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Development of the Precerebellar Nuclei in the Rat: III. The Posterior Precerebellar Extramural Migratory Stream and the Lateral Reticular and External Cuneate Nuclei

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ABSTRACT

Sequential thymidine radiograms from rats injected on day E15 and killed thereafter at daily intervals up to day E22 were analyzed to trace the migratory routes and settling patterns of neurons of the lateral reticular nucleus and the external cuneate nucleus. The neurons of the lateral reticular and external cuneate nuclei originate in the primary precerebellar neuroepithelium at the same site as the inferior olivary neurons but follow a different migratory route. The labeled young neurons that are produced on day E15 (the last one-third of the total) join the posterior precerebellar extramural migratory stream. The cells move circumferentially over the wall of the medulla in a ventral direction and by day E17 reach the midline and cross it beneath the inferior olive. The crossing cells apparently continue to migrate circumferentially on the opposite side. One complement of these cells begins to form a ventrolateral extramural condensation on day E19. By day E20 some cells begin to penetrate the parenchyma and settle as neurons of the lateral reticular nucleus. The settling of the lateral reticular neurons continues on the following day, and by day E22 all the cells destined for the lateral reticular nucleus have penetrated the parenchyma. A dorsomedial-to-ventrolateral neurogenetic gradient is indicated for the settling lateral reticular neurons.

Another complement of migrating cells continues dorsally and forms a condensation on day E19 that we interpret as the external cuneate component of the crossed stream. These cells begin to penetrate the parenchyma on day E20, and by days E21 and E22 two components of the external cuneate nucleus are identifiable—the dorsal and ventral external cuneate nuclei. The neurons of the lateral reticular and external cuneate nuclei differ from neurons of all the other precerebellar nuclei in that their cerebellar projection is predominantly ipsilateral. We speculate that the axons of all precerebellar neurons are genetically specified to cross the midline ventrally to provide a contralateral efferent projection, but this is modified in the case of the ipsilaterally projecting lateral reticular and external cuneate neurons by the cell bodies following their neurites to the opposite side.

Key words: cell migration, external cuneate nucleus, lateral reticular nucleus, neurogenesis, thymidine autoradiography

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The *lateral reticular* nucleus lies alongside the inferior olive dorsolaterally. It was first described by Clarke (1858) and, according to Walberg ('52), Gudden obtained evidence in the 1880s that the lateral reticular nucleus sends fibers to the cerebellum by way of the inferior cerebellar peduncle. Brodal ('43), following similar earlier attempts, distinguished within the nucleus a magnocellular, parvicellular, and subtrigeminal component. Walberg ('52) examined the nucleus in 15 mammalian species and found considerable interspecies variability in the size of the nucleus. He claimed that all regions consist of small, medium, and large cells, but in many mammals the large cells tend to be concentrated dorsomedially and the smaller cells ventrolaterally. In the rat (Kapogianis et al., '82) the parvicellular component is situated ventrally, the magnocellular division dorsomedially, and the subtrigeminal component, containing predominantly medium-sized cells, dorsolaterally. The lateral reticular nucleus receives afferents from the spinal cord and some medullary and midbrain structures (reviewed by Flumerfelt, '82; Røste et al., '85); the spinal projection has been confirmed in the rat (Shokundi et al., '85). In the rat (Hrycyshyn et al., '82) the projection from the lateral reticular nucleus to the cerebellum is topographically organized and the projection to the vermis is more massive than to the hemispheres. There is some evidence that the parvicellular division of the lateral reticular nucleus projects in the cat to the lobules of the cerebellum representing the hindlimbs and the magnocellular division to the lobules representing the forelimbs (Brodal, '75). This is in agreement with a lesion study in the cat (Corvaja et al., '77) that showed that destruction of the magnocellular region of the nucleus produced maximal postural asymmetry in the forelimbs, whereas lesions affecting the parvicellular division produced mainly postural abnormalities in the hindlimbs. Most of these studies agree that the projection of the lateral reticular nucleus to the cerebellum is predominantly ipsilateral (Clendenin et al., '74; Chan-Palay et al., '77; Dietrichs and Walberg, '79). But there is also a smaller contralateral component present, partly attributable to collaterals (Payne, '83). The study of the development of the lateral reticular nucleus has been a neglected subject. Our quantitative thymidine radiographic investigation in adults (Altman and Bayer, '78) indicated that the neurons of this nucleus are generated over a 3-day period between days E13 and E15, with about 35% of the cells being generated on day E15.

Anatomical (Liu, '56; Grant, '62) and physiological (Holmqvist et al., '63; Cooke et al., '71a,b; Rosén and Sjölund, '73) studies have established that the *external* (or lateral) *cuneate nucleus* provides a topographically organized proprioceptive relay from the muscles of the forelimb and the neck to the cerebellum. In the rat (Campbell et al., '74) neck muscles are represented in the rostrolateral pole of the nucleus, arm and shoulder muscles posteromedially, and forearm and hand muscles more posteriorly. According to Grant ('62) and Rinvik and Walberg ('75) the fibers of the external cuneate nucleus terminate ipsilaterally in a topographic manner in the posterior part of the anterior lobe and the anterior part of the posterior lobe, and in the paramedian lobule. The pattern of external cuneate projection to the cerebellum is similar in the rat and is almost exclusively ipsilateral (Payne, '83). To our knowledge the only developmental study of the external cuneate nucleus concerns the time of origin of its neurons in the rat (Altman and Bayer, '80). With quantitative long-survival thymidine radiography we have established that the bulk of its neurons (nearly 70%) is generated on day E15, significantly later than the neurons of the main cuneate nucleus (peak on day E13). The superficial or extramural precerebellar migratory stream has not been hitherto implicated as the source of neurons of either the external cuneate nucleus or the lateral reticular nucleus.

MATERIALS AND METHODS

The material used in this study was identical with that described in detail in the first paper of this series (Altman and Bayer, '87a). Special use was made of sequential radiograms from rats labeled with ^{3}H-thymidine on day E15 and killed thereafter at daily intervals up to day E22.

RESULTS

The posterior extramural migratory stream

In rats injected on day E15 and killed 2 hours later, the heavily labeled cells of the primary precerebellar neuroepithelium (pcp in Figs. 1A, 2A) are surrounded by a zone of darkly staining unlabeled cells. The latter region was previously (Altman and Bayer, '87b) identified as the postmitotic premigratory zone, consisting of neurons of the inferior olive (iop in Figs. 1A, 2A) generated on day E14 or earlier. In rats injected on day E15 and killed 1 day later (Fig. 1B), the unlabeled olivary premigratory neurons are no longer seen; presumably they have joined the intramural olivary migratory stream. By day E17, as seen in rats injected on day E15 and killed 2 days later, the unlabeled cells have settled in their final location in the inferior olive (IO in Figs. 1C, 2C). By this time, a subpial band of cells has appeared beneath the inferior olive, composed of labeled cells. This zone is identified, on the basis of observations made in coronal sections (Figs. 3, 4), as the posterior precerebellar extramural migratory stream (pes).

Abbreviations

aes	anterior extramural migratory stream
ca	caudal
cp	primordium of the fourth ventricle choroid plexus
ecm	external cuneate extramural migratory stream
EC	external cuneate nucleus
ECd	dorsal external cuneate nuclei
ECv	ventral external cuneate nuclei
IO	inferior olive
iom	inferior olivary intramural migratory stream
iop	inferior olivary premigratory zone
LR	lateral reticular nucleus
lrm	lateral reticular extramural migratory stream
ME	medulla
pcp	precerebellar primary neuroepithelium
pcs	precerebellar secondary neuroepithelium
pcsc	caudal precerebellar secondary neuroepithelium
pcsr	rostral precerebellar secondary neuroepithelium
pes	posterior extramural migratory stream
PO	pontine region
ro	rostral
v4	fourth ventricle
v4p	posterior fourth ventricle
VS	principal sensory nucleus of the trigeminal

Fig. 1. Parasagittal radiograms through the primary (pcp) and secondary (pcsr) precerebellar neuroepithelia of rats labeled with ^{3}H-thymidine on day E15 and killed 2 hours (**A**), 1 day (**B**), and 2 days (**C**) later. Lines in C indicate the approximate coronal planes of the sections illustrated in the corresponding figures. Paraffin. Scale: 200 μm.

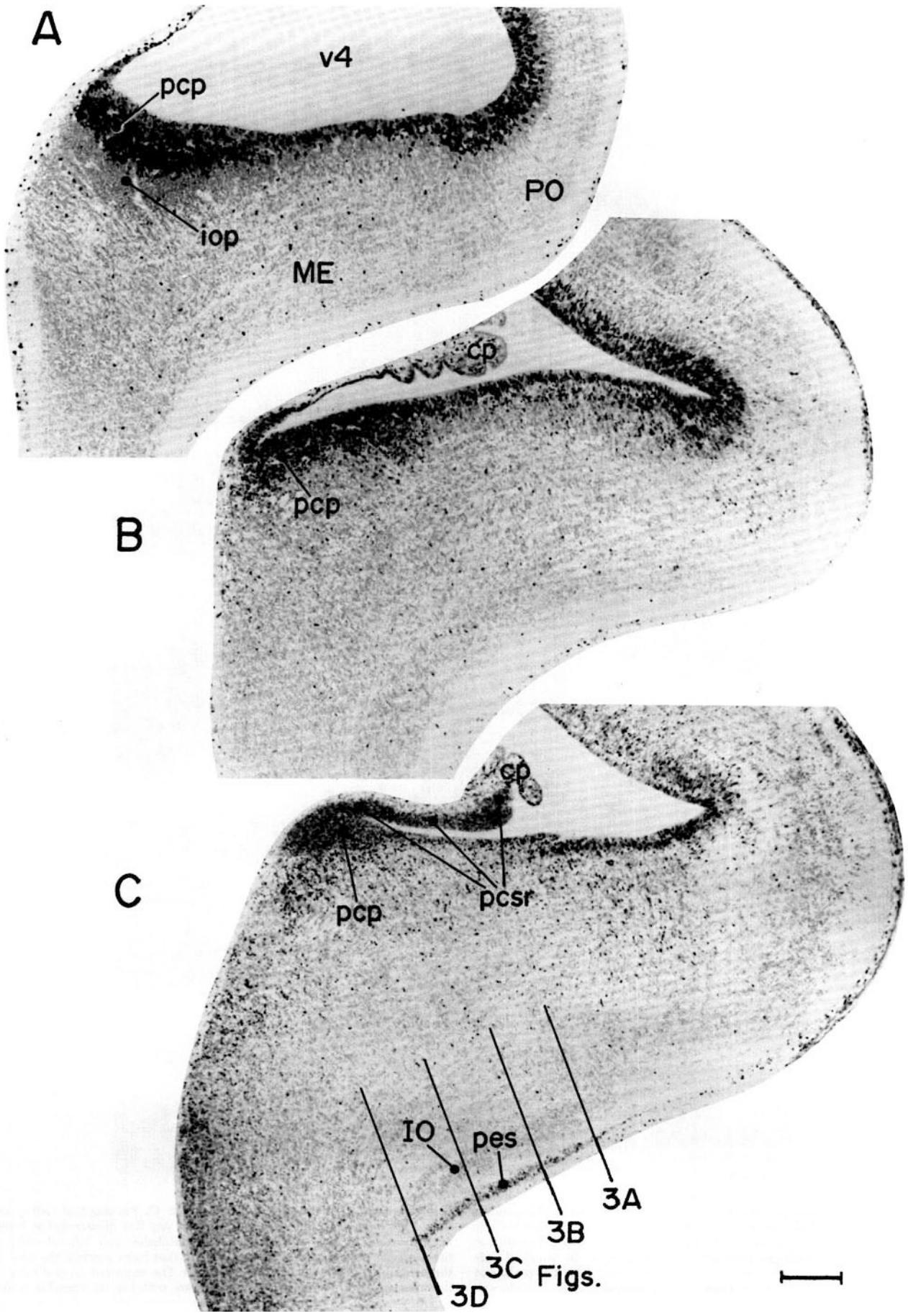


Figure 1

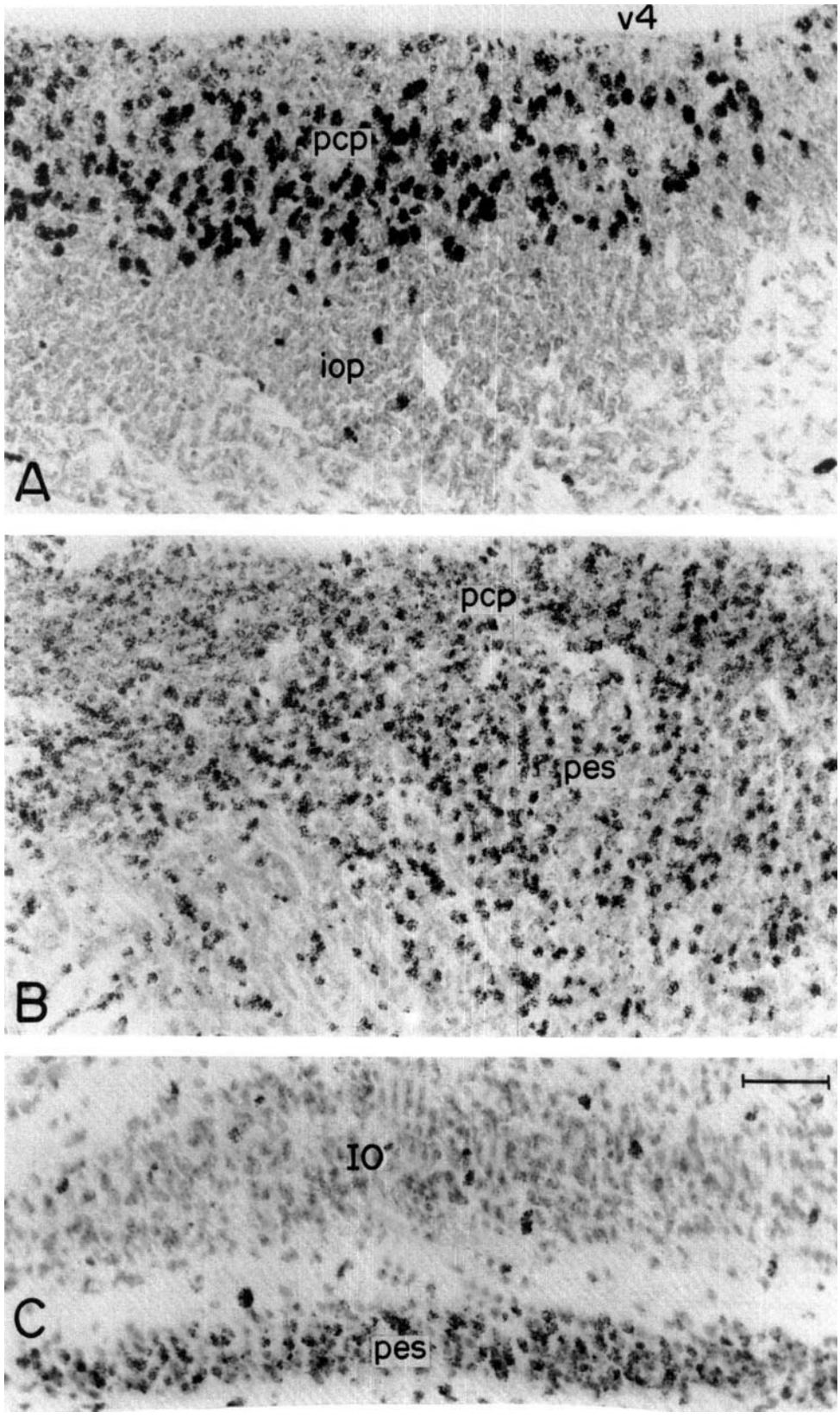
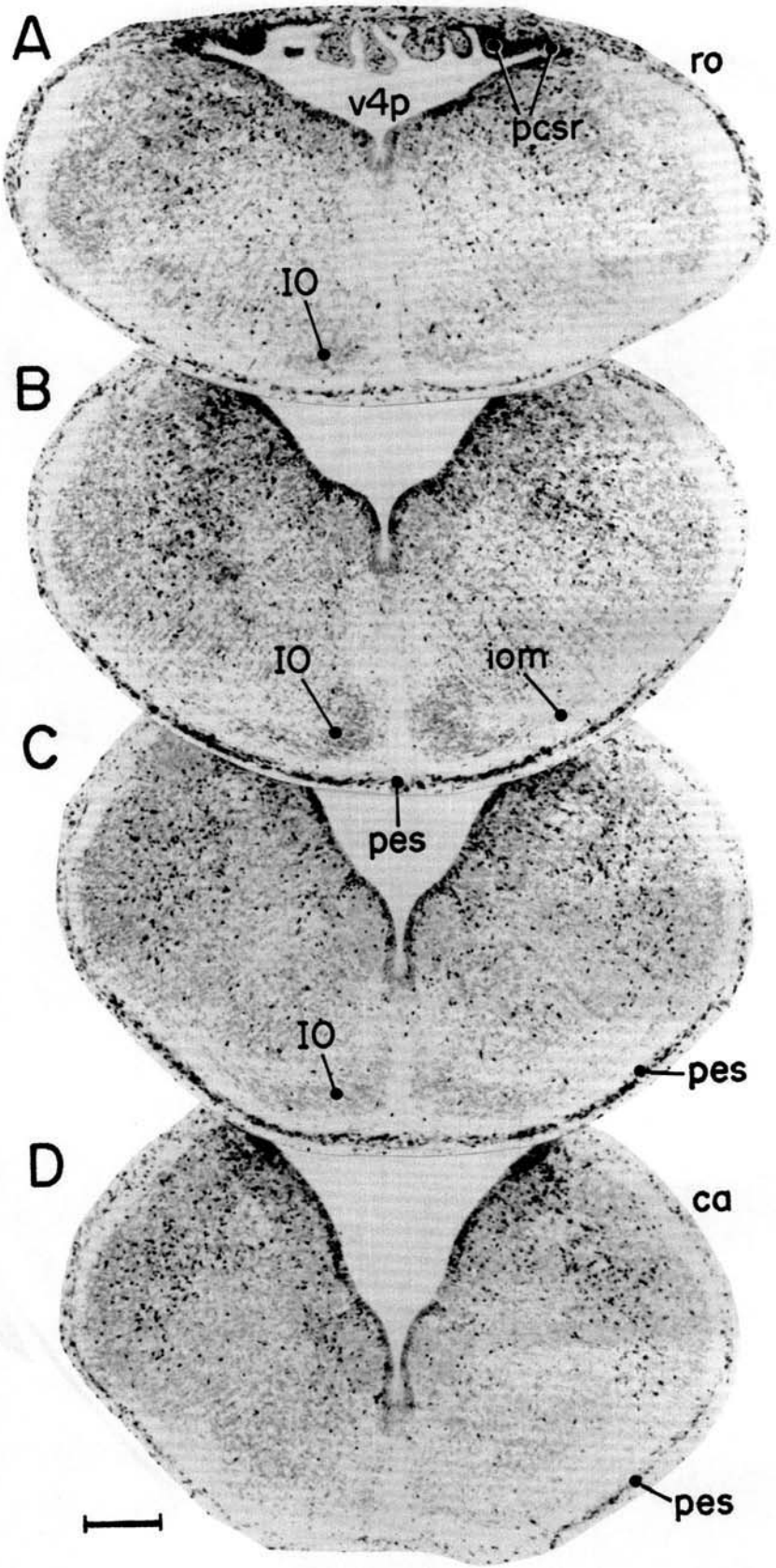


Fig. 2. **A:** Parasagittal radiogram from a rat labeled with ^{3}H-thymidine on day E15 and killed 2 hours later with heavily labeled (mitotic) cells in the precerebellar primary neuroepithelium (pcp) and unlabeled (postmitotic) cells in the inferior olivary premigratory stream (iop). **B:** Matched radiogram from a rat labeled on day E15 and killed on day E16. The proliferating cells of the precerebellar primary neuroepithelium show considerable label dilution. The former region of the inferior olivary premigratory zone is now occupied by a new wave of labeled and unlabeled cells forming the posterior extramural migratory stream (pes). **C:** Parasagittal radiogram from a rat labeled on day E15 and killed on day E17 (illustrated at lower magnification in Fig. 1C) to show the unlabeled and labeled cells of the posterior extramural migratory stream that have reached the base of the medulla beneath the inferior olive (IO). The scattered labeled cells in the inferior olive may be glial cells (compare with Fig. 4). Paraffin. Scale: 50 μm.



(E17). The labeled cells of the posterior extramural migratory stream now form a semicircle around the lower half of the medulla under the unlabeled inferior olive. Paraffin. Scale: 200 μm.

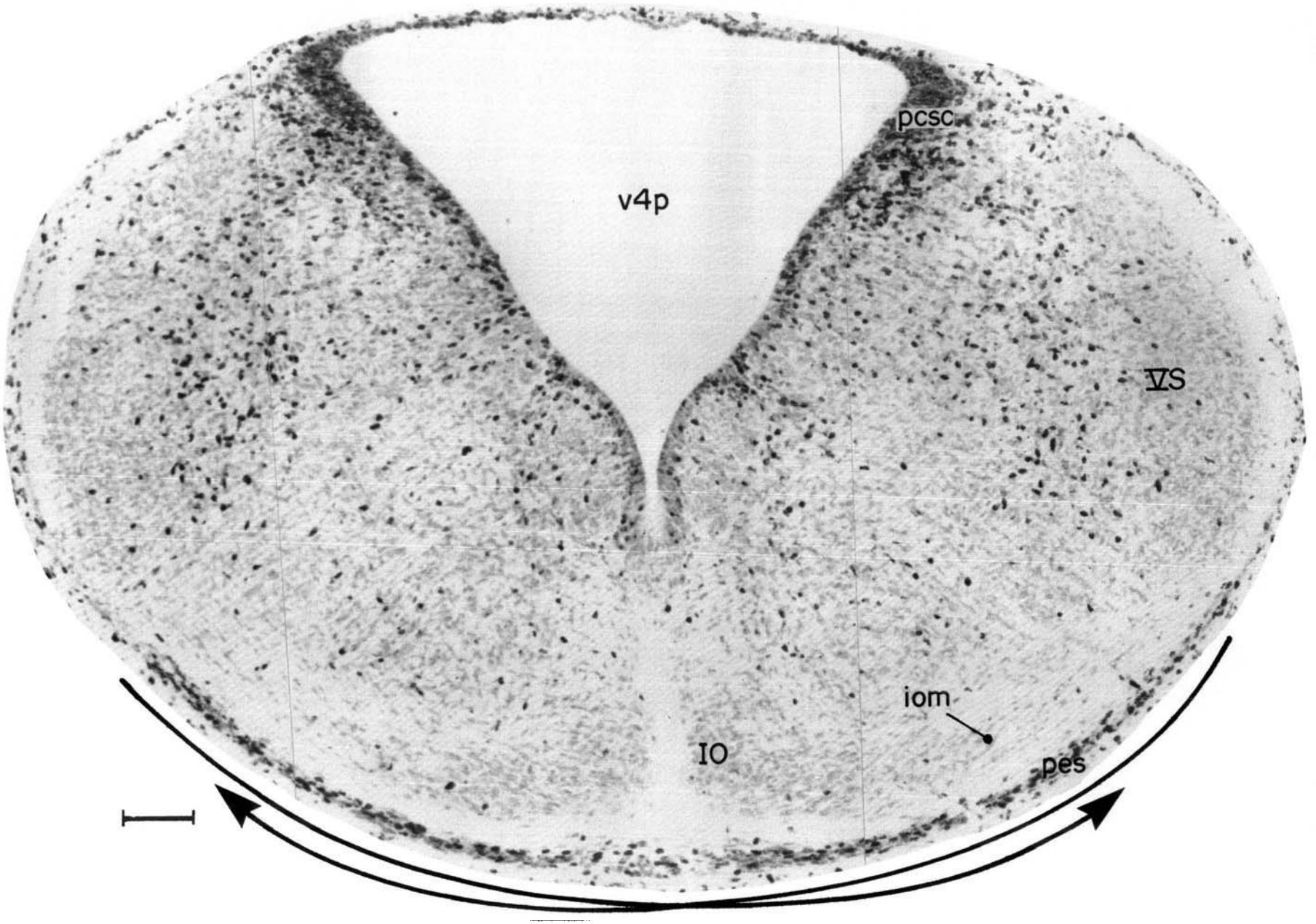


Fig. 4. Coronal radiogram, from a rat labeled on day E15 and killed on day E17, through the midportion of the inferior olive. The cells of the posterior extramural migratory stream (some unlabeled, most of them labeled) cross the midline ventrally. We postulate that the cells originating on one side cross over to the opposite side (arrows). Paraffin. Scale: 100 μm.

The posterior precerebellar extramural migratory stream is distinguished from the later-appearing anterior precerebellar extramural migratory stream that courses toward the basal pons (Altman and Bayer, '87c). In rats injected on day E15 and killed on day E16, the former site of the unlabeled premigratory olivary cells (iop in Fig. 2A) is now occupied by round and vertically oriented, spindle-shaped cells—some unlabeled, others showing light or intermediate labeling (pes in Fig. 2B). These cells move around the wall of the upper half of the medulla and by day E17 form a semicircle of extraparenchymal cells (most of them labeled, some unlabeled) from rostral to caudal (Fig. 3A–D) along the entire length of the inferior olive. On the subsequent day, as seen in rats injected on day E15 and killed on day E18, most of the cells have left the midline region and can be traced farther dorsolaterally (Figs. 5, 6). This observation allows two interpretations: (1) after the migratory cells have reached and crossed the midline they reverse their course and move backward, or (2) the cells originating on either side cross to the opposite side where they move forward. We have adopted the latter interpretation as the more likely of these alternatives (Fig. 4). We propose that the posterior extramural migratory stream has two components, the lateral reticular (lrm) and external cuneate (ecm) migratory streams (Figs. 5, 6) and that these cells settle on the succeeding days at two sites—ventrolaterally as the neurons of the lateral reticular nucleus and dorsolaterally as the neurons of the external cuneate nucleus.

The settling of the lateral reticular nucleus neurons

In rats injected on day E15 and killed on day E19 the posterior extramural migratory stream is greatly reduced (and at many levels is no longer present) in the midline (Fig. 7). As we noted earlier, we interpret the lower of the two lateral cell streams and condensations as the presettling neurons of the lateral reticular nucleus (lrm in Figs. 5–7). By the next day, in rats injected on day E15 and killed on day E20 (lrm; Figs. 8, 10A) some of these cells are still in subpial position while others have penetrated the parenchyma as the settling labeled neurons of the lateral reticular nucleus (LR in Figs. 8, 10A). The settling of the lateral reticular neurons generated on day E15 continues on day E21 (Fig. 10B) but a subpial condensation is still present. Interestingly, the settled cells tend to be heavily labeled (LR in Fig. 10B) while the presettling cells are lightly labeled (lrm in Fig. 10B). This observation, combined with the fact that the earlier-settled cells (LR in Figs. 10, 11) are unlabeled after injection on day E15, indicates that there is a dorsomedial-to-ventrolateral neurogenetic gradient in the lateral reticular nucleus. The unlabeled cells (the two-thirds of the population generated on days E13 and E14; Altman and Bayer, '78: Fig. 3) settle dorsomedially, and the labeled cells (those generated on day E15) settle sequentially ventrolaterally. By day E22 all the cells destined for the lateral reticular nucleus have penetrated the parenchyma (LR in Fig. 11). An exception is a cluster of labeled cells that appears to be arrested near the midline (asterisk in Figs. 10B, 11). The fate of these few labeled cells has not been determined.

The settling of the external cuneate nucleus neurons

The external cuneate condensation of the posterior extramural migration is recognizable by day E18 (ecm in Figs. 5, 6) and becomes more pronounced on day E19 (Fig. 7). By day E20 these cells begin to settle to form the external cuneate nucleus (EC in Figs. 8A, 12A) but the migratory stream is still not exhausted. By days E21 and E22 two components of the external cuneate nucleus are identifiable, tentatively designated as the dorsal and ventral external cuneate nuclei (ECd and ECv in Fig. 12B,C).

DISCUSSION

Our thymidine radiographic demonstration that the neurons of the inferior olive are no longer labeled on day E15, whereas a high proportion of the cells of the posterior extramural migratory stream are labeled, indicates that this stream is not composed of young olivary neurons, as was hitherto assumed (Essick, '12; Harkmark, '54; Ellenberger et al., '69; Altman and Bayer, '78). In the preceding paper of this series (Altman and Bayer, '87b) we have presented evidence that neurons of all divisions of the inferior olive, not just some of them, as Harkmark ('54) believed, derive from the intramural migratory stream. Indeed, most of the cells of this intramural migration have settled in the olive by day E17 when the posterior extramural migratory stream reaches the midline ventrally.

The present findings based on sequential thymidine radiography indicate that the posterior extramural migratory stream is the source of neurons of two other precerebellar structures—the lateral reticular nucleus and the external cuneate nucleus. The cells destined to reach these two structures supplying mossy fibers to the cerebellum first assemble as extramural cell condensations ventrolaterally and dorsolaterally and thereafter penetrate the parenchyma. Since two-thirds of the lateral reticular nucleus neurons are generated before day E15 (Altman and Bayer, '80), while the bulk of the external cuneate nucleus neurons are generated on day E15 (Altman and Bayer, '78), we assume that most of the unlabeled cells of the posterior extramural migratory stream represent lateral reticular neurons and most of the labeled cells external cuneate neurons. In the lateral reticular nucleus the early-forming (unlabeled) cells settle dorsomedially, and the late-forming (labeled) cells ventrolaterally.

The significance of the presence of extramural migratory cells across the midline ventrally was difficult to interpret in the past when it was believed that this stream was composed of inferior olivary neurons, because the settled olivary neurons do not extend to the midline. Our observations suggest that these cells cross the midline and settle contralaterally—one contingent ventrolaterally, as the neurons of the lateral reticular nucleus, and another contingent dorsolaterally, as the neurons of the external cuneate nucleus. The alternative interpretation—that the cells generated on one side cross the midline and then swing back, and some settle ventrolaterally while others retrace their steps all the way dorsally, to settle, after a delay of several days, near their site of origin—does not seem plausible. But our interpretation—namely, that cells generated on one side cross to the opposite side, and in the case of the external cuneate nucleus practically circumnavigate the entire medulla—also requires an explanation because such a crossing is presently unknown in any other region of the developing mammalian brain. (The anterior extramural migratory stream does not cross; Altman and Bayer, '87c.)

A speculative interpretation starts with the difference in the laterality of inferior olivary and basal pontine gray projection to the cerebellum, on the one hand, and that of

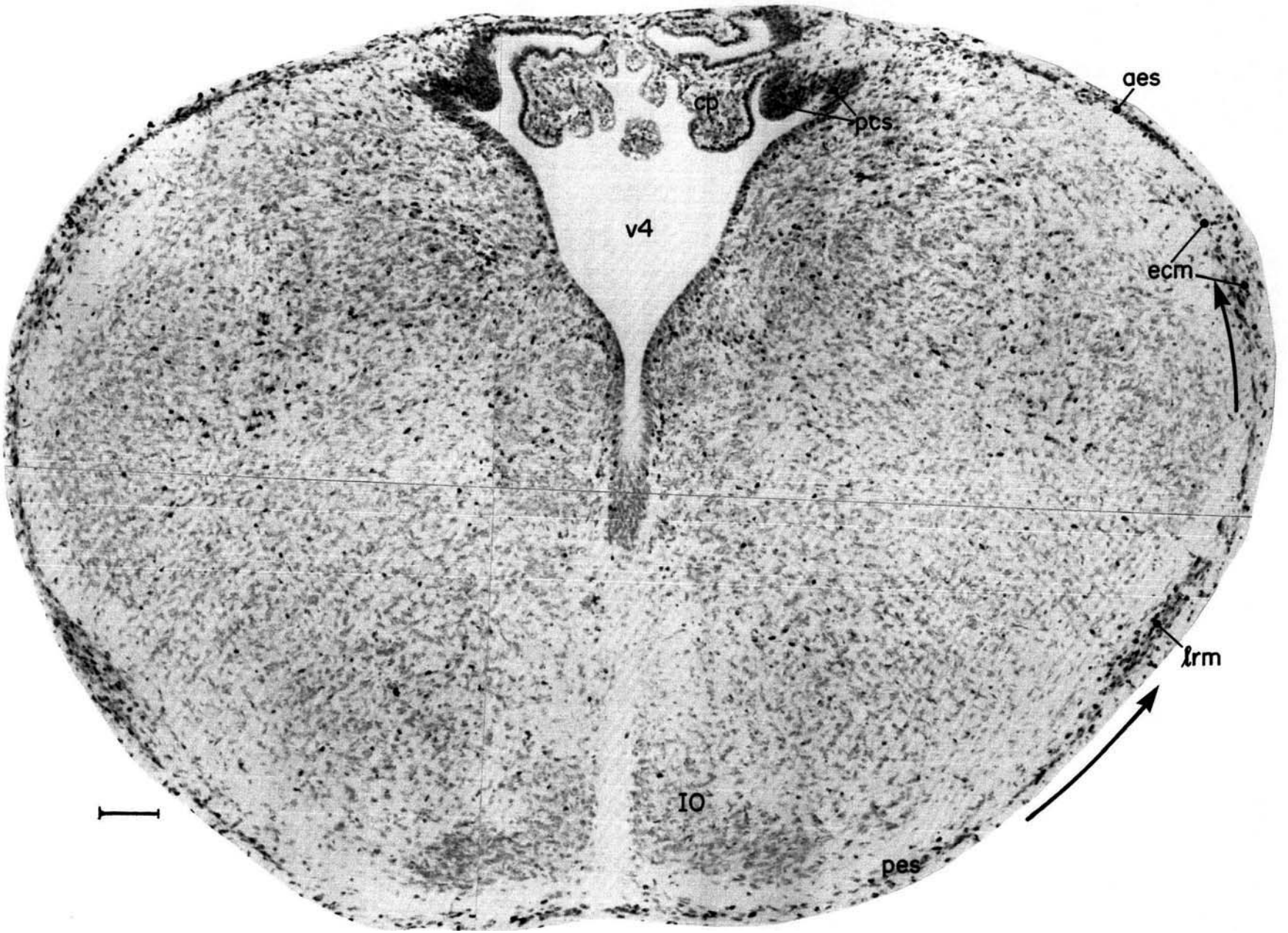


Fig. 5. Midcoronal radiogram through the inferior olive from a rat labeled with ^{3}H-thymidine on day E15 and killed on day E18. The posterior extramural migratory stream (pes) contains few cells ventrally but forms two clusters laterally. We designate the ventrolateral cluster as the lateral reticular component of this stream (lrm) and the dorsolateral cluster as its external cuneate component (ecm). Further dorsolaterally is another stream, designated as the anterior extramural migratory stream (aes), derived from the secondary precerebellar neuroepithelium (Altman and Bayer, '87a) and having a different destination. Paraffin. Scale: 100 μm.

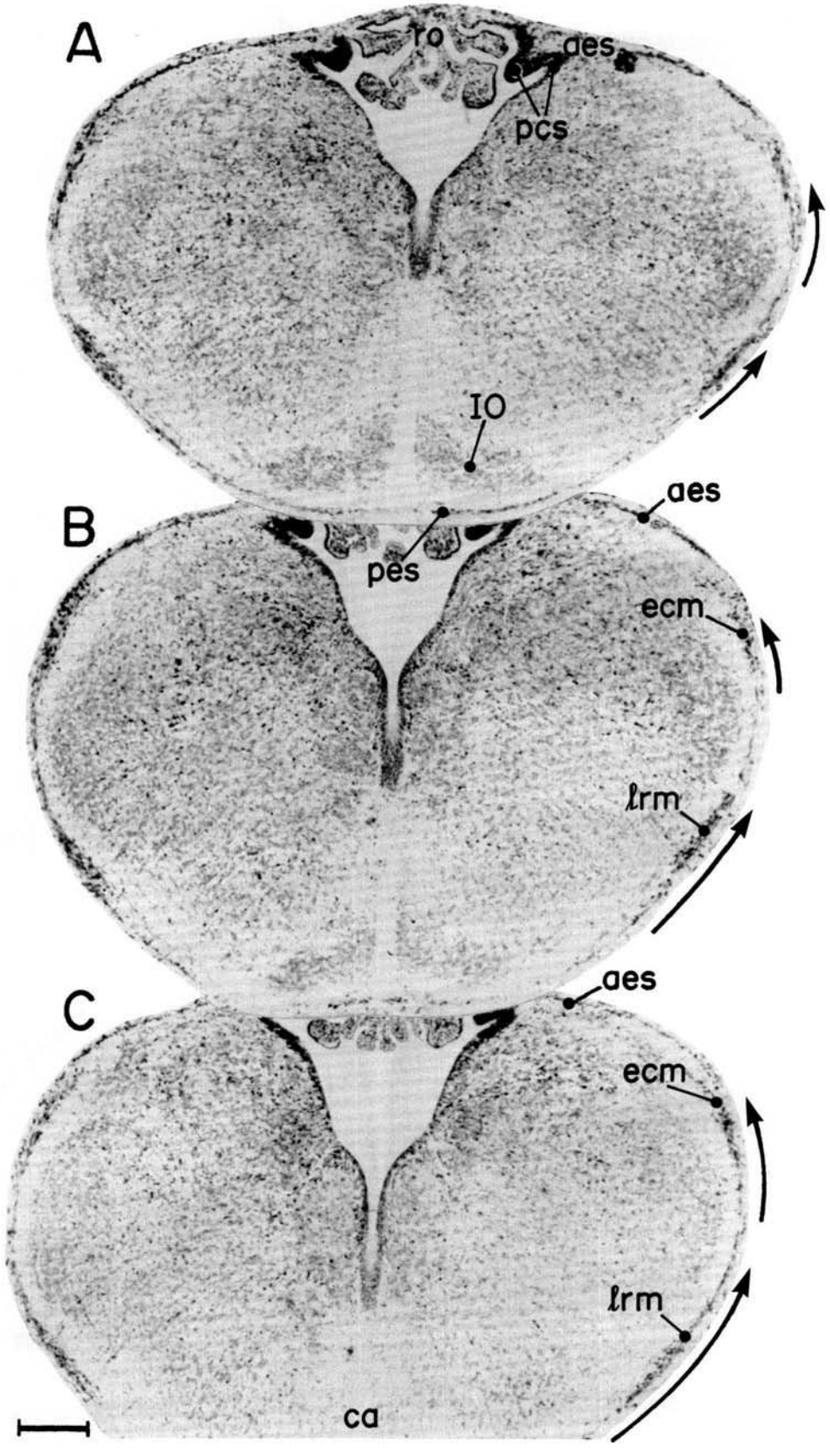


Fig. 6. Coronal radiograms from rostral (A) to caudal (C), from a rat labeled on day E15 and killed on day E18. B is shown at higher magnification in Figure 5. Paraffin. Scale: 200 μm.

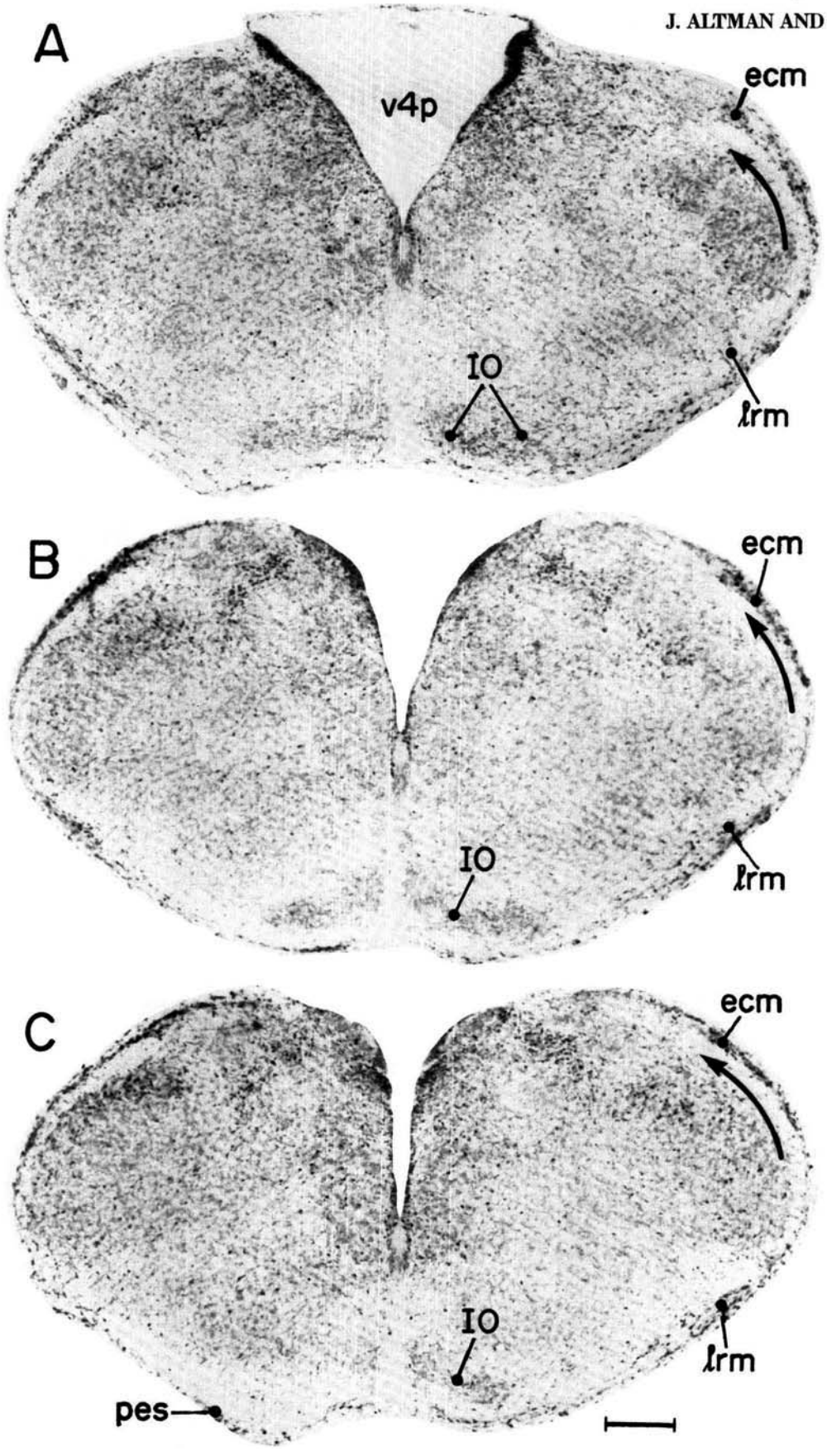


Fig. 7. Coronal thymidine radiograms from rostral (A) to caudal (C), from a rat labeled on day E15 and killed on day E19. Arrows indicate the presumed direction of migration. B is shown at higher magnification in Figure 9B. Paraffin. Scale: 200 μm.

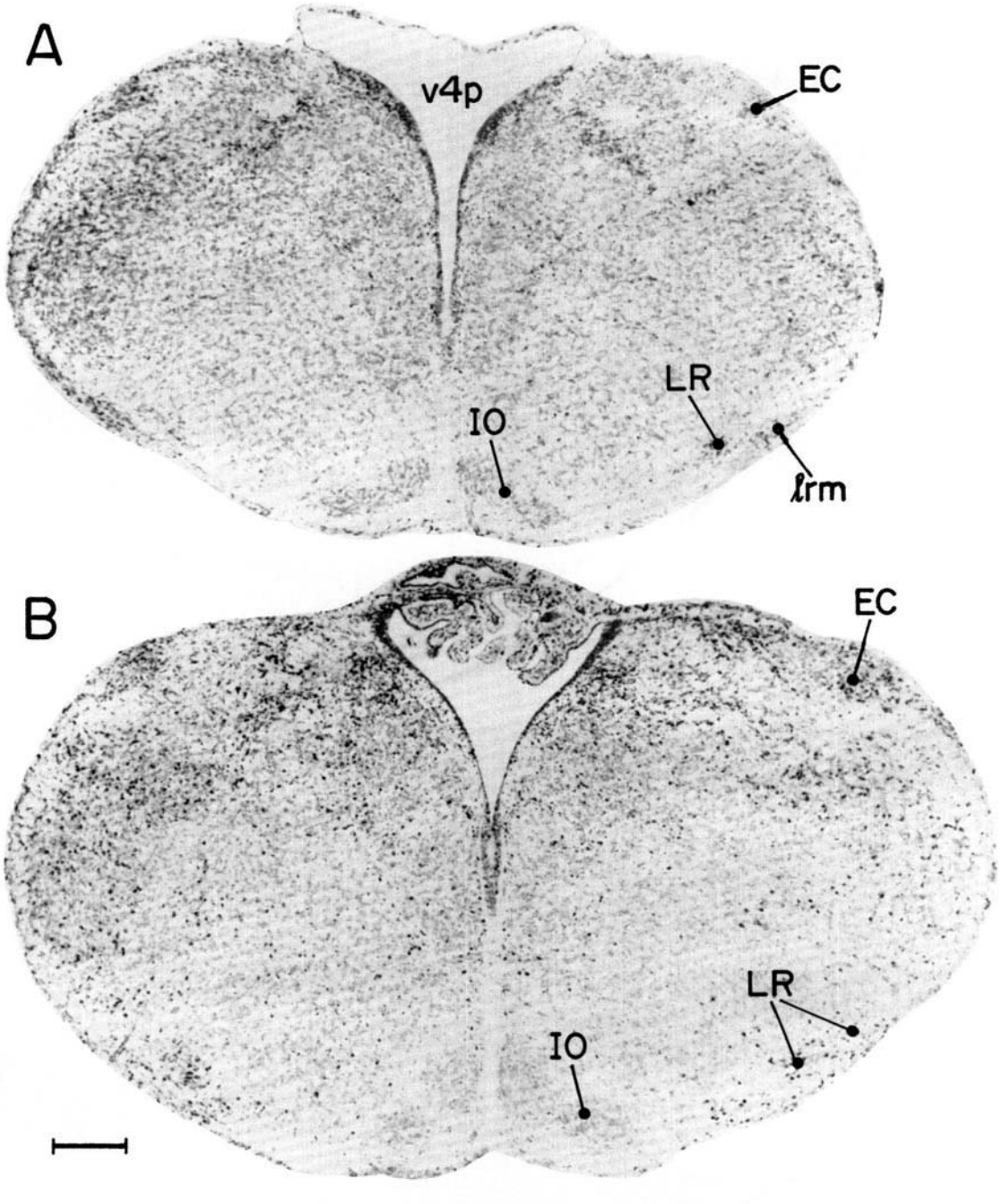


Fig. 8. **A:** Coronal thymidine radiogram showing the settling of the labeled neurons of the lateral reticular nucleus (LR) and external cuneate nucleus (EC) in a rat labeled on day E15 and killed on day E20. **B:** Matched radiogram from a labeled on day E15 and killed on day E21. Paraffin. Scale: 200 μm.

the lateral reticular nucleus and external cuneate nucleus, on the other. In the rat, the axons of the inferior olive terminate as climbing fibers predominantly (Chan-Palay et al., '77) or exclusively (Campbell and Armstrong, '83; Payne, '83) in the contralateral cerebellum. Similarly, the majority of pontine gray mossy fibers terminate contralaterally (Eisenman, '81; Azizi et al., '81; Payne, '83). In contrast, the mossy fiber projection from the lateral reticular nucleus (Chan-Palay et al., '77; Payne, '83) and the external cuneate nucleus (Grant, '62; Rinvik and Walberg, '75, in the cat; Payne, '83, in the rat) is mostly ipsilateral. Our speculation is that all precerebellar neurons are specified to send their axons to the opposite side. The axons of the inferior olivary and pontine gray neurons presumably decussate after their cell bodies have settled ipsilaterally. In contrast, the predominantly ipsilateral projection of the lateral reticular

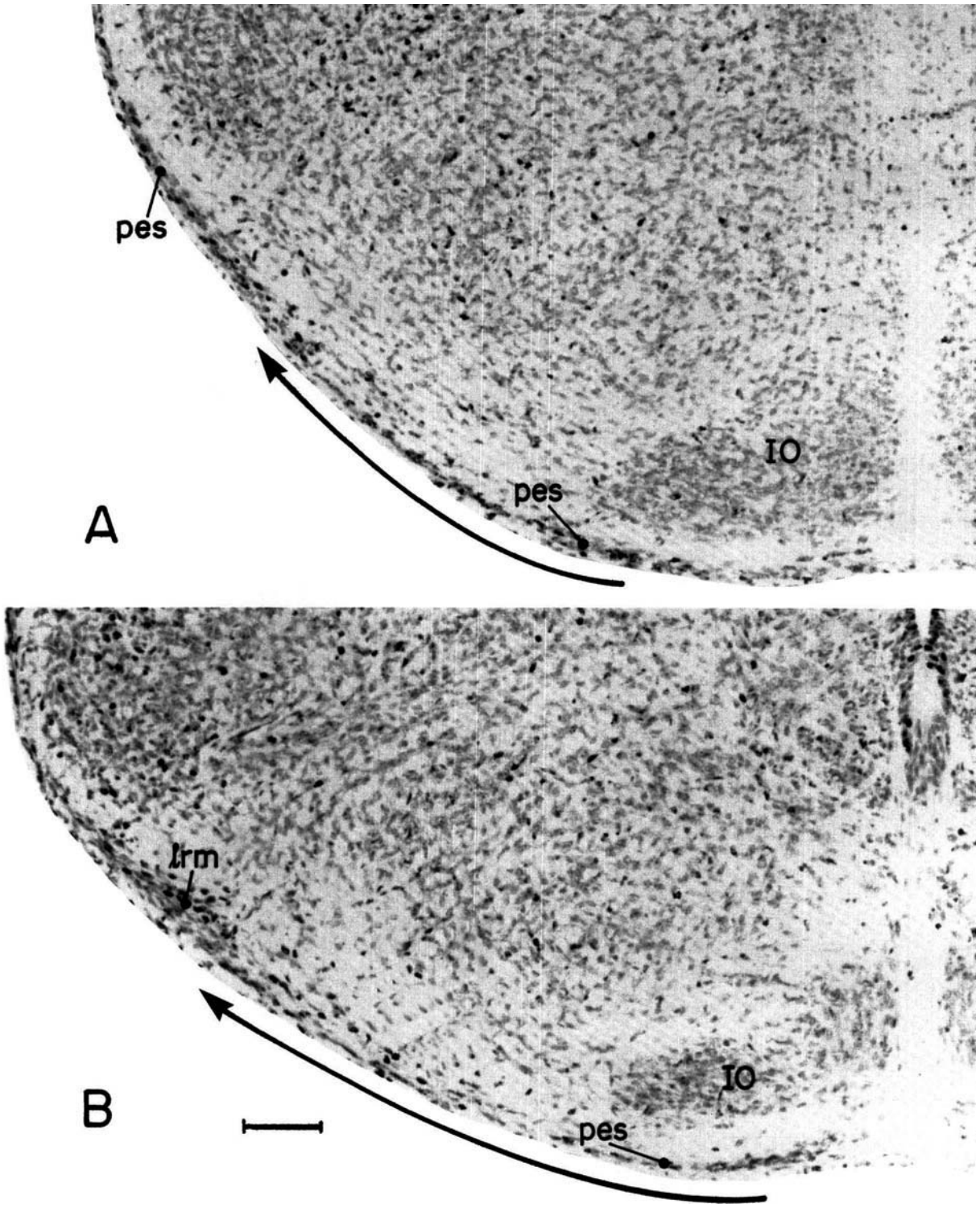


Fig. 9. Sequential radiograms (continued in Figs. 10, 11) tracing the settling of the cells of the lateral reticular component (lrm) of the posterior precerebellar extramural migratory stream (pes). **A:** From a rat labeled on day E15 and killed on day E18. **B:** From a rat labeled on day E15 and killed on day E19. Paraffin. Scale: 100 μm.

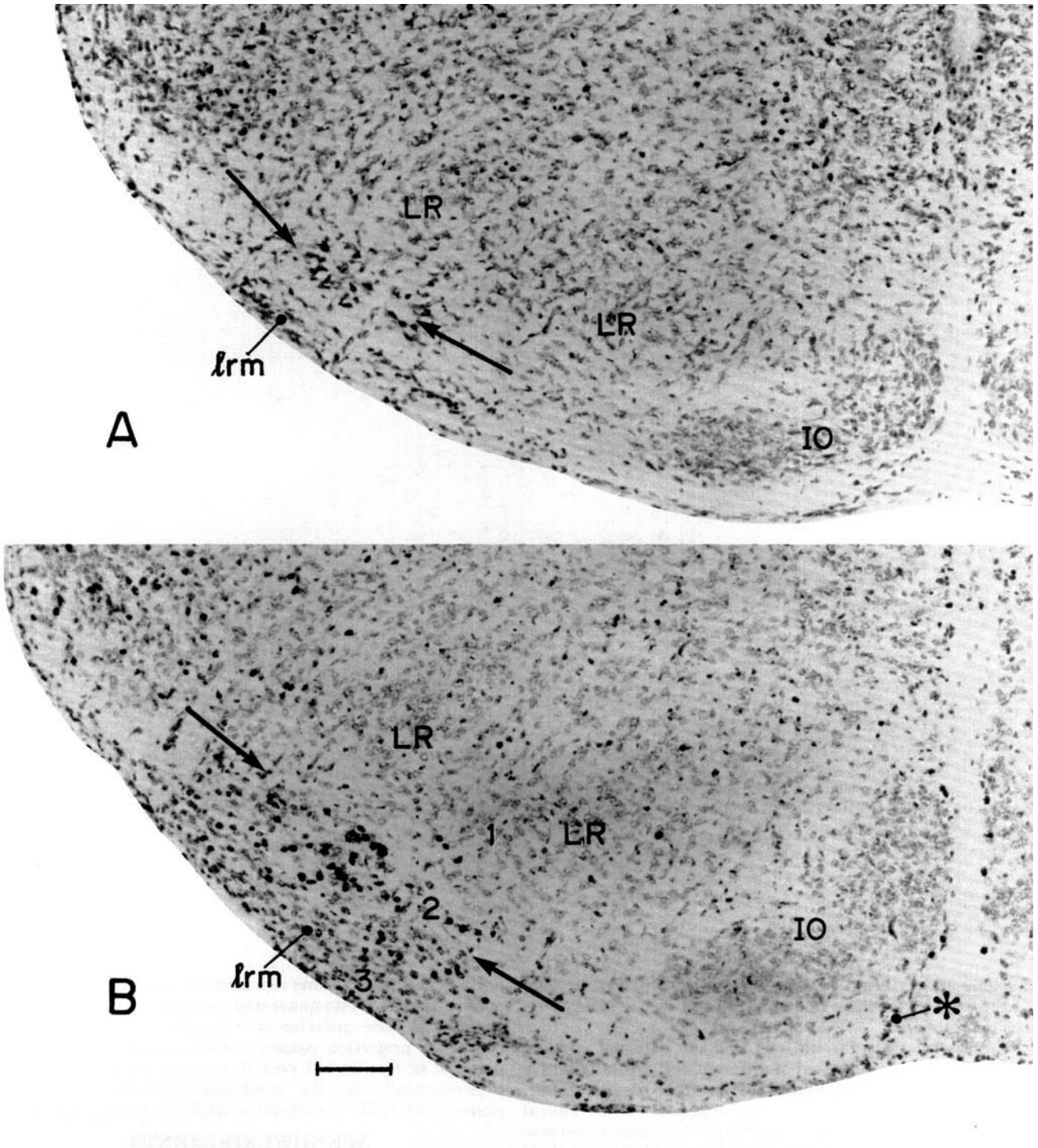


Fig. 10. Continuation of sequential thymidine radiograms shown in Figure 9. **A:** From a rat labeled on day E15 and killed on day E20. **B:** From a rat labeled on day E15 and killed on day E21. The unlabeled lateral reticular neurons (LR and 1) are settled dorsomedially. The settling of the second complement of heavily labeled lateral reticular neurons (arrows and 2) is evident on day E20 and continues on day E21. On these days a fair proportion of the later-generated lightly labeled cells are still in the migratory zone (3). Asterisk indicates a small cluster of unidentified labeled cells. Paraffin. Scale: 100 μm.

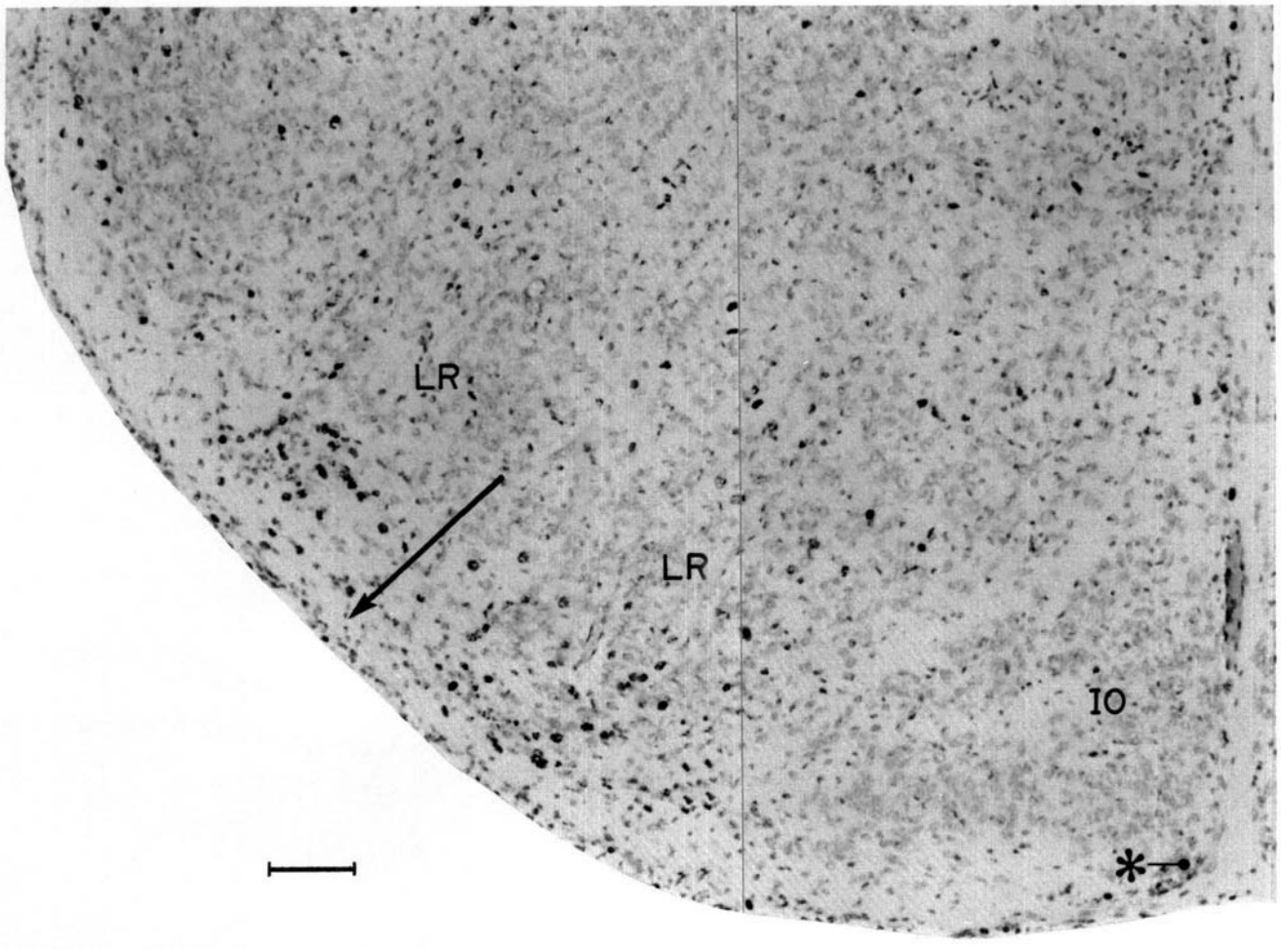


Fig. 11. Continuation of the sequential thymidine radiograms shown in Figures 9 and 10. Animal labeled on day E15 and killed on day E22. By this age practically all the labeled cells of the migratory stream have settled in the lateral reticular nucleus (LR). Arrow indicates the dorsomedial-to-ventrolateral neurogenetic gradient in the lateral reticular nucleus. Asterisk indicates a small cluster of unidentified labeled cells. Paraffin. Scale: 100 μm.

nucleus and external cuneate nucleus is achieved in spite of the crossing of their fibers by the cell bodies settling on the opposite side.

The lateral reticular nucleus and the external cuneate nucleus are each composed of different cell types and have subdivisions. We have referred earlier to the magnocellular, parvicellular, and subtrigeminal components of the lateral reticular nucleus, the rostrolateral, posteromedial, and posterior divisions of the external cuneate nucleus, and their differential topographic projection to the cerebellum. In perinatal rats we have found a dorsomedial-to-ventrolateral neurogenetic gradient in the lateral reticular nucleus. These neurons are not mature enough at this age to distinguish them in terms of size. It is tempting to speculate that the early-generated neurons represent the magnocellular component and the late-generated neurons the parvicellular component. The question of a possible difference in the cerebellar projection patterns of early and late-generated neurons of the lateral reticular nucleus can be resolved experimentally by the combined thymidine autoradiographic and HRP histochemical double labeling technique.

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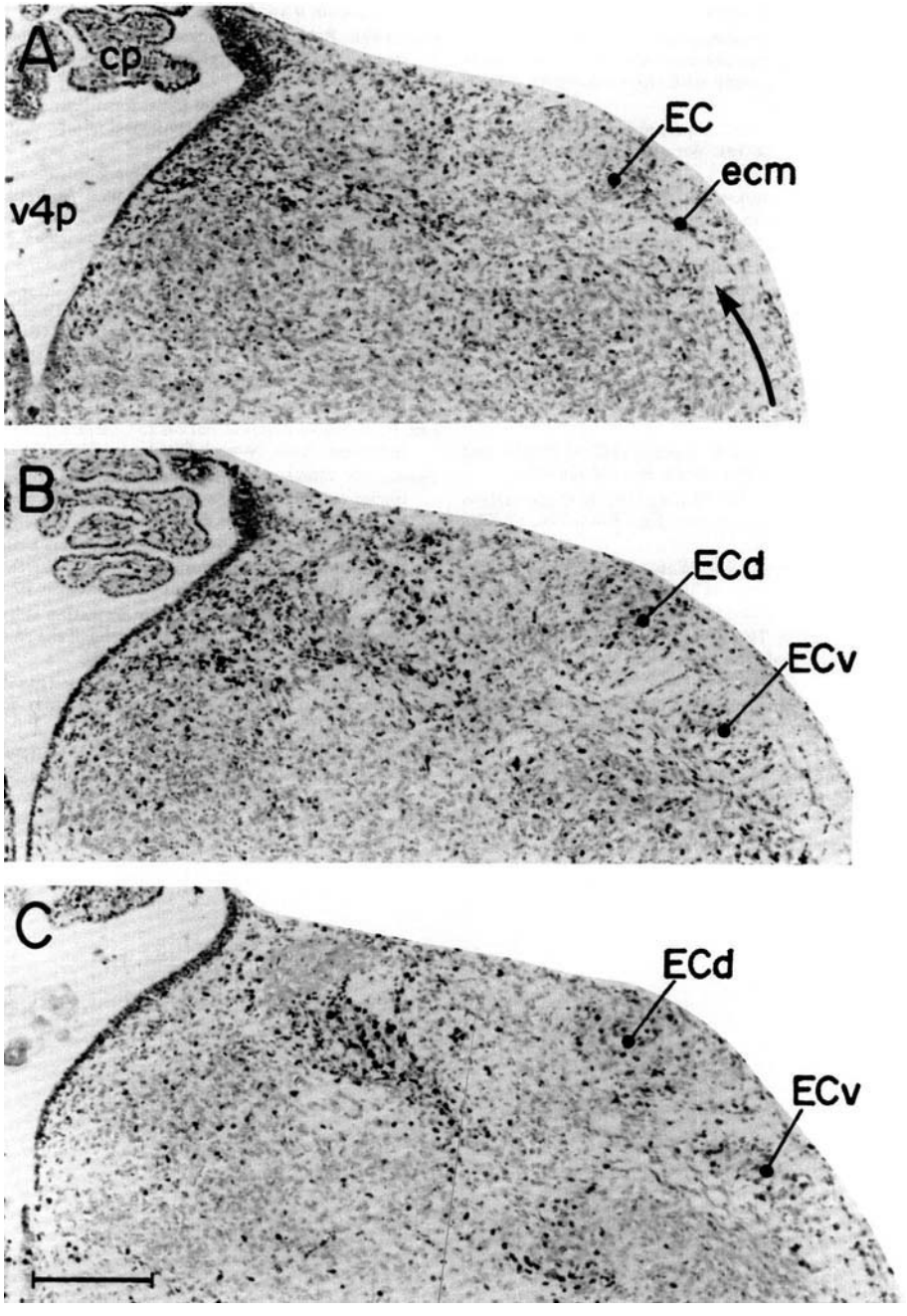

Fig. 12. Coronal radiograms from rats labeled on day E15 and killed on days E20 (A), E21 (B), and E22 (C) to show the settling of neurons of the external cuneate nucleus. Paraffin. Scale: 200 μm.

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