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Time of Origin of Neurons of the Rat Superior Colliculus in Relation to Other Components of the Visual and Visuomotor Pathways

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Summary. Groups of pregnant rats were injected with two successive daily doses of ^{3}H-thymidine from gestational day 12 and 13 (E12 + E13) until the day before parturition (E21 + 22) in order to label all the multiplying precursors of neurons. At 60 days of age the proportion of neurons generated (or no longer labelled) on specific days was determined in the separate layers of the superior colliculus. Neurogenesis begins with the production of a few large multipolar neurons in layers V and IV on day E12; the bulk (87%) of these cells are generated on day E13. This early-produced band of large neurons, the intermediate magnocellular zone, divides the superior colliculus into two cytogenetically distinct regions. In both the deep and the superficial superior colliculus neuron production is relatively protracted. In the deep superior colliculus neuron production peaks on day E15 in layer VII, on day E15 and E16 in layer VI, and on day E16 (the large neurons excluded) in layer V, indicating an inside-out sequence. In the superficial superior colliculus peak production time of layer III cells is on day E15 and of layer IV cells on day E16; peak production time of both layer I and II is on day E16 but in the latter region neuron production is more prolonged and ends on day E18. One interpretation of these results is that the two pairs of superficial layers are produced in an outside-in sequence. These three cytogenetic subdivisions of the superior colliculus may be correlated with its structural-functional parcellation into an efferent spinotectal, a deep somatomotor and a superficial visual component.

A comparison of neurogenesis in different components of the visuomotor and visual pathways of the rat indicates that the motor neurons of the extraocular muscles, the abducens, trochlear and oculomotor nuclei, and neurons of the nucleus of Darkschewitsch are produced first. Next in line are source neurons of efferents to the bulb and the spinal cord: those of the Edinger-Westphal nucleus and the intermediate magnocellular zone of the superior colliculus. These are followed by the relay neurons of the dorsal nucleus of the lateral geniculate body. The neurons of the superficial superior colliculus and of the visual cortex implicated in visual sensori-motor integrations are produced last.

Key words: Superior colliculus – Neurogenesis – Thymidine radiography – Visual system development

In preceding investigations of the time of origin of neurons in the rat brain, we have established the birth dates of neurons in the following sensory and motor structures directly involved in visual functions: the abducens nucleus (Altman and Bayer 1980a), the trochlear nucleus, the oculomotor nucleus, the Edinger-Westphal nucleus, the nucleus of Darkschewitsch (Altman and Bayer 1980c), and the dorsal and ventral nuclei of the lateral geniculate body (Altman and Bayer 1979). In addition we have obtained quantitative data on the temporal order of neurogenesis in the following brain stem structures secondarily involved in visuomotor functions: the vestibular nuclei, the nucleus prepositus hypoglossi (Altman and Bayer 1980b), and the parabigeminal nucleus (Altman and Bayer 1980c).

The present study deals with the chronology of neurogenesis in the different layers of the rat superior colliculus, and completes our datings of neuron production in the major subcortical components of the visual and visuomotor systems (the retina excepted). This provides us with the opportunity to examine the possible role of the precise chronology of neurogenesis in components of this pathway in relation to the morphogenetic organization of the rest of the visuomotor and visual systems.

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In this attempt we shall follow the pattern set in the preceding paper (Altman and Bayer 1981) in which we noted a close correlation between the spatial order of cytogenetic gradients within different components of the central auditory system and their tonotopic organization.

There is an extensive literature on the structural and functional organization of the mammalian superior colliculus (recently reviewed by Sprague et al. 1972; Goldberg and Robinson 1978; Gordon 1975). The superior colliculus is a laminated structure but the layers are not as numerous or discrete in mammals as they are in the optic tectum of many lower vertebrates. The stratum zonale, stratum opticum and stratum griseum intermedium are often classified as the superficial layers; the stratum album intermedium, stratum griseum profundum and stratum album profundum as the intermediate and deep layers or just the deep layers. These two (or three) zones appear to differ in their connections, physiological properties and behavioral functions. The optic fibers terminate in the superficial zone where the most effective stimuli are moving targets (Marchiafava and Pepeu 1966; Straschill and Taghavy 1967). The receptive fields are smaller superficially within this zone (Humphrey 1968; Gordon 1973), and they do not respond to eye movement; in contrast the cells beneath them have larger receptive fields and respond to eye movements in a specific direction (Schiller and Koerner 1971; Cynader and Berman 1972; Wurtz and Goldberg 1972). In the intermediate zone cells are present that respond not only to visual but also to auditory and somatic stimuli (Gordon 1973; Dräger and Hubel 1975). The retinotopic representation and representation from the face area and the rest of the body are in register (Gordon 1973; Dräger and Hubel 1975, 1976; Finlay et al. 1978); the somatosensory fibers terminate principally in the stratum album intermedium (Antonetty and Webster 1975). Other inputs were described from neck muscle and extraocular muscle afferents (Abrahams and Rose 1975) and from the cerebral cortex. Fibers from the cortical visual areas arise in layer V (Gilbert and Kelly 1975; Raczkowski and Diamond 1978) and terminate in both the superficial and deep zones (Kawamura et al. 1974).

Not only are there differences in the afferent organization of the superficial and deeper layers of the superior colliculus but their efferents differ too. The major descending projections from the superior colliculus are to the reticular formation, the pontine nuclei and the spinal cord (Papez and Freeman 1930; Altman and Carpenter 1961; Waldron and Gwyn 1969; Kawamura and Brodal 1973) and the inferior olive (Graham 1977; Weber et al. 1978). The descending fibers originate in cell bodies located in the stratum opticum and in the intermediate and deeper layers (Hashikawa and Kawamura 1977; Kawamura and Hashikawa 1978; Weber et al. 1978); these are the cells that appear to project to the vicinity of the oculomotor and abducens nucleus (Edwards and Henkel 1978). The tectospinal fibers may originate from the larger neurons in the intermediate and deep layers (Abrahams and Rose 1975; Weber et al. 1978; Rhoades and DellaCroce 1980). In contrast, the cells of origin of the ascending projections to the thalamus, in particular the pulvinar (Harting et al. 1973; Glendenning et al. 1975; Kawamura and Kobayashi 1975), the pretectal nuclei and the lateral geniculate nuclei (Graham 1977; Perry 1980) were traced to the superficial layers of the superior colliculus. The projections to these different rostral structures may originate in different layers of the superficial zone (Raczkowski and Diamond 1978; Albano et al. 1979). A projection to the centrum medianum has also been described (Graham 1977; Niimi et al. 1970) but this has been traced to the dorsomedial portion of the stratum griseum profundum (McGuiness and Krauthammer 1980). This complex laminar organization of the superior colliculus is relevant to its development because available descriptions and our results indicate a correspondingly complex sequence in cytogenesis and morphogenesis.

The time of origin of neurons of the superior colliculus (or the optic tectum) has been investigated with thymidine radiography in the chick (Fujita 1964; LaVail and Cowan 1971), the mouse (DeLong and Sidman 1962; Taber Pierce 1973) and the rat (Brückner et al. 1976; Mustari et al. 1979). In the chick temporal differences were noted in the origin of neurons of the superficial, intermediate and deep layers, together with gradients in the rostrocaudal, ventrodorsal and lateromedial planes (Fujita 1964; LaVail and Cowan 1971). Such differences in the time of origin of neurons in the different layers of the superior colliculus of rodents were denied (DeLong and Sidman 1962) or thought to be not pronounced (Mustari et al. 1979). Our quantitative data indicate a complex pattern of cytogenetic gradients in the rat superior colliculus which resembles the gradients noted in the chick optic tectum.

Methods

Purdue-Wistar pregnant rats were injected subcutaneously with two successive daily doses of ^{3}H-thymidine (specific activity, 6.0 Ci/mM; dose, 5 μCi/g body weight) between 9:00–11:00 a.m. on

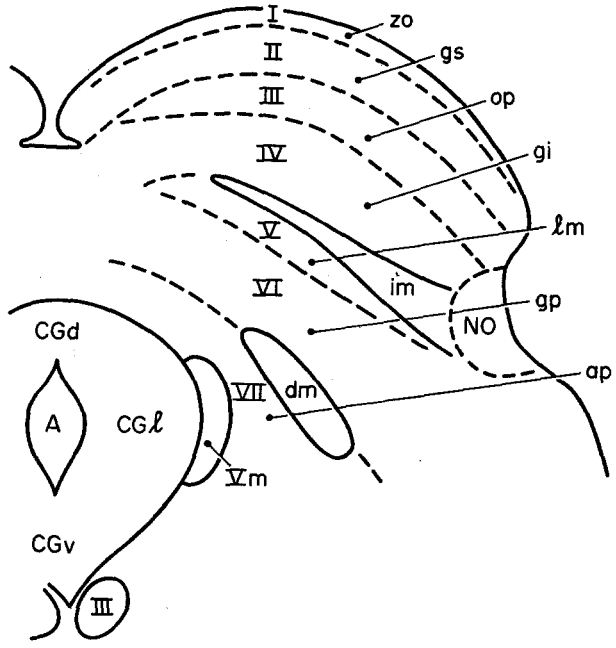


Fig. 1. Laminar organization of the rat superior colliculus

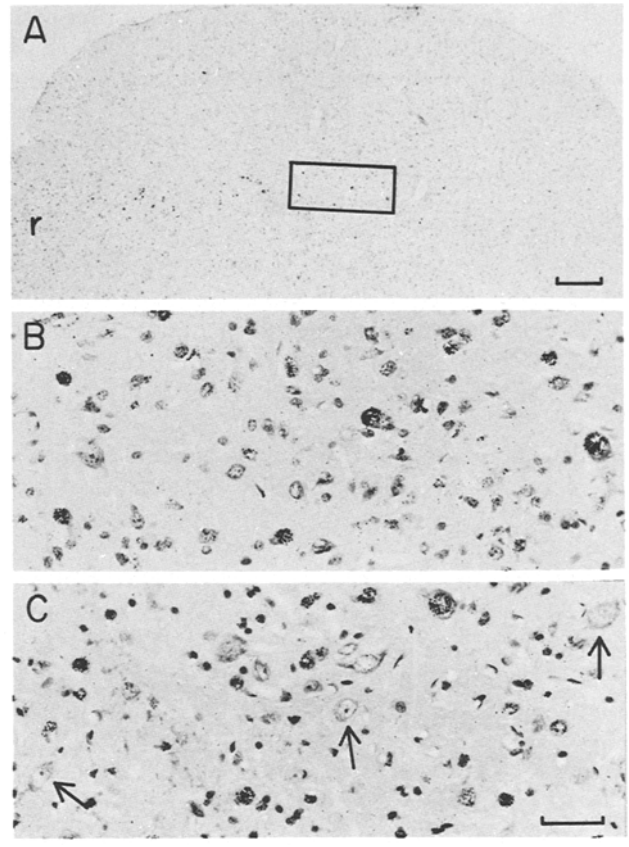


Fig. 2. A Low power photomicrograph of the superior colliculus in sagittal section from a rat injected on days E12 + 13. The enclosed heavily labelled large cells of the intermediate magnocellular zone are shown at higher magnification in **B. C** Some of the large neurons of the im are no longer labelled (arrows) in this animal injected on days E13 + 14. Scales: **A** 200 μm; **B** and **C** 50 μm

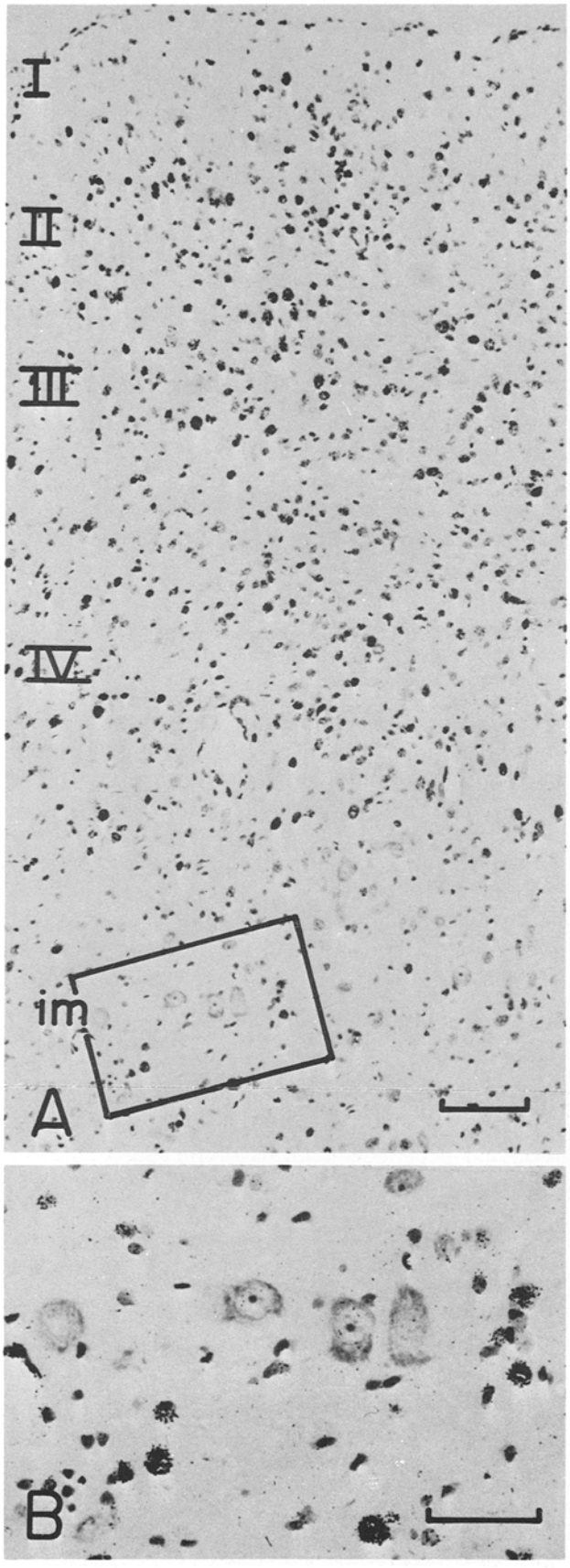
the following gestational ages: E12 + 13, E13 + 14 . . . E21 + 22. (The day of sperm positivity was counted as E1.) The progeny of at least two dams/injection group were killed at the constant postnatal age of 60 days by cardiac perfusion with 10% neutral formalin. The brains were embedded in paraffin, sections were cut at 6 μm serially in the three planes and every fifteenth section was saved. Successive sections were stained with cresyl voilet and hematoxylin-eosin for examination without nuclear emulsion or were prepared for autoradiography. The latter procedure has been described elsewhere (Altman 1964). Briefly, deparaffinized sections were coated with Kodak NTB-3 emulsion in the dark, exposed for 90 days with a dessicant, developed with D-19, and stained with hematoxylin-eosin.

Coronal sections from approximately the middle portion of the superior colliculus in the anteroposterior plane were selected from 6 male rats per injection group for quantitative purposes; the additional material was used for qualitative assessments. The number of labelled and unlabelled cells was counted separately in the middle portion of the superior colliculus in the mediolateral plane in the seven layers of the superior colliculus (Kanaseki and Sprague 1974; Fig. 1). In all instances a minimum of 100 (up to several hundred) cells were classified in each layer in all the animals. The estimation of the proportion of cells differentiating (ceasing to divide) on a particular day was based on the progressively delayed comprehensive labelling procedure. The rationale of this procedure is that as long as virtually all the cells of a selected brain region can be labelled (in the populations studied here nearly 100% of labelling can be accomplished with two successive daily injections) all the cells are considered to be primitive precursors that have not started to differentiate. When with delayed onset of injections all cells can no longer be tagged, the proportion of cells that can no longer be labelled as a result of a single day delay is taken to be the complement that differentiated on the previous day. As an example, the cells arising on day E15 are determined as follows: E15 = (E15 + 16) − (E16+ 17).

Previous examination of our quantitative results indicated that the sequence of neuron generation in various nuclei was often more clearly indicated in the data from individual animals than in the pooled data. This apparent variability between animals might be due to differences in the exact age of the pooled individuals or their exact developmental stage (differences were often noted within littermates). Accordingly, we employed a statistical procedure, the sign test (Conover 1971), to determine the consistency of sequential neuron production in pairs of superior collicular strips regardless of the chronological grouping of the individual animals. This test is based on paired comparisons (X, Y) within individual animals. The comparisons are grouped into 3 categories: (1) $X > Y$, "–" comparison; (2) $X < Y$, "+" comparison; (3) $X + Y$, "0" comparison. The zero comparisons are discarded and, depending on the total number of remaining "–" and "+" comparisons, either a binomial distribution or a normal approximation is used to calculate probabilities (p's).

Results

The lamination pattern of the rat superior colliculus is not distinct. The cells characterizing different layers are not sharply segregated from each other and the fibrous layers do not offer clear landmarks



because they contain an appreciable concentration of neuronal perikarya. The stratum zonale (layer I) is composed of sparsely packed small cells and similar cells are concentrated more densely in the stratum griseum superficiale (layer II). The typical cells of the stratum opticum (layer III) are larger, spindle-shaped (with horizontal orientation in the coronal plane) and usually have pale nuclei. The stratum griseum intermediale (layer IV) contains a high concentration of small cells together with other types. The cell population of the stratum lemnisci (layer V) is quite heterogeneous and includes many large, multipolar cells, particularly laterally. The stratum griseum profundum (layer VI) is characterized by intermediate-size multipolar cells. The stratum album profundum (layer VII) contains mostly large cells (but they do not reach the size of some of those seen in layer V).

In the group injected on days E12 + 13, label concentration was very light over the cells of the superior colliculus, with the exception of the large multipolar neurons situated in a zone extending from the nucleus of the optic tract laterally over layer V (Fig. 1). These cells of the intermediate magnocellular zone tended to be heavily labelled (Fig. 2A, B). Some of these large neurons were no longer labelled in the E13 + 14 group (Fig. 2C) and they were typically unlabelled in the group injected on days E14 + 15 (Fig. 3). Most of the other cells of the superior colliculus were labelled in the latter group, including the large multipolar neurons in the vicinity of layers VI and VII, what we designate as the deep magnocellular zone (Fig. 4). In the group injected on days E15 + 16 unlabelled cells were seen in increasing numbers in layer VII, and in the group injected on days E16 + 17 also in layers VI, V and III (Fig. 5). In the E16 + 17 group labelled cells were still numerous in layers IV and II surrounding the stratum opticum. These were small neurons and in this group the labelled cells that were seen in the stratum opticum itself tended to be of the same small type. Two bands of labelled cells in layers II and IV were a prominent feature in the group injected on days E17 + 18, and they were still seen in most (though not all) of the animals injected on days E18 + 19.

Our quantitative results (Fig. 6) showed that the large neurons of the intermediate magnocellular zone originate between days E12 and E14, with 87% of the cells being generated on day E13 (Fig. 6A). Because

Fig. 3. A Cells are heavily labelled in the superficial layers of the superior colliculus (sagittal section) in this rat injected on days E14 + 15, except the large neurons of the im. The latter shown at higher magnification in **B**. Scales: **A** 100 μm; **B** 50 μm

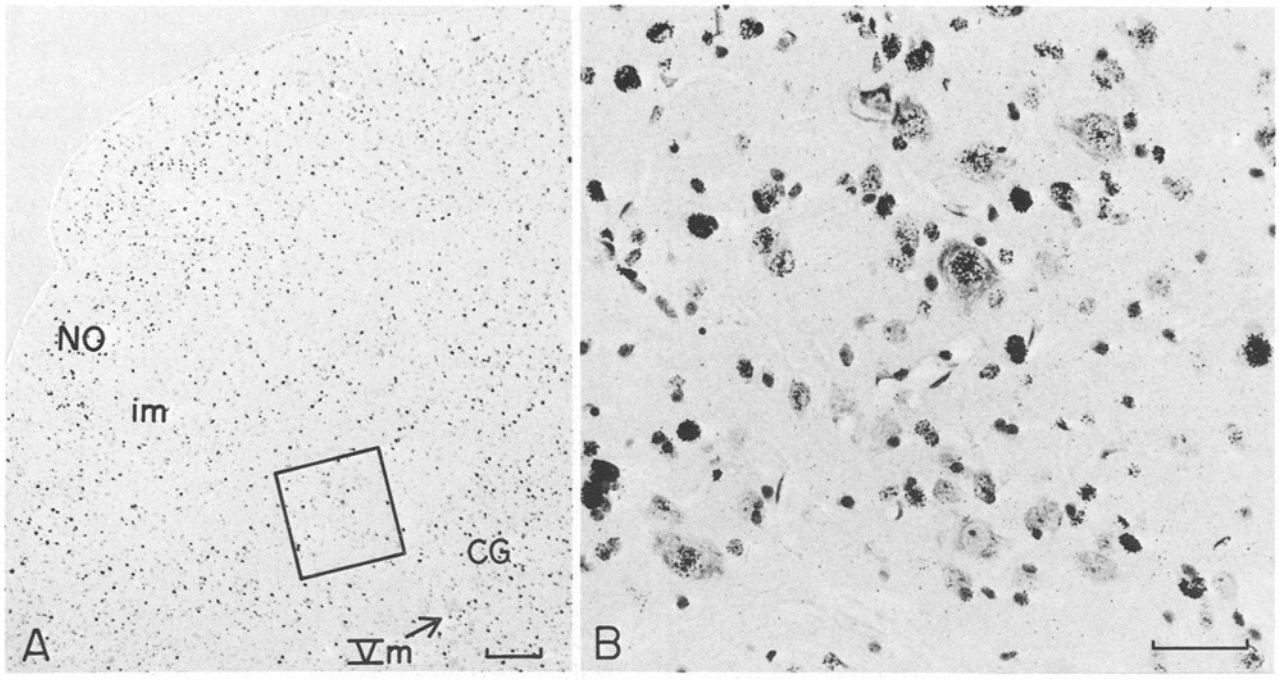


Fig. 4. **A** Coronal section from a rat injected on days E14 + 15. The large neurons of the im are no longer labelled, but many of the dm (enclosed) are still labelled. The latter region shown at higher magnification in **B**. Scales: **A** 200 μm; **B** 50 μm

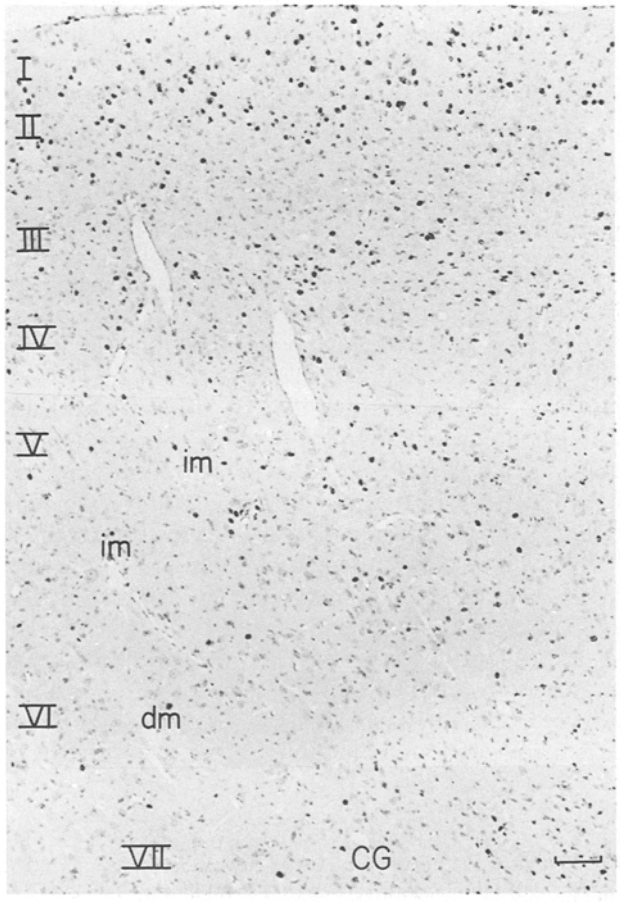


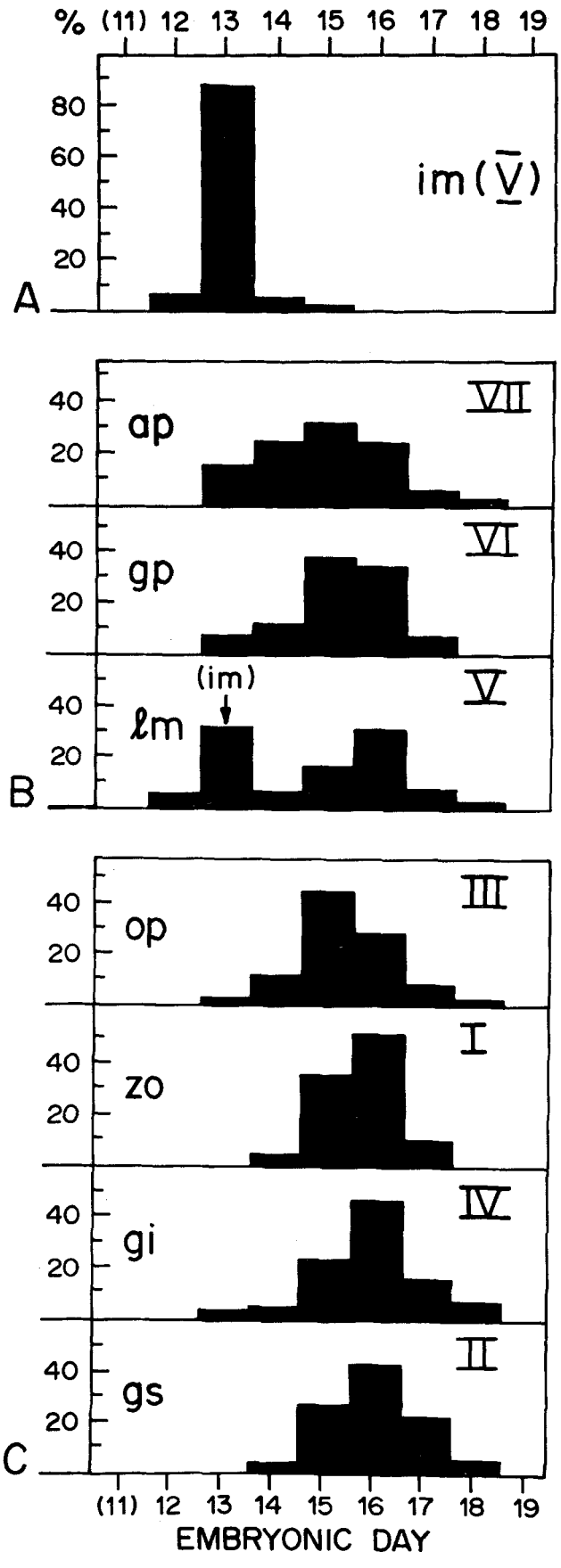
Fig. 5. Laminar differences in the proportion of labelled and unlabelled cells in a rat injected on days E16 + 17. Scale: 100 μm

of its unique cytogenetic properties (early and rapid generation time) it is distinguished from the seven traditional layers of the superior colliculus. We found it convenient to subdivide the latter into the deep layers (Fig. 6B) and the superficial layers (Fig. 6C).

In the deep superior colliculus neuron production extended over a protracted period. Peak production time of neurons of layer VII was on day E15 and the population as a whole was produced significantly earlier ($p < 0.003$) than layer VI. The neurons of layer V constituted two populations: the early-generated magnocellular neurons, which were also counted separately (Fig. 6A), and the other cells. Apparent peak production time of the latter was on day E16 (Fig. 6B). Hence, if we exclude the magnocellular cells, the neurons of the deep superior colliculus are produced in an inside-out pattern in relation to the aqueduct.

In the superficial superior colliculus the time of production of neurons of layers IV and II was not statistically different. The cytogenesis of layer III neurons antedated layers IV and II ($p < 0.0001$), and layer I neurons were produced significantly ahead of layer II ($p < 0.0001$) but not of layer IV (Fig. 6C). Thus, the results suggest a sandwich pattern in the cytogenesis of the superficial layers of the superior colliculus, possibly two subregions with an outside-in pattern.

Cell counts were also made in the nucleus of the optic tract. Its cells are generated between days E13



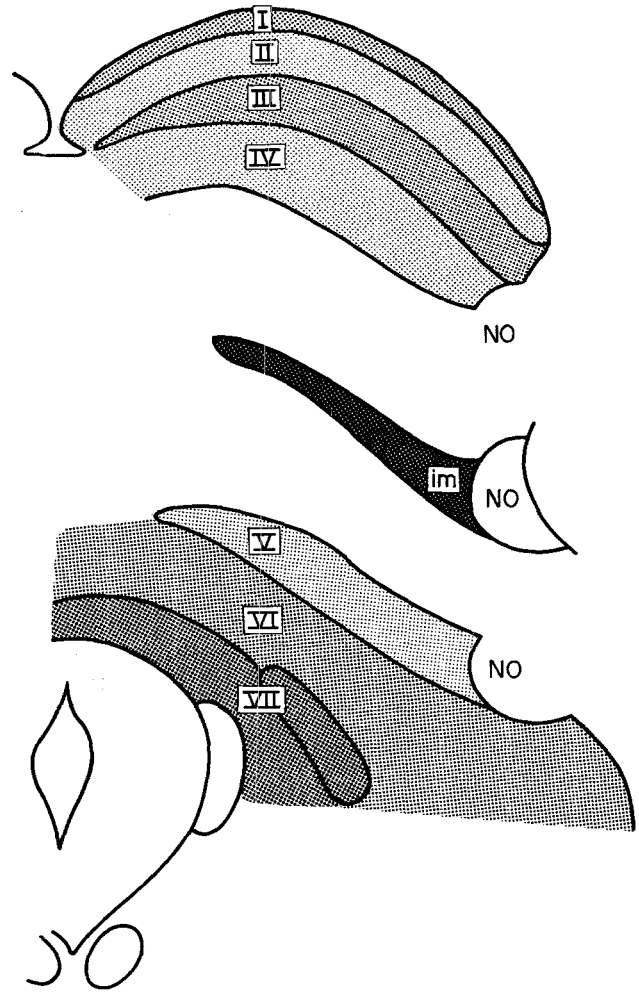


Fig. 7. Parcellation of the superior colliculus into three cytogenetic zones on the basis of chronology of neuron production and laminar gradients. Compare with Figs. 1 and 6

and E16 with a peak on day E15. The neurons of this nucleus are produced significantly later than those of the intermediate magnocellular zone ($p < 0.0001$), concurrently with layer VII and significantly ahead of all the other layers of the superior colliculus ($p < 0.003$–0.0001). The results suggest that the superior colliculus is divisible into three cytogenetic zones (Fig. 7).

The quantitative data were based on cell counts in coronal sections at midcollicular levels. However, there were considerable differences in lamination and in labelling patterns from rostral to caudal. This

Fig. 6A–C. Time of origin of neurons in the intermediate magnocellular zone (**A**), and in the layers of the deep (**B**) and superficial (**C**) superior colliculus. The cell counts in layer V included the large neurons that were counted also separately as the intermediate magnocellular zone

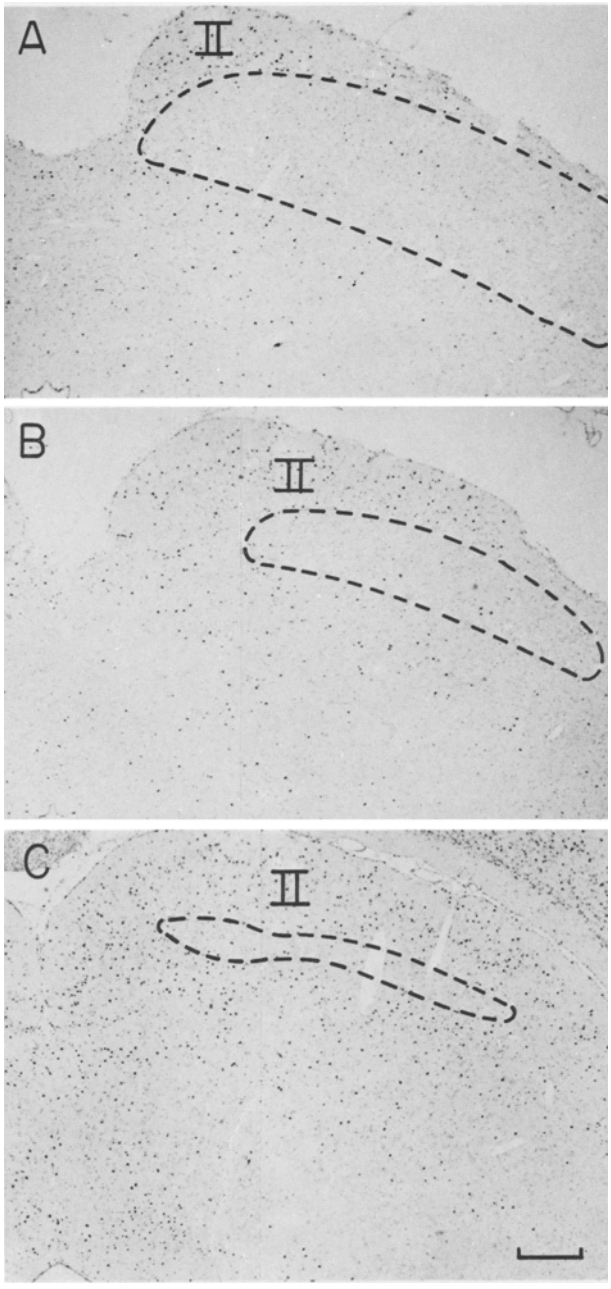


Fig. 8A–C. Differences in laminar organization and labelling pattern from rostral (**A**) to caudal (**B**); coronal sections from a rat injected on days E16 + 17. CThe unlabelled zone of cells beneath layer II becomes narrower proceeding from rostral (posterior pretectal nucleus) to caudal (stratum opticum). Scale: 300 μm

is illustrated in Fig. 8 in a rat injected on days E16 + 17. At midcollicular level (Fig. 8C) the labelled zone of layer II is extensive and the unlabelled zone of layer III is narrow. But more rostrally (Fig. 8B) the unlabelled zone widens and as the level of the posterior pretectal nucleus is reached (Fig. 8A) layer II is disappearing and the unlabelled zone expands further. We do not know whether or not the unlabelled cells of the posterior pretectal nucleus are related to those of the stratum opticum of the superior colliculus.

Discussion

The time span of neuron production obtained in this study is in good agreement with previous reports by Brückner et al. (1976) and Mustari et al. (1979). Both groups of investigators reported that cell production in the rat superior colliculus begins on day E12. The cessation of neurogenesis was placed between days E18 and E20 by Brückner et al. and on day E17 by Mustari et al. Our results indicated a time span between day E12 and E18, with very few cells produced on the first and the last day. However, our data and interpretations differ in regard to the question of the presence of cytogenetic gradients in the rodent superior colliculus. Brückner et al. were not able to identify clear gradients while Mustari et al. stated that more of the cells contributing to the deeper layers were generated early, and more of the superficial cells were generated late. They also noted a gradient from rostrolateral to caudomedial. Both teams of investigators denied the presence of the type of complex gradients that were described in the optic tectum of the chick (Fujita 1964; LaVail and Cowan 1976). This was largely in agreement with the earlier claim of DeLong and Sidman (1961) that neurons in all layers of the mouse superior colliculus are generated simultaneously.

Undoubtedly, the type of clear laminar gradient which has been repeatedly described in the rodent cerebral cortex (Angevine and Sidman 1962; Berry and Rogers 1965; Hicks and D'Amato 1968; Bisconte et al. 1972) is not present in the rodent superior colliculus. This may be at least partly due to the fact that the lamination itself is very imprecise in the mammalian superior colliculus, in contrast to the avian optic tectum which has sharp laminar boundaries and where cytogenetic gradients have been described. Nevertheless, our quantitative data indicate that laminar gradients are also discernible in the rat superior colliculus and that they may be as complex, though not necessarily identical with those reported in the optic lobe of chicks. Fujita (1964) and LaVail and Cowan (1976) described differences in the time of origin of neurons in the optic tectum of the chick between the deep layers (early), the superficial layers (intermediate), and the intermediate layers (late). In addition, LaVail and Cowan also noted inside-out and outside-in gradients within the three developmental zones. In agreement with the

latter classification, our results suggest the existence of three cytogenetic zones in the rat superior colliculus. We have named the earliest region the intermediate magnocellular zone. Its large cells are not restricted to a single layer but can be traced from the nucleus of the optic tract, where it is most pronounced, through layers V and IV. Recent studies with different techniques have suggested that these early-generated large multipolar neurons are the source of fibers of the tectospinal tract (Abrahams and Rose 1975; Weber et al. 1978; Rhoades and DellaCroce 1980).

The intermediate magnocellular zone seems to be the dividing line between the deep and the superficial superior colliculus. The deep superior colliculus is composed of layers V–VII, and these are arranged in an inside-out pattern in relation to the aqueduct (Fig. 7). The stratum lemnisci of the deep superior colliculus has been functionally related to somesthetic input (Gordon 1973; Dräger and Hubel 1975, 1976; Finlay et al. 1978). The deep superior colliculus has also been implicated in the control of eye movements (Schiller and Koerner 1971; Wurtz and Goldberg 1972; Robinson 1972; Straschill and Rieger 1973; Roucoux and Crommelinck 1976; Mohler and Wurtz 1976). The inside-out gradient observed in this region is reminiscent of that seen in the cerebral cortex (Angevine and Sidman 1961) and differs from the complex gradient that we obtained in the superficial superior colliculus. We described the latter as a sandwich pattern composed of two subregions with an outside-in pattern. An alternative interpretation is that layer IV is related to the intermediate magnocellular zone; like the latter, layer IV is composed of cells with descending efferents, specifically to the region of the extraocular motor nuclei (Edwards and Henkel 1978), the reticular formation (Kawamura and Hashikawa 1978), and the inferior olive (Weber et al. 1978). The cells of the superficial superior colliculus are intimately related to the optic tract, and also receive afferents from the cerebral cortex (Harting et al. 1973; Kawamura et al. 1974) and send ascending efferents to the thalamus (Kawamura and Kobayashi 1975; Raczkowski and Diamond 1978). Thus there is a relationship between the structural and functional parcellation of the superior colliculus (Casagrande and Diamond 1974) and its cytogenetic subdivisions. It is possible that the different horizontal zones of the superior colliculus are derived from different germinal matrices; but this question has to be investigated in embryonic materials. In addition to these laminar gradients LaVail and Cowan (1976) also described a ventrolateral to dorsomedial gradient in the chick. We have observed differences in the rat in labelling pattern between rostral and caudal

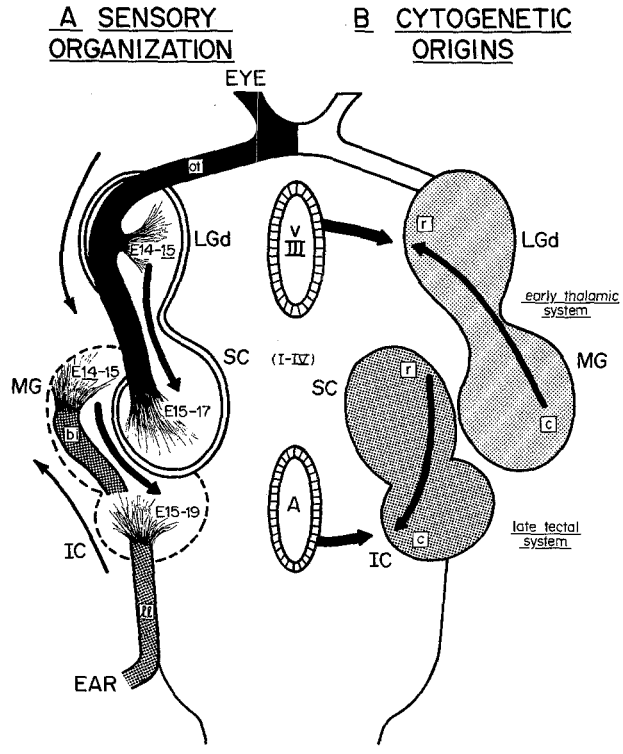
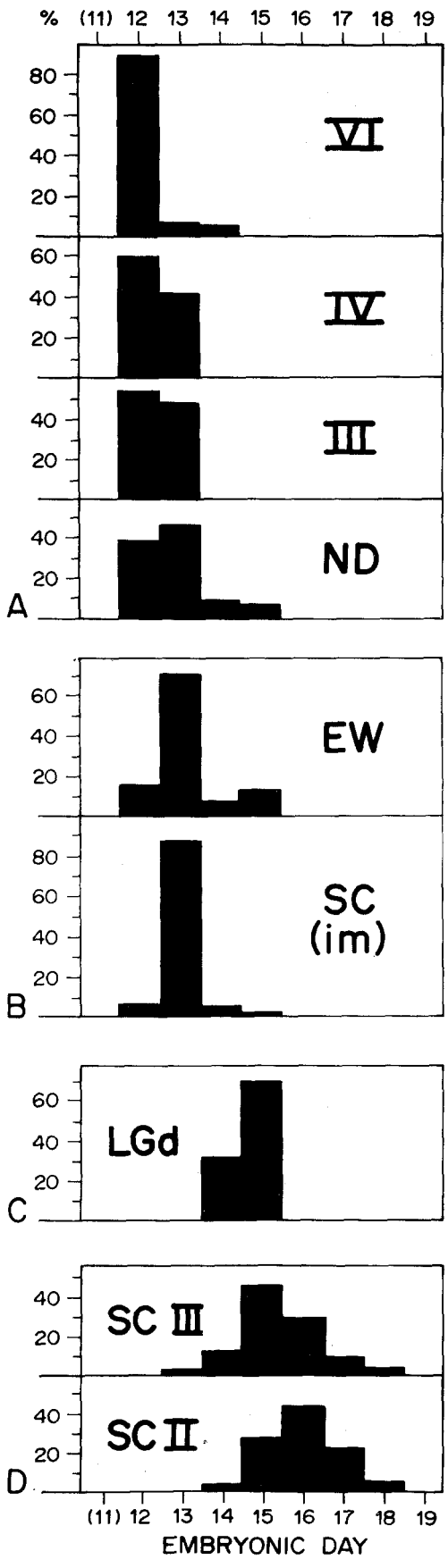


Fig. 9A, B. Relationship between the location of the primary afferents of the auditory and visual systems, and the time of origin of neurons and cytogenetic gradients in the auditory and visual components of the thalamus and the tectum. **A** The earlier production of neurons of the lateral geniculate body than the superior colliculus could be related to the earlier arrival there of optic tract fibers, but this relationship does not hold for the auditory system where the distal medial geniculate body is produced earlier than the proximal inferior colliculus. **B** An alternative interpretation focuses on differences in the time of production of neurons in the thalamus (early) and tectum (late) and mirror image gradients in these two systems

sections (Fig. 8) but interpreted them to be due to differences in the width of different laminae rather than as true gradients in the mediolateral or anteroposterior planes.

There are similarities and differences in neurogenesis between the tectal and the thalamic nuclei of the visual and auditory systems. In both sensory systems (Fig. 9A) neurons originate earlier in the thalamus (the lateral and medial geniculate bodies) than in the tectum (the superior and inferior colliculi). The traditional assumption that the optic lobe is phylogenetically older than the lateral geniculate body and that is cells should therefore arise earlier is contradicted by this evidence. We have entertained the possibility that the obtained gradient between the lateral geniculate body and the superior colliculus may be related to the circumstance that the retina is closer to the lateral geniculate nucleus than the superior colliculus and that the later arrival of optic



tract fibers in the superior colliculus (Lund and Bunt 1976) is associated with delayed neurogenesis. But this principle is counterindicated by our findings in the auditory system where the neurons of the medial geniculate body are generated before the neurons of the inferior colliculus even though the relation of these two structures to the source of sensory input is reversed (Fig. 9A). An alternative interpretation focuses on differences in the cytogenesis of the thalamus and the tectum (Fig. 9B). The neurons of the medial and lateral geniculate nuclei are produced relatively early, with a caudal-to-rostral gradient (Altman and Bayer 1979). In contrast, the neurons of the superior and inferior colliculi are produced relatively late, and with a rostral-to-caudal gradient (Altman and Bayer 1981; this paper). Moreover, in the thalamus the relay neurons of the auditory system are produced before the neurons of the visual system whereas in the tectum this relationship is reversed. Apparently, general developmental principles of the dorsal thalamus and the tectum govern the order of neurogenesis in their auditory and visual components with no obvious relation to the temporal or spatial order of neural development in the sensory systems with which they become later connected.

A comparison of the present results with our preceding study (Altman and Bayer 1981) suggests important differences in the early cytogenetic organization of the visual and auditory systems. In the auditory system we found a relationship between cytogenesis and tonotopic organization in the inferior colliculus, the medial geniculate body and several other structures (Altman and Bayer 1981); we were not able to detect a relationship between cytogenesis and retinotopic organization in the superior colliculus (this study) or in the lateral geniculate body (Altman and Bayer 1979). Contrariwise, we noted a relationship between cytogenesis and functional organization in the visuomotor and visual pathways (Fig. 10) which does not have its obvious parallel in the auditory system. The earliest generated neurons of the visuomotor system are those forming the nuclei controlling the extraocular muscles. The neurons of the abducens, trochlear and oculomotor nuclei are produced on days E12 + 13 with a caudal-to-rostral gradient (Altman and Bayer 1980c). A similar pattern is shown also in the nucleus of Darkschewitsch, a

Fig. 10A–D. Summary diagram of the chronology of neuron production in some components of the visuomotor and visual pathways. Neurons of the motor nuclei of the extraocular muscles and the ND are produced first (**A**). The neurons supplying descending efferents to the medulla and spinal cord are produced next (**B**). The "relay" neurons of the LGd (**C**) are produced next but before the sensorimotor "integrative" neurons of the superficial superior colliculus (**D**)

structure whose connections and functions are not known. The next group of structures are the Edinger-Westphal nucleus and the intermediate magnocellular zone of the superior colliculus. For some time it was believed that the neurons of the Edinger-Westphal nucleus are the source of parasympathetic outflow to the ciliary ganglion, which supplies fibers to the muscles of pupillary constriction and lens accomodation (Warwick 1954). However, recent studies (Loewy and Saper 1978; Sugimoto et al. 1978) indicate that few of the cells of the Edinger-Westphal nucleus have this role; rather they provide a descending projection to several medullary nuclei and the spinal cord. It is tempting to speculate that neurons of both the Edinger-Westphal nucleus and of the intermediate magnocellular zone of the superior colliculus are involved in motor functions related to head movements. The sensory relay neurons of the lateral geniculate body are produced next, and the last produced elements are those of the superior colliculus and the visual cortex (work in progress) where the integration between visual and visuomotor functions are supposed to occur.

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Abbreviations

A, aqueduct
ap, stratum album profundum (layer VII)
bi, brachium of the inferior colliculus
c, caudal
CGd, central gray, pars dorsalis
CGl, central gray, pars lateralis
CGv, central gray, pars ventralis
dm, deep magnocellular zone
EW, Edinger-Westphal nucleus
gi, stratum griseum intermediale (layer IV)
gp, stratum griseum profundum (layer VI)
gs, stratum griseum superficiale (layer II)
IC, inferior colliculus
im, intermediate magnocellular zone
LGd, lateral geniculate nucleus, pars dorsalis
ll, lateral lemniscus
lm, stratum lemnisci (layer V)
MG, medial geniculate nucleus
ND, nucleus of Darkschewitsch
NO, nucleus of the optic tract
op, stratum opticum (layer III)
ot, optic tract
r, rostral
SC, superior colliculus
vIII, third ventricle
ZO, stratum zonale (layer I)
III, oculomotor nucleus
IV, trochlear nucleus
Vm, mesencephalic nucleus of the trigeminal
VI, abducens nucleus

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