

ERGs because of nasal deviation of the gaze, and the responses through this electrode (No. 1) were always recorded as control. The eye of subjects was deviated to the nasal side by  $35^\circ$  and was fixed by gazing at a visual target marked on the inner surface of an adapting dome. *Results and discussion.* 2 series of recordings were typically shown in figures 1 and 2. Responses through the electrode 1 were normal ERGs (control). They consisted of a faint a-wave, a prominent b-wave and oscillatory potentials. A faint slow wave on the response through the electrode 6 was an appearance of the visually evoked cortical potential (VECP). It was noted that, on the recordings of 3, 4 (figure 1) and of 2, 3, 4, 5 (figure 2), several wavelets appeared. The implicit times of positive peaks were measured and were 13–15, 18–20, 24–26, 30–31, 37–38 and 44–46 msec in turn. Among them, the latter 3 (7–8 msec interval) were the rest of the oscillatory potentials superimposed on the remaining and slightly reversed b-wave of a low amplitude, because of an excess deviation of the visual axis to the nasal side. However, the initial 2 or 3 peaks on these recordings are difficult to identify as special parts of ERGs from the following reasons. We are inclined to consider that these wavelets on an early phase might be the potentials from the optic nerve. 1. No wavelets corresponding to these were observed on the early phase of upper traces. If these wavelets are parts of ERGs, they should appear more prominently on the recordings through the electrode 1. 2. These wavelets have not appeared on the recordings from the position 6 and 7. This suggested that the wavelets were different from VECP. The implicit times were too short to suggest that they are parts of VECP. 3. If these are potentials from extraocular muscles, they should appear also on the latter phase and appear on responses of the position 1, because

the eye was deviated to the nasal side. In this case, the external rectal muscle is antagonizing and the internal rectal muscle is an acting one. The action potential of the antagonizing muscle is weaker than that of the acting muscle. Another reason to exclude the muscle potentials is that the action potentials of extraocular muscles are as fast as 300–800 Hz<sup>6</sup>. The action potential of periocular muscle is similar to that of skull muscle, and is 5–10 Hz<sup>6</sup>. This is quite different from the fast wavelets of this study. The action potentials of periocular muscles are responses which do not synchronize with photo-stimuli. 5. Another possibility is that these are responses from the visual tract of higher level, for example, the lateral geniculate body (LGB). But LGB is anatomically far from the lateral canthus of the eye, and responses of LGB consist of slow waves as VECP. The nasal deviation of the visual axis pushes the optic nerve near to the lateral canthus. This phenomenon has usually been observed by a computer-assisted tomography, and is convenient for the electrodes on the lateral canthus to pick up potentials from the optic nerve.

We are interested in these early, fast wavelets recorded from the lateral canthus during ERG-neutralization, and consider a high possibility that these are the optic nerve potentials. Until now all trials to record clinically action potentials of the optic nerve have failed, for example, inserting electrodes into the nasal and oral cavity. Hence, we suggest the importance of further investigation of these wavelets and a possibility of clinical use, although the signal/noise ratio is low and more advance in recording techniques is needed.

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## Alternating activity between neurons of lateral geniculate nucleus and Superior colliculus in rabbit

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*Summary.* In rabbits, simultaneous recordings of unitary activity of lateral geniculate nucleus and superior colliculus revealed that some neurons of these structures presented fluctuations in their firing pattern which are opposite in phase.

Among mammals, two neural networks play a role in the processing of visual information: they are retino-tectal and retino-cortical<sup>3–6</sup>. The retino-tectal system is involved in oculo-motor functions<sup>7,8</sup> whereas the retino-geniculo-cortical pathway primarily serves perceptual functions<sup>9</sup>. The relationship between these 2 networks is not fully understood<sup>10–12</sup>. Thus, the aim of this study was to demonstrate by simultaneous recording from the *lateral geniculate nucleus* (L.G.N.) and the *Superior colliculus* (S.C.) that the occurrence of spike activity for some cells in one structure is time-locked to an absence of discharge at the other site; that is, some geniculate and collicular neurons present fluctuations in their neural activity which are opposite in phase.

*Methods.* The experiments were conducted on pentobarbital-anesthetized and paralyzed rabbits. 2 tungsten micro-electrodes were lowered into the L.G.N. and S.C. In the S.C., all cells described in this study were recorded from the superficial layers, i.e. zonale, superficial gray and optic as determined by the morphology of the field potential<sup>13</sup>; electrode site was verified by histological

examination. Unit recordings were identified primarily on the basis of the waveform<sup>14</sup>. Cells were activated by full-field 'ON' and 'OFF' illumination (4 foot candle at the cornea) and electrical stimulation of the retina (trans-retinal stimulation), visual cortex and the optic nerve at its exit from the eye. In the L.G.N., response to optic nerve stimulation permitted differentiation between relay cells (P) and interneurons (I), which gave repetitive responses or a burst to a single afferent volley<sup>15</sup>. The method of mapping the receptive field of some of the cells has been described elsewhere<sup>16</sup>.

*Results.* 36 pairs of simultaneously recorded units were investigated (36 collicular units and 31 from the L.G.N., since some geniculate neurons were coupled with more than one collicular cell). 16 pairs of cells exhibited a clearly opposite phase pattern of discharge. Examples of alternating activity between geniculate and collicular neurons is shown in Figure 1A for three different pairs. The cells of the first pair (tracing 1, 2, Figure 1) both responded by a brief burst to light 'ON' with identical latencies (see dot), indicating that the same retinal chan-

nel converged on them. Later during the 'ON' period, the geniculate and collicular neurons underwent alternate changes. The alternating activity of geniculate and collicular neurons was more evident when the 'OFF' stimulus applied (Figure 1, tracings 1 and 2). In both cells, 'OFF' responses (dots) were followed by short periods of high frequency discharge separated by silent periods. The most intriguing observation was that the high rate of impulses in one unit coincided in time with spike-free periods in the other. This alternating fluctuation lasted up to 800 msec after the initial 'OFF' step. The most frequent case of alternating activity was encountered when collicular 'ON' response fell between 2 periods of activity in the L.G.N. neurons; this was also found with multi-unit recordings. The example of tracings 3 and 4 (Figure 1) shows that the 'ON' response of the collicular cell (tracing 4) appeared as soon as firing in the geniculate unit (tracing 3) ended. Another pattern of alternating activity is provided by the two cells illustrated in tracings 5 and 6 which were both most effectively stimulated by moving spots. The back and forth movement of a light spot elicits responses at every passage of the light. These specific conditions evoked a high frequency burst which did not occur simultaneously in the 2 structures. Half the units were tested for sensitivity to moving targets; all of these exhibited an alternating pattern of activity. The responsiveness of the same cells to full field 'ON' and 'OFF' stationary illumination showed that geniculate cell activity decreased when the collicular neuron exhibited an increase in firing rate (tracings 7 and 8).

'ON' and 'OFF' retinal channels may both be activated by light and electrical stimulation of the retina (T.R.S.). The latency of the response evoked by T.R.S. is determined by the polarity of the pulse (cornea negative or

positive) according to the receptive field type<sup>16-17</sup>. This property was used to modify the latencies of the evoked activity and spike-free periods observed simultaneously in the L.G.N. and S.C. An example of a pair of cells responding to T.R.S. is shown in Figure 1, B, C. The time course of the response to an anodal (A.S.) pulse of the geniculate interneuron (I) (Figure 1, B, tracings 1, 3, 5) had a spike-free period of 40 msec; it was during this silent pause that the collicular cell responded very regularly with a brief burst (tracings 2, 4, 6). Reversing the polarity of the stimulating pulse (i.e. cathodal C.S.) changed the time of appearance of the responses, but the alternating pattern of firing between the two cells was

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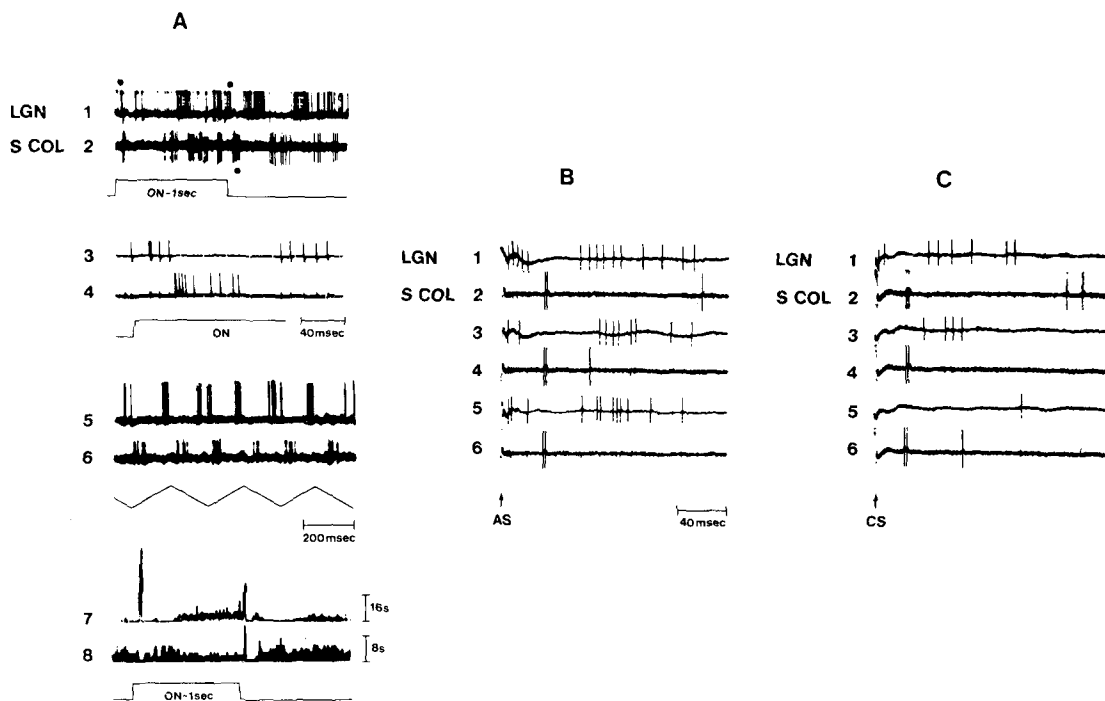


Fig. 1. A Examples of 3 pairs of cells simultaneously recorded from L.G.N. (P) (tracings 1, 3, 5, 7) and S.C. (tracings 2, 4, 6, 8). Tracings 1, 2 and 5, 6 were obtained from 4 to 5 superimposed sweeps. Tracings 3-4: single sweep. Units from tracings 7 and 8 are the same as are shown in tracings 5 and 6. The geniculate neuron responded to 'ON' and 'OFF' throughout its receptive field with no direction specificity. The collicular cell's receptive field was rather wide and its response to a stationary light spot was feeble (see tracing 8). Both receptive fields were not overlapping. Bin width 2 msec.

B-C L.G.N. unit is an I cell. A.S. anodal polarization of the retina, C.S. cathodal polarization of the retina, voltage unchanged. Single sweep for each tracing.

maintained. Tracings 3, 4, 5 and 6 illustrate that the occurrence of spontaneous activity of the collicular cell is associated with a decrease in activity of the geniculate neuron. In tracings 4 and 6 (Figure 1, B, C), it is shown that occasionally the collicular neuron presented a spike at 70 msec which coincided with a delayed discharge (tracing 3) or a complete absence of activity (tracing 5) in the geniculate neuron.

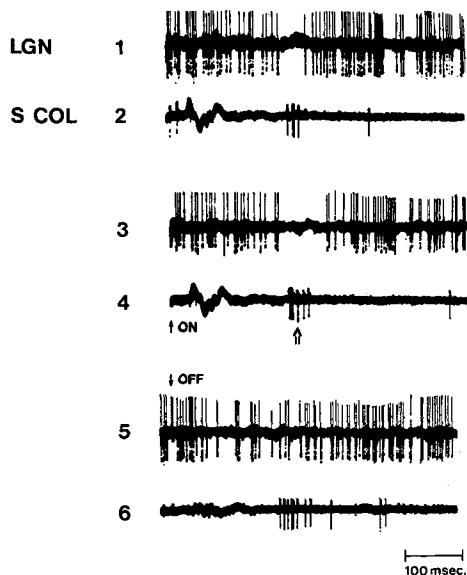


Fig. 2. Simultaneous recordings from L. G. N., P cell (tracings 1, 3, 5) and S. C. (tracings 2, 4, 6). Following an 'ON' step, the geniculate neuron presented a transient interruption of its activity. The burst of the collicular cell occurred while the geniculate cell was prevented from firing. All tracings were obtained from 4 to 5 superimposed sweeps. The polarity of the collicular evoked potentials to the 'ON' stimulus (tracings 2, 4) and the absence of a distinguishable 'OFF' response (tracing 6) confirm that the collicular unit is located very superficially in the S.C.

The example in Figure 2 provides additional insight into the mechanism underlying this alternating type of activity between the L.G.N. and S.C. The geniculate unit shown in Figure 2 (tracings 1, 3, 5) responded rather weakly to 'ON' and 'OFF' stimuli but was capable of firing at any moment for 1 sec following the 'ON' stimulus, except for a short period of time between 195 and 240 msec. In comparison, the collicular cell (Figure 2, tracings 2-4), recorded simultaneously, exhibited a very slow rate of firing. Its highest period of excitation occurred with a long latency (195 msec) and thus, precisely during the silent period of the geniculate neuron. No such alternating effects were observed from the opposite (OFF) stimulus (tracings 5 and 6).

**Discussion.** Application of an 'OFF' stimulus shows that the cessation of activity of the geniculate cell is not associated with an increase of excitability of a collicular cell and vice versa. Thus, it seems that direct mutually inhibitory relationships between the L.G.N. and S.C. cannot be involved, although such connections may exist<sup>18</sup>. Furthermore, electrical stimulation through the recording electrodes fails to elicit a response in the complementary unit. The 2 remaining most likely sites to which these alternating effects may be attributed are: the retina and the visual cortex. Although the retina cannot be disregarded, it is interesting to point out in this respect that the response in Figure 1 (tracings 6 and 8) as well as Figure 2 are not typical of retinal ganglion cells, and that abolition of cortical function with 3 M KCl application results in a disruption of the normal firing pattern of geniculate neurons<sup>19</sup>. These results suggest a possible involvement of the superior colliculus in scanning processes of the eye<sup>20</sup> which mediate pattern perception.

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## Vestibular units during decompensation<sup>1</sup>

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**Summary.** Typical modifications of the unitary discharge of vestibular units have been recorded following the transection of the spinal cord of hemilabyrinthectomized and compensated guinea-pigs. These results support the concept that the spinal cord is essential in the compensation of the symptoms resulting from a lesion of one labyrinth.

Previous research<sup>2,3</sup> has demonstrated that the spinal cord is involved in the mechanism of compensation of the motor deficits resulting from a previous hemilabyrinthectomy. In fact, it has been observed that spinal cord transection at the mid-thoracic level, after compensation of the symptoms produced by lesion of one labyrinth, will be followed by the reappearance of some of these same symptoms. This new stage has been identified as the decompensation period. Furthermore, cutting the spinal afferent pathways in a hemilabyrinthectomized and compensated animal provokes clear-cut modifications of the field potentials generated by electrical stimulation of the ampullar receptors of the intact side and recorded from

the vestibular nuclear complexes of both sides. The effects induced by the transection of the cord consist of facilitation of  $N_1$  or  $N_1-N_2$  waves<sup>4</sup> recorded from the vestibular nuclei of the intact side and inhibition of the evoked potentials in the vestibular nuclei of the deafferented side. Therefore, it is evident that the compensation of the vestibular deficits is controlled by the output of the vestibular nuclei, which in turn is dependent upon the influence of the spinal cord.

The purpose here is to describe the results of series of experiments carried out with the aim of analyzing the behavior of the vestibular units during the compensated and decompensated stages. Ether anesthesia of 75