

A further experiment on four inbred lines, namely N1, N2, Y1, and Y2, some being the same as those discussed above, gave a heritability in the broad sense of 0.303. A 4 × 4 diallel cross of all the possible hybrids between these four inbred lines was set up and analysed according to the procedure of GRIFFING⁹ for general and specific combining abilities (Table II). The general combining ability component was significant, showing the importance of the additive genetic variance σ_A^2 . The value of the heritability in the narrow sense, namely σ_A^2/σ_P^2 came to 0.098, and in the broad sense 0.119.

Table I. (a) Mean durations of copulation (in min) for the 5 inbred lines. Each mean is based on 26 observations

Generation	Lines					Total mean
	N1	N2	D5	G5	Y2	
1	18.6	15.8	21.0	20.0	18.4	18.5
2	20.0	17.6	21.9	19.2	18.1	19.4
Combined mean	19.3	16.7	21.4	19.5	18.2	18.9

(b) Analysis of variance combining the two generations

Source	d.f.	M.S.	F	P
Lines	4	172.754	12.34	< 0.1%
Error	255	14.003		

These various experiments clearly show that the duration of copulation is controlled genetically with a heritability probably in the region of 0.15 to 0.20. The low value obtained in the diallel cross is perhaps surprising, but it must be remembered that the heritability of a trait is a property of the population under study and not of the trait itself.

Table II. Analysis of variance for a 4 × 4 diallel cross (omitting the 4 inbred lines following model 3 of GRIFFING⁹)

Source	d.f.	M.S.	F	P
General combining ability	3	25.383	3.38	< 2.5%
Specific combining ability	2	10.825	1.43	
Reciprocal effects	6	16.467	2.17	~ 5.0%
Error	109	7.594		

Résumé. Une série d'expériences tend à montrer que chez *Drosophila melanogaster* la structure génétique joue un rôle déterminant dans la durée de l'accouplement.

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⁹ B. GRIFFING, Aust. J. biol. Sci. 9, 463 (1956).

Nystagmus Evoked in the Rabbit by Electrical Stimulation of the Lateral Geniculate Body

In previous publications^{1,2} we have shown that uni-lateral stimulation of the optic nerve, optic tract or superior colliculus in the rabbit produces 'central nystagmus'. Since the majority of optic fibres run through or synapse in the corpus geniculatum laterale (CGL), it was expected that electrical excitation of this structure would also evoke a nystagmus response. Central nystagmus was first elicited from the so-called 'diencephalic nystagmogenic area'³. The question arises whether this region is also part of the optic pathway, in view of the identification of central nystagmus as a subclass of optic nystagmus⁴.

Systematic exploration of the CGL with concentric stainless steel electrodes gave the results shown in Figure 1. In plane D (atlas of MONNIER and GANGLOFF⁵), the threshold intensity fell markedly when the electrode, moving downward, penetrated into the CGL, and rose again when the ventral border of this structure was pierced. However, positive responses with a low threshold were also encountered outside the CGL, especially in the optic radiation.

The nystagmogenic area, marked in Figure 1 medial to the lateral geniculate body, was originally delineated with

the help of unipolar electrodes³. It is evident that this area comprises not only part of the CGL, but also trans-geniculate fibres, running to the superior colliculus and the oculomotor and vestibular nuclei.

Among all susceptible structures, the CGL and the optic radiation manifest the lowest threshold and are therefore the most suitable substrate for studying central nystagmus. The great sensitivity of the optic radiation is rather surprising because this region contains only fibres. However, MANNI et al.⁶ have described a nystagmogenic area in the cortex of the rabbit. After destruction of this region, degenerating fibres were found inter alia in the

¹ J. GUTMAN, F. BERGMANN, M. CHAIMOVITZ, and A. COSTIN, Exp. Neurol. 8, 132 (1963).

² F. BERGMANN, A. COSTIN, J. GUTMAN, and M. CHAIMOVITZ, Exp. Neurol. 9, 386 (1964).

³ J. LACHMANN, F. BERGMANN, and M. MONNIER, Am. J. Physiol. 193, 328 (1958).

⁴ F. BERGMANN, A. COSTIN, and M. CHAIMOVITZ, Exp. Neurol., in press.

⁵ M. MONNIER and H. GANGLOFF, Atlas for Stereotaxic Brain Research on the Conscious Rabbit (Elsevier, Amsterdam 1961).

⁶ E. MANNI, G. B. AZZENA, and C. DESOLE, Arch. ital. Biol. 102, 645 (1964).

CGL⁷. Therefore, it is possible that in addition to the optic fibres arising from the retina, a second nystagmus pathway originating from the cortex passes through the lateral geniculate. If, indeed, stimulation of the optic radiation activates such corticofugal fibres, the great sensitivity of this region may be due to crowding of these

fibres or to their close proximity to the neurons of the CGL.

The much higher intensities needed for points outside the CGL or the optic radiation, suggest that spreading current has caused activation of the cortical nystagmus circuit or of the optic pathway.

It is also noteworthy that the superior colliculus responds much less readily². From this structure, nystagmus can usually be evoked only if auxiliary measures (darkness or enhancement by drugs) are employed. These are superfluous if one stimulates the CGL.

On the other hand, the nystagmus evoked from the CGL depends on the rate of stimulation in a way closely resembling the responses from other parts of the optic pathway^{1,8}. Thus, in Figure 2 the optimal frequency lies again between 40–60 cycles/sec.

Since in the chiasm of the rabbit the optic fibres undergo an almost complete decussation, almost all fibres reaching the right CGL originate from the left eye. Therefore, stimulation of the right CGL, like stimulation of the left optic nerve, invariably produces eye movements to the left. The effect of monocular illumination from a stationary light source depends on which side is exposed. Nystagmus elicited from the right CGL is strongly depressed by illumination of the right eye, but is little affected by light shining on the left eye, in accordance with previous observations on the asymmetric character of photic inhibition of central nystagmus⁹ (Table).

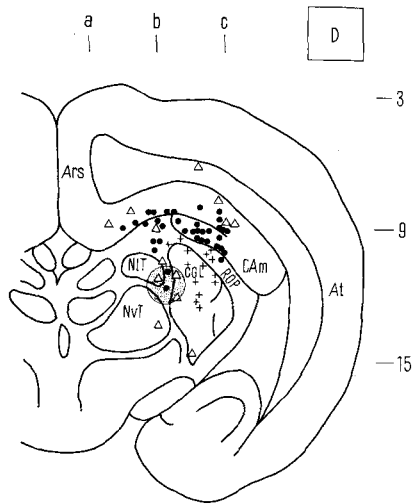


Fig. 1. Localization of nystagmogenic points in the rabbit's diencephalon. Transverse section through the lateral geniculate body (plane D of MONNIER and GANGLOFF⁵). +, Points in the CGL and the optic radiation where nystagmus can be evoked by electrical stimulation at low intensity (0.02–0.2 mA); •, points from which a response is elicited only at higher intensities (0.4–1.2 mA); Δ, refractory points. Distance between top letters, 3 mm; right-hand scale indicates mm below surface of the skull. Original 'nystagmogenic area'³ is located at a depth of about 12 mm, as shown by the stippled circle. Abbreviations: Ars, area retrosplenialis; At, area temporalis; CAM, cornu ammonis; CGL, corpus geniculatum laterale; NIT, nucleus lateralis thalami; NvT, nucleus ventralis thalami; ROP, radiatio optica.

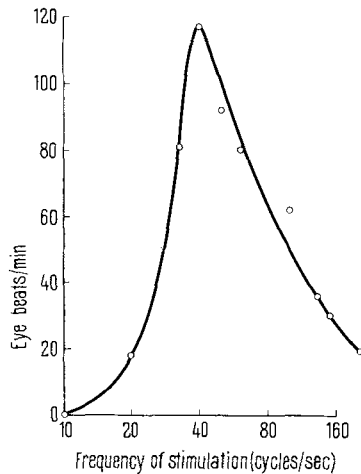


Fig. 2. Number of eye beats as function of frequency of stimulation at the lateral geniculate body. Male rabbit, 2.6 kg; concentric electrodes at left cD (see Figure 1), at a depth of 12 mm below surface of the skull; intensity of current 0.15 mA; pulse duration 2 msec; stimulation period 1 min. Above 60 c/s, the response was not sustained. At 60 c/s, nystagmus died out after 55 sec; at 100 and 150 c/s after 45 sec; and at 200 c/s after 25 sec.

Asymmetric effect of constant illumination on nystagmus, evoked from the lateral geniculate body

The right CGL was stimulated for 1 min by a pair of concentric electrodes at a rate of 40 cycles/sec; pulse duration 2 msec; current strength 0.05 mA; eye movements to left. Where indicated, the eyes were covered with small black hoods. Intensity of illumination 200 lux

Condition of eyes	Eye beats/min
Both eyes covered	90 + 34 ^a
Left eye illuminated	82 + 26
Right eye illuminated	9
Both eyes illuminated	2

^a These figures read as follows: 90 beats during stimulation period of 1 min; afternystagmus 34 beats.

Résumé. La stimulation électrique du corps géniculé latéral et de la radiation optique provoque des mouvements nystagmiques contraversifs. Cette réponse est inhibée fortement par l'illumination de l'œil ipsilatéral.

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⁷ E. MANNI, G. B. AZZENA, and M. L. ATZORI, Arch. ital. Biol. 103, 136 (1965).

⁸ F. BERGMANN, J. LACHMANN, M. CHAIMOVITZ, and J. GUTMAN, Exp. Neurol. 3, 487 (1961).

⁹ F. BERGMANN, A. COSTIN, J. GUTMAN, and M. CHAIMOVITZ, Confin. Neurol., 25, 403 (1965).