from the more proximal part even though there is no external anatomical differentiation between these 2 regions. The myoelectric complexes observed oral to the sub-serosal lymphoid formations had similar durations of the phases of the MMC and the frequency of the slow waves to those previously described for the ileum in carnivores[4,5]. The last part (about 10 cm) of the intestine in the ferret caudal to the lymphoid formations exhibited a pattern of colonic electrical activity similar to that previously described in the dog[3,6] and other species[10]. The oral limit of the serosal lymphoid formation thus appears to be a good indicator or the transition from ileum to colon.

This change in electrical activity was observed despite the absence of a caecum and an ileo-colonic sphincter in the ferret. The presence of a sphincter and the anatomical differentiation into small and large intestine does not appear to be necessary for the generation of typical small and large intestinal electrical activity patterns. This is confirmed by results showing the absence of both colonic motor changes and bowel habits after ileo-colonic sphincterectomy in dog (unpublished results).

a A histological change was observed at the point of functional transition from small to large intestine. At this point the continuity of the muscle layers was disrupted by a band of connective tissue which may be considered as an 'electrical insulator'. This insulator prevents slow waves and spike propagation from the ileum to the colon in a manner similar to that observed at the ileo-colonic sphincter on the dog[8]. There can be no electrotonic spread of the myoelectric complex to the last 10 cm of intestine in the ferret.

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Taste responsiveness of the transplanted supernumerary leg in the fleshfly *Sarcophaga bullata*[1]

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Summary. Ectopic legs were produced on the abdomen of the fleshfly *Sarcophaga bullata* by transplantation of prothoracic leg imaginal discs. Stimulation of the tarsal chemoreceptors of these ectopic legs with sucrose solution resulted in the extension of the host proboscis indicating the functional connectivity of the sensory axons.

During development of the nervous system, the growing axons navigate towards and find their target tissues; having reached a given target, they establish specific patterns of connectivity. Proper functioning of the nervous system depends upon the appropriateness of these connections. How axons actually navigate and establish specific connectivity is still far from clear[3,4]. Taste reponsiveness in flies seems to be a promising system for the analysis of 2 fundamental problems of developmental neurobiology, namely, axonal navigation and neuronal specificity. In flies, taste receptors (chemosensory hairs with water, sugar and salt receptors) are located on the tarsal segments of the legs. When a hungry or thirsty fly lands on a potential food or water source these sensilla send impulses to the central nervous system which results in the extension of the fly's proboscis to initiate feeding[5]. This is called the proboscis extension response (PER). A positive PER is an indication of the existence of sensory axons in the leg as well as their specific connectivity with the central neurons. To study the developmental aspects of neural connectivity supernumerary legs were produced by ectopic transplantation[6] of leg imaginal discs in the fleshfly *Sarcophaga bullata* and the taste responsiveness of the chemosensilla on these legs was examined. The results reported here indicate that the growing sensory axons have made appropriate connections with the central interneurons, at least to some extent.

Materials and methods. Prothoracic leg imaginal discs from donor larvae (red spiracle stage, about 4–6 h before pupariation) were dissected out in sterile *Drosophila* Ringer's[7] solution and transplanted onto 2–3-h-old prepupae[6]. The operated hosts were kept in the environmental chamber till adult emergence (about 12 days post operation). The newly emerged host flies had their wings clipped off. The dorsal thorax of each fly was glued on to the tip of a wooden stick and it was left overnight starving before testing the PER the next morning. The flies were tested for

Proboscis extension response of host flies upon stimulation of their tarsal chemosensilla of transplanted or in situ legs

Test solution	Physiological status	PER of in situ prothoracic leg of the host fly	PER of transplanted leg
Distilled water	Thirsty and hungry	6 (15)	3 (10)
Sucrose solution			
0.15 M	Hungry	6 (15)	2 (9)
0.5 M	Hungry	6 (15)	3 (11)
1.0 M	Hungry	6 (15)	3 (11)
1.0 M sodium chloride solution	Thirsty and hungry	0 (15)	0 (11)

PER is expressed on a scale of 0–6. The numbers in parentheses represent number of flies responding out of a test number of 15 flies. (2nd column from the right) or the number of flies having a fully developed ectopic leg which could be tested (extreme right-hand column). PER score is not average of tested flies. Each fly in the parentheses exhibited the same response.

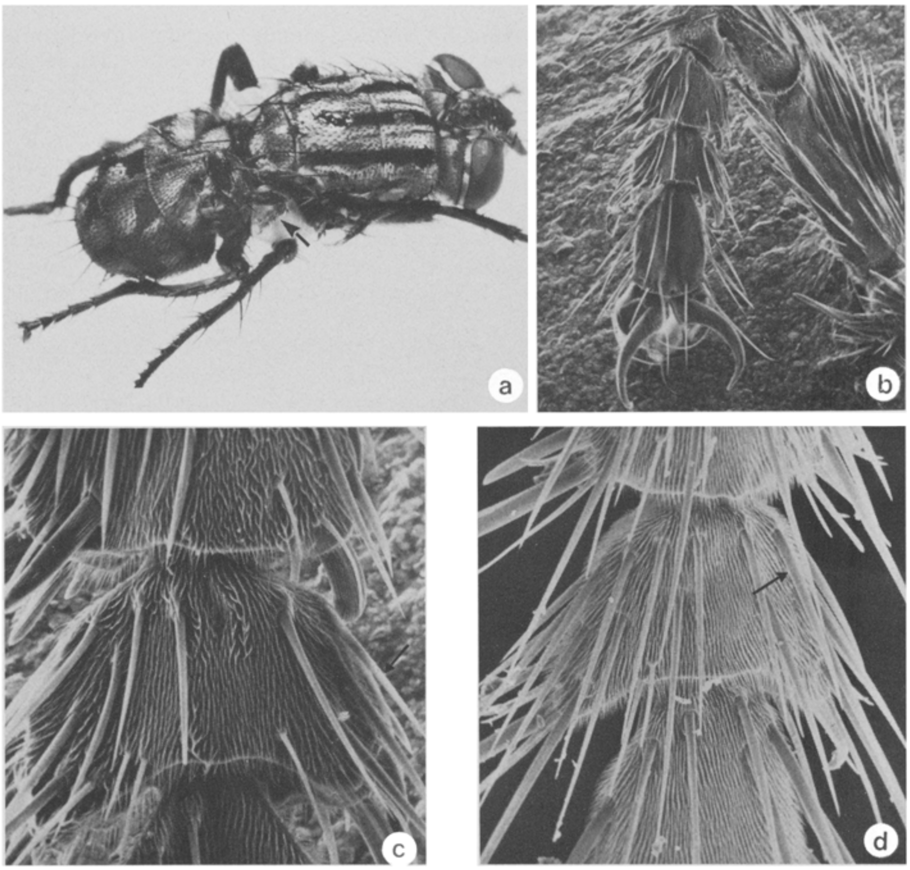
PER under 2 physiological conditions - thirsty and hungry or hungry. The taste sensilla on the tarsi of their transplanted or in situ prothoracic legs were exposed to distilled water, 1.0 M sodium chloride solution or sucrose solution of different concentrations. A tiny drop of test solution was placed on the tarsal sensilla by means of a brush made of a single human eye brow hair. PER was scored on an arbitrary scale of 0 (no response) to 6 (full response)[8]. For microscopical observations, the gold-coated legs were examined in a Cambridge Stereoscan S4-10 scanning electron microscope operated at an accelerating voltage of 20 kV and photographed on Kodak plus-X pan professional film.

Results and discussion. Ectopic transplantation of leg imaginal discs resulted in the development of fully everted, well differentiated supernumerary legs on the host flies (figure, a, b). The tarsi of these legs contained chemosensory hairs like the in situ leg (figure, c, d). PER test results are summarized in the table. At least 15 flies were used in the experiment and all the flies were tested for each solution. It can be seen that the transplanted legs responded to both distilled water and sucrose solution. However, the PER is only partial irrespective of the physiological status of the fly and the concentration of the sucrose solution. None of the transplanted legs showed a full PER with a score of 6.

Earlier reports[6,9] on transplanted supernumerary legs in flies demonstrated the existence of nerve connection between the ectopic leg and the host's thoracic ganglion; and recently[10] it was shown in the fleshfly that this nerve projects directly into the appropriate neuromere of the thoracic ganglion. The behavioral studies of this report indicate that the sensory axons from the taste sensilla establish specific connectivity with proper interneurons of the host's ganglion, because without such connectivity even a partial PER is not possible. It should also be noted that the partial PER is not due to any stimulus to mechano sensilla because application of 1.0 M NaCl solution fails to produce any response.

Analogous studies using homeotic mutants of *Drosophila melanogaster* and their supernumerary organs also demonstrate the existence of sensory axons from the sensilla at ectopic sites[11-14] and their functional connectivity with the central interneurons[12,15]. In the case of these homeotic mutants, the imaginal discs from which the supernumerary organs develop have larval nerves connecting them with the central ganglia, and it has been suggested that these larval nerves provide guidance to the growing adult sensory nerves[16]. On the other hand, the supernumerary legs produced by ectopic transplantation as reported in this study did not have their usual pioneer axons during development because the larval nerves of their imaginal discs were severed before transplantation. In spite of this, the growing axons were able to reach the host's thoracic ganglion and established specific connectivity.

What kind of guidance did they have? In *Drosophila* when the larval nerves between imaginal discs and CNS are severed the adult axons grow guided by the nearest larval nerves[17]. It is possible that a similar mechanism might provide guidance to the growing sensory axons of the transplanted leg imaginal discs. Still, this does not explain how the axons from the transplanted prothoracic leg enter directly into the prothoracic neuromere[10], and, having entered, how the axons make appropriate connections with central neurons without which even the partial PER exhibited by the transplanted legs would be impossible. Although only future experiments will clarify these points the prospect of using the system of transplanted leg imaginal discs for the investigation of axonal navigation and neuronal specificity looks very promising.



a Supernumerary leg (arrow) with the host fly. × 6. *b* Supernumerary leg. × 40. *c* Tarsi of supernumerary leg. × 100. *d* Tarsi of in situ leg. × 100. Arrow: chemosensilla.

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Response properties of visual units in the anterior dorsolateral thalamus of the chick *(Gallus domesticus)*

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Summary. Receptive fields of neurons in the anterior dorsolateral thalamus (DLA) of the chick were plotted and their response properties analyzed. The average size was 18°×13° but there were some wide-field units. DLA cells were classified as detectors of 1. general movement (uniform-field), 22%; 2. general movement (centre-periphery), 22%; 3. moving dark objects, 29%; 4. direction, 8%; and 5. illumination, 19%.

Anatomical investigations have revealed the existence of 2 major ascending visual pathways in the avian brain: the tectofugal (retina-optic tectum-n. rotundus-ectostriatum) and the thalamofugal (retina-anterior dorsolateral thalamus-hyperstriatum)[2-4] which has been compared with the mammalian geniculostriate projection[5,6], despite the lack until recently[7] of any knowledge concerning the properties of DLA neurons. The study reported here aimed at the elucidation of DLA unit properties as a part of a survey of visual structures of the diencephalon.

In the avian thalamus, most retinal ganglion (r.g.) fibres terminate in the contralateral n. lateralis anterior (LA), the n. dorsolateralis anterior, pars magnocellularis (DLAmc) and pars lateralis (DLL) and the lateral portion of the pretectal region[8]. LA, DLAmc and DLL have been given the name 'n. opticus principalis thalami' but the participation of the LA in this complex has been questioned[3,4]. Webster[4] divided the pigeon DLA into a retino-receptive part incorporating a superficial lamina and a core. He hypothesized that fibres from the former terminate in the other 2 areas. Furthermore, following lesions in the hyperstriatum (Wulst) he found retrograde degeneration in the DLA but not in the LA. In view of this, the LA was excluded from the study of DLA properties reported here.

Material and methods. Experiments were performed on 2-10-day-old Warren sex-link chicks of *Gallus domesticus* under urethane anaesthesia (1 g/kg b. wt given i.m. at the beginning of the experiment with further hourly injections of up to $\frac{1}{5}$ of that dose). As a rule, 10 min were allowed to pass before the resumption of the search for visual units after supplementary injections and no injections were given during unit recordings. The chicks were placed in a head-holder conforming with Andrew's stereotaxic coordinates[9]. The eyelids of the left eye were securely reflected, the nictitating membrane was removed and pupil dilatation was obtained with 2.5% atropine sulphate. A few curarized, artificially respired birds were also used. A thin film of silicone fluid (60×10^3 centistokes) prevented corneal drying. A window was opened in the skull, allowing the tungsten microelectrode access to the DLA of the right-hand side.

Receptive fields (r.f.) were initially plotted on a translucent plastic hemisphere (diameter=57 cm), the centre of which was occupied by the retina of the stimulated eye. For more accurate r.f. determinations a translucent screen was used at 57 or 114 cm. Stimulation was provided by projected targets – light or dark (spots, edges, etc.). The 'on' and the 'off' of spots were controlled by an electromechanical shutter and their movement by a combination of a feedback controlled electromechanical device, a Dove prism and a mirror on a universal lock[10]. At various instances and at the end of the experiment small electrolytic lesions were made and electrode positions were calculated from them in cresyl-violet-stained sections of the brain.

Results and observations. Of 86 DLA units, 74 (86%) possessed mainly circular, elliptical and, sometimes, irregular fields with diameters between 3°×3° and 33°×26° and averaging 18°×13° (restricted-field units, figure, A). R.f. were distributed over much of the visual space but mostly anteriorly (nasally) and above the horizontal meridian. Two-thirds of these units possessed fields differentiated into a central area and a periphery; one-third possessed uniform fields. The remaining 12 units (14%) responded to stimulation of much or the whole of the visual field (wide-field units).

R.f. organization and the response to moving stimuli suggested the following classification of DLA units: 1. Uniform-field general movement detectors (22% of the total), responding indiscriminately to small moving spots, bars or edges irrespective of contrast. – 2. Centre-periphery general movement detectors (22%), with properties similar to the pigeon 'concentric' r.g. units[11] except that the DLA neurons possessed larger r.f. and peripheries not always regularly shaped and only occasionally antagonistic to the centre. – 3. Dark object detectors (uniform-field, 29%), showing preference for large dark edges or other large targets entering the r.f. – 4. Directional movement detectors (8%), exclusively uniform-field, similar to r.g. directional detectors[11,12]. – 5. Illumination detectors (mostly wide-field, 19%), responsive to the 'on' or 'off' of diffuse light but not to small flashing or moving stimuli. Their responses were proportional to stimulus size and intensity.