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

S. Pateromichelakis[1]

Ethology and Neurophysiology Group, School of Biological Sciences, University of Sussex, Falmer, Brighton (E. Sussex, England), 28 July 1980

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].

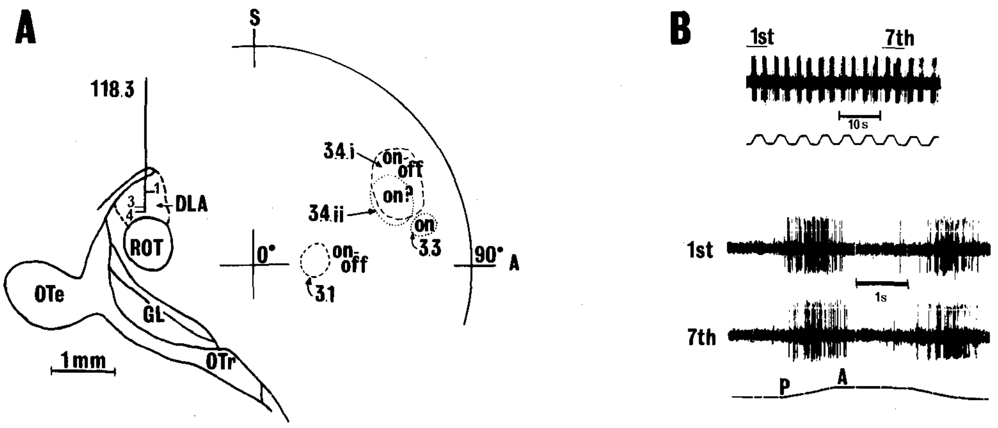
Webster[4] divided the pigeon DLA into a retino-receptive part incorporating a superficial lamina and a core. He hypothesized that fibres from the former terminate in the other 2 areas. Furthermore, following lesions in the hyperstriatum (Wulst) he found retrograde degeneration in the DLA but not in 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 ⅕ 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.



A The positions in the DLA (left) and the visual field (right) of 4 units isolated during 3 different placings of the microelectrode during a single penetration (units 118.3.1, 118.3.2, 118.3.4i and 118.3.4ii). The last 2 units were encountered in the same electrode position. Unit 118.3.2 did not respond to visual stimulation and is omitted. All units were uniform field with the exception of 118.3.4i which possessed an 'on-off' centre and an 'off' periphery. The responses indicated are to flashes of a white spot. OTe, optic tectum; ROT, n.rotundus; DLA, anterior dorsolateral thalamic complex; GL, n.lateralis geniculatus ventralis; OTr, optic tract; S, superior pole of the visual field; A, anterior pole.
B Responses of a non-adapting unit from the DLA to a series of stimulus presentations (top) of which the 1st and the 7th (marked by a bar) are shown, at a different time scale, below. Stimulus: a $3° \times 20°$ light bar moving along its short axis across the receptive field at 27°/sec. Movement started outside the receptive field from a posterior (P) to an anterior (A) (i.e. nasal) position. The stimulus then returned to its original position.

Reports of monosynaptic retinal inputs ot the DLA[2-4] invite a comparison of its properties with those of the r.g. cell layer. In both structures adaptation to stimulus repetition was usually low (figure 1, B, and Miles[12]), a characteristic shared with neurons of the mammalian dorsolateral geniculate (LGd) and contrasting with the rapid adaptation in the avian tectofugal pathway[13]. On the other hand, differences between r.g. cells and those of the DLA were found when the relationship was examined between average firing rate and target velocity: of 7 tonic units analyzed, 5 produced responses (in terms of impulses per sec of stimulation) which were exponential functions of target velocity with exponent values between 0.66 and 0.76. Similar values have been obtained in the chick ventral lateral geniculate nucleus[10] which receives both retinal and tectal inputs. Under identical conditions, Miles[12] calculated values of 0.35–0.50 for ganglion cells of the de-efferented chick retina. This suggests that the DLA is a significant relay in the transformation of the retinal signal as it is transmitted to the telencephalon.
Avian r.g. cells possess r.f. of small diameters (2°–6°), concentric organization, high movement sensitivity and considerable target specificity[11,12]. Of chick DLA receptive fields, 57% were organized into a centre and a periphery but less rigorously than r.g. cells; a high degree of movement specificity was seen as well as some target specificity (class 3 units). In the hyperstriatum field differentiation has disappeared, sensitivity to motion is universal but r.f. size is a matter of disagreement with reported diameters either lower than 10°[14] or $60° \times 36°$ on average[15].
An apparent anomaly in the progressive modification of unit properties in the thalamofugal pathway is the large dimensions of some DLA r.f. (class 5 units). Such fields have also been reported in the pigeon DLA[7]. However, as the DLA retino-receptive area is restricted[4,8], most units would tend to be isolated in the non-retino-receptive part. It is therefore proposed that polysynaptic inputs converge on some neurons of the DLA contributing to larger field diameters.
Jassik-Gerschenfeld et al.[7] reported that pigeon DLA units did not show any directional preferences; r.f. organization was also higher than in the chick; in both species some surrounds fired independently of the centre. The pigeon DLA has been credited by other authors with many small-field units and considerable directional sensitivity although the LA appears to have been included in this sample[16]. Such diverging reports of DLA unit properties can only be explained by the multiplicity of anatomical, and by implication, functional subunits within this area[3,4,8] or by species differences.

1 Present address: Rayne Institute, King's College Hospital Medical School, 123, Coldharbour Lane, London SE 5, England.
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