Visual Receptive Fields from Cells of a Marsupial (*Didelphis virginiana*) Superior Colliculus

As part of a developing survey of information processing throughout the marsupial visual pathways 72 cells of the superior colliculus of *Didelphis virginiana*, the common American opossum, were studied. A broad range of receptive field geometries and response properties were found represented among them. Described here are 51 of these cells, those for which complete survey information under uniform conditions was gathered.

Twelve animals, both male and female, of weights 0.8–3.5 kg were studied under mild general anesthesia: 6 ml/kg body weight of 20% ethyl carbamate in saline. Quantitative information was taken only when ready flexure of the forepaw could be ellicited. This anesthetic state was found from earlier work to be no more detrimental to cell responsiveness than decerebrate and encéphale isolé techniques[1].

Once mounted in a stereotaxic frame giving complete access to both monocular and binocular fields, the pupils were dilated with 1% cyclopentolate hydrochloride, and the eyes refracted and fitted with contact lenses to bring the retinae into conjugacy with the 114 cm testing plane. For plotting purposes, horizontal and vertical zero were taken relative to an axis projecting from the inferior border of the optic disc, through the center of the pupil. Although eye movements were rarely encountered, the field boundaries were rechecked frequently for interim displacement.

An aperture 4 × 4 mm, made directly over the left superior colliculus and resealed with 4% agar gel, gave passage to the stainless steel microelectrodes (40 mΩ) used to record from and to mark single cell response sites. These sites were later localized histologically by Prussian blue reactions seen in the frozen sections made of each brain.

The receptive field of each collicular cell was mapped using a $^1/_2$°, 10 m candle spot against a 1 m candle background. Response to additional visual stimuli, diffuse and discrete, light and shadow and of various edge geometries and areas were also measured. A range of auditory (e.g. clicks, tones) and tactile (e.g. localized movement of the fur both countralaterally and ipsilaterally) stimuli were given during the survey of each cell as well.

Forty-six cells of the sample described here could be classified into 3 geometric catagories: (1) homogeneous response fields; those giving the same form of response (e.g. only 'on', only 'off' or always 'on' and 'off') throughout their receptive fields; (2) concentric geometry fields, having opposing center and surround responses; and (3) fields of asymmetric geometry. Table I gives the occurrance of these classes and their subtypes within this sample, together with the diameters and eccentricities from the reference axis each group displayed. The Figure shows the distribution of these classes in visual space, indicating the orientation of directional or meridional selectivities when present[2].

Table II summarizes the specialized response properties of these cells and their frequencies of occurance within the classes. These properties included intermodality responsiveness[3] of the single cell being tested (all in this sample responded photically, 7 to both photic and auditory stimuli and 2 at all 3 modality stimuli); the occurrance of rapid habituation[4]; directional or meridional selectivity[2]; the maximally effective stimulus velocities; and the capability of certain of these cells to be driven by stimuli to either eye.

Special mention should be made of those cells of the asymmetric class above, each of the 3 studied having a nearly vertical division of its internal response geometry, specifically: (1) a pure 'off' response in the anterior zone and a pure 'on' response in the posterior zone; (2) an 'on-off' response throughout the anterior zone and an 'off' response, only, in the posterior zone; (3) a pure 'on' response in the anterior zone and a pure 'off' response in the posterior zone. The individuality of such zones (e.g. as in (2) above, habituation of the posterior zone to local photic stimuli while the anterior zone continued to respond

Table I. Distribution of photically responding cells of a marsupial (*D. virginiana*) superior colliculus by receptive field geometry

Field geometry	N	%	Diameter $\bar{x}$°	Diameter range°	Eccentricity $\bar{x}$°	Eccentricity range°
(1) Homogeneous 'on'	30	58	85.7 $\sigma = \pm 44.8$	6–167	22.2	0–70.1 $\sigma = \pm 14.9$
Homogeneous 'off'	1	2	98.5		25.3	
Homogeneous 'on-off'	2	4	40.0	20–60	55.5	40.8–70.2
(2) 'On' center, 'off' surround	3	6	63.3	45– 90	23.7	11.2–40.0
'On' center, 'on-off' surround	3	6	119.6	102.5–147	24.3	7.1–40.3
'On-off' center, 'off' surround	3	6	80.2	41.5–111	14.4	2.8–25.3
'On-off' center, 'on' surround	1	2	83.0		32.3	
(3) Asymmetric	3	6	100.2	39.5–135	40.0	22 –69.9
Not classified geometrically	5	10				
Total	51	100				

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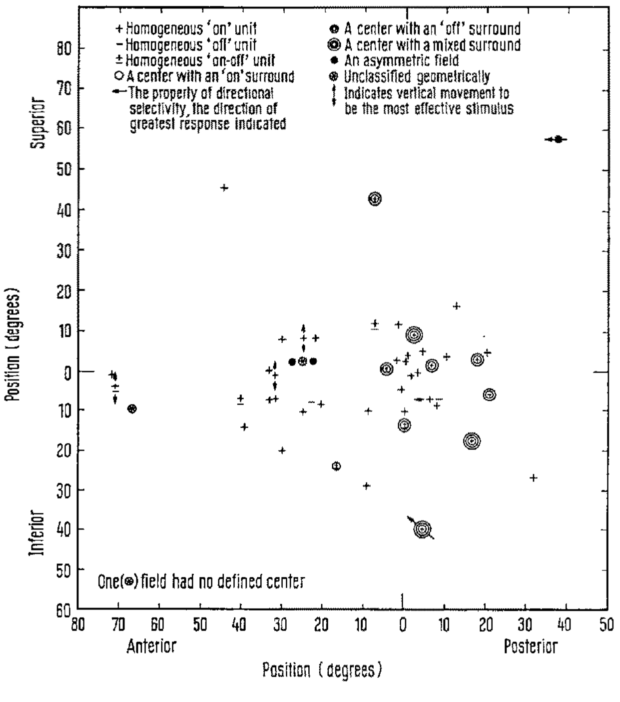
Table II. The occurrance of special response properties among photically responding cells of a marsupial (*D. virginiana*) superior colliculus

Field geometry	N	Intermodality:		Rapid	Selectivity of:		Average	Binocularly
		Auditory	Tactile	habituation	Meridian	Direction	optimum velocity (°/sec)	driven
(1) Homogeneous 'on'	30	4	1	8	2	1	75	9
Homogeneous 'off'	1	0	0	0	0	0	170	0
Homogeneous 'on-off'	2	1	0	2	1	0	70	1
(2) 'On' center, 'off' surround	3	0	0	1	0	0	83	0
'On' center, 'on-off' surround	3	0	0	1	0	1	48	0
'On-off' center, 'off' surround	3	1	0	1	0	0	87	0
'On-off' center, 'on' surround	1	0	0	0	0	0	180	0
(3) Asymmetric	3	1	1	1	0	1	50	0
Not classified geometrically	5	0	0	1	0	0		1
Total	51	7	2	15	3	3		11



Distribution and properties of 50 visual receptive fields of cells of the superior colliculus of the marsupial *D. virginiana*.

to these same stimuli) suggests that these fields may be composites of several ganglion cell inputs as described at the lateral geniculate level of the rabbit by Arden[5].

Finally, 5 fields of this sample responded too inadequately to discrete stimuli to be classified geometrically; they most commonly displayed a rapid, bursty kind of activity, often inhibited by gross or moving stimuli, or to changes of ambient illumination. The subtility of inhibition and proneness to habituate rapidly made these cells difficult to describe quantitatively. Only 1 could be driven binocularly and 1 responded to auditory and tactile as well as photic stimuli.

Histologically, the cells of this study were localized in the 3 dorsalmost layers of the superior colliculus: the stratum zonale, stratum griseum superficiale and the stratum opticum as defined by Tsai[6].

From this initial survey it appears then that the superior colliculus of *D. virginiana*, a long enduring (Eocene period) marsupial, incorporates receptive field geometries and properties similar to those of certain placentals (e.g. the rabbit[7]). These specialized properties include rapid habituation, intermodality responsiveness (auditory and/or tactile in addition to visual), selectivity for meridional or a particular direction of movement, delimited ranges of velocity response, ambient illumination sensitivity and, for 20% of the cells sampled, the capability to be driven by stimuli to either eye[8].

Zusammenfassung. Einzelne Zellen in der Region des superior colliculus des Beuteltieres *Didelphis virginiana* können von der linken oder auch rechten Retina stimuliert werden. Diese Zellen verfügen über eine gut entwickelte intermodale Reaktionsfähigkeit, Selektivität gegenüber gerichteter Bewegung und rasche Gewohnheitsbildung. Zellpopulationen derselben Region repräsentieren eine grosse Anzahl von «receptive field»-Geometrien.

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[8] This work was supported by U.S.P.H.S. Grants Nos. NB06983 and NB05416.