AGE-RELATED NEURONE-LOSS AND THE OCCURRENCE OF DARK AND LIGHT NEURONES IN THE GANGLIA OF CRANIAL NERVES AND AUTONOMIC NERVOUS SYSTEM: A COMPARATIVE EVALUATION OF THEIR DEVELOPMENTAL AND GROWTH CHANGES

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ABSTRACT: Senescent-decline in the nervous-system functions is very frequently attributed to age-related neurone-loss. Processes and mechanisms involved in neuro-degeneration form part of the structural frame-work for interpreting the functional consequences. The literature concerning this matter are confusing and contradicting. The behaviour of cranial nerve ganglia was studied using neuro-histological techniques. On the evidence available in the present study, the dark cells are considered as active ones; the light cells are considered as those which have failed to establish functional projections, inactive, dying, dead or degenerating ones. Probably it is during the medium-sized stage of cell growth, the peripheral and central processes (of axons) begin to grow from the cell body and attempt to get established in their projection fields. The light cells have appeared among the very-small cells just on the day of hatching. This probably signifies the possible attempt to eliminate the growing cells since they are no longer needed to replace larger categories of cells which have already well-developed neuronal connections at this stage. It is assumed that the time of appearance of light cells might be indirectly related to the onset of establishment of active functional connections of neurones and to the functional importance of the organs which it supplies. *(JUMMEC 1998 1&2: 22-46)*

KEYWORDS: Neurone-Loss and Ageing, Dark and Light Neurones, Sensory and Autonomic Ganglia

Introduction

Senescent-decline in the nervous-system functions is very frequently attributed to age-related neurone loss. Processes and mechanisms involved in neuro-degeneration form part of the structural framework for interpreting the functional consequences of age-related changes in other parameters. The literature concerning age-related neurone loss give confusing and sometimes contradicting data and therefore, remain with controversy (1, 2, 3, 4, 5, 6). However, age-related neurone-loss represents a structural basis of senescent-decline in nervous system functions.

Dark and Light types of neurones, based on staining properties have been documented in many vertebrates (7, 8, 9, 10) including primates (11, 12). A few investigators (9, 13, 14) have found differences in chemical constituents in these two types of neurones in sensory ganglia of rodents. Similar observations have been reported in mammals (9, 15, 16) and reptiles (17).

The significance of Dark and Light neurones in different ganglia in different animal species has been controversial in available literature. Dual embryonic origin (of epidermal placode and of neural crest origin) (18), as fixation artefacts (19), difference in central and peripheral projections (20, 21), different sensory functions (22, 23), different histogenetic characteristics (10), difference in distribution of cytoplasmic organelles and relative density of cytoplasm (8, 12, 24), fluid shift between cells and the surrounding extra-cellular spaces (25) have been offered as different hypotheses. From available literature, there is no report of a study in the whole life cycle of any one animal species so as to infer a conclusive significance of this dual cytology of neurones. All these works have been done in adult animals or in certain stages of development or growth.

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This work was carried-out at the Department of Anatomy, Faculty of Medicine, University of Khartoum, Sudan, in collaboration with the University of Leiden, Netherlands

Therefore, it is thought useful to study this aspect in different ganglia related to different functions, in the whole life cycle of any one animal species during embryonic development through adult, so as to infer the conclusive significance and hypothesis regarding the occurrence of this dual cytology and to see whether their occurrence is related to age-changes. This has been really rewarding to achieve this conclusive information from the results obtained as described below. However, the discussion is restricted to some useful points (rather than description) in order to simplify a great deal of repetition. (However, the detailed descriptions in relation to individual ganglia can be found elsewhere.) The results in the present study can be of great value to correlate and evaluate the functional status of similar ganglia during development and in relevant clinical conditions and ageing in the human.

Material and methods

The chicks *Gallus gallus domesticus*, White Leghorn breed were used in this study. Fertilised eggs were collected in groups of 25 - 30, and incubated at a temperature of 37.5 degree Centigrade. The date and time while beginning the incubation were recorded every time when a new set of eggs was kept for incubation. After every 24 hours from this time, it was considered as Embryonic Day 1 (E1), Embryonic Day 2 (E2) etc till hatching (H). Embryos from E3 till hatching were removed carefully without causing damage and fixed in 10 % formaldehyde solution at least for two weeks. Larger (older) embryos were cut transversely into suitable smaller pieces and labelled serially for future orientation. The tissues of older embryos (i.e., E15 and onwards till adult) were usually decalcified after fixation. In the adult, and in those belonging to later stages of development, the head at the level of C6 was separated and the brain was exposed by a longitudinal cut on the skull by means of a thin bone-saw, to facilitate proper fixation of the brain tissue. After making paraffin blocks, serial sections of 8 - 10 microns were stained by Cresyl Fast Violet for Nissl granules.

Only a few selected stages which showed some remarkable changes are described in this work. These include E6, E8, E10, E13, E15, E18, chick on the day of hatching and adult. In all, three animals in each group, having a total of twenty four animals were used. Ganglia of both sides in each animal were used for observation. Average of the results of all six ganglia is described in the results. Every section of the ganglion was observed, drawn and the cells were plotted in diagram with the help of light microscope having a camera lucida attachment. Different categories of neurones were classified into Dark and Light neurones according to the difference in the intensity of cytoplasmic stain. Each of these types is again subdivided into various subclasses (according to size) represented in the diagram by a symbol. Only those cells having a clear nucleus and a nucleolus were counted. Dimensions of cells were measured with the help of an eye piece graticule. The following categories of cells (based on average dimensions) were classified. Tiny (< 5 microns), very small (6 - 10 microns), small (11 - 15 microns), medium sized (16 - 20 microns), big (21 - 25 microns), very big (26 - 30 microns), large (31 - 35 microns), very large (36 - 40 microns), giant (41 - 45 microns), gigantic (46 - 50 microns), gigantic giant (> 51 microns).

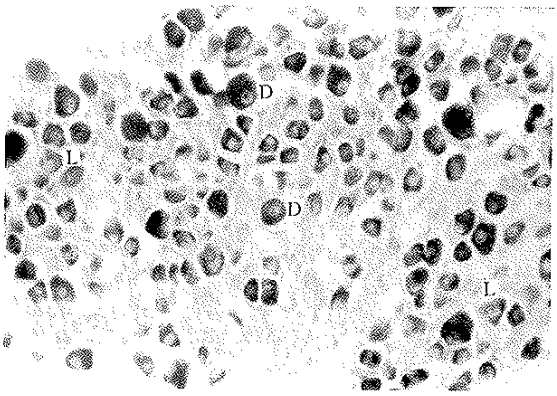

Figure 1. Shows Dark (D) and Light (L) cells observed in the ganglion

The following sensory and autonomic ganglia have been studied.

Trigeminal (Sensory)
Genicular (Sensory)
Vestibular (Sensory)
Acoustic (Sensory)
Prox. G. Comp.of N. IX and X (Sensory)
Petrous (Sensory)
Nodose (Sensory)
Ciliary (Parasympathetic)
Superior Cervical (Sympathetic)

Results

The ganglion showed great difference in different age groups of animals and in different areas of the same ganglion. These changes during successive embryonic days, on the day of hatching and in the adult situation were studied in greater detail. The most striking changes are as follows. When the dark neurones alone are present in the ganglion, they are represented just by their numbers; when they are mixed with light neurones, D= dark neurones, and L= light neurones.

1. Trigeminal Ganglion

The trigeminal ganglion could be recognised clearly on E6 while it had a rostro-caudal length of 0.376 mm and a volume of 0.0485 mm^3. The ganglion had 73862 cells, all which were dark type. In all, there were 4923 (6.67

%) tiny cells, 24453 (33.11 %) very small ones, 41267 (55.87 %) small ones, and 3219 (4.36 %) medium sized ones. On E8, the ganglion had a length of 0.600 mm, a volume of 0.1414 mm^3 and had 259405 cells. Among these cells, 259327 (99.97 %) were dark type and 78 (0.03 %) were light ones. In all, there were 63347 (24.42 %) tiny cells, 168400 (64.92 %) very small ones, 23973 (D= 23970 + L= 3) (9.24 %) small ones and 3685 (D= 3610 + L= 75) (1.42 %) medium sized ones. On E10, the ganglion had a length of 0.594 mm and a volume of 0.1909 mm^3. There were 101199 cells. Among them, 100603 (99.41 %) cells were dark type, and 596 (0.59 %) were light ones. In all, there were 581 (0.57 %) tiny cells, 17067 (16.86 %) very small ones, 59443 (D= 59095 + L= 348) (58.74 %) small ones, 24043 (D= 23804 + L= 239) (23.76 %) medium sized ones, 52 (D= 45 + L= 7) (0.05 %) big ones and 13 (D= 11 + L= 2) (0.01 %) very big ones. On E13, the ganglion had a length of 0.780 mm, a volume of 0.4641 mm^3 and had 84493 cells. Among these cells, 52199 (61.78 %) were dark type and 32294 (38.22 %) were light ones. In all, there were 510 (0.6 %) tiny cells, 27203 (32.2 %) very small ones, 25841 (D= 10824 + L= 15017) (30.58 %) small ones, 22442 (D= 9856 + L= 12586) (26.56 %) medium sized ones, 7062 (D= 3131 + L= 3931) (8.36 %) big ones, 1140 (D= 503 + L= 637) (1.35 %) very big ones, 283 (D= 163 + L= 120) (0.33 %) large ones, 4 (D= 3 + L= 1) very large ones, and 8 (D= 6 + L= 2) gigantic type. On E15, the ganglion had a length of 1.300 mm, a volume of 0.2004 mm^3 and had 62441 cells. Among these cells, 34032 (54.5 %) were dark type and 28409 (45.5 %) cells were light ones. In all, there were 1004 (1.61 %) tiny ones, 19330 (30.96 %) very small ones, 17374 (D= 5046 + L= 12328) (27.82 %) small ones, 16694 (D= 5742 + L= 10952) (26.74 %) medium sized ones, 5554 (D= 1833 + L= 3721) (8.89 %) big ones, 2479 (D= 1071 + L= 1408) (3.98 %) very big ones.

On E18, the ganglion had a length of 1.300 mm, a volume of 0.7688 mm^3 and had 306498 cells. Among these cells, 288252 (94.05 %) were dark type and 18246 (5.95 %) were light ones. In all, there were 113491 (37.03 %) tiny cells, 106003 (34.59 %) very small ones, 49614 (D= 43706 + L= 5908) (16.18 %) small ones, 32053 (D= 22305 + L= 9748) (10.46 %) medium sized ones, 4346 (D= 2154 + L= 2192) (1.42 %) big ones, 964 (D= 578 + L= 386) (0.31 %) very big ones and 27 (D= 15 + L= 12) large ones. On the day of hatching, the ganglion had a length of 1.950 mm, a volume of 0.7873 mm^3 and contained 58779 cells. Among these cells, 36116 (61.44 %) were dark type and 22663 (38.56 %) were light ones. In all, there were 781 (1.33 %) tiny cells, 17223 (D= 12288 + L= 4935) (29.3 %) very small ones, 19557 (D= 11275 + L= 8282) (33.27 %) small ones, 14890 (D= 8138 + L= 6752) (25.33 %) medium sized ones, 3841 (D= 1856 + L= 1985) (6.53 %) big ones, 1733 (D= 1116 + L= 617) (2.95 %) very big ones, 679 (D= 605 + L= 74) (1.16 %) large ones, and 75 (D= 57 + L= 18) (0.13 %) very large ones. In the adult situation, the ganglion had a length of 3.750 mm, a volume of 2.7904 mm^3 and had 36826 cells. Among these cells, 29475 (80.04 %) were dark type and 7351 (19.96 %) were light ones. In all, there were 548 (1.49 %) tiny ones, 5512 (D= 3886 + L= 1626) (14.97 %) very small ones, 3576 (D= 2539 + L= 1037) (9.71 %) small ones, 6167 (D= 4567 + L= 1600) (16.75 %) medium sized ones, 522 (D= 435 + L= 87) (1.42 %) big ones, 4381 (D= 3568 + L= 813) (11.9 %) very big ones, 3996 (D= 3277 + L= 719) (10.85 %) large ones, 10191 (D= 8841 + L= 1350) (27.67 %) very large type, 10 (D= 7 + L= 3) (negligible) giant cells, 1917 (D= 1803 + L= 114) (5.21 %) gigantic type of cells and 6 (D= 4 + L= 2) cells of gigantic giant type in the ganglion.

2. *Geniculate Ganglion*

The geniculate ganglion could be clearly recognized on E6 while it had a rostro-caudal length of 0.176 mm and a volume of 0.0055 mm^3. The ganglion had 3428 cells and all of them were dark type. In all, there were 95 (2.77 %) tiny cells, 1232 (35.94 %) very small ones, 1815 (52.95 %) small ones, and 286 (8.34 %) medium sized ones. On E8, the ganglion had a length of 0.208 mm and a volume of 0.0049 mm^3. The ganglion had 6705 cells, all of which were dark type. In all, there were 1952 (29.11 %) tiny cells, 3111 (46.4 %) very small ones, 1542 (23 %) small ones and 100 (1.49 %) medium sized ones. In a few sections in the rostral part of the ganglion, the cells were more crowded towards their periphery. On E10, the ganglion had a length of 0.243 mm and a volume of 0. 0054 mm^3. The ganglion had 1361 cells and all of them were dark type.). In all, there were 81 (5.95 %) tiny cells, 160 (11.76 %) very small type, 677 (49.74 %) small ones), 343 (25.2 %) medium sized ones and 100 (7.35 %) big ones. On E13, the ganglion had a length of 0.270 mm and a volume of 0.0180 mm^3. The ganglion had 4764 cells of which 4252 (89.25 %) were dark type and 512 (10.75 %) were light ones. In all, there were 78 (1.64 %) tiny cells, 1841 (38.64 %) very small type, 774 (D= 693 + L= 81) (16.25 %) small ones, 964 (D= 807 + L= 157) (20.24 %) medium sized ones, 1017 (D= 765 + L= 252) (21.35 %) big ones, 61 (D= 45 + L= 16) (1.28 %) very big ones and 29 (D= 23 + L= 6) (0.61 %) large ones. On E15, the ganglion had a length of 0.250 mm and a volume of 0.0071 mm^3. It had 2869 cells of which 1442 (50.26 %) were dark type and 1427 (49.74 %) were light ones. In all, there were 98 (3.42 %) tiny cells, 935 (32.59 %) very small type, 515 (D= 150 + L= 365) (17.95 %) small ones, 908 (D= 147 + L= 761) (31.65 %) medium sized ones, 317 (D= 74 + L= 243) (11.05 %) big ones, and 96 (D= 38 + L= 58) (3.35 %) very big ones. On E18, the ganglion had a length of 0.300 mm, a volume of 0.0418 mm^3 and contained 17592 cells. Among these cells, 16543 (94.04 %) were dark type, and 1049 (5.96 %) were light ones. In all, there were 8092 (46 %) tiny cells, 5533 (31.45 %)

very small type, 2288 (D= 1971 + L= 317) (13.01 %) small ones, 1559 (D= 920 + L= 639) (8.86 %) medium sized ones, 106 (D= 20 + L= 86) (0.6 %) big ones and 14 (D= 7 + L= 7) (0.08 %) very big ones. On the day of hatching, the ganglion had a length of 0.350 mm, a volume of 0.0264 mm^3 and contained 2093 cells. Among these cells, 1112 (53.13 %) were dark type and 981 (46.87 %) were light ones. In all, there were 20 (0.96 %) tiny cells, 183 (D= 59 + L= 124) (8.74 %) very small type, 328 (D= 69 + L= 259) (15.67 %) small ones, 603 (D= 289 + L= 314) (28.81 %) medium sized ones, 480 (D= 301 + L= 179) (22.93 %) big ones, 473 (D= 368 + L= 105) (22.6 %) very big ones, 2 (0.1 %) large ones, 1 very large ones and 3 (0.15 %) giant dark type of cells. In the adult situation, the ganglion had a length of 0.550 mm, a volume of 0.0457 mm^3, and contained 1021 cells. Among these cells, 904 (88.54 %) were dark type and 117 (11.46 %) were light ones. In all, there were 15 (1.47 %) tiny cells, 7 (0.69 %) very small type, 36 (D= 22 + L= 14) (3.53 %) small ones, 96 (D= 84 + L= 12) (9.4 %) medium sized ones, 22 (D= 13 + L= 9) (2.15 %) big ones, 212 (D= 194 + L= 18) (20.76 %) very big ones, 198 (D= 175 + L= 23) (19.39 %) large ones, 349 (D= 315 + L= 34) (34.18 %) very large ones, 2 (D= 1 + L= 1) (negligible) giant ones, and 84 (D= 78 + L= 6) (8.23 %) gigantic type of cells.

3. Acoustic Ganglion

The acoustic ganglion could be clearly recognised on E6 while it had a rostro-caudal length of 0.312 mm and a volume of 0.0085 mm^3. The ganglion had 10060 cells and all of them were dark type. In all, there were 334 (3.32 %) tiny cells, 4710 (46.82 %) very small ones, 4841 (48.12 %) small ones and 175 (1.74 %) medium sized ones. On E8, the ganglion had a length of 0.416 mm, a volume of 0.0165 mm^3 and contained 20415 cells and all of them were dark type. In all, there were 5863 (28.72 %) tiny cells, 9660 (47.32 %) very small ones, 4728 (23.16 %) small ones and 164 (0.8 %) medium sized ones. In most of the sections, the larger sized cells were more numerous medially mixed with a few tiny cells, whereas compactly arranged tiny cells were found laterally. On E10, the ganglion had a length of 0.558 mm, a volume of 0.0287 mm^3 and contained 42668 cells, and all of these cells were dark type. In all, there were 6495 (15.22 %) tiny cells, 33229 (77.88 %) very small type), and 2944 (6.9 %) small ones. On E13, the ganglion had a length of 0.600 mm and a volume of 0.0537 mm^3 and contained 39097 cells. Among these cells, 36809 (94.15 %) were dark type, and 2288 (5.85 %) were light ones. In all, there were 325 (0.83 %) tiny cells, 16320 (41.74 %) very small type, 20640 (D= 18817 + L= 1823) (52.79 %) small ones 8) and 1812 (D= 1347 + L= 465) (4.63 %) medium sized ones. On E15, the ganglion had a length of 0.700 mm, a volume of 0.0769 mm^3 and 49313 cells. Among these cells, 47807 (96.95 %) were dark type and 1506 (3.05 %) were light ones. In all, there were 6482 (13.14 %) tiny cells, 28864 (58.53 %) very small, 8808 (D= 8290 + L= 518) (17.86 %) small ones, 4640 (D= 3969 + L= 671) (9.41 %) medium sized ones, 474 (D= 193 + L= 281) (0.96 %) big ones and 45 (D= 9 + L= 36) (0.09 %) very big ones. On E18, the ganglion had a length of 0.720 mm, a volume of 0.2386 mm^3 and 220338 cells. Among these cells, 220314 (99.99 %) were dark type and 24 (0.01 %) were light ones. In all, there were 57962 (26.31 %) tiny cells, 93394 (42.39 %) very small, 63328 (D= 63318 + L= 10) (28.74 %) small ones, 5617 (D= 5603 + L= 14) (2.55 %) medium sized ones and 37 (0.02 %) big (dark) cells. In some of the sections, smaller cells were found to be more numerous in the medial part of the ganglion whereas the larger cells were found to be more in their lateral part. On the day of hatching, the ganglion had a length of 0.910 mm, a volume of 0.1568 mm^3 and 26701 cells. Among these cells, 13037 (48.83 %) were dark type and 13664 (51.17 %) were light ones. In all, there were 219 (0.82 %) tiny cells, 3977 (D= 840 + L= 3137) (14.89 %) very small, 16771 (D= 8018 + L= 8753) (62.81 %) small ones, 5714 (D= 3943 +L= 1771) (21.4 %) medium sized ones and 20 (D= 17 + L= 3) (0.07 %) big ones. In the adult situation, the ganglion had a length of 1.000 mm, a volume of 0.1420 mm^3 and 14633 cells. Among these cells, 14524 (99.26 %) were dark type and 109 (0.74 %) were light ones. In all, there were 3329 (22.76 %) tiny cells, 6617 (D= 6557 + L+ 60) (45.22 %) very small ones, 4488 (D= 4450 + L= 38) (30.67 %) small ones and 199 (D= 188 + L= 11) (1.36 %) medium sized ones.

4. Vestibular Ganglion

The vestibular ganglion could be recognised on E6 while it had a rostro-caudal length of 0.304 mm and a volume of 0.0094 mm^3. The ganglion had 32924 cells. Among these cells, 32916 (99.98 %) were dark type and 8 (0.02 %) were light ones. In all, there were 2220 (6.74 %) tiny cells, 14803 (44.96 %) very small ones, 15197 (46.16 %) small ones and 704 (2.14 %) medium sized ones. On E8, the ganglion had a length of 0.480 mm and a volume of 0.0240 mm^3, and contained 42695 cells, and all of these cells were dark type. In all, there were 874 (2.05 %) tiny cells, 30870 (72.3 %) very small ones, 10750 (25.18 %) small ones and 201 (0.47 %) medium sized ones. On E10, the ganglion had a length of 0.963 mm, a volume of 0.0442 mm^3 and 61936 cells and all of these cells were dark type. In all, there were 10268 (16.58 %) tiny cells, 40467 (65.34 %) very small ones, 9418 (15.21 %) small ones and 1783 (2.88 %) medium sized ones. In a few sections of the ganglion the larger sized cells were more at their periphery while the smaller cells were more in their centre. On E13, the ganglion had a length of 1.020 mm, a volume of 0.1232 mm^3 and 43894 cells. Among these cells, 40267 (91.74 %) were dark type and 3627 (8.26 %) were light ones. In all, there were 2674 (6.09 %) tiny cells, 27480 (62.61 %) very small ones, 9251 (D= 6818 + L= 2433) (21.08 %) small ones, 3655 (D= 2665 + L= 990) (8.33 %) medium sized ones, 763 (D= 583 + L= 180) (1.74 %) big ones and 71 (D= 47 + L= 24) (0.16 %)

very big ones. Many smaller groups of cells were observed in the ventral part of some sections of the ganglion. On E15, the ganglion had a length of 0.940 mm, a volume of 0.0770 mm^3 and 53439 cells. Among these cells, 47465 (88.82 %) were dark type and 5974 (11.18 %) were light ones. In all, there were 3449 (6.45 %) tiny cells, 31886 (59.67 %) very small ones, 10090 (D= 7501 + L= 2589) (18.88 %) small ones, 5654 (D= 3195 + L= 2459) (10.58 %) medium sized ones, 1609 (D= 953 + L= 656) (3.01 %) big ones, and 751 (D= 481 + L= 270) (1.41 %) very big ones. On E18, the ganglion had a length of 1.230 mm, a volume of 0.3874 mm^3 and 237191 cells. Among these cells, 234877 (99.02 %) were dark type and 2314 (0.98 %) were light ones. In all, there were 91241 (38.47 %) tiny cells, 100958 (42.56 %) very small type, 32555 (D= 31988 + L= 567) (13.73 %) small ones, 10248 (D= 8981 + L= 1267) (4.32 %) medium sized ones, 1827 (D= 1491 + L= 336) (0.77 %) big ones and 362 (D= 218 + L= 144) (0.15 %) very big ones. On the day of hatching, the ganglion had a length of 1.200 mm, a volume of 0.2079 mm^3 and 18067 cells. Among these cells, 4871 (26.96 %) were dark type and 13196 (73.04 %) were light ones. In all, there were 105 (0.58 %) tiny cells, 4179 (D= 428 + L= 3751) (23.13 %) very small type, 4987 (D= 924 + L= 4063) (27.6 %) small ones, 6640 (D= 2178 + L= 4462) (36.75 %) medium sized, 1531 (D = 693 + L= 838) (8.47 %) big, 498 (D= 425 + L= 73) (2.76 %) very big ones and 127 (D= 118 +L= 9) (0.7 %) large ones. In the adult situation, the ganglion had a length of 1.290 mm, a volume of 0.2325 mm^3 and 12483 cells. Among these cells, 12189 (97.64 %) were dark type and 294 (2.36 %) were light ones. In all, there were 1183 (9.48 %) tiny cells, 4935 (39.53 %) very small ones, 3800 (D= 3645 + L= 155) (30.44 %) small ones, 1961 (D= 1860 + L= 101) (15.71 %) medium sized ones, 182 (D= 168 + L= 14) (1.46 %) big ones, 295 (D= 278 + L= 17) (2.36 %) very big ones and 127 (D= 120 + L= 7) (1.02 %) large ones.

5. Proximal Ganglionic Complex of Cranial Nerves IX and X

The proximal ganglionic complex of cranial nerves IX and X could be recognised on E6 while it had a rostro-caudal length of 0.328 mm and a volume of 0.0078 mm^3. The ganglion had 17905 cells all of which were dark type. In all, there were 785 (4.38 %) tiny cells, 8222 (45.92 %) very small type, 8444 (47.16 %) small cells and 454 (2.54 %) medium sized ones. On E8, the ganglion had a length of 0.360 mm, a volume of 0.0236 mm^3 and contained 31016 cells all of which were dark type. In all, there were 492 (1.59 %) tiny cells, 22987 (74.11 %) very small type, 7342 (23.67 %) small ones and 195 (0.63 %) medium sized ones. On E10, the ganglion had a length of 0.612 mm, a volume of 0.0445 mm^3 and 28813 cells all of which were dark type. In all, there were 2810 (9.75 %) tiny cells, 18610 (64.59 %) very small type, 7019 (24.36 %) small ones and 374 (1.3 %) medium sized ones. On E13, the ganglion had a length of 0.660 mm, a volume of 0.0676 mm^3 and 26208 cells (P. D= 388843). Among these cells, 19277 (73.55 %) were dark type and 6931 (26.45 %) were light ones. In all, there were 302 (1.15 %) tiny cells, 13166 (50.24 %) very small type, 6342 (D= 2956 + L= 3386) (24.2 %) small ones, 5142 (D= 2274 + L= 2868) (19.62 %) medium sized ones, 1161 (D= 537 + L= 624) (4.43 %) big ones and 95 (D= 42 + L= 53) (0.36 %) very big ones. On E15, the ganglion had a length of 0.660 mm, a volume of 0.0505 mm^3 and 24677 cells. Among these cells, 16770 (67.96 %) were dark type and 7907 (32.04 %) were light ones. In all, there were 281 (1.14 %) tiny cells, 7451 (30.19 %) very small type, 5435 (D= 4221 + L= 1214) (22.02 %) small cells, 8131 (D= 3905 + L= 4226) (32.95 %) medium sized ones, 3282 (D= 867 + L= 2415) (13.3 %) big ones, 82 (D= 38 + L= 44) (0.33 %) very big ones, 9 (D= 5 + L= 4) (0.04 %) large ones and 6 (0.02 %) very large ones. On E18, the ganglion had a length of 0.900 mm, a volume of 0.2469 mm^3 and 106131 cells. Among these cells, 103947 (97.94 %) were dark type and 2184 (2.06 %) were light ones. In all, there were 37646 (35.47 %) tiny cells, 36189 (34.1 %) very small ones, 17228 (D= 16518 + L= 710) (16.23 %) small ones 12344 (D= 11356 + L= 988) medium sized ones, 2018 (D= 1657 + L= 361) (1.9 %) big ones and 706 (D= 581 + L= 125) (0.67 %) very big ones. On the day of hatching, the ganglion had a length of 0.980 mm, a volume of 0.2480 mm^3 and 17536 cells. Among these cells, 10354 (59.04 %) were dark type and 7182 (40.96 %) were light ones. In all, there were 182 (1.04 %) tiny cells, 2136 (D= 945 + L= 1191) (12.18 %) very small type, 4620 (D= 2251 + L= 2369) (26.35 %) small ones, 6380 (D= 3942 + L= 2438) (36.38 %) medium sized ones, 3142 (D= 2185 + L= 957) (17.92 %) big ones, 1013 (D= 799 L= 214) (5.78 %) very big ones and 63 (D= 50 + L= 13) (0.36 %) large ones. In the adult situation, the ganglion had a length of 1.300 mm, a volume of 0.6408 mm^3 and 13105 cells. Among these cells, 10757 (82.08 %) were dark type and 2348 (17.92 %) were light ones. In all, there were 509 (3.88 %) tiny cells, 3192 (D= 2517 + L= 675) (24.36 %) very small type, 2658 (D= 2047 + L= 611) (20.28 %) small ones, 2641 (D= 2052 + L= 589) (20.15 %) medium sized ones, 1052 (D= 1004 + L= 48) (8.03 %) big ones, 1664 (D= 1494 + L= 170) (12.7 %) very big ones, 1196 (D= 987 + L= 209) (9.13 %) large ones and 193 (D= 147 + L= 46) (1.47 %) very large ones.

6. Petrous Ganglion

The Petrous ganglion could be recognised on E6 while it had a rostro-caudal length of 0.336 mm and a volume of 0.0077 mm^3. The ganglion had 7778 cells all of which were dark type. In all, there were 205 (2.64 %) tiny cells, 3681 (47.33 %) very small ones, 3484 (44.79 %) small ones and 408 (5.25 %) medium sized ones. On E8, the ganglion had a length of 0.360 mm, a volume of 0.0118 mm^3 and had 8379 cells, all of which were dark type. In all, there were 106 (1.27 %) tiny cells, 3446 (41.13 %) very small ones, 4579 (54.65 %) small ones, 235 (2.8 %) medium sized ones and 13 (0.16 %) big ones. On E10, the ganglion had a length of 0.360 mm, a volume of 0.0157 mm^3 and had

6866 cells. Among these cells, 6858 (99.88 %) were dark type and 8 (0.12 %) were light ones. In all, there were 839 (12.22 %) tiny cells, 3244 (47.25 %) very small ones, 2218 (D = 2211 + L = 7) (32.3 %) small ones, 476 (D = 475 + L = 1) (6.93 %) medium sized ones and 89 (1.3 %) big ones. On E13, the ganglion had a length of 0.370 mm, a volume of 0.0243 mm^3 and had 10022 cells. Among these cells, 7960 (79.43 %) were dark type and 2062 (20.57 %) were light ones. In all, there were 128 (1.28 %) tiny cells, 6191 (61.78 %) very small ones, 1843 (D = 853 + L= 990) (18.39 %) small ones, 1015 (D= 440 + L = 575) (10.13 %) medium sized ones, 789 (D= 326 + L= 463) (7.87 %) big ones and 56 (D = 22 + L = 34) (0.56 %) very big ones. On E15, the ganglion had a length of 0.450 mm, a volume of 0.0425 mm^3 and had 8126 cells. Among these cells, 6673 (82.12 %) were dark type and 1453 (17.88 %) were light ones. In all, there were 399 (4.91 %) tiny cells, 3097 (38.11 %) very small ones, 2030 (D = 1556 + L = 474) (24.98 %) small ones, 2366 (D = 1521 + L = 845) (29.12 %) medium sized ones, 221 (D = 93 + L = 128) (2.72 %) big ones and 13 (D = 7 + L= 6) (0.16 %) very big ones. On E18, the ganglion had a length of 0.470 mm, a volume of 0.0561 mm^3 and had 32203 cells. Among these cells, 31462 (97.7 %) were dark type and 741 (2.3 %) were light ones. In all, there were 10948 (34 %) tiny cells, 9937 (30.86 %) very small ones, 6333 (D = 6136 + L = 197) (19.67 %) small ones, 3917 (D = 3577 + L = 340) (12.16 %) medium sized ones, 756 (D = 635 + L= 121) (2.35 %) big ones and 312 (D = 229 + L = 83) (0.97 %) very big ones. On the day of hatching, the ganglion had a length of 0.540 mm, a volume of 0.0548 mm^3 and had 3859 cells. Among these cells, 1711 (44.34 %) were dark type and 2148 (55.66 %) were light ones. In all, there were 42 (1.09 %) tiny cells, 459 (D = 50 + L = 409) (11.89 %) very small ones, 1087 (D = 288 + L= 799) (28.17 %) small ones, 1872 (D = 992 + L = 880) (48.51 %) medium sized ones, 313 (D = 258 + L = 55) (8.11 %) big ones and 86 (D = 81 + L = 5) (2.23 %) very big ones. In the adult situation, the ganglion had a length of 0.940 mm, a volume of 0.2390 mm^3 and had 2992 cells. Among these cells, 1870 (62.5 %) were dark type (D= 7824) and 1122 (37.5 %) were light ones. In all, there were 52 (1.74 %) tiny cells, 235 (D = 85 + L = 150) (7.85 %) very small ones, 749 (D = 304 + L = 445) (25.03 %) small ones, 1516 (D = 1053 + L = 463) (50.67 %) medium sized ones, 349 (D = 291 + L = 58) (11.66 %) big ones and 91 (D = 85 + L = 6) (3.04 %) very big ones.

7. Nodose Ganglion

The nodose ganglion could be recognised on E6 while it had a rostro-caudal length of 0.496 mm, a volume of 0.0127 mm^3 and 10740 cells. Among these cells, 9225 (85.89 %) were dark type and 1515 (14.11 %) were light ones. In all, there were 161 (1.5 %) tiny cells, 2488 (23. 17 %) very small ones, 4545 (D= 3731 + L= 814) (42.32 %) small ones and 3546 (D= 2845 + L= 701) (33.02 %) medium sized ones. On E8, the ganglion had a length of 0.536 mm, a volume of 0.0251 mm^3 and had 17167 cells. Among these cells 16958 (98.78 %) were dark type and 209 (1.22 %) were light ones. In all, there were 116 (0.68 %) tiny cells, 6425 (37.43 %) very small ones, 6729 (D= 6645 + L= 84) (39.2 %) small ones, 3735 (D= 3627 + L= 108) (21.76 %) medium sized ones and 162 (D= 145 + L= 17) (0.92 %) big ones. On E10, the ganglion had a length of 0.603 mm, a volume of 0.0484 mm^3 and had 16181 cells. Among these cells, 16014 (98.97 %) were dark type and 167 (1.03 %) were light ones. In all, there were 135 (0.83 %) tiny cells, 4774 (29.5 %) very small ones, 7626 (D= 7584 + L= 42) (47.13 %) small ones, 2370 (D= 2300 + L= 70) (14.65 %) medium sized ones, 1226 (D= 1178 + L= 48) (7.58 %) big ones and 50 (D= 43 + L= 7) (0.31 %) very big ones. On E13, the ganglion had a length of 0.630 mm, a volume of 0.0474 mm^3 and contained 8972 cells. Among these cells, 6613 (73.71 %) were dark type and 2359 (26.29 %) were light ones. In all, there were 94 (1.05 %) tiny cells, 3812 (42.49 %) very small ones, 2504 (D= 1645 + L= 859) (27.91 %) small ones, 1656 (D= 714 + L= 942) (18.46 %) medium sized ones, 587 (D= 229 + L= 358) (6.54 %) big ones, 271 (D= 99 + L= 172) (3.02 %) very big ones and 48 (D= 20 + L= 28) (0.53 %) large ones. On E15, the ganglion had a length of 0.740 mm, a volume of 0.0870 mm^3 and had 46803 cells. Among these cells, 44857 (95.84 %) were dark type and 1946 (4.16 %) were light ones. In all, there were 979 (2.09 %) tiny cells, 35572 (76 %) very small ones, 4964 (D= 4388 + L= 576) (10.39 %) small ones, 5027 (D= 3769 + L= 1258) (10.74 %) medium sized ones, 204 (D= 128 + L= 76) (0.44 %) big ones, 43 (D= 14 + L= 29) (0.09 %) very big ones and 14 (D= 7 + L= 7) (0.03 %) large ones. On E18, the ganglion had a length of 0.790 mm, a volume of 0.1071 mm^3 and had 80720 cells. Among these cells, 79253 (98.18 %) were dark type and 1467 (1.82 %) were light ones. In all, there were 30278 (37.51 %) tiny cells, 25074 (31.06 %) very small ones, 16309 (D= 15800 + L= 509) (20.2 %) small ones 6921 (D= 6154 + L= 767) (8.57 %) medium sized ones, 1778 (D= 1594 + L= 184) (2.2 %) big ones, 322 (D= 315 + L= 7) (0.4 %) very big ones and 38 (0.05 %) large ones. On the day of hatching, the ganglion had a length of 1.350 mm, a volume of 0.1368 mm^3 and had 11464 cells. Among these cells 7808 (68.11 %) were dark type and 3656 (31.89 %) were light ones. In all, there were 66 (0.58 %) tiny cells, 351 (D= 259 + L= 92) (3.06 %) very small type, 1855 (D= 908 + L= 947) (16.18 %) small ones, 4253 (D= 2709 + L= 1544) (37.1 %) medium sized ones, 2574 (D= 1654 + L= 920) (22.45 %) big ones, 2053 (D= 1903 + L= 150) (17.91 %) very big ones and 312 (D= 309 + L= 3) (2.8 %) large ones. In the adult situation, the ganglion had a length of 2.100 mm, a volume of 1.4497 mm^3 and had 9130 cells. Among these cells, 8784 (96.21 %) were dark type and 346 (3.79 %) were light ones. In all, there were 275 (3.01 %) tiny cells, 1526 (16.71 %) very small ones, 1551 (D= 1527 + L= 24) (16.99 %) small ones, 2342 (D= 2245 + L= 97) (25.65 %) medium sized ones, 973 (D= 902 + L= 71)

(10.66 %) big ones, 1500 (D= 1418 + L= 82) (16.43 %) very big ones, 505 (D= 467 + L= 38) (5.53 %) large ones, 413 (D= 388 + L= 25) (4.52 %) very large ones, and 45 (D= 36 + L= 9) (0.49 %) giant ones.

8. Ciliary Ganglion (Parasympathetic)

The ciliary ganglion could be recognised on E6 while the ganglion had a rostrocaudal length of 0.240 mm and a volume of 0.0174 mm^3. The ganglion had 16629 cells all of which were dark type. In all, there were 2053 (12.35 %) tiny cells, 8820 (53.04 %) very small ones, 5707 (34.32 %) small ones, and 49 (0.29 %) medium sized ones. On E8, the ganglion had a length of 0.296 mm, a volume of 0.0274 mm^3 and had 17646 cells all of which were dark type. In all, there were 114 (0.65 %) tiny cells, 9452 (53.56 %) very small ones, 5684 (32.21 %) small ones and 2396 (13.58 %) medium sized ones. On E10, the ganglion had a length of 0.387 mm, a volume of 0.0261 mm^3 and had 23618 cells all of which were dark type. In all, there were 2918 (12.35 %) tiny cells, 14152 (59.92 %) very small ones, 4337 (18.36 %) small ones, and 2211 (9.36 %) medium sized ones. On E13, the ganglion had a length of 0.460 mm, a volume of 0.0758 mm^3 and had 21867 cells. Among these cells, 21093 (96.46 %) were dark type, and 774 (3.54 %) were light ones. In all, there were 156 (0.71 %) tiny cells, 14142 (64.67 %) very small ones, 5124 (D= 4559 + L= 565) (23.43 %) small ones, 2256 (D= 2057 + L= 199) (10.32 %) medium sized ones, and 189 (D= 179 + L= 10) (0.86 %) big ones. On E15, the ganglion had a length of 0.510 mm, a volume of 0.0674 mm^3 and had 9365 cells. Among these cells, 6909 (73.77 %) were dark type, and 2456 (26.23 %) were light ones. In all, there were 413 (4.41 %) tiny cells, 2519 (26.9 %) very small ones, 3355 (D= 1887 + L= 1468) (35.82 %) small ones, 3062 (D= 2078 + L= 984) (32.7 %) medium sized ones, 9 (D= 6 + L= 3) (0.1 %) big ones, and 7 (D= 6 + L= 1) (0.07 %) very big ones. On E18, the ganglion had a length of 0.540 mm, a volume of 0.2390 mm^3 and had 186557 cells. Among these cells, 186379 (99.9 %) were dark type and 178 (0.1 %) were light ones. In all, there were 155843 (83.54 %) tiny cells, 16125 (8.64 %) very small ones, 9924 (D= 9923 + L= 1) (5.32 %) small ones, 3315 (D= 3237 + L= 78) (1.78 %) medium sized ones, 935 (D= 876 + L= 59) (0.5 %) big ones, and 415 (D= 375 + L= 40) (0.22 %) very big ones. On the day of hatching, the ganglion had a length of 0.600 mm, a volume of 0.0903 mm^3 and had 10521 cells. Among these cells, 5610 (53.32 %) were dark type and 4911 (46.68 %0 were light ones. In all, there were 319 (3.03 %0 tiny cells, 2867 (D= 1486 + L= 1381) (27.25 %) very small ones, 3361 (D= 1639 + L= 1722) (31.95 %) small ones, 2976 (D= 1594 + L= 1382) (28.29 %) medium sized ones, 856 (D= 472 + L= 384) (8.14 %) big ones and 142 (D= 100 + L= 42) (1.35 %) very big ones. In the adult situation, the ganglion had a length of 0.660 mm, a volume of 0.2977 mm^3 and contained 2535 cells. Among these cells, 2079 (82.01 %) were dark type and 456 (17.99 %) were light ones. In all, there were 259 (10.22 %) tiny cells, 336 (13.25 %) very small ones, 313 (D= 249 + L= 64) (12.35 %) small ones, 605 (D= 449 + L= 156) (23.87 %) medium sized ones, 373 (D= 274 + L= 99) (14.71 %) big ones, 195 (D= 150 + L= 45) (7.69 %) very big ones, 234 (D= 178 + L= 56) (9.23 %) large ones and 220 (D= 184 + L= 36) (8.68 %) very large ones.

9. Superior Cervical Ganglion (Sympathetic)

The Superior Cervical Ganglion could be recognised on E6 while it had a rostro-caudal length of 0.560 mm and a volume of 0.0083 mm^3 and, had 14489 cells all of which were dark type. In all, there were 687 (4.74 %) tiny cells, 5986 (41.31 %) very small type, 7250 (50.04 %) small ones, and 566 (3.9 %) medium sized ones. On E8, the ganglion had a length of 0.600 mm, a volume of 0.0325 mm^3 and had 30832 cells all of which were dark type. In all, there were 5230 (16.96 %) tiny cells, 12194 (39.55 %) very small type, 13190 (42.78 %) small ones and 218 (0.71 %) medium sized ones. On E10, the ganglion had a length of 0.657 mm, a volume of 0.0387 mm^3 and had 47681 cells all of which were dark type. In all, there were 10832 (22.72 %) tiny cells, 31144 (65.32 %) very small ones, 3929 (8.24 %) small ones and 1776 (3.72 %) medium sized ones. On E13, the ganglion had a length of 0.580 mm, a volume of 0.0582 mm^3 and had 39322 cells all of which were dark type. In all, there were 347 (0.88 %) tiny cells, 22999 (58.49 %) very small ones, 12004 (30.53 %) small ones and 3972 (10.1 %) medium sized ones. On E15, the ganglion had a length of 0.690 mm, a volume of 0.1075 mm^3 and had 74974 cells all of which were dark type. In all, there were 1292 (1.72 %) tiny cells, 59282 (79.01 %) very small ones, 11798 (15.72 %) small ones and 2602 (3.47 %) medium sized ones. On E18, the ganglion had a length of 0.720 mm, a volume of 0.1963 mm^3 and had 127722 cells. Among these cells, 127231 (99.62 %) were dark type and 491 (0.38 %) were light ones. In all, there were 38420 (30.08 %) tiny cells, 42647 (33.39 %) very small ones, 44575 (D= 44252 + L= 323) (34.9 %) small ones and 2080 (D= 1912 + L= 168) (1.63 %) medium sized ones. On the day of hatching, the ganglion had a length of 0.810 mm, a volume of 0.1166 mm^3 and had 55244 cells. Among these cells, 18172 (32.89 %) were dark type and 37072 (67.11 %) were light ones. In all, there were 675 (1.22 %) tiny cells, 38083 (D= 9404 + L= 28679) (68.94 %) very small ones, 15240 (D= 7086 + L= 8154) (27.59 %) small ones, and 1246 (D= 1007 + L= 239) (2.26 %) medium sized ones. In the adult situation, the ganglion had a length of 1.430 mm, a volume of 0.4928 mm^3 and had 34374 cells. Among these cells, 18271 (53.15 %) were dark type and 16103 (46.85 %) were light ones. In all, there were 475 (1.38 %) tiny cells, 20026 (D= 8228 + L= 11798) (58.26 %) very small ones, 12481 (D= 8365 + L= 4116) (36.31 %) small ones, 1212 (D= 1057 + L= 155) (3.53 %) medium sized ones and 180 (D= 146 + L= 34) (0.52 %) big ones.

Table 1. Illustrates the total number of dark and light cells in the trigeminal ganglion in different age groups of animals in the ontogeny of the chick

Size / Age	Tiny <5u	Very small 6-10u	Small 11-15u	Medium 16-20u	Big 21-25u	Very big 26-30u	Large 31-35u	Very large 36-40u	Giant >40u	Total Number	Grand Total
E6-D	4923	24453	41267	3219	0	0	0	0	0	73862	
E6-L	0	0	0	0	0	0	0	0	0	0	73862
E8-D	63347	168400	23970	3610	0	0	0	0	0	259327	
E8-L	0	0	3	75	0	0	0	0	0	78	259405
E10-D	581	17067	59095	23804	45	11	0	0	0	100603	
E10-L	0	0	348	239	7	2	0	0	0	596	101199
E13-D	510	27203	10824	9856	3131	503	163	3	6	52199	
E13-L	0	0	15017	12586	3931	637	120	1	2	32294	84493
E15-D	1004	19330	5046	5742	1833	1071	0	0	0	34026	
E15-L	0	0	12328	10952	3721	1408	0	0	0	28409	62435
E18-D	113491	106003	43706	22305	2154	578	15	0	0	288252	
E18-L	0	0	5908	9748	2192	386	12	0	0	18246	306498
H-D	781	12288	11275	8138	1856	1116	605	57	0	36116	
H-L	0	4935	8282	6752	1985	617	74	18	0	22663	58779
A-D	548	3886	2539	4567	435	3568	3277	8841	1814	29475	
A-L	0	1626	1037	1600	87	813	719	1350	119	7351	36826

(D = Dark cells E=Embroynic age H=Day of hatching A=Adult)

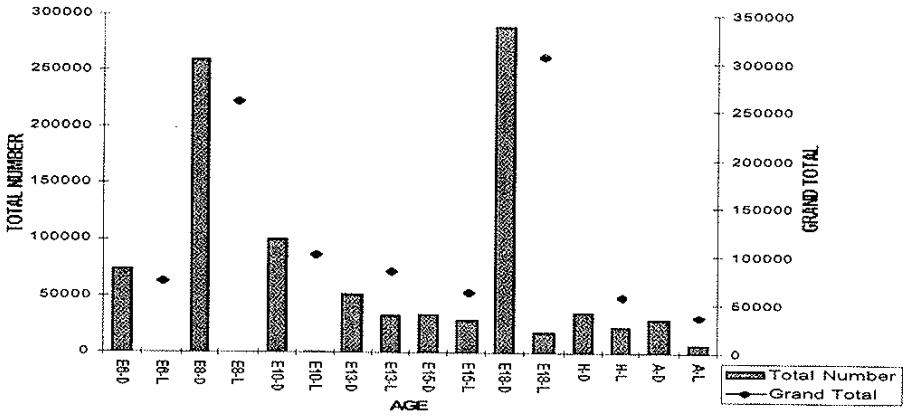

Figure 1 A. Total number of dark & light cells in the trigeminal ganglion in different age groups of animals in the ontogeny of the chick

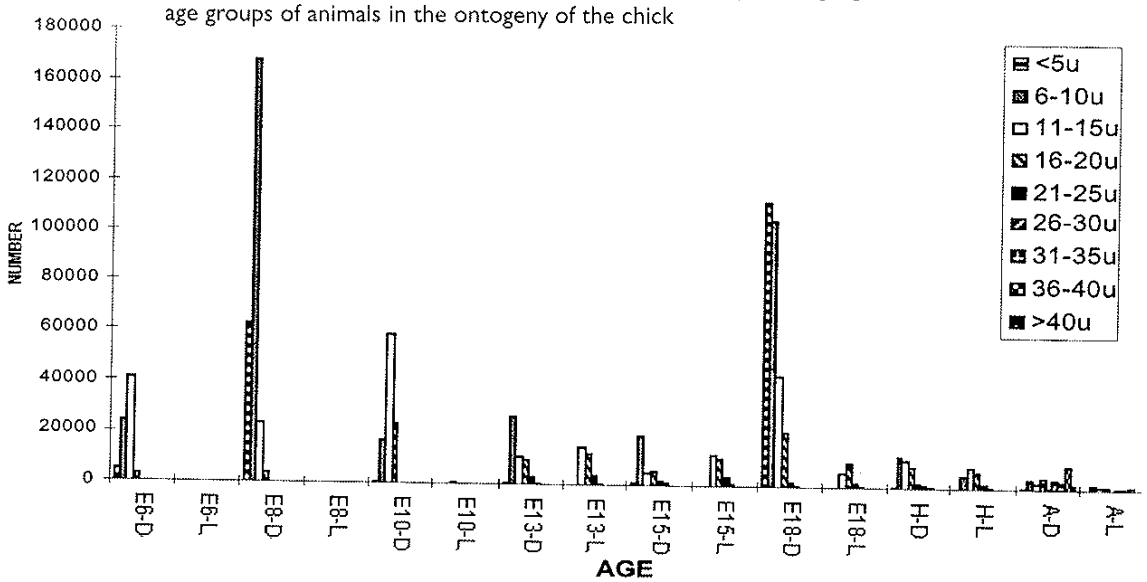

Figure 1B. Total number of dark & light cells in the trigeminal ganglion in different age groups of animals in the ontogeny of the chick

Table 2. Illustrates the total number of dark and light cells in the genicular ganglion in different age groups of animals in the ontogeny of the chick

Size / Age	Tiny <5u	Very small 6-10u	Small 11-15u	Medium 16-20u	Big 21-25u	Very big 26-30u	Large 31-35u	Very large 36-40u	Giant >40u	Total Number	Grand Total
E6-D	95	1232	1815	286	0	0	0	0	0	3428	
E6-L	0	0	0	0	0	0	0	0	0	0	3428
E8-D	1952	3111	1542	100	0	0	0	0	0	6705	
E8-L	0	0	0	0	0	0	0	0	0	0	6705
E10-D	81	160	677	343	100	0	0	0	0	1361	
E10-L	0	0	0	0	0	0	0	0	0	0	1361
E13-D	78	1841	693	807	765	45	23	0	0	4252	
E13-L	0	0	81	157	252	16	6	0	0	512	4764
E15-D	98	935	150	147	74	38	0	0	0	1442	
E15-L	0	0	365	761	243	58	0	0	0	1427	2869
E18-D	8092	5533	1971	920	20	7	0	0	0	16543	
E18-L	0	0	317	639	86	7	0	0	0	1049	17592
H-D	20	59	69	289	301	368	2	1	3	1112	
H-L	0	124	259	314	179	105	0	0	0	981	2093
A-D	15	7	22	84	13	194	175	315	79	904	
A-L	0	0	14	12	9	18	23	34	7	117	1021

(D = Dark cells E=Embroynic age H=Day of hatching A=Adult)

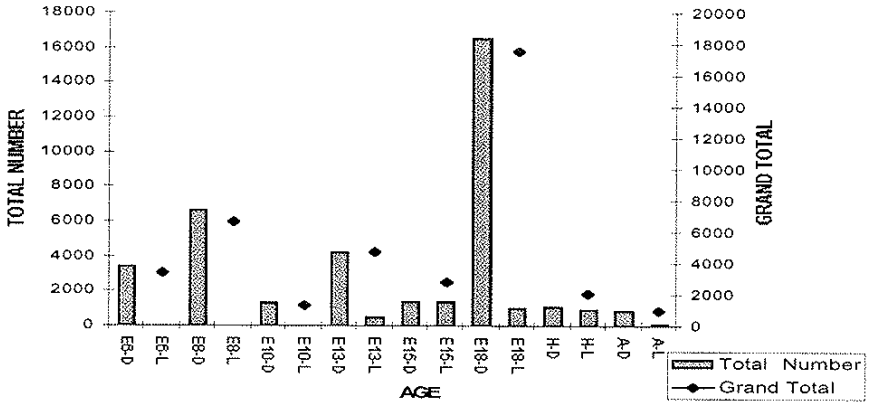

Figure 2 A. Total number of dark & light cells in the genicular ganglion in different age groups of animals in the ontogeny of the chick

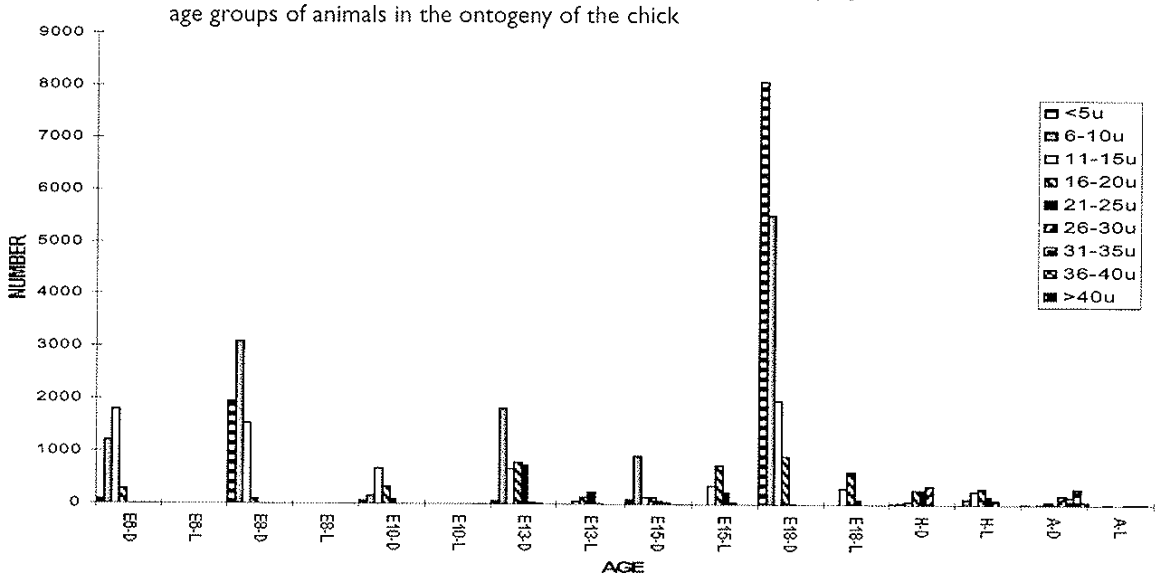

Figure 2B. Total number of dark & light cells in the genicular ganglion in different age groups of animals in the ontogeny of the chick

Table 3 Illustrates the total number of dark and light cells in the acoustic ganglion in different age groups of animals in the ontogeny of the chick

Size / Age	Tiny <5u	Very small 6-10u	Small 11-15u	Medium 16-20u	Big 21-25u	Very big 26-30u	Large 31-35u	Very large 36-40u	Giant >40u	Total Number	Grand Total
E6-D	334	4710	4841	175	0	0	0	0	0	10060	
E6-L	0	0	0	0	0	0	0	0	0	0	10060
E8-D	5863	9660	4728	164	0	0	0	0	0	20415	
E8-L	0	0	0	0	0	0	0	0	0	0	20415
E10-D	6495	33229	2944	0	0	0	0	0	0	42668	
E10-L	0	0	0	0	0	0	0	0	0	0	42668
E13-D	325	16320	18817	1347	0	0	0	0	0	36809	
E13-L	0	0	1823	465	0	0	0	0	0	2288	39097
E15-D	6482	28864	8290	3969	193	9	0	0	0	47807	
E15-L	0	0	518	671	281	36	0	0	0	1506	49313
E18-D	57962	93394	63318	5603	37	0	0	0	0	220314	
E18-L	0	0	10	14	0	0	0	0	0	24	220338
H-D	219	840	8018	3943	17	0	0	0	0	13037	
H-L	0	3137	8753	1771	3	0	0	0	0	13664	26701
A-D	3329	6557	4450	188	0	0	0	0	0	14524	
A-L	0	60	38	11	0	0	0	0	0	109	14633

(D = Dark cells E=Embroynic age H=Day of hatching A=Adult)

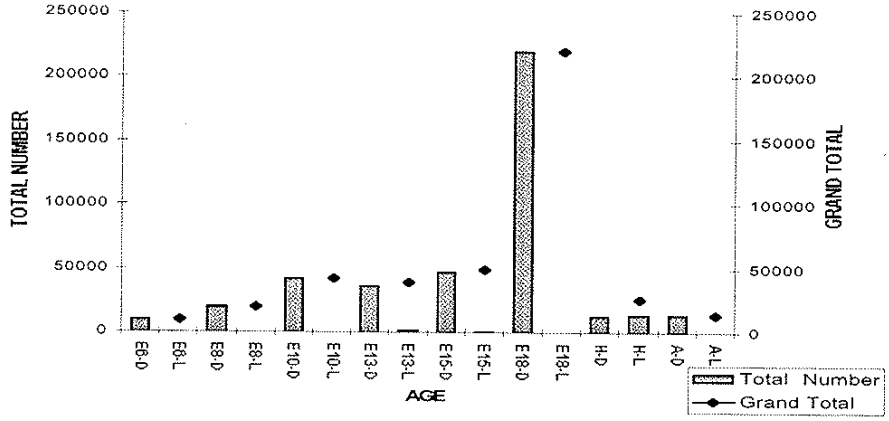

Figure 3 A. Total number of dark & light cells in the acoustic ganglion in different age groups of animals in the ontogeny of the chick

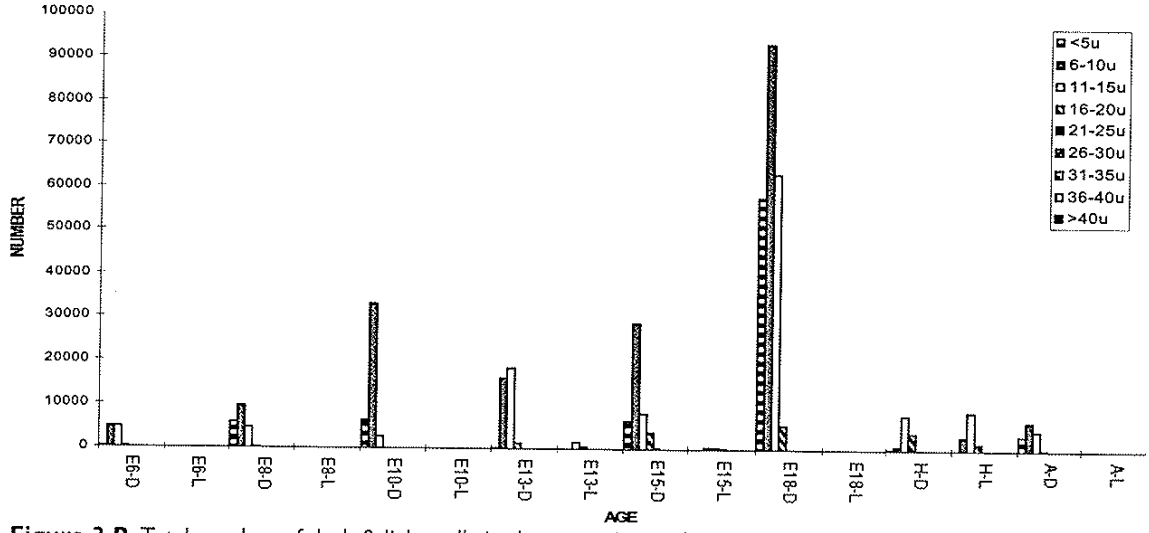

Figure 3 B. Total number of dark & light cells in the acoustic ganglion in different age groups of animals in the ontogeny of the chick

Table 4 Illustrates the total number of dark and light cells in the vestibular ganglion in different age groups of animals in the ontogeny of the chick

Size / Age	Tiny <5u	Very small 6-10u	Small 11-15u	Medium 16-20u	Big 21-25u	Very big 26-30u	Large 31-35u	Very large 36-40u	Giant >40u	Total Number	Grand Total
E6-D	2220	14803	15197	696	0	0	0	0	0	32916	
E6-L	0	0	0	8	0	0	0	0	0	8	32924
E8-D	874	30870	10750	201	0	0	0	0	0	42695	
E8-L	0	0	0	0	0	0	0	0	0	0	42695
E10-D	10268	40467	9418	1783	0	0	0	0	0	61936	
E10-L	0	0	0	0	0	0	0	0	0	0	61936
E13-D	2674	27480	6818	2665	583	47	0	0	0	40267	
E13-L	0	0	2433	990	180	24	0	0	0	3627	43894
E15-D	3449	31886	7501	3195	953	481	0	0	0	47465	
E15-L	0	0	2589	2459	656	270	0	0	0	5974	53439
E18-D	91241	100958	31988	8981	1491	218	0	0	0	234877	
E18-L	0	0	567	1267	336	144	0	0	0	2314	237191
H-D	105	428	924	2178	693	425	118	0	0	4871	
H-L	0	3751	4063	4462	838	73	9	0	0	13196	18067
A-D	1183	4935	3645	1860	168	278	120	0	0	12189	
A-L	0	0	155	101	14	17	7	0	0	294	12483

(D = Dark cells E=Embroynic age H=Day of hatching A=Adult)

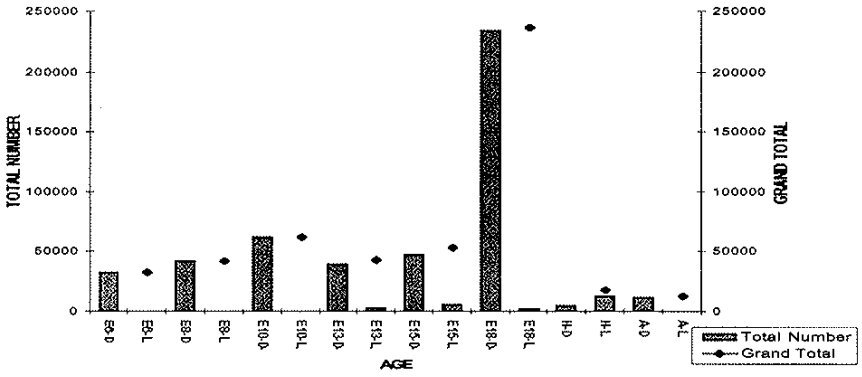

Figure 4A. Total number of dark & light cells in the vestibular ganglion in different age groups of animals in the ontogeny of the chick

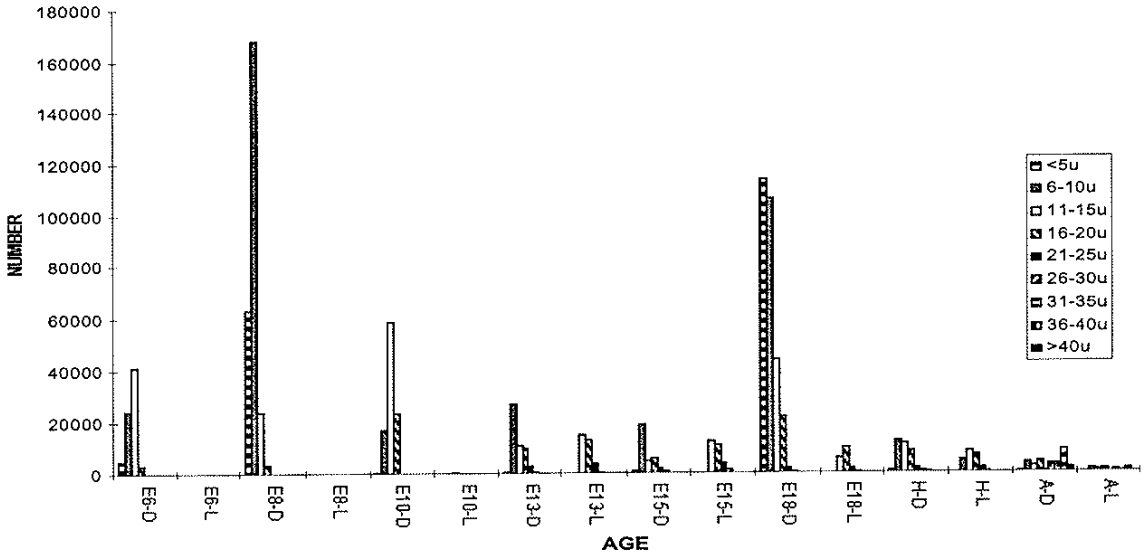

Figure 4 B. Total number of dark & light cells in the vestibular ganglion in different age groups of animals in the ontogeny of the chick

Table 5. Illustrates the total number of dark and light cells in the proximal ganglionic complex of cranial nerves IX & X in different age groups of animals in the ontogeny of the chick

Size / Age	Tiny <5u	Very small 6-10u	Small 11-15u	Medium 16-20u	Big 21-25u	Very big 26-30u	Large 31-35u	Very large 36-40u	Giant >40u	Total Number	Grand Total
E6-D	785	8222	8444	454	0	0	0	0	0	17905	
E6-L	0	0	0	0	0	0	0	0	0	0	17905
E8-D	492	22987	7342	195	0	0	0	0	0	31016	
E8-L	0	0	0	0	0	0	0	0	0	0	31016
E10-D	2810	18610	7019	374	0	0	0	0	0	28813	
E10-L	0	0	0	0	0	0	0	0	0	0	28813
E13-D	302	13166	2956	2274	537	42	0	0	0	19277	
E13-L	0	0	3386	2868	624	53	0	0	0	6931	26208
E15-D	281	7451	4221	3905	867	38	5	2	0	16770	
E15-L	0	0	1214	4226	2415	44	4	4	0	7907	24677
E18-D	37646	36189	16518	11356	1657	581	0	0	0	103947	
E18-L	0	0	710	988	361	125	0	0	0	2184	106131
H-D	182	945	2251	3942	2185	799	50	0	0	10354	
H-L	0	1191	2369	2438	957	214	13	0	0	7182	17536
A-D	509	2517	2047	2052	1004	1494	987	147	0	10757	
A-L	0	675	611	589	48	170	209	46	0	2348	13105

(D = Dark cells E=Embroynic age H=Day of hatching A=Adult)

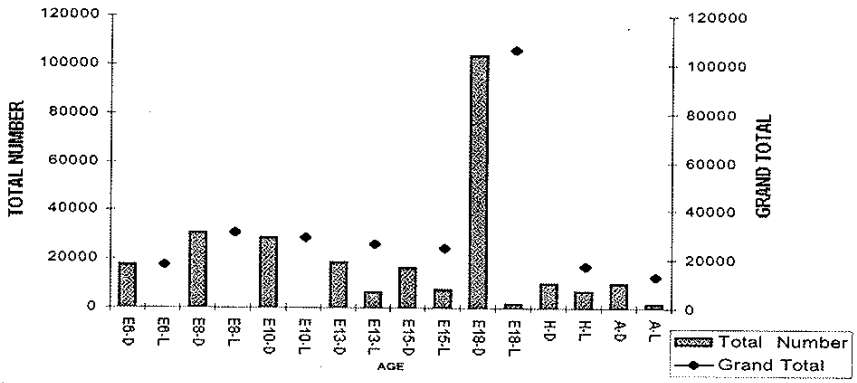

Figure 5A. Total number of dark & light cells in the proximal ganglionic complex of cranial nerves IX & X in different age groups of animals in the ontogeny of the chick

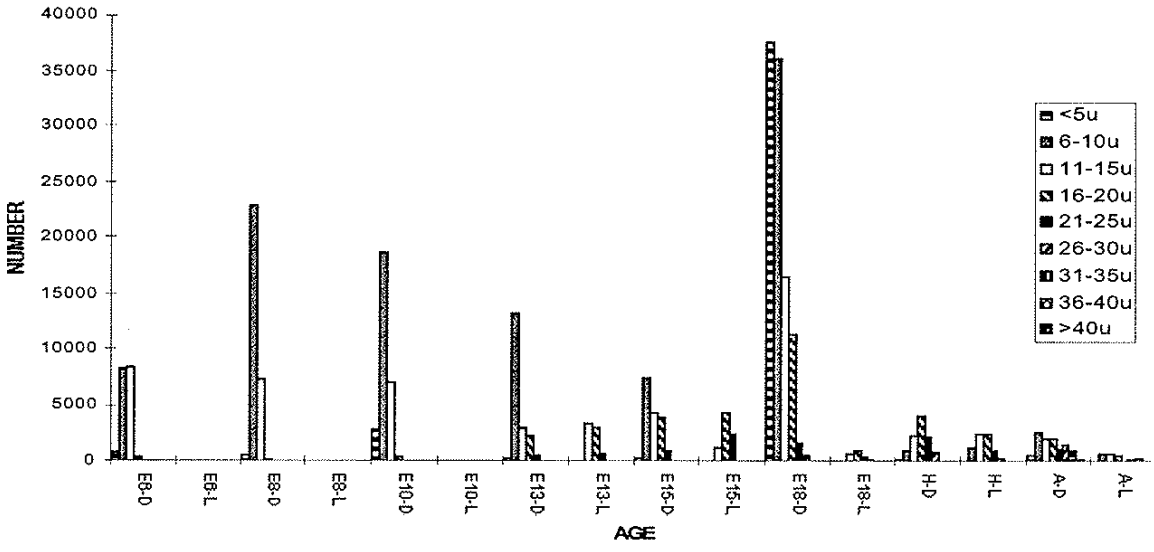

Figure 5B. Total number of dark & light cells in the proximal ganglionic complex of cranial nerves IX & X in different age groups of animals in the ontogeny of the chick

Table 6. Illustrates the total number of dark and light cells in the petrous ganglion in different age groups of animals in the ontogeny of the chick

Size / Age	Tiny <5u	Very small 6-10u	Small 11-15u	Medium 16-20u	Big 21-25u	Very big 26-30u	Large 31-35u	Very large 36-40u	Giant >40u	Total Number	Grand Total
E6-D	205	3681	3484	408	0	0	0	0	0	7778	
E6-L	0	0	0	0	0	0	0	0	0	0	7778
E8-D	106	3446	4579	235	13	0	0	0	0	8379	
E8-L	0	0	0	0	0	0	0	0	0	0	8379
E10-D	839	3244	2211	475	89	0	0	0	0	6858	
E10-L	0	0	7	1	0	0	0	0	0	8	6866
E13-D	128	6191	853	440	326	22	0	0	0	7960	
E13-L	0	0	990	575	463	34	0	0	0	2062	10022
E15-D	399	3097	1556	1521	93	7	0	0	0	6673	
E15-L	0	0	474	845	128	6	0	0	0	1453	8126
E18-D	10948	9937	6136	3577	635	229	0	0	0	31462	
E18-L	0	0	197	340	121	83	0	0	0	741	32203
H-D	42	50	288	992	258	81	0	0	0	1711	
H-L	0	409	799	880	55	5	0	0	0	2148	3859
A-D	52	85	304	1053	291	85	0	0	0	1870	
A-L	0	150	445	463	58	6	0	0	0	1122	2992

(D = Dark cells E=Embroynic age H=Day of hatching A=Adult)

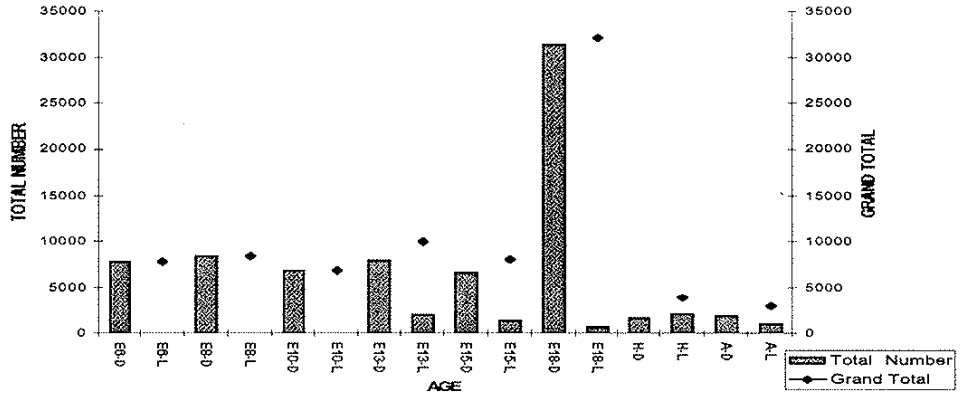

Figure 6A. Total number of dark & light cells in the petrous ganglion in different age groups of animals in the ontogeny of the chick

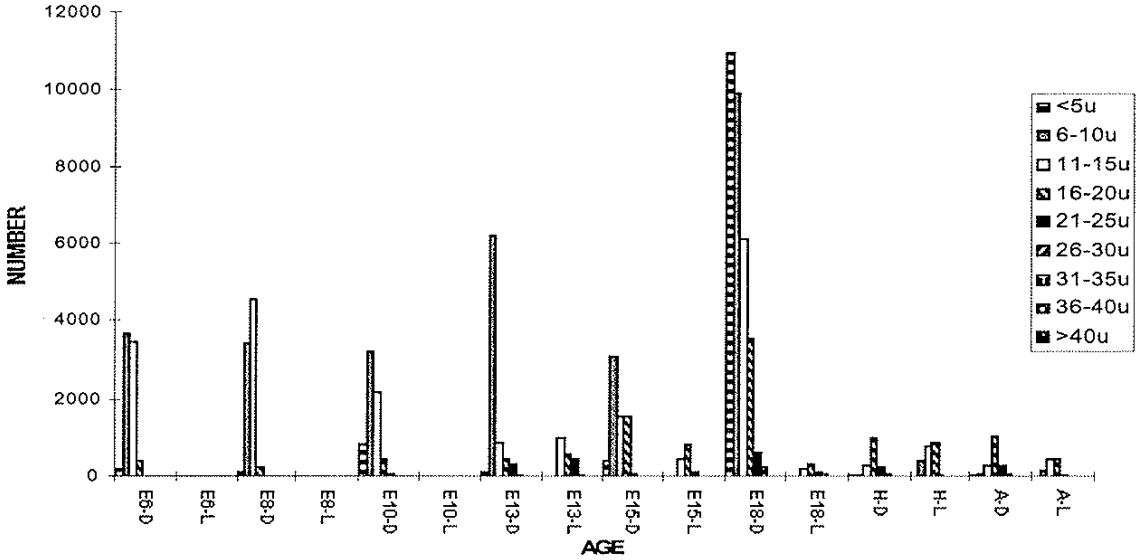

Figure 6B. Total number of dark & light cells in the petrous ganglion in different age groups of animals in the ontogeny of the chick

Table 7. Illustrates the total number of dark and light cells in the nodose ganglion in different age groups of animals in the ontogeny of the chick

Size / Age	Tiny <5u	Very small 6-10u	Small 11-15u	Medium 16-20u	Big 21-25u	Very big 26-30u	Large 31-35u	Very large 36-40u	Giant >40u	Total Number	Grand Total
E6-D	161	2488	3731	2845	0	0	0	0	0	9225	
E6-L	0	0	814	701	0	0	0	0	0	1515	10740
E8-D	116	6425	6645	3627	145	0	0	0	0	16958	
E8-L	0	0	84	108	17	0	0	0	0	209	17167
E10-D	135	4774	7584	2300	1178	43	0	0	0	16014	
E10-L	0	0	42	70	48	7	0	0	0	167	16181
E13-D	94	3812	1645	714	229	99	20	0	0	6613	
E13-L	0	0	859	942	358	172	28	0	0	2359	8972
E15-D	979	35572	4388	3769	128	14	7	0	0	44857	
E15-L	0	0	576	1258	76	29	7	0	0	1946	46803
E18-D	30278	25074	15800	6154	1594	315	38	0	0	79253	
E18-L	0	0	509	767	184	7	0	0	0	1467	80720
H-D	66	259	908	2709	1654	1903	309	0	0	7808	
H-L	0	92	947	1544	920	150	3	0	0	3656	11464
A-D	275	1526	1527	2245	902	1418	467	388	36	8784	
A-L	0	0	24	97	71	82	38	25	9	346	9130

(D = Dark cells E=Embroynic age H=Day of hatching A=Adult)

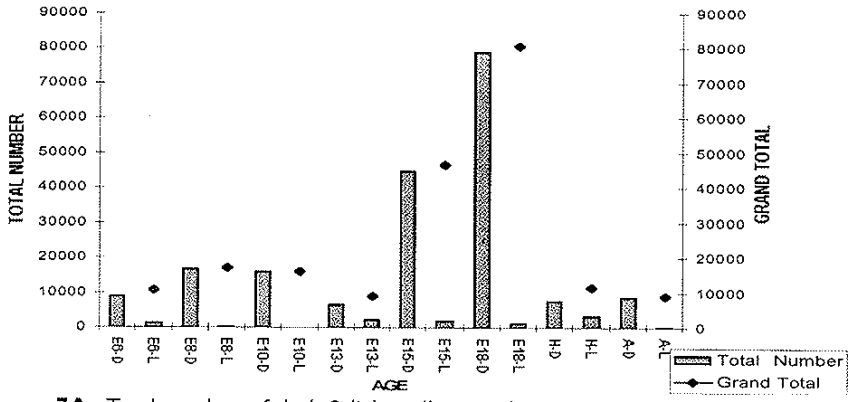

Figure 7A. Total number of dark & light cells in nodose ganglion in different age groups of animals in the ontogeny of the chick

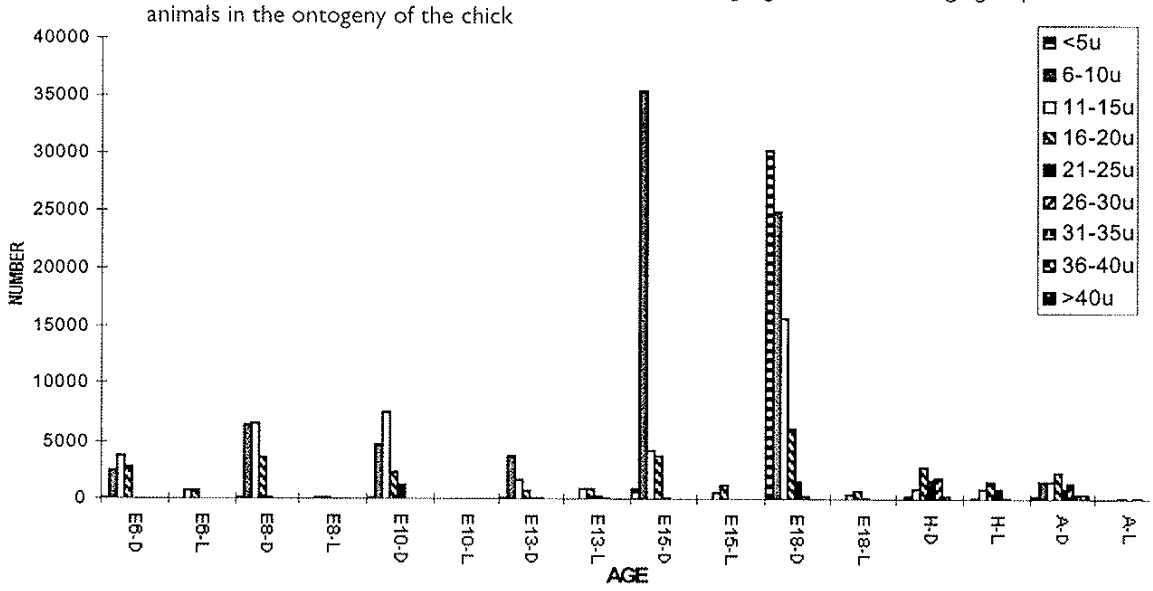

Figure 7B. Total number of dark & light cells in nodose ganglion in different age groups of animals in the ontogeny of the chick

Table 8. Illustrates the total number of dark and light cells in the ciliary ganglion in different age groups of animals in the ontogeny of the chick

Size / Age	Tiny <5u	Very small 6-10u	Small 11-15u	Medium 16-20u	Big 21-25u	Very big 26-30u	Large 31-35u	Very large 36-40u	Giant >40u	Total Number	Grand Total
E6-D	2053	8820	5707	49	0	0	0	0	0	16629	
E6-L	0	0	0	0	0	0	0	0	0	0	16629
E8-D	114	9452	5684	2396	0	0	0	0	0	17646	
E8-L	0	0	0	0	0	0	0	0	0	0	17646
E10-D	2918	14152	4337	2211	0	0	0	0	0	23618	
E10-L	0	0	0	0	0	0	0	0	0	0	23618
E13-D	156	14142	4559	2057	179	0	0	0	0	21093	
E13-L	0	0	565	199	10	0	0	0	0	774	21867
E15-D	413	2519	1887	2078	6	6	0	0	0	6909	
E15-L	0	0	1468	984	3	1	0	0	0	2456	9365
E18-D	155843	16125	9923	3237	876	375	0	0	0	186379	
E18-L	0	0	1	78	59	40	0	0	0	178	186557
H-D	319	1486	1639	1594	472	100	0	0	0	5610	
H-L	0	1381	1722	1382	384	42	0	0	0	4911	10521
A-D	259	336	249	449	274	150	178	184	0	2079	
A-L	0	0	64	156	99	45	56	36	0	456	2535

(D = Dark cells E=Embroynic age H=Day of hatching A=Adult)

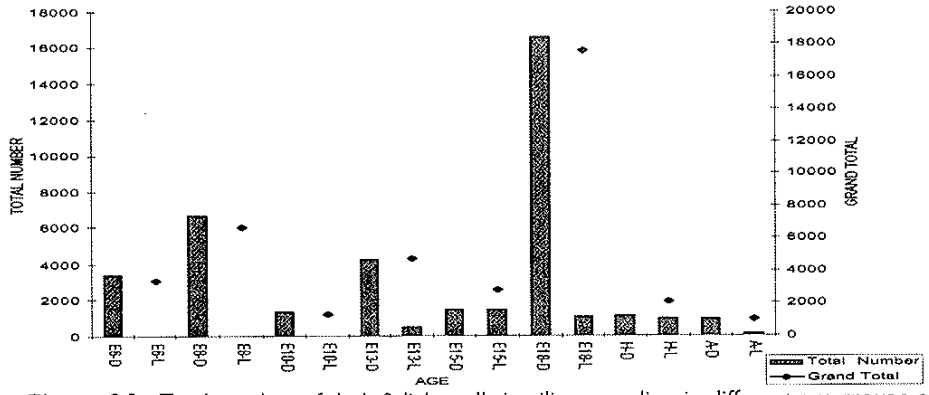

Figure 8A. Total number of dark & light cells in ciliary ganglion in different age groups of animals in the ontogeny of the chick

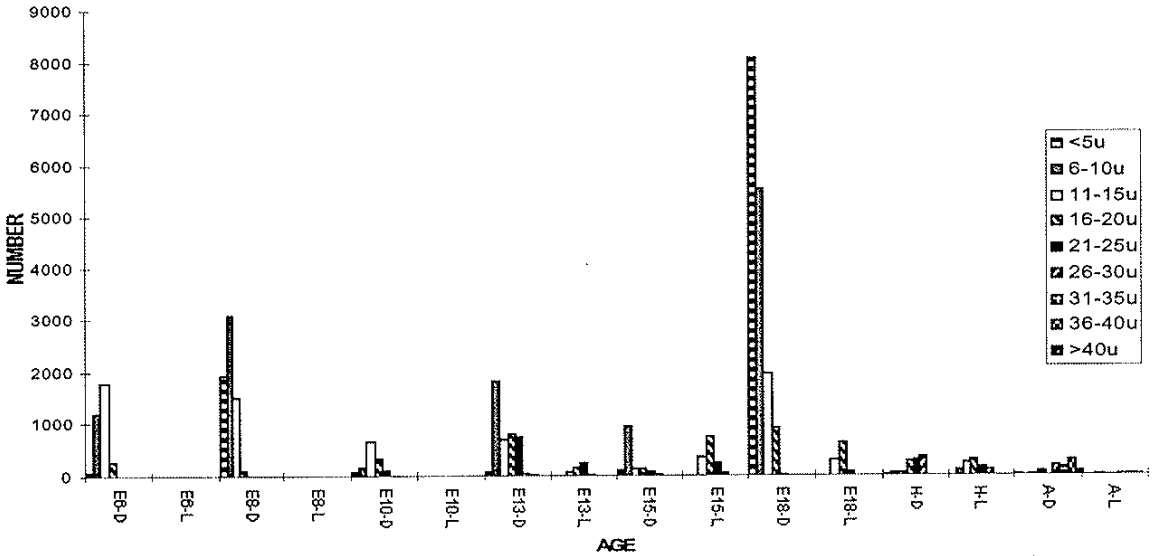

Figure 8B. Total number of dark & light cells in ciliary ganglion in different age groups of animals in the ontogeny of the chick

Table 9. Illustrates the total number of dark and light cells in the superior cervical ganglion in different age groups of animals in the ontogeny of the chick

Size / Age	Tiny <5u	Very small 6-10u	Small 11-15u	Medium 16-20u	Big 21-25u	Very big 26-30u	Large 31-35u	Very large 36-40u	Giant >40u	Total Number	Grand Total
E6-D	687	5986	7250	566	0	0	0	0	0	14489	
E6-L	0	0	0	0	0	0	0	0	0	0	14489
E8-D	5230	12194	13190	218	0	0	0	0	0	30832	
E8-L	0	0	0	0	0	0	0	0	0	0	30832
E10-D	10832	31144	3929	1776	0	0	0	0	0	47681	
E10-L	0	0	0	0	0	0	0	0	0	0	47681
E13-D	347	22999	12004	3972	0	0	0	0	0	39322	
E13-L	0	0	0	0	0	0	0	0	0	0	39322
E15-D	1292	59282	11798	2602	0	0	0	0	0	74974	
E15-L	0	0	0	0	0	0	0	0	0	0	74974
E18-D	38420	42647	44252	1912	0	0	0	0	0	127231	
E18-L	0	0	323	168	0	0	0	0	0	491	127722
H-D	675	9404	7086	1007	0	0	0	0	0	18172	
H-L	0	28679	8154	239	0	0	0	0	0	37072	55244
A-D	475	8228	8365	1057	146	0	0	0	0	18271	
A-L	0	11798	4116	155	34	0	0	0	0	16103	34374

(D = Dark cells E=Embroynic age H=Day of hatching A=Adult)

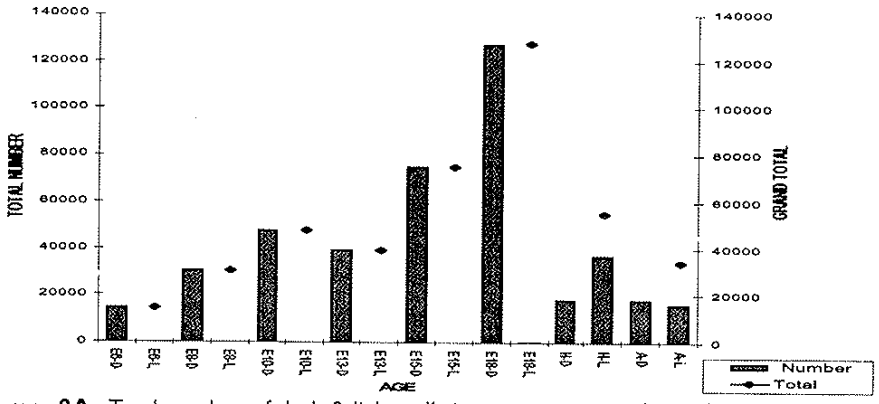

Figure 9A. Total number of dark & light cells in superior cervical ganglion in different age groups of animals in the ontogeny of the chick

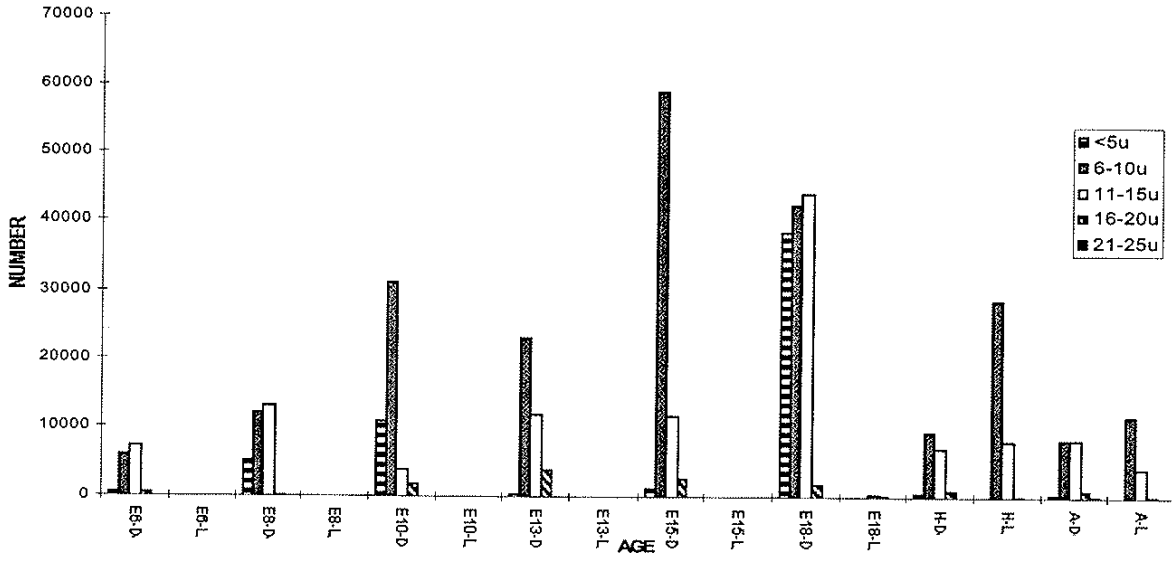

Figure 9B. Total number of dark & light cells in superior cervical ganglion in different age groups of animals in the ontogeny of the chick

Discussion

A. Dark and Light Cells

In general, by a critical analysis and evaluation of the results in all the ganglia studied in the present series of investigation, it is assumed that

a. the dark cells represent a group of functionally active cells which might proliferate, grow, mature, establish proper connections and continue to perform their functions. However, these cells may lose their activity and become inactive or die at any stage of their development, growth or activity and change to a light coloured cell on staining.

b. the light cells represent a group of inactive, dying, dead or degenerating cells. In many situations, the occurrence of light cells in the ganglion for the first time is associated with loss of cells. These cells might become inactive or die due to some inherent defects developed within themselves or to some adverse factors found in the micro-environment. These light cells are found to appear around the time when the cells begin to establish their projections and represent those which fail to establish functional connections. However, sometimes when the adverse factors are rectified, these cells which have at first started to lose their functions might be re-activated and become normal active cells again and, therefore, might turn to be a dark type.

i. by re-activation of their same original cell-processes which have first failed to establish a functional projection into their peripheral field of innervation, by rectifying the defects (found either within the cells themselves or in their micro-environment) by developing some favourable conditions, or

ii. by the development of new collateral branches from the main process, which might grow new and establish functional connections to their innervation fields.

A brief explanation is given below to illustrate the factor: b given above, i.e., to show that the light cells (inactive cells) might revert to dark cells (active ones). As an example, please refer to the results of the superior cervical ganglion on the day of hatching (H) and in the adulthood(A). Please note the number of total cells (55244 on H, 34374 in A), dark cells (18172 on H, 18271 in A) and light cells (37072 on H, 16103 in A), and the proliferative capacity which is represented by the number of tiny cells (675 on H, 475 in A) in these stages (H and reduced in A). This indicates that the number of dark cells have increased in the adulthood whereas the light cells have reduced, in comparison to that observed on the day of hatching. This is clearly suggestive of the assumption that some of the light cells have changed themselves to become an active type again (i.e., dark cells), probably by establishing a viable functional connection as a result of newly-formed collateral branches as a result of some favourable micro-environment, or by regaining the functional capacity of the original fibres by a process of re-activation, after the fibres have started to lose their functional capacity. Almost similar results can be noticed in the vestibular ganglion, proximal ganglionic complex of cranial nerves IX and X, petrous ganglion, nodose ganglion etc. However, in these ganglia, the increased number of tiny cells in the adulthood in comparison to that observed on the day of hatching might suggest that the increased number of dark cells in the adult situation might be related either to a re-activation of light cells (inactive cells) as explained above, or to the growth, maturation and establishment of active functional connections of the new-generation of tiny cells, or by both these processes.

The following evidences are presented in support of this assumption about the significance of the dark and light groups of cells. However, these statements are given in the form of brief points in order to avoid unnecessary long descriptions which might also need repetitions for every ganglion studied. Later, the facts are described in relation to some of the relevant available literature. Whenever necessary, for more details, the results of that particular ganglion may be verified and the facts be confirmed. The percentage or ratio of the dark and light cells in the ganglion in any age group may be found in the description of the results.

1. During the periods of active proliferation and growth especially in the early stages of development, while there is a continuous increase in the total number of cells, all the cells among all categories found in the ganglion are dark type; no light cells are found during these active periods of development. Therefore, the dark cells are considered as a group of active cells which might divide, proliferate, grow, mature and thereby help to increase (or add) the number of all classes of cells in the ganglion. It may be noticed that the light cells begin to appear in the respective ganglia just after the stages given below. The time of appearance of light cells in the ganglion is presumed to be related to the time of their failure to establish functional connections. The beginning of establishment of such connections should be earlier than the time of occurrence of these light cells in the ganglion. Of course, this period varies from one ganglion to the other. The following description shows the developmental stages where all the ganglion cells are dark type after which the light cells begin to appear.

Trigeminal ganglion	E6, probably the establishment of functional connection begins early.
Geniculate ganglion:	E6, E8, E10
Vestibular ganglion:	E6, E8, E10; Please refer to the explanation given for the presence of a few (8) light cells on E6

Acoustic ganglion:	E6, E8, E10
Prox. G. Comp. of IX and X:	E6, E8, E10
Petrous ganglion:	E6, E8
Nodose ganglion:	Light cells are found even on E6; Probably the establishment of functional projections begins very early, even before E6. Thus this is the first ganglion to developfunctional connections, possibly related to its supply tovital organs such as heart, lungs and alimentary canal and its importance.
Ciliary ganglion:	E6, E8, E10
Superior cervical ganglion:	E6, E8, E10, E13, E15; Very late appearance of light cells

Exceptionally, in certain stages of development, in some of these ganglia (given below), the number of cells are reduced instead of a continuous increase, indicating probably the presence of an active phagocytic process which would remove the inactive or dead cells (so-called light cells) during developmental period. However, the light-cell stage is not represented in them probably because the phagocytosis is so active and so-fast to leave this light-cell stage for clear observation. These developmental stages probably represent some critical periods (in that particular ganglion) in their attempt to establish functional projection to their innervation fields. It may be noticed that most of these periods of cellular loss are just before the occurrence of light cells in the ganglion.

Geniculate ganglion:	E10
Prox. G. Comp. of N. IX and X:	E10
Superior cervical ganglion:	E13

2. As soon as the light cells have appeared in the ganglion, the total cells have reduced in number representing a loss of cells which, in turn, suggests that these light cells play a role in the loss or reduction of cells in the ganglion, or in other words, these light cells might represent a group of resting, inactive, dying, dead or degenerating cells which will, in course of time, be removed from the ganglion by phagocytes. It may be noticed that the loss or reduction in the total number of cells in the ganglion is occurring around the time when the light cells make their first appearance.

Trigeminal ganglion:	E10, the very few (78 cells) negligible number of light cells ound on E8 probably have formed justthen, which is the beginning of cell death where the total cells, however, are greater in number.
Geniculate ganglion:	E15, the few (512 cells) light cells found on E13 probably is the beginning of an observable cell death. The cell loss found on E10 is explained in the Discussion; probably the removal is too fast so as not to observe the light-cell stage.
Vestibular ganglion:	E13
Acoustic ganglion:	E13
Prox. G. Comp. of N. IX and X:	E13
Petrous ganglion:	E10
Nodose ganglion:	Light cells are found even on E6; earlier stages are not observed in this ganglion.
Ciliary ganglion:	E13
Superior cervical ganglion:	A few (491 cells = 0.38 %) light cells have appeared only on E18, which is probably the beginning of the appearance of light cells, however, on the day of hatching a gross reduction in the total number of cells having an increased number of light cells is found. However, in the earlier stages of cell loss (E13) light cells are not found.

3. On E18, there is usually a greatly reduced number of light cells (compared to E15) in relation to the tremendously increased number of dark cells (predominantly smaller categories), most of which are probably phagocytes (please refer to Part C : Removal of Dead Cells in the end) (also assumed from the present results found on the day of hatching where there is a great loss in the total number of cells in the ganglion). It is possikåe that the phagocytic activity is so great and so-fast that the light cell stage is not always observable since most of these inactive cells are actively removed from the vicinity of the ganglion before they become observable. This is a constant feature in all the ganglia in order to free the tissue from the noxious effects of the remnants of dead cells before the delicate and young animal is exposed to an independent living on the day of hatching.

This is true in all the ganglia studied except a small difference observed in the superior cervical ganglion where the light cells have appeared for the first time only on E18.

4.a. But on the day of hatching, there is usually a greater proportion of light cells in the ganglion while there is a greatly reduced total number of cells because most of the unwanted cells have been removed by the greatly increased phagocytic activity found around E18. During post-hatching period, the light cells are greater in

number. Probably, most of these light cells are in a temporary resting or inactive stage; many of them might become active functional cells again. It is also assumed that a proportion of the smaller categories of dark cells might represent the continued presence of phagocytes, ready to remove the inactive or dead cells.

This is true in all the ganglia studied except Geniculate ganglion where some differences are found. That is, here in the geniculate ganglion greatest number of light cells are found on E15; later the light cells reduced in number throughout embryonic development, on the day of hatching as well as in the adult situation.

b. The tiny cells are found to be always dark. The very small type of cells are also found to be dark through the whole embryonic period till E18. Later, however, the light cells have appeared among the very small type also on the day of hatching, but they may or may not continue to be present in the adult situation. This might imply that even though the very small type of cells appear to keep themselves to be an active group till the day of hatching, and be ready to replace the dead cells occurring as a result of several adverse factors, cell death and degeneration begin among these cells also as from the day of hatching. It may be assumed that normally there cannot be any more necessity for the establishment of new functional projections after the day of hatching since all these connections might have been already established by this time while the animal is ready to lead an independent living. Therefore, there is no need for further growth and maturation of this smaller category of cells and the cell death begins even among this very small type of cells as from the day of hatching. Thus the appearance of light cells among this group just on the day of hatching is suggestive of evident cellular inactivity, death and degeneration process.

Trigeminal ganglion:	True : Continue to be present in the adult
Geniculate ganglion:	True : Disappear in the adult
Vestibular ganglion:	True : Disappear in the adult
Acoustic ganglion:	True : Continue to be present in the adult
Prox. G. Comp of IX and X:	True : Continue to be present in the adult
Petrous ganglion:	True : Continue to be present in the adult
Nodose ganglion:	True : Disappear in the adult
Ciliary ganglion:	True : Disappear in the adult
Superior cervical ganglion :	True : Continue to be present in the adult

5. Even the larger classes of cells (having a diameter greater than 30 microns) whenever they have appeared in the ganglion contain both dark as well as light cells. (However, the dark and light cells are also found among smaller classes as well). This contradicts the descriptions of many earlier workers (26, 27, 28) that the ganglion contains small dark cells and large light cells and also contradicts their attribution of different functions to these cells because, in the present study the dark and light cells are found distributed among all categories whose diameter is greater than 10 microns irrespective of their small or large size. Therefore, such classification and functional attribution are disputed.

Trigeminal ganglion:	E13, E18, on the day of hatching and adult; on E15 these larger classes of cells have totally disappeared
Geniculate ganglion:	E13 and adult; on E15 and E18 the larger classes of cells have totally disappeared; on the day of hatching only dark cells are found.
Vestibular ganglion:	On the day of hatching and adult when these larger classes of cells have appeared.
Acoustic ganglion:	Such large class of cells has never appeared in the ganglion
Prox. G. Comp. of IX and X:	E15, day of hatching and adult when the larger classes of cells have appeared. On E18 these larger classes have totally disappeared
Petrous ganglion:	Such large class of cells has never appeared
Nodose ganglion:	E13, E15, day of hatching and adult when these larger classes of cells have appeared. On E18 only dark cells are found among them.
Ciliary ganglion:	In the adult, only when these larger classes of cells have appeared
Superior cervical ganglion:	Such large class of cells has never appeared

6. The light cells continue to be present in the ganglion even in the adult situation while the total number of cells also continue to reduce. This is probably due to cellular inactivity and death as a result of ageing process while the functional reduction or functional loss is found in all organs including the organs of special sensibility and nervous control. This factor is uniformly noticed in all the ganglia studied.

7. The number of light cells lost in the ganglion is almost equal to the loss in the total number of cells, at a stage

while the proliferation has stopped or reduced as evidenced by the number of tiny cells. Even though such condition is observed in a few instances in the whole investigation, this cannot be neglected as invalid because such incidence or circumstance cannot be expected to occur frequently in a constantly changing life cycle in the ontogeny, when such a change has to coincide with the time of observation.

Petrous ganglion: and Superiorcervical ganglion:	Compare the results on the day of hatching and the and adult situation, at a time while the tiny cells are almost equal in number which indicates the stoppage of proliferative activity.

8. In the early stages of development, only dark cells are found in all the ganglia studied in the present series of investigation indicating that these are active cells. The light cells appear only after certain period of embryonic growth, probably at a time when the cells fail to establish proper functional projection onto their innervation fields. For example, in the present study, the structural evidence of the occurrence of light cells in the trigeminal ganglion on E8 seems to coincide with the appearance of physiological evidence occurring on the same embryonic day (E8) of exhibiting reflexogenic response to tactile stimulus of the beak of the chick embryo (29). Similarly there are suggestions (22,26) that the placode-derived neurones in the trigeminal ganglion have well-established peripheral projections by the end of the first week of incubation. In contrast, the neurones derived from the neural crest in the trigeminal ganglion (30, 31) do not cease dividing until the seventh day of incubation. It may be recalled that the process-formation of neurones begins after the terminal mitosis which is considered as neurone's birth date (31). Even though there is a slight variation in these suggestions given by different workers, it may be assumed that such degeneration is quite likely to happen around the seventh day of incubation. Thus the coincidence of appearance of light cells in the trigeminal ganglion in the present study indicating cell death on their failure to form proper connections suits very well with all these descriptions. However, similar physiological observations and reports for other ganglia are not available in the literature in order to make a comparison with the results in other ganglia studied in the present series of investigation.

9. It may also noticed that the light cells appear in the ganglion for the first time usually among small and medium sized cells (having a diameter of 11 - 20 microns) and later once they grow into larger classes, the light cells continue to be present among them. This is suggestive that the establishment of functional projection begins during this stage and that once they are unable to make functional connections, these cells become inactive or die and change into light coloured cells on staining. Such light cells may represent cellular inactivity or death. The light cells among larger classes may also represent cellular inactivity or death during successive growth periods, before establishing functional connections which may be due to any defect, either within the cell, in the micro-environment, inadequate supply of nerve growth factor (neurotrophic factor), or to ageing process in the case of adult.

10. However, it may be thought that the period of active cell loss (death) coincides with the period of active establishment of functional connections and in the present study, this period varies from ganglion to ganglion. This may be judged by the time of occurrence of light cells for the first time in the ganglion. However, this active establishment of functional connections may extend for longer periods as indicated by greater cellular loss in other stages. The following stages show the time of first appearance of light cells in the ganglion.

Trigeminal ganglion:	E8
Geniculate ganglion:	E13
Vestibular ganglion:	E6, even though light cells are missing on E8 and E10
Acoustic ganglion:	E13
Prox. G. Comp. of N. IX and X:	E13
Petrous ganglion:	E10
Nodose ganglion:	E6, early and frank appearance of light cells
Ciliary ganglion:	E13
Superior cervical ganglion:	E18

The descriptions of the dark and light neurones by different investigators in different animals vary greatly in available literature. Some of these conflicting views from the literature which are considered more useful are described below. Some investigators (9, 26) have described in the trigeminal ganglion of the chick that the large neurones contain many isolated clumps of basophilic material in a neurofilament-rich cytoplasmic matrix having a diameter ranging from 19 - 40 microns and that the smaller neurones having a diameter ranging from 11 - 30 microns tend to be multipolar and have a greater concentration of ribosomes and granular endoplasmic reticulum which are dispersed through a dense matrix. Based on their staining properties, these larger ones are called light neurones and the smaller ones are called dark neurones. In the adult rats, trigeminal neurones have been classified into dark and light types on the basis of distribution of cytoplasmic organelles within the neurones and on the relative density of cytoplasm (7, 12, 24). In a comparative ultra-

structural study of the trigeminal ganglion (8) small dark cells were densely packed with rough endoplasmic reticulum and ribosomes, and large light cells with a dispersed and occasionally clumped ergastoplasm. It may be noticed that the classification (9, 26) of dark (small) and light (large) neurones overlap in size. However, all the above investigators have found that the dark (smaller) neurones have a greater concentration of ribosomes and granular endoplasmic reticulum, which is suggestive of a more active role than that of their lighter (larger) counterparts. This observation also supports the present results that the dark cells represent a group of active cells and the light cells represent a group of resting, inactive, dying, dead or degenerating cells.

However, in subsequent reports on human autopsied trigeminal ganglia, it was not easy for these workers (25) to readily identify dark and light neurones. The majority of cells were intermediate in appearance. On rare occasions when they did observe these two neuronal types, the cells differed only in their cytoplasmic density and not in the arrangement of any of their organelles. These observations led these investigators to conclude that the dark and light cells were not real entities, but resulted from fluid-shifts between the cells in question and the surrounding extra-cellular spaces. By the same token, other investigators (32, 33) working with cat and monkey trigeminal ganglia found that if proper tissue fixation techniques were used, there were no base for classifying the trigeminal neurones into dark and light cell types. It is possible that these conflicting reports given by different investigators may be attributed to the species difference of the experimental animals used.

There has been suggestions(26) that shortly before hatching (E18 onwards), there appears two classes of interposed neurones characteristic of the mature trigeminal ganglion : large light types and small dark type. Neither of these two populations corresponds uniquely to either of the two segregated populations (large peripherally and distally located cells, and small centrally and proximally located groups) found in the embryo. In the present study in the chick, the dual cytology of neurones (dark and light cells) is found in all the ganglia studied. They were observed not only in the mature ganglia (from 18th day of incubation to adult) as stated by earlier investigators (9, 26, 27, 30, 34, 36), but also in earlier developmental stages (please refer to the results). It is not clear whether the above workers failed to observe these classes of cells in earlier developmental stages because of unreliable staining techniques or whether they did not attempt to investigate their presence during early embryonic periods. It is also noticed in the present investigation that in the early stages of development, only dark cells are found in all the ganglia. The light cells begin to appear only after certain period of embryonic growth which varies from ganglion to ganglion : probably the time of their occurrence coincides with their failure to establish proper functional projection to their innervation fields. For example, in the present study in the trigeminal ganglion, the light cells have appeared for the first time on E8 which seems to coincide with the day (E8) of establishment of functional connections as observed on the basis of the presence of reflexogenic responses to tactile stimulus of the beak (29).

It is frequently suggested (18, 26, 27, 30, 31, 37, 38) that the large light and small dark neurones found in the trigeminal ganglion are correlated with the dual embryonic origin as derived from both the epidermal placode and neural crest. Through most of the second week of development the large cells are found in the distal and ventro-lateral parts of the ganglion and the small cells are found in the proximal (core) and medio-dorsal parts (39, 40). Even though the present study is not aimed at finding out the embryological origin of these two categories of cells, the segregation of large cells in the distal and ventro-lateral parts and the small cells in the proximal (core) and medio-dorsal parts of the ganglion is evident from the present results similar to these findings.

Also there is both circumstantial and direct evidence that cytological dichotomy in the adult ganglion is not based on separate embryological origin. First, other sensory ganglia that are exclusively of neural crest origin such as trunk dorsal root ganglia, or of placodal origin such as acoustic ganglion have both dark and light types of neurones in the present study. Similar view has been advocated by previous investigators (41, 42) also. In addition, the light and dark neurones are found interspersed at random throughout the ganglion during embryonic development and post-hatching periods in the present study, whereas the segregation of crest and placode-derived neurones (small dark and large light cells respectively) are found only in the embryo. Both transplantation experiments (27) and birth-date analysis (31) have proved that neurones from each of these anlagen retain their original separate locations during later stages of development and maturation. Thus the dual cytology of the mature trigeminal ganglion is not based on separate embryonic origins.

Since there is no clear evidence of trigeminal neuron projection to the solitary nuclear complex which normally receives only visceral input (43, 44, 45), there should be no visceral neurones in the trigeminal ganglion. The work on trigeminal ganglion (28) have demonstrated that the trigeminal ganglion had the smallest proportion of dark cells (46.8 %) whereas in the proximal ganglionic complex of the cranial nerves IX and X and the distal ganglion of cranial nerve IX the proportion of the dark cells was much greater (84.7 % and 70.3 % respectively).

Since these two ganglia have both somatic and visceral neurones (46) the large proportion of small dark cells suggests that at least some of the dark cells are visceral neurones. In a work on spinal ganglia (47), the visceral neurones had a tendency to be smaller than somatic neurones. If this is true, then the larger portion of dark cells in the proximal ganglionic complex of cranial nerves IX and X observed by the above workers suggests that this ganglion has more visceral neurones than the distal ganglion of cranial nerve IX. The specific functional attribution for the neurones, based only on size difference (small and large cells) or staining properties (dark and light cells) as suggested by the above-mentioned workers, however, could not be confirmed in the present study because of the following reasons : a) In the present investigation in the chick in the adult situation, even though the proportion of dark cells in the proximal ganglionic complex of cranial nerves IX and X (82.08 %) and that of the petrous ganglion of cranial nerve IX (62.5 %) are very close to the observations of the above mentioned workers in the same ganglia, the proportion of the dark cells found in the trigeminal ganglion (80.04 %) in the present study is quite different from that (46.8 %) observed by these investigators. This suggests that such proportion of dark and light cells in the ganglion might not be a constant factor so as to generalise their functional significance as has been suggested by them, or such changes could be due to species difference of the experimental animals as well. b) In the above-mentioned ganglia as well as in other ganglia studied in the present series of investigation, the proportion of dark and light cells shows a constant fluctuation through the whole ontogeny, i.e., during embryonic period, on the day of hatching as well as in the adult situation. Therefore, similar observation done at any one stage of the whole life cycle cannot prove valuable or give concrete evidence for such functional attribution for any cell. c) Again, this proportion of dark and light cells in the same ganglion is strikingly different in the adult situation even that observed on the day of hatching. The fluctuations in the number of these cells observed during development are considered as a necessary change for the establishment of a suitable functional organisation in the animal. However, similar suggestion cannot be attributed to an animal on the day of hatching, a stage while the animal is already prepared for an independent living (just as the adult animals themselves). d) In the adult situation, in all the ganglia studied in the present series of investigation, there is not only a change in the proportion of dark and light cells but also a great reduction in the total number of cells in the ganglion. Similar variation again confirms that such method of functional attribution of cells, that too found just on one stage of a long life-cycle, and just on the basis of their staining characteristics cannot be validated because this staining characteristics may change in different conditions such as change in pH and functional state of that particular cell. Thus, on analysing the results in the present series of investigation, it is assumed that the light cells represent a group of resting, inactive, dying, dead or degenerating cells and the dark cells represent a group of functionally active cells in the ganglion. It is also assumed that the time of appearance of light cells in the ganglion is directly related to the onset of establishment of functional connections whose importance is related to the organs which their fibres supply, for example, early appearance of light cells in the nodose ganglion is probably related to the functional importance of the vagus nerve which supplies the vital organs such as the heart, lungs and alimentary canal which should be properly innervated as early as possible.

It is also thought useful to quote the views of a few earlier investigators on Cell Death and Degeneration, and Removal of Dead Cells in order to complete the full evaluation of the dark and light cells. In this view, the following points are given for relevant reference.

B. *Cell Death and Degeneration*

One feature of development of many parts of the nervous system is the occurrence of two opposing processes : cellular proliferation which leads to the production of large numbers of neurones and massive cellular degeneration which results in the loss of many of these same neurones. These two processes ultimately control the final number of neurones of a neural centre. Even though no attempt was taken to investigate the purpose, reasons or ways of causing cell death which occur in different ganglia studied in the present series of investigation, the suggestions of some of the earlier investigators which are found suitable are given below in order to supplement the present assumption derived from a critical analysis of all these results. In the present study, cell death occurs mainly around E10 - E13 after which the ganglion prepares itself for a massive phagocytic activity which nearly comes to an end by the day of hatching. This resembles the descriptions (48) that there are corresponding and parallel changes in the brain stem auditory nuclei and their peripheral ganglionic projections.

The observations (48, 49, 50, 51) support the idea that it is the events in the target tissue (i.e., the periphery) which normally regulate cell survival. They demonstrated that the periphery both controls the proliferation and initial differentiation of undifferentiated cells and also provides the conditions necessary for continued growth and maintenance of neurones in stages following the first outgrowth of neurites. Several experiments (49, 52, 53, 54, 55, 56, 57, 58, 59) have led to a general acceptance of the idea that neuronal death regulates nerve cell numbers in response to peripheral demands by eliminating those nerve cells whose fibres

fail to establish proper peripheral connections. There are evidences (51, 53, 60) suggesting that events at the target tissue controlling normal cell-death, involve the notion of either a competition between neurones for a limited number of synaptic sites and / or for a limited amount of trophic substances supplied by the target. Failure of the neurones to either make or receive the appropriate synaptic connections has been attributed to most neuronal deaths during embryogenesis (51,61). It also seems more likely that the main function of cell death in this system is probably to remove redundant neurones which though being in the correct muscle, have failed to form a contact (62). According to this argument, the nervous system is programmed to over-produce cells in order to saturate the target and insure that all muscle fibers become innervated. The cell death presumably plays a role in the normal formation of orderly connections.

In some experiments (52, 60) in which it has been possible to experimentally enlarge the projection fields of the neuronal population, or to increase the number of afferents which it receives (a technique known to experimental neuro-embryologists as " peripheral over-loading or peripheral enlargement") the number of neurones found in the population at later stages of development has been significantly greater than normal. In contrast to these experiments, peripheral ablation experiments (48,57,58,60) have shown that the severity of the normal neuronal degeneration is much increased resulting in the additional cell death usually occurring over the same period as the naturally occurring neuronal loss. That is, natural cell death is known to be greatly enhanced by peripheral depletion.

From the available evidence, it is convincing to accept the idea that the peripheral influences, peripheral demands, trophic factors supplied by the target organs etc are important factors in controlling the neuronal death and the number of functional neurones available in the ganglia and that the neuronal death plays a role in the normal formation of orderly connections.

C. Removal of Dead Cells

Several investigators have suggested that macrophages are important in removing debris of dead cells (63). Different sources of these macrophages have been suggested. One possibility is the transformation of mononuclear leucocytes in the circulatory system into tissue macrophages (64, 65, 66, 67). It has also been demonstrated (68) many radioactively labelled mononuclear leukocytes can infiltrate into nervous system and aggregate around damaged nervous tissue. There is also electron-microscopic evidence that the leukocytes invade nervous system by crossing through the wall of the blood capillaries (69). It has also been demonstrated in an ultra-structural study (70) that the phagocytic cells contain neuronal debris that exhibit most of the characteristics of mononuclear leukocytes. The phagocytic activity of the satellite cells in the chick embryonic spinal ganglia are attributed to the removal of cellular debris of degenerated cell (71) during early development. There are also reports (72, 73) that phagocytosis is accomplished by glial cells. However, some investigators (74) believe that the degenerating cells produce hydrolytic enzymes for their own degeneration. Therefore, there is obvious reason to believe that the leukocytes from the blood stream can penetrate through the wall of the capillaries into the nervous system and function as tissue macrophages to remove the neuronal debris during cell death and that the glial and satellite cells also can act as phagocytes.

Acknowledgement

The author wishes to express his sincere and unlimited gratitude to Professor. Dr. Dubbeldam JL, University of Leiden, Netherlands for his continued generosity, guidance, co-operation and support throughout this study. His continued efforts and encouragement to make it as part of a thesis for the award of a DSc degree of Leiden University are greatly appreciated.

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