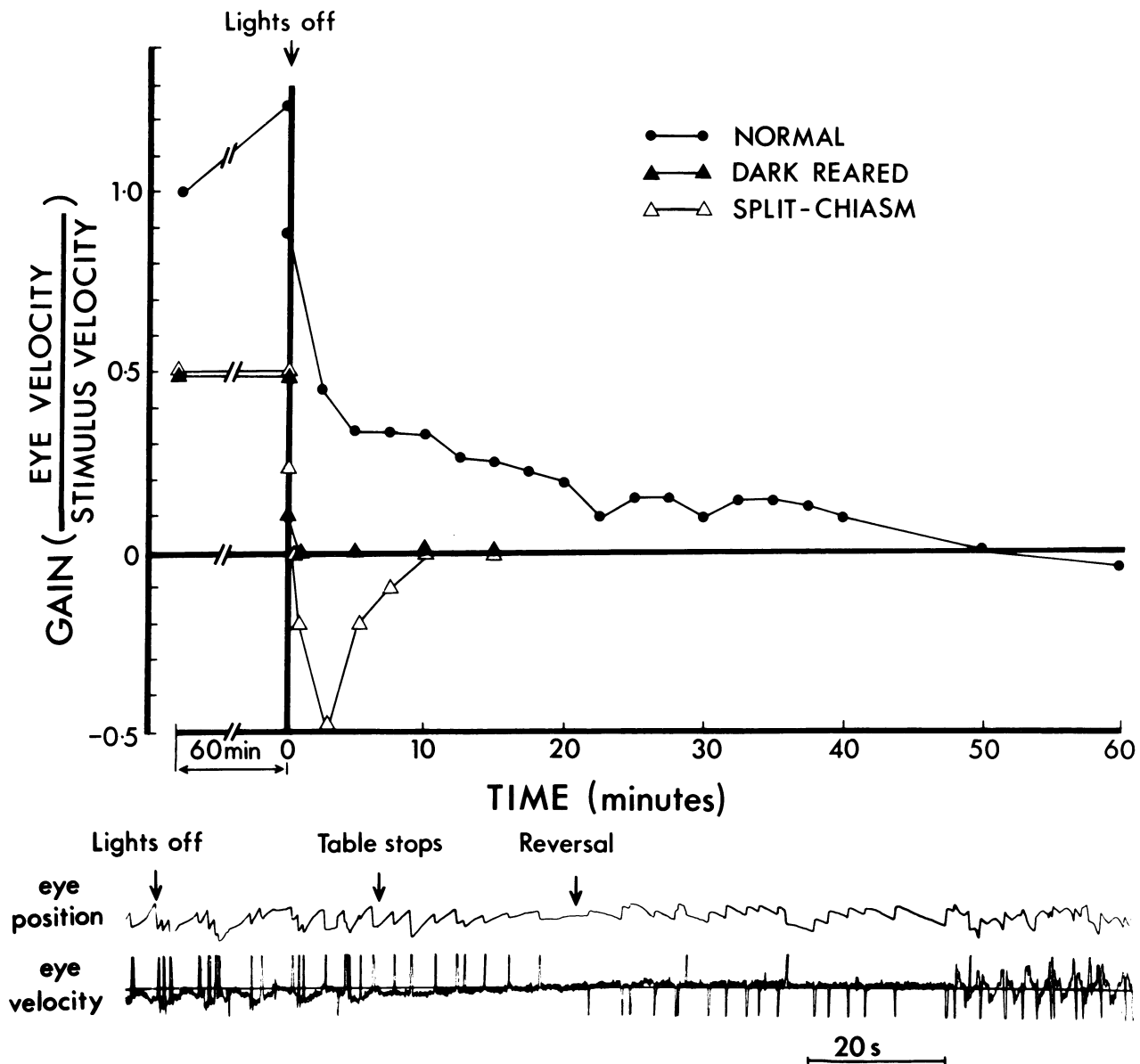


Fig. 9. After 1 h of optokinetic stimulation (without concurrent vestibular stimulation) the normal cats developed an after-nystagmus in the same direction as the original OKN that lasted for about 50 min (*filled circles*). Neither the dark-reared (*filled triangles*) nor the split-chiasm animals (*open triangles*) displayed anything like such a long-lived after-nystagmus in this direction. The graphs are averages of all animals after both medial and lateral visual optokinetic stimulation. The reversal of direction of after-nystagmus in the case of the split-chiasm cat is further illustrated by the records below the graph. This example was obtained after an adaptation procedure in which both the table and the drum were moving (see central traces of Fig. 5). The table continued to rotate sinusoidally for about 30 s after the lights were extinguished (between the "lights off" and "table stops" arrows). During this time the balance indeed appeared shifted. However, only 1 min after the lights were turned off, the after-nystagmus reversed direction (arrow labelled "reversal") and subsequent vestibular testing revealed a balance shift in the opposite direction. This change does not appear in Fig. 5 since it is so short lived

only the gain quickly recovered its original value (*filled circles*). Normal animals subjected to prolonged rotation in the dark as a control did not show this substantial decrease.

Dark-reared Cat. Having confirmed that the gain of the normal cat was indeed adaptable and could be

easily and quickly manipulated in our apparatus we subjected the dark-reared animals to a similar treatment. We took advantage of the fact that the gain of the VOR of the dark-reared cat was much lower than that of a normal cat (0.3 over the range 0.05–1.2 Hz; *filled circles* Fig. 10B; see also Harris and Cynader 1981). Forced rotation of the animal in the light while

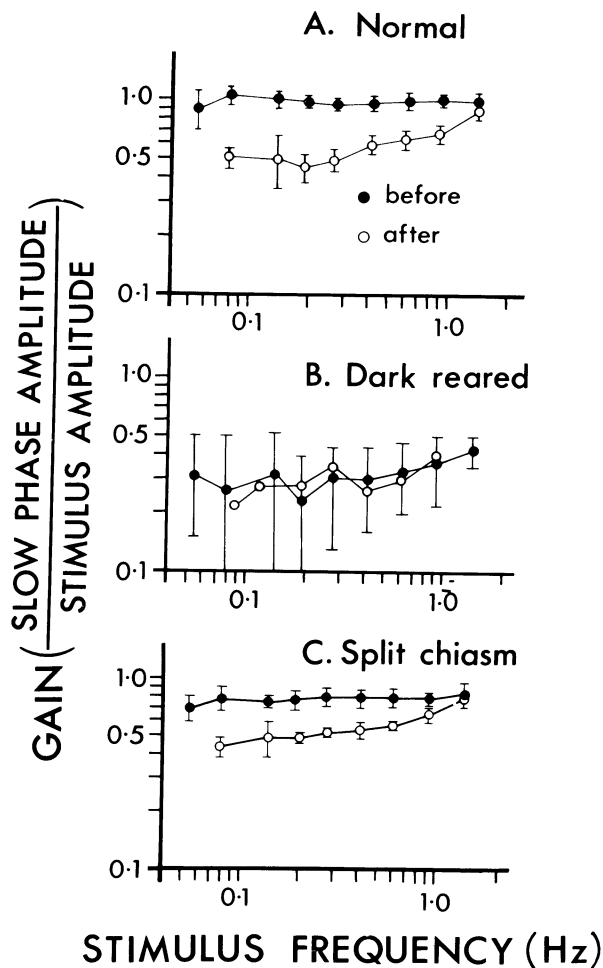


Fig. 10A-C. Modification of the gain of the vestibulo-ocular reflex of the normal cat **A** was achieved by rotating the optokinetic drum with the animal. The visual stimulus was therefore stationary with respect to the animal and suppressed the vestibulo-ocular response. When the VOR was tested in the dark after 2 h of adaptation, the gain was indeed found to have fallen (*open circles*) from the initial values (*filled circles*). The adapting frequency was 0.2 Hz. The VOR of the dark-reared cat **B** appeared not to be susceptible to modification. Forced rotation in the light (causing temporary enhancement of the VOR to a gain of one) had no effect on the gain measured subsequently in the dark (*open circles*). The open circles were in fact obtained after several weeks of living in a normal environment (see text) during which time several attempts were made to raise the gain by forced rotation. Filled circles represent the gain of the VOR measured in the dark before any visual experience. Modification of the gain of the VOR of the split-chiasm cat **C** was achieved, as in the normal cat, by rotating the optokinetic drum with the animal

leaving the drum stationary thus introduced a visual-vestibular conflict. The rotation in the light indeed produced a reasonable gain measured in the light (when both optokinetic and vestibular cues were available) but, as soon as the lights were extinguished, the gain of the VOR resumed its original

low level. This is shown in Fig. 10B. The filled circles, obtained before the forced rotation, overlap closely the open circles obtained after. There was thus no modification of the gain of the VOR of the dark-reared cat using a paradigm that was effective in the modification of the gain of the normal cat.

We confirmed the unmodifiability of the gain of the VOR of the dark-reared cat in quite a different way. After the animal had been studied he was released into a normally-lit cat colony. Under these conditions, each natural head movement of the animal was a stimulus for VOR modification. Each head movement evoked visual and vestibular cues for the generation of corrective eye movements. In a normal cat such a continuous conflict of visual and vestibular information modifies the VOR extremely rapidly. Analogous experience has no effect on the VOR of the dark-reared cat. Even after 5 months of free visual experience the gain remained below 0.5 throughout the range of frequencies measured (see Fig. 12, Harris and Cynader 1981). The results indicate that the gain of the vestibulo-ocular reflex of the dark-reared cat is as unmodifiable as is its balance.

Split-chiasm Cat. Subjecting the split-chiasm cat to exactly the same procedure as described above for the normal cat produced a long-lasting change in gain of the VOR very similar to that produced in a normal animal. The split-chiasm cat was rotated sinusoidally at 0.2 Hz with stabilized vision (drum rotating in phase with the table) for 2 h. The induced visual-vestibular conflict was effective in reducing the gain of the VOR by a similar amount to that of the normal cat. This is shown in Fig. 10C. It will be noticed that neither the split-chiasm cat nor the normal cat completely suppressed their VOR. Such large-scale modification presumably requires very much longer periods of exposure to the modifying stimulus.

Discussion

There are two aspects of the vestibulo-ocular reflex (VOR) that we have shown to be modifiable independently from one another in the normal cat: the *gain* and the *balance* of the reflex. Visual deprivation abolishes modifiability of either of these aspects in the cat. Surgical section of the crossed visual pathways (achieved by splitting the optic chiasm) leaves the ability to modify the gain of the reflex but abolishes modifiability of the balance. Either dark rearing or midsagittal chiasm section severely reduces the duration of optokinetic after-nystagmus.

The Control of the Gain of the Vestibulo-ocular Reflex

The adult vestibulo-ocular reflex has recently been shown to be extremely adaptable in both man (Gonshor and Melvill Jones 1971, 1976b), cat (Melvill Jones and Davies 1976), monkey (Miles and Fuller 1974), rabbit (Ito et al. 1974; Collewijn and Kleinschmidt 1975) and even non-mammalian species (Dieringer and Precht 1979). The output of the vestibular end organs are multiplied by a common value to produce the *gain*. This value can be changed by atypical visual exposure, as when, for example, our normal cats were force-rotated with stabilized vision producing a visual-vestibular conflict (Fig. 10A). This is also what happens when wearing reversing prisms requires the gain to become negative (Melvill Jones and Davies 1976), or magnifying or minifying lenses require the gain to rise or fall (Miles and Fuller 1974; Gauthier and Robinson 1975). Several possible mechanisms for modification of VOR gain include those proposed by Ito (1972) and Lisberger and Miles (1980) which involve the cerebellum. It now seems that the mechanism by which the VOR's gain is changed is certain to depend on an intact cerebellum, particularly the cerebellar flocculus (e.g., Ghelarducci et al. 1975; Ito et al. 1973). Lesions of this area abolish the ability to modify the gain of the VOR in response to vision (Ito et al. 1974; Takemori and Cohen 1974; Hassul et al. 1976; Robinson 1976). Curiously, however, if the gain is changed (by visual experience) and then the flocculus is *immediately* removed, the gain returns to the *previous* value (Robinson 1976). This finding suggests that the previous baseline value is, in fact, stored elsewhere. A distinction must be made between relatively short-term changes brought about, for example by reversing prisms, or various lenses, and the very long-term standards to which these changed values are referred and to which the system reverts in the absence of the flocculus. Dark rearing leaves the ability to suppress or enhance the VOR while the animal is in the light but abolishes the system by which these adaptive changes are maintained in darkness. It may be that one of the consequences of dark-rearing is simply to prevent visual input from influencing the cerebellar neurones which play an important role in VOR modification. It is known in other contexts that one effect of dark rearing is to reduce the sensitivity of neurones in the cat superior colliculus to visual input. This may be brought about by a competitive interaction between visual afferents and those from other sense modalities such as audition (Cynader 1979; Harris and Rauschecker 1981). If a similar loss of visual respon-

Table 1. Modifiability of the gain and balance of the vestibulo-ocular reflex

	Gain	Balance
Normal cat	Yes	Yes
Dark-reared cat	No	No
Split-chiasm cat	Yes	No
Flocculectomized cat (Haddad and Robinson 1977)	No	Yes

siveness occurred in the cerebellum of dark-reared cats it would provide a mechanism for the lack of VOR gain modifiability we observed.

One might maintain that the low VOR gain of the dark-reared cat, itself represents an adaptive response to its rearing conditions. There is after all, no incentive to maintain a VOR gain of one when the animal is in darkness. However, a normal cat placed in darkness for a prolonged period showed little VOR gain alteration (Harris and Cynader 1981), and the dark-reared cats studied here could not achieve an adaptive increase of VOR gain even after prolonged visual exposure.

The Control of the Balance of the Vestibulo-ocular Reflex

We have shown a dissociation between modifiability of the gain and balance of the VOR since our split-chiasm cats were able to modify the VOR gain but not its balance. Dark-reared cats were also found to be unable to change the balance of their VOR in response to our visual procedure (Figs. 3 and 4). Normal 4 month old kittens cannot modify their VOR balance (Berthoz et al. 1975) in terms of compensation for hemilabyrinthectomy. However, since the gain of the VOR has become roughly appropriate by this age (Flandrin et al. 1979), it would appear that the *gain* is modifiable at this time: the mechanisms for control of gain and balance of the VOR appear to mature at different rates. The neural mechanisms involved in balance changes remain uncertain. Haddad and Robinson (1977) have demonstrated that the cerebellum is *not* the site for the modification of the balance since lesions of the cerebellum that abolish gain modifiability do not prevent cats from compensating for the *balance* change induced by hemilabyrinthectomy. There is thus a *double* dissociation between gain and balance modifiability which is summarised in Table 1. We have demonstrated that the modifiability of the balance of the VOR is abolished by the unlikely expedient of surgical section of the crossed visual

pathways at the level of the chiasm. The ipsilateral visual projections that this operation spares are relatively modern in their phylogenetic appearance. However, visual information conveyed by these remaining projections mediates some aspects of optokinetic nystagmus (OKN) (Harris et al. 1980) and also permits modification of the *gain* of the VOR.

The mechanism involved in the balance modification appears to be closely linked with the mechanisms underlying optokinetic after-nystagmus (OKAN). Both dark-reared and split-chiasm animals showed unusually short-lived OKAN as well as an inability to modify their VOR's balance. Indeed it appears that the changes of OKAN in these animals are largely sufficient to account for the unmodifiability of VOR balance. OKAN has been shown to interact with vestibulo-ocular responses in the monkey (Young and Henn 1976; Raphan et al. 1977, 1979) and man (Young and Henn 1974; Cohen et al. 1978). After bilateral labyrinthectomy (after which there can of course be no VOR in response to angular acceleration) optokinetic after-nystagmus is also found to be abolished (Cohen et al. 1973; Collewyn 1976; Zee et al. 1976), further indicating close links between the vestibular and OKAN systems.

Neuronal activity in the vestibular nuclei, normally closely associated with vestibulo-ocular eye movements (Fuchs and Kimm 1975; Waespe and Henn 1977a), also parallels optokinetic nystagmus (Keller and Daniels 1975; Allum et al. 1976; Waespe and Henn 1977a) and optokinetic after-nystagmus (Waespe and Henn 1977b). The cerebellum, unneeded for the control of the VOR balance (Haddad and Robinson 1977) is also unnecessary for this visual response since it is still obtained after cerebellectomy (Keller and Precht 1978).

The results from the dark-reared cat which performs OKN using crossed visual pathways (Harris et al. 1980) and the split chiasm cat which uses uncrossed visual pathways suggest that both long-lived OKAN and VOR balance modification may depend on a comparison of the activity of crossed and uncrossed visual pathways. Since neither of the above groups have both sets of visual inputs available, they share the inability to modify VOR balance. This hypothesis suggests that decorticate cats which are characterised by completely crossed projections to the NOT (Hoffman et al. 1977) might also lack the ability to modify VOR balance.

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