RELATIONSHIPS BETWEEN THE CAUDATE NUCLEUS AND
THE FRONTAL CORTEX IN MACACA MULATTA

By

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INTRODUCTION

One of the best defined experimental syndromes following cortical ablation is "the frontal lobe syndrome" in the Rhesus monkey. In this laboratory, French (1959 a and b) has recently investigated this syndrome with particular emphasis on the problem of localization. It was found that bilateral removal of Brodmann's area 9 was sufficient to cause a typical frontal lobe syndrome, consisting mainly of: (1) increased rate of locomotor activity, and (2) deficit in the so-called delayed-response test. Removal of area 6 does not produce this same clinical picture. The problem of localization of this syndrome is complicated by the fact that any cortical lesion causes secondary degeneration of neurons and fiber tracts which are associated with the damaged area. Thus the "frontal lobe syndrome" may not be solely attributable to the removal of a circumscribed cortical area, but a number of associated cortical and subcortical centers must be considered part of the substrate which is to be localized.

Among the most striking connections of the frontal lobes are the thalamo-cortical projections which emanate from the nucleus medialis dorsalis (Walker, 1940). Surprisingly, however, bilateral destruction of this nucleus (Chow, 1954; Peters et al, 1956) fails to produce a deficit equivalent or even faintly similar to the "frontal lobe syndrome". If correct, these observations would seem to indicate that connections other than the thalamo-frontal may have a significant role in the development of impaired function.

Connections with the caudate nucleus have become more prominent in the current discussion for these reasons: (1) The caudate nucleus has been unintentionally encroached upon by frontal lobe lesions in many

previous studies of the "frontal lobe syndrome" (Ruch and Shenkin, 1943; Richter and Hines, 1939; Davis, 1951). (2) Lesions restricted to the caudate nucleus (Rosvold et al., 1956) have been shown to cause a deficit similar to the ones caused by removal of frontal cortex alone. (3) There are claims in the literature concerning projections of the caudate nucleus upon the frontal cortex (Mettler et al., 1952).

This third argument seems to be rather crucial for an understanding of the "frontal lobe syndrome" and the present investigation was designed to further elucidate caudate-frontal relationships. Before describing the outline of our study, it is desirable to present a short survey of the present state of knowledge concerning fiber connections of the caudate nucleus.

FIBER CONNECTIONS OF THE CAUDATE NUCLEUS

The caudate nucleus together with the putamen forms the corpus striatum. It consists of a rather homogenous mass of small and large cells, the former being more numerous in a ratio of 20 to 1. The small cells, of Golgi II type, are said to be mainly receptive, i.e. the synaptic target of afferent connections. In contrast, the large neurons are considered "efferent", that is to say, cells which by virtue of their long axones carry the bulk of caudate information to distant areas.

Afferent connections:

(1) From the substantia nigra. This connection has been traced by retrograde and anterograde degeneration methods and the best study in this regard is by Rosegay (1944).

(2) From the thalamus. The existence of thalamo-striatal projections is a relatively old claim of classical neuroanatomy. Several nuclei, such as the anterior, the medialis dorsalis, and the centrum medianum, have been invoked by various authors. More recently Powell and Cowan (1956) have shown evidence in monkey, cat and rat that caudate lesions produce retrograde degeneration in the centralis lateralis, paracentralis, and centralis medialis. In view of the controversial situation, it seems safe to accept in a general way the existence of thalamic afferents and the intralaminar system as their tentative origin. Such a link with the diffuse thalamic system, if confirmed, would bring the caudate nucleus into direct connection with the brainstem reticular formation.

(3) From the cerebral cortex. Such connections have been observed by means of Wallerian degeneration techniques and strychnine-neuronography. There seems to be two pathways by which cortical impulses, particularly from the frontal areas, may reach the head of the caudate nucleus: (1)

collaterals of fibers descending in the internal capsule, and (2) the subcallosal bundle. It should be emphasized, however, that such connections—if they really exist—must be numerically of minor significance since a number of competent neuroanatomists (Wilson, 1914; Krieg, 1954; and Smythies et al., 1957) have been unable to confirm their existence. The issue is discussed by Kodama (1927) and by Mettler (1942). The following cortical-caudate pathways have been stated in the literature:

- (a) from area 9 (Mettler, 1935; Mettler, 1947)
- (b) from area 6 (Mettler, 1947)
- (c) from area 4s (Dusser de Barenne, 1938)
- (d) from area 2s, 3s, and 8s (Glees, 1945)
- (e) from gyrus preceus (Stratford, 1954)
- (f) from cingulate gyrus (Nauta, 1953)

In view of the above mentioned connections between the frontal lobes and the head of the caudate nucleus, one should mention the findings of Whitlock and Nauta (1956) regarding analogous relationships between the temporal lobe (middle and inferior gyrus) and the tail of the caudate nucleus.

Efferent connections:

(1) To the pallidum. This pathway has long been recognized in normal as well as experimental material. More recently Papez (1942) has discussed the pertinent findings.

(2) To the substantia nigra and subthalamic nucleus. Reports concerning these connections loom widely in clinical literature. Papez (1942) has also accepted their existence. However, a careful evaluation renders any subcortical connections, other than the pallidal, rather doubtful. In view of this, it seems safe to assume that the downstream effects of caudate excitation must undergo a pallidal synapse before reaching more

widespread areas of the brainstem.

(3) To the cerebral cortex. There are as many claims as denials regarding caudate-cortical projections. This somewhat controversial situation prompted us to reinvestigate the problem and further discussion of this point will be found in the subsequent paragraphs.

Figure 1. Schematic diagram of presently accepted fiber pathways of the caudate nucleus.

MATERIAL AND METHODS

The success of retrograde degeneration studies in tracing thalamo-cortical projections was mainly responsible for selecting the same technique for an analysis of caudate-cortical relationships. The main advantage of the Nissel method is its high degree of reliability. Cortical lesions can be made with optimal precision and the occurrence of retrograde cell changes in the caudate nucleus would be the most trustworthy indicator for the existence of fiber connections. The following paragraphs will give a detailed description of methodology.

Ten monkeys of the genus Macaca mulatta were used in this investigation. Four monkeys (nos. 249, 250, 258 and 260) had bilateral surgical ablation of area 6 (see figure 2). Four monkeys (nos. 247, 253, 254 and 262) had bilateral surgical ablation of area 9 (see figure 3). Seven of these monkeys survived for periods from 209 to 346 days. One (no. 247) was sacrificed at 73 days when he became severely ill. One monkey was normal (no. 256). One monkey, under aseptic conditions and by means of a series of ten operations over a two year period, was totally decorticated (no. 50-10) and had survived removal of frontal cortex by 30 days. When sacrificed the brains were perfused with formalin under deep nembutal anesthesia and then removed in toto. They were then dehydrated in alcohol, embedded in celloiden and sectioned coronally at a thickness of thirty micra. Every second section was saved and stained with thionin. Cortical lesions were reconstructed and reported by French (1959).

The optical system employed in taking cell counts consisted of a 20x objective and a 12.5x ocular equipped with a reticule, thus providing a magnification of 250x. For cell counts, all of the cells in a single square of the reticule were counted thus sampling a field measuring 1600 square micra. When considering the thickness of the section, samples were

Figure 2. Reconstruction of lesions of the cortical surface in animals of the area six group. The lines drawn from lower right to upper left indicate the region of the ablation in the left hemisphere. The lines drawn from lower left to upper right indicate the region of ablation in the right hemisphere. Zones of cross hatching show the approximate extent of bilateral lesions. In this figure there is no attempt to represent removal of cortex lying within sulci.

Figure 3. Reconstruction of lesions of the cortical surface in animals of the area nine group. The lines drawn from lower right to upper left indicate the region of the ablation in the left hemisphere. The lines drawn from lower left to upper right indicate the region of the lesion in the right hemisphere. Zones of cross hatching show the approximate extent of bilateral lesions. In this figure there is no attempt to represent removal of cortex lying within sulci.

taken from a block of tissue of 48,000 cubic micra. The caudate was studied from anterior to posterior at each of nine levels on coronal planes. Since the nucleus may extend more anteriorly in one hemisphere than in that of the opposite side, coronal sections through the brain would not necessarily cut through both nuclei at comparable levels. This difference in position was eliminated by taking as the first level in each nucleus the most anterior section in which the nucleus had clearly defined borders. The succeeding eight levels were chosen at intervals of 300 micra, or every tenth ensuing section. This procedure was followed on all brain material. In counting cells, a neuron was counted only if its nucleolus appeared within the field demarcated by the lines of the reticule. Both large and small cells were counted and no attempt was made to differentiate cell size. Glial cells were easily distinguished from nerve cells and were not included in the cell count. Following each count, the microscope was thrown out of focus and the slide moved to a different area of the nuclei under investigation. The microscope was refocused and the cells counted in that field. If a blood vessel made up a majority of the field focused upon, that field was eliminated and another sample taken (see figure 4).

Two different analyses were performed on this material.

Analysis I

An attempt was made to determine differences in cell counts in the caudate nucleus with respect to area 6 or 9. The caudate was taken as a whole except in respect to laterality. From the four animals with lesions of area 6, a total of fifty fields were counted from the caudate nucleus of each hemisphere at each level. The number of fields counted from any one animal having the ablation of area 6 was determined using tables of random numbers. The number of cells per field was tabulated in relation

Fig. 1a.

Coronal section (ref. to nr. 4 in Fig. 1b) of monkey brain showing midline structures and left striatum. Hatched = Head of caudate nucleus.

Fig. 1b.

Sanittal view of caudate nucleus, reconstructed from coronal sections. Vertical lines represent levels (1-9) at regular 0.3 mm intervals, from which cell counts were taken.

Fig. 1c.

Absence of any regional difference in cell population between animals with area 6 and area 9 lesions.

Fig. 1d.

The counting was done with a reticule of 40 μ total base length at a magnification of 250x. Fifty samples were taken at each level.

Figure 4. Method of Cell Counting

to hemisphere, level, and areal lesion involved. A similar procedure was followed on the animals having the ablation of area 9 and the values obtained were tabulated in a similar manner. Twenty-five fields were counted in each hemisphere at each level from both the decorticated animal and the normal animal. These data were also tabulated and used in graphs for comparison. The data thus obtained from these cell counts were subjected to an analysis of variance which compared the cell population between levels, areal lesion, hemisphere and all possible combinations of these factors in the animals with frontal lesions. The results obtained will be discussed later in this paper, but at present it can be stated that no significant differences in the factors could be found between area 6 and area 9 and between the right and left hemispheres.

In order to rule out the possibility that the investigator was not holding the criteria for a cell constant throughout the investigation, a reliability test was performed. This consisted of counting fifty different fields at two time intervals from an initial count and then analyzing for any significant differences in the values obtained. The time intervals chosen were one hour and twenty-four hours, for it was felt that (1) the examiner would be most likely to make an error after counting for one hour, and (2) he would be likely to make an error if counts were done over a two day period. Fifty counts were taken, the results tabulated, and the values obtained concealed from the examiner to prevent biased opinion on succeeding counts. One hour and twenty-four hours later similar counts were taken and the results tabulated in a similar manner. The values obtained were then analyzed by means of a chi square test.

Analysis II

An attempt was made to see if any focal differences, not demonstrated in analysis I, could be found in the cell population of the caudate nucleus. For this investigation the caudate nuclei of the animals with lesions of area 6 and 9 were further subdivided. The nucleus at each level was divided in dorsal lateral, dorsal medial, ventral lateral and ventral medial quadrants. (See fig. 4) This division into quadrants was accomplished by taking two consecutive coronal sections at each of the nine levels used previously in analysis I. This in effect, if hemisphere is disregarded, provides four cross-sectional samples of the caudate nucleus at each level. By random selection a different quadrant was outlined in opaque paint on each of the four cross-sections of the nucleus.

Use of the two hemispheres interchangeably is valid when considering that no significant differences could be found between hemispheres, as has been demonstrated in analysis I. That is, any conclusion drawn from the analysis of any specific quadrant in one hemisphere can be applied to the corresponding quadrant of the nucleus in the other hemisphere. The optical system, random choice of animals for counts, criteria of a cell, and technique of counting cells were all the same as previously described. However, instead of fifty counts from each hemisphere as in analysis I, twenty-five counts were obtained from each quadrant. The number of fields counted in any one animal was again determined by tables of random numbers. Data obtained were tabulated in respect to quadrant, level, and area of surgical lesion. In a similar manner to analysis I, an analysis of variance was applied to the data.

To determine the reproducibility of the results obtained, and as a check on the reliability of the investigator, an investigation was

performed identical to the one described above. All markings on the slides were removed and the material reorganized in the manner described for analysis II. Data were tabulated and analyzed as previously described.

RESULTS

Absence of cytological changes in the caudate nucleus

It was fairly obvious that by looking at the slides microscopically that the cells of the caudate nucleus appeared normal in size and population. There was no sign of cell atrophy, scar formation or phagocytosis in the head of the caudate nucleus of any animal with surgical ablation of either area 6 or 9 (see figure 5). In the animal which had total decortication the caudate nucleus was reduced in size and showed an increase in the cell population as compared to the normal animal and animals with lesions of area 6 and 9. The cells were also slightly smaller and darker staining, suggesting a slight degree of atrophy.

Cell population studies

Since no qualitative changes could be noted microscopically in the frontal animals, it was decided to study the nucleus caudatus quantitatively. This was done in two stages.

Analysis I

The head of the caudate nucleus was examined in both hemispheres to rule out the possibility of dominance of one hemisphere and to determine if changes could be found at any level through the caudate nucleus. Using an analysis of variance, no significant differences were noted at any of the nine levels and no difference could be demonstrated between the two hemispheres of the animals with lesions of area 6 and area 9, (level of confidence = 0.05). Graphs of the cell distribution in the animals with lesions and normals were essentially identical (figure 6). The decorticated animal showed a slightly larger amount of cells per unit area, thus confirming the impression obtained by mere investigation.

To rule out the possibility that the negative results were due to a variation in the investigator's criteria of a cell, a reliability test was run which demonstrated that the criteria of a cell was being held constant as well after one hour as twenty-four hours. Thus, the identity of findings between normal and operated animals can not be attributed to bias on the part of the examiner.

Analysis II

The assumption was made that the head of the caudate nucleus may not be homogenous throughout, but consisted of subdivisions similar to the thalamus, i.e. with differential projections to the cortex and subcortical areas. If this were true, only small foci in the caudate could be expected to react to removal of frontal cortex, and such focal changes could be easily overlooked in a global survey such as had been made in analysis I. The head of the caudate nucleus was therefore subdivided by a midsagittal and a midtransverse plane into four main fragments (see figure 4) which were then examined at each of the previous nine coronal levels, thus dividing the caudate nucleus into 36 small areas.

The cell density per unit area, as plotted in figure 5, showed similar distribution curves throughout these areas in frontal animals and the statistical analysis of the material (analysis of variance) made it clear that no significant differences existed.

100 X

ABLATION OF AREA 6

ABLATION OF AREA 9

NORMAL

200 X

Figure 5. Photographs of the head of the caudate nucleus showing absence of changes in cell population in the caudate nucleus following areal ablation of area six and nine of the frontal cortex in Macaca Mu latta.

There is no difference between normal animals and those with frontal lesions. (The counts of both area 6 and area 9 groups are added together in this analysis.)

This as well as the previous graph shows no difference between normal and frontal animals. The decorticated monkey has an increased cell population per unit area due to shrinkage of the caudate.

Regional differences of cell population were tested on the basis of this subdivision into 2 dorsal and 2 ventral sectors. Cell counts were taken separately from these sectors at each level.

This as well as the previous graph shows no difference between normal and frontal animals. The decorticated monkey has an increased cell population per unit area due to shrinkage of the caudate.

Figure 6. Cell Population Curves

DISCUSSION

Any evaluation of caudate-cortical relationship must begin with the findings in the decorticated preparation where any essential dependency of the caudate nucleus upon the cerebral cortex would inevitably be manifested by atrophic changes in the caudate nucleus. Previous investigators such as Holmes (1901) and Rothmann (1923), working on dogs, and von Monakow (1925), working in cats and rabbits, have found no alteration of the caudate nucleus in this condition. In our decorticated monkey there are some uncontestable changes. The volume of the caudate nucleus is noticeably reduced as compared to the volume of a normal control nucleus. On the other hand, there is no reduction, but rather an increase, in cell population per unit area. These findings can best be explained by the disappearance of fiber bundles of cortical origin or destination which traverse the interstitial spaces of the caudate nucleus prior to entering the internal capsule. The majority of such fibers apparently have no direct relation with the cells of the caudate nucleus although minimal cell atrophy of caudate neurons may be indicative of collateral nerve endings. Nevertheless, in agreement with the aforementioned authors, it can be stated that the caudate nucleus is essentially independent of cerebral cortex even if the existence of collateral linkage is admitted.

In view of this situation, it is not surprising that the main results of this investigation concerning the reactions in the caudate nucleus secondary to localized ablations of the frontal cortex were negative in character. Contrary to the positive findings in the nucleus medialis dorsalis thalami, there was no evidence of retrograde or any other type of atrophy of caudate cell bodies.

A similar study of caudate frontal lobe connections was made by Tankard and Harman (1955) in five monkeys with the following lesions: (1) all isocortex, (2) area 9, (3) area 9 and dorsal part of area 10, (4) areas 6, 8, 9 and 10, and (5) orbital surface.

These authors found statistically significant reductions of caudate neurons in animals 1, 4 and 5, which had in common the large size of the ablation and the removal of area 10. They concluded that "retrograde degeneration of caudate nucleus appears to be related exclusively to removal of the lower portion of Brodmann's area 10..... The orbital part.....is related to the rostral half of the caudate head, the lateral part to its caudal moiety." In other words, these authors obtained negative results in regard to area 9 and these are in agreement with our observations; they also have positive results concerning area 10 which we shall discuss in a moment.

To what extent are the negative findings final and conclusive? The absence of retrograde changes proves that there are no essential projections between the caudate nucleus and area 9. By this we mean there are no connections which are so important that the cell body ceases to exist after the interruption of its axon. Thus far, the only essential connection of the caudate nucleus which could be demonstrated satisfactorily is the one with the pallidum, illustrated in figure 1. On the other hand, the limitations of retrograde degeneration studies should be mentioned here. They are particularly important in cases where the lesion does not interrupt all or most of the connections of a cell. Under this condition the cell body undergoes little changes in structure and continues to function over the still viable paths. Connections of this kind are called sustaining by Rose and Woolsey (1959). Consider the

20 following three possibilities

Figure 7. Possible caudate cortical relationships. (A) Essential cortical projection determined by retrograde degeneration. (B) Sustaining cortical projections only shows retrograde degeneration if both areas of cortex removed simultaneously. (C) Sustaining cortical and subcortical projections which does not show retrograde degeneration if only cortex removed.

of caudate cortical relationship: (A) essential cortical projections, (B) sustaining cortical projections, and (C) sustaining cortical and subcortical projection (figure 7). Obviously, the technique utilized in this study was adequate to establish type A and B connections, the latter by using completely decorticated controls. However, retrograde studies would fail to detect any difference in type C connections unless both cortical and subcortical projection areas were destroyed simultaneously. Certainly, based on our present study, the existence of type C caudate projections could not be precluded and will remain the subject of future research.

The positive findings of Tankard and Harman (1955) regarding area 10 deserve some further comments. Unfortunately, they are based on a very small number of cases, each representing a different type of lesion. Also the authors fail to mention the presence of chromatolysis and gliosis and our own findings in the decorticated animal would render such findings doubtful. It seems therefore, that this caudato-orbitofrontal projection system as "statistically verified" by Tankard and Harman is in need of further support. Fortunately, Mettler and coworkers (1958) and Purpura (1958) were able to provide additional data. Electric shocks to the caudate nucleus are reported to produce evoked responses in area 10 of the Rhesus monkey and the short latency is suggestive of direct transmission. The criticism which seems to apply to this kind of experiment is that corticofugal or corticopetal fibers of passage may be responsible for these responses rather than genuine cells of the caudate nucleus. Certainly far more convincing electrophysiological work has to be presented before the caudate-cortical pathway can be accepted as a morphological reality. These critical considerations--far from being

complete--serve to underline the technical difficulties which one encounters in the study of central connections.

A final problem should be briefly mentioned. It was pointed out in the introduction that the caudate nucleus may be part of the neural circuit affected in the frontal lobe syndrome. Would the absence of direct connections between caudate and frontal cortex invalidate this hypothesis? This question leads into a new set of problems concerned with indirect caudate-cortical relationships which could well afford an explanation of complex behavior. Such an indirect pathway may involve one or more synapses in the pallidum and thalamus. It is also certain to require further experimental research.

SUMMARY

1. An investigation of caudate-cortical pathways was undertaken in conjunction with other anatomical studies on the problem of localization of the "frontal lobe syndrome" in the Rhesus monkey.
2. A review of caudate fiber connections establishes the paucity of trustworthy information and the controversial status of cortical relationships in particular.
3. Our studies of retrograde and other cell changes in the caudate nucleus were undertaken in two series of four Rhesus monkeys with histologically verified lesions in Brodmann's area 6 and 9 of frontal cortex. Furthermore, two animals, one completely decorticated and one normal, served as controls.
4. No evidence of retrograde degeneration, cell atrophy, scar formation or phagocytosis, could be found microscopically in the caudate nucleus of any animal.
5. Extensive cell counts at nine coronal levels of the caudate failed to show generalized or focal differences in density of cells in the test animals. No quantitative or qualitative changes suggesting caudate-cortical pathways could be demonstrated in any animal.

TABLES

TABLE I
SUMMARY OF DATA FROM ANALYSIS I

<u>SOURCE</u>	<u>df</u>	<u>ss</u>	<u>ms</u>	<u>F</u>
Plane (P)	7	37.2	5.3	1.55
Hemisphere (S)	1	0.3	0.3	0.008
Group (G)	1	0.2	0.2	0.005
P x S	7	17.1	2.4	0.07
P x G	7	47.1	6.7	1.97
G x S	1	1.6	1.6	0.5
P x G x S	7	33.1	4.7	1.38
Replication	1568	5307.5	3.4	
Total	1599	5444.1		

Legend: Plane (P) is the analysis of data in respect to the coronal level.

Hemisphere (S) is the analysis of data in respect to the right or left hemisphere.

Group (G) is the analysis of data comparing areas six and nine.

Analysis of the interactions of these factors is designated by the respective letters i.e. P x S is the analysis of the interaction of plane and hemisphere.

TABLE II
SUMMARY OF THE DATA FROM ANALYSIS II-A

<u>SOURCE</u>	<u>df</u>	<u>ss</u>	<u>ms</u>	<u>F</u>
Plane (P)	8	153.6	19.2	6.62
Width (W)	1	721.4	72.1	24.97
Height (H)	1	86.7	86.7	29.90
Group (G)	1	18.2	18.2	6.28
P x W	8	40.1	5.0	1.72
P x H	8	44.7	5.6	1.93
P x G	8	27.1	3.4	1.17
W x H	1	0.2	0.2	1
W x G	1	18.2	18.2	6.28
H x G	1	0.3	0.3	1
P x W x H	8	25.4	3.2	1.10
P x W x G	8	23.4	2.9	1.00
W x H x G	1	1.0	1.0	1
P x H x G	8	38.2	4.8	1.66
P x W x G x H	8	47.0	5.9	2.03
Replication	1728	5025.3	2.9	
Total	1799	5621.8		

Legend: Plane (P) is the analysis of data in respect to the coronal level.

Width (W) is the analysis of the data in respect to the medial and lateral parts of the nucleus.

Height (H) is the analysis of the data in respect to the dorsal and lateral parts of the nucleus.

Group (G) is the analysis of data comparing areas six and nine.

Analysis of the interactions of these factors is designated by the respective letters i.e. P x W is the analysis of the interaction of plane and width.

TABLE III

SUMMARY OF THE DATA FROM ANALYSIS II-B

<u>SOURCE</u>	<u>df</u>	<u>SS</u>	<u>MS</u>	<u>F</u>
Plane (P)	8	168.0	21.0	8.08
Width (W)	1	45.1	45.1	17.35
Height (H)	1	51.7	51.7	19.88
Group (G)	1	4.8	4.8	1.85
P x W	8	28.7	3.6	1.38
P x H	8	55.0	6.9	2.65
P x G	8	33.8	4.2	1.62
W x H	1	6.2	6.2	2.38
W x G	1	0.2	0.2	1
H x G	1	0.1	0.1	1
P x W x H	8	20.1	2.5	1
P x W x G	8	43.0	5.4	2.08
W x H x G	1	26.1	26.1	10.04
P x H x G	8	47.0	4.6	1.77
P x W x H x G	8	34.8	4.4	1.69
Replication	1728	4489.5	2.6	
Total	1799	5054.1		

Legend: Plane (P) is the analysis of data in respect to the coronal level.

Width (W) is the analysis of the data in respect to the medial or lateral parts of the nucleus.

Height (H) is the analysis of the data in respect to the dorsal or ventral parts of the nucleus.

Group (G) is the analysis of data comparing areas six and nine.

Analysis of the interactions of these factors is designated by the respective letters i.e. P x W is the analysis of the interaction of plane and width.

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