The Reticular Formation of the Brain Stem
Anatomical Aspects and Functional Correlations

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A. BRODAL

Oslo, June 1956

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The Reticular Formation of the Brain Stem Anatomical Aspects and Functional Correlations[1]

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Introduction

The relation between phrenology and the reticular formation of the brain stem may seem remote. Yet, questions of localization of functions to particular anatomical structures are important considerations to each of these subjects. While this statement will be willingly accepted as far as it concerns phrenology its relevance to the reticular formation will probably be questioned by many, since it is still usual to think of this part of the brain as an entirely diffuse aggregation of cells and fibres. One of the purposes of this account will be to show that this is not the case.

I would like to express my gratitude to the William Ramsay Henderson Trust and particularly to Professor G. J. Romanes, the Chairman of the trust, for providing this opportunity to review the present status of our knowledge of the anatomy of the reticular formation. Since there are still large gaps in this knowledge, any conclusions reached must of necessity be provisional. The value of attempting a survey of this kind at a time when new data are still being collected, may, in fact, be found more in the opportunity that such an enterprise offers to draw attention to questions still unsolved and to programmes for further research, than to enumerate the facts that have been actually established. From this point of view it is particularly desirable to evaluate the anatomical data in the light of the large amount of physiological information that has been brought forward in the last ten years. For structural features only become meaningful when considered in relation to function, and conversely, a complete understanding of any function requires a profound knowledge of the structures by which this function is mediated. Any attempt to correlate anatomical and physiological data meets with considerable difficulties

[1] The essence of this publication was presented as two lectures under the auspices of the William Ramsay Henderson Trust at the University of Edinburgh in May 1956.

and to a large extent the results must remain hypothetical. Since, however, science progresses by the development of working hypotheses it may still be useful to make assumptions and to put forward suggestions, even if future research may prove them to be false.

Before entering the difficult field of anatomical-physiological correlations, I shall, in the first part of my discussion, follow the safer road formed by the anatomical observations since these, on the whole, rest on fairly solid foundations. The anatomical data presented here are culled from many sources and include results obtained at the Anatomical Institute of the University of Oslo.

The Reticular Formation: Definitions

Nowadays the term "reticular formation of the brain stem" is commonly used in a very vague manner, and its connotation differs according to whether it is used by anatomists or by physiologists. Yet it should be made clear in any discussion to what the term refers.

It is appropriate to recall that the name "reticular formation" had its origin in anatomy before the turn of the century. The expression has generally been taken to comprise those areas of the brain stem which are characterized structurally by being made up of diffuse aggregations of cells of different types and sizes, separated by a wealth of fibres travelling in all directions. Circumscribed groups of cells, such as the red nucleus or the facial nucleus, formed of relatively closely packed units of a more or less uniform size and type, are not considered to be part of the reticular formation, which forms, so to speak, a sort of matrix in which the "specific" nuclei and the more conspicuous tracts, e.g. the medial longitudinal fasciculus, are embedded. According to this definition, the chief criterion for considering a cellular area to be part of the reticular formation is its structure, and from this point of view some fairly well circumscribed nuclei, such as the lateral reticular nucleus and the nucleus reticularis tegmenti pontis, rightly belong to it although they are usually omitted when the term reticular formation is taken in the sense used by physiologists. The situation is, however, less clear with regard to certain other cell groups. Some of these, in spite of their reticular structure, are given specific names and thus tend to be separated from the general mass termed the reticular formation, such for example is the nucleus of the raphe. In some instances it is a matter of taste whether a particular nuclear group is included in the reticular formation or not.

On account of this uncertainty Olszewski (1954) has suggested that the epithet "reticular" be omitted altogether, especially as a closer scrutiny reveals that the so-called reticular formation can be subdivided into a number of fairly circumscribed cellular areas which can be referred to as nuclei. It may also be objected that the various reticular nuclei are presumably functionally different

and for this reason should not be grouped together. However, so little is known at the present time of the functions of the various areas of the reticular formation that it would be premature to attempt a subdivision on a functional basis, and since there are many structural and presumably, therefore, also functional, similarities between the several "nuclei" of the reticular formation, it may still be useful to group them together in a common term. Whether the name of the particular nucleus has the affix "reticular" or not is of little importance. The term "reticular formation" when used in this account will be employed in the classical sense mentioned above, even though the phrase is not entirely satisfactory, and in the future it may be possible to devise a more adequate nomenclature.

Opinions differ as to the definition of the term "brain stem". In this account the term will be used in a macroscopic sense, i.e. as comprising the medulla oblongata, the pons and the mesencephalon. This seems justified also because it is uncertain whether the so-called reticular nuclei of the diencephalon are homologous to the reticular formation of the mesencephalon, pons and medulla.

Methods

Many methods may be used to study the anatomical organization of the reticular formation. On account of its peculiar structure certain of those difficulties, which are also met with in the study of other parts of the central nervous system, make themselves particularly felt when we attempt to unravel the detailed anatomy of the reticular formation.

The study of normal material furnishes the necessary basis for any experimental investigation whether its purpose is to clarify anatomical or physiological problems. A mapping of the reticular formation from a cytoarchitectonic point of view, i.e. a grouping of cells according to their type and distribution as they appear in Nissl-stained sections, is a first and essential step. Also in normal material the Golgi method may give valuable information concerning the form and arrangement of the processes of nerve cells, the variations of these in cells belonging to different groups, as well as demonstrating areas of termination of afferent fibres and revealing important points concerning synaptic relationships.

Without some knowledge of the connexions of the various cell groups of the reticular formation with other parts of the nervous system, the data obtained by the use of normal material remain of limited value. For reliable information on fibre connexions we have to turn to *experimental studies*. Thus the main course followed by afferent fibres may be brought out by the use of the *Marchi method*, which enables one to trace to the reticular formation fibres degenerating as a result of lesions in other parts of the brain (e.g. the cerebral cortex). While

several workers have followed myelinated fibres in this way, unmyelinated fibres escape recognition, and the actual terminations cannot be determined since the terminal portions of the fibres are unmyelinated. These difficulties can be overcome by the use of *silver impregnation methods*, such as those of Glees and Nauta (method of terminal degeneration). The latter method gives clear pictures of the course of degenerating fibres and some information on the mode of termination. The Glees method in our experience is particularly well suited to the demonstration of the terminal ramifications and the terminal boutons of degenerating fibres. In favourable cases it may demonstrate even the cells on which particular degenerating fibres terminate. However, in this respect the reticular formation is not very suitable since large as well as small boutons may be present normally on a single cell (Pl. I, Fig. 1*a*), a feature illustrated long ago by Cajal (his Fig. 436, vol. I). Also normal boutons may appear in many forms, as rings, as solid dots, and as boutons en passage (Pl. I, Fig. 1*b*). The extent of the variation between normal boutons is so great (at least in the cat) that it is difficult to recognize degenerating forms from the normal (Rossi and Brodal, 1956*a*). We are, therefore, left with the demonstration of degeneration in the finest terminal fibres (Pl. I, Figs. 1*d* and 1*e*) as the only reliable indication of the site of termination of degenerating afferents. While this is sufficient to establish the terminal area, details of the synaptic pattern escape recognition. In the lateral reticular nucleus the situation is somewhat better. Unequivocal signs of degeneration in terminal boutons (Pl. I, Figs. 3*a* and 3*b*) can be identified on the cell somata as well as on the cell processes (Brodal, 1949).

The efferent connexions from the reticular formation may also be studied with the Marchi method when lesions are made in the reticular formation. On account of the large number of fibre systems passing through this part of the brain, damage to which cannot be excluded, any conclusions from the study of lesions remain to some extent uncertain. A more reliable method which has been used by some authors is to identify *retrograde changes* in the cells of the reticular formation following interruption of its efferent fibres. One may study either the *acute changes*, occurring in the course of a few days, or one may wait for the *later disintegration* of the affected cells and record the cell loss. The difficulties encountered vary in the two methods. With short survival times it is not easy to distinguish cells showing slight changes from the normal, since the latter may show considerable variations, particularly with respect to their content of Nissl-material. In the past these minor variations frequently appear to have been considered as pathological. When the late changes are studied there is no great difficulty in evaluating even a moderate cell loss if it occurs unilaterally. When it is bilateral the situation is different, since comparisons with normal controls are of limited value unless the cell loss is very marked.

In our own studies we have employed the *modified Gudden method*, described previously (Brodal, 1939, 1940*a*). By operating on very young animals (cats 8-14 days old or somewhat more) and killing them after 5-10 days, one takes advantage of the fact that the nerve cells in such animals are much more susceptible to axonal injury than those in the adult. Cells whose axons have been cut usually display a characteristic histological picture a few days after the injury, and disintegrate some days subsequently. Consequently the area affected may be entirely free from cells after a few days, if all its cells project to or through the region which has been destroyed. For example, massive degeneration of cells occurs in the inferior olive following ablation of the cerebellum (Brodal, 1940*b*). In adult animals one does not see this rapid disintegration but after some weeks there is only a partial cell loss, the remaining cells being atrophic (Brodal, 1939). It appears from our studies on the reticular formation, to be presented below, that its cells react to injury of their axons in the manner described above.[1]

A complete loss of cells of this type has been observed in certain areas of the lateral reticular nucleus of young kittens and rabbits (Pl. III, Fig. 6, Brodal, 1943). In other parts of the reticular formation that have been studied so far, a complete loss of cells does not occur since adjacent neurons send their fibres to different terminal stations. In these cases we have, therefore, used short survival times to establish the presence of acute retrograde cellular changes as, for example, in the study of the long ascending and descending fibres taking origin from the reticular formation. In order to avoid interpreting normal but slightly tigrolytic cells as pathological, we have recorded only cells presenting the fully developed picture of retrograde changes: tigrolysis, peripheral displacement of the nucleus usually combined with flattening and some degree of swelling of the perikaryon. Such changes can be seen in young animals in all types of cells of the reticular formation. Figures 9 (Pl. IV) and 10 *e-h* (Pl. V) show representative examples.

It is obvious that by using this strict criterion only minimal values are obtained, but on the other hand, the risk of attributing the origin of interrupted fibres incorrectly to areas from which they do not arise is avoided.[2] There is

[1] Becker (1952) claims that the atrophic cells seen in the olive of the adult cat following cerebellar lesions are actually not affected by axonal retrograde changes, but are to be considered as affected by transneuronal changes. According to this author the complete loss of cells in the olive found in very young animals is due to the young cells being more susceptible to deprivation of their afferents. Quite apart from the fact that cerebello-olivary fibres, whose existence is a prerequisite for the appearance of transneuronal changes in the olive after cerebellar lesions, have never been demonstrated (see Brodal, 1954; Walberg, 1956), Torvik (1956*a*) has shown that the disintegration of olivary cells following interruption of (descending) afferents in young animals takes place in an entirely different manner from the retrograde changes. If the likely assumption is made that the situation is similar in the reticular formation, then we feel that the retrograde changes which we have observed are actually due to the interruption of efferent fibres.

[2] A problem of some relevance to studies of this type is whether transection of an axon has to take place proximal to the first collateral in order to produce retrograde changes. In newborn

little doubt that, in the reticular formation the study of retrograde changes is the only reliable method for the determination of the origin of efferent fibres and the Marchi method is of limited value for this purpose. If we are to make the pattern of organization within the reticular formation manifest, an exact knowledge of the sites of origin of efferent and the termination of afferent fibres is of primary importance. But information of this kind by itself is not sufficient to clarify structural organization.

Data obtained by the experimental methods that have been described give the main pathways, the high-roads so to speak, of the reticular formation. They tell us very little about what may be called the intrinsic organization, the smaller roads, the innumerable circuitous paths and tracks which are available for the passage of nervous impulses. The presence of intercalated or "association" cells of various types, the direction and pattern of distribution of dendrites from cells and collaterals from their axons, imply an amazing complexity of potential paths for nervous impulses. Yet, we are not justified in assuming that we are here dealing with an arrangement so disordered that it is hopeless to attempt a more complete analysis. Data that will be mentioned later make it appear that the cells are indeed arranged according to a definite plan. At the present time these problems can only be studied by the classical Golgi method.

The difficulties to be met with in using the Golgi method are well known. With any modification of the method it is purely a matter of chance which elements are impregnated, and one can never be sure that those visible are completely impregnated and show all their processes. As a consequence a large amount of material is always needed, and very many sections have to be prepared. It is also frequently difficult to decide exactly which area is being studied since borders between nuclei and cell groups may be indistinct. This difficulty makes itself particularly felt in an area like the reticular formation. However, if we are to obtain really useful and detailed information and are not content with sweeping generalizations which, as we have learnt from the history of natural science, are apt to be misleading, it is essential to take into account the topographical features when making Golgi studies of the reticular formation. The recent Golgi studies of the Scheibels, that will be considered later, make it clear that valuable information can be obtained in this way. Even if studies of this kind are laborious and extremely time-consuming, there is little doubt that they will prove of the utmost value for our understanding of the reticular formation, not least for the interpretation of electrophysiological observations. On the other hand, the problems of dendritic potentials and related questions

animals this does not seem necessarily to be true. Indeed, it appears that the transection of one of the branches of a bifurcating axon may suffice to produce such changes. This conclusion is drawn from observations on the efferent fibres from the red nucleus (Brodal and Gogstad, 1954) as well as findings made in the reticular formation to be dealt with below (Brodal and Rossi, 1955; Torvik and Brodal, 1957).

that are attracting lively interest at present among neurophysiologists, when solved and considered in connexion with the outcome of Golgi studies, may furnish valuable information.

On the borders of anatomy are fields whose cultivation may also be fruitful for the understanding of the reticular formation. So far relatively little is known of possible differences in *chemical transmitters* among the nerve cells in the central nervous system. Yet, it is conceivable that there may be variations of this kind among the cells of the reticular formation which are of importance in their function. Studies along this line may again be rewarding in spite of the great technical difficulties. It is also conceivable that there may be differences among cells of the reticular formation with regard to their *enzymatic equipment*, differences similar to those which have been found recently among cells in the cerebellum by Robins and his collaborators (Robins and Smith, 1953; Robins, Smith and Yen, 1956). Finer structural differences between types of cells may be revealed by the *electron microscope*, although here again the problem of identifying the structures observed with the familiar patterns known from the light microscope is frequently a major one.

Anatomy

The early anatomists paid relatively little attention to the reticular formation and it was only after physiological demonstrations during the last 10 years had shown the reticular formation to be a very complex part of the brain that renewed interest was directed to studies of its structure. There is, consequently, little cause for wonder that our knowledge of its structural organization is still far from complete though new data are steadily forthcoming. It is not possible, and would not be feasible, to present here all these data in their full complexity, so in this account I shall deal chiefly with those aspects which appear to be most important, and shall include some of the results of work carried out in the Anatomical Institute in Oslo. An attempt will be made to arrive at some conclusions concerning the major features in the organization of the reticular formation and to answer some of the many questions which arise in connexion with a study of this complex. Most of these questions are subordinate to the overriding question: Has the reticular formation a completely diffuse structural organization? From reading most of the physiological papers the impression is gained that the authors think of the reticular formation as a sort of entity, a diffuse structure. Although some qualifications are made implicitly, to the effect that certain areas are more closely related to certain functions, physiologists have on the whole been little concerned with the structural basis of the phenomena they have observed. Yet, almost every piece of anatomical information brought forward in recent years tends to show that the reticular formation is not only complexly built, but that regions of it differ considerably

with regard to their structural organization. If this be so, it is a fact of the greatest importance for the understanding of the functional organization of the reticular formation.

1. Cytoarchitectonics

While some previous authors have outlined certain cellular groups of the reticular formation and have given them specific names (see e.g. Kappers, Huber and Crosby, 1936; Pitts, 1940; Jacobsohn, 1909, and Gagel and Bodechtel, 1930, in man), the first systematic attempt at mapping the entire reticular formation has been made in recent years by Olszewski and his collaborators (Meessen and Olszewski, 1949, rabbit; Olszewski and Baxter, 1954, and Olszewski, 1954, man). On the basis of serial Nissl-stained sections the reticular formation has been subdivided into a series of more or less circumscribed cell groups, referred to as nuclei. Some of them undoubtedly correspond more or less completely to groups described by earlier workers, but differently labelled. Unfortunately no correlations are made with older descriptions but as the chief aim of these recent studies is to provide a frame of topographical references for studies on the reticular formation, no great harm is done.

The very fact that it is possible to undertake a subdivision of the reticular formation into a number of particular cell groups forms a strong argument against the assumption that functionally the reticular formation is diffusely organized. This holds true, even if some of the boundaries shown are, and of necessity will have to be, rather arbitrary. The photomicrographs from Olszewski's and Baxter's atlas on the human brain stem, for example, show that while some borders stand out very clearly, there are others which seem to be less convincing. To what extent the subdivisions distinguished are significant will have to be decided from correlations with studies based on other methods.

According to Olszewski (1954), familiarity with the structural subdivision of the reticular formation in any of the four mammals, rabbit, cat, monkey or man makes it simple to recognize the corresponding cell groups in any of the others. Although this is probably true as far as the more conspicuous groups are concerned, there is nevertheless reason to assume that there may be certain species differences with regard to the degree of development of individual groups or even that certain groups may be present in some species and absent in others.[1] Thus to mention one feature only which has been frequently commented upon, the giant cells which are so prominent in the reticular formation of the cat and rabbit are far less conspicuous in man. We are, however,

[1] It is interesting to note in this connexion that some of the names of cellular groups used by Meessen and Olszewski (1949) in the rabbit are not found in Olszewski and Baxter's (1954) atlas of the human brain stem. Instead a certain number of new names for reticular nuclei are introduced, presumably in order not to suggest, prematurely, homologies between cell groups in rabbit and man.

still waiting for the anatomist who has sufficient patience and endurance to undertake a comparative cytoarchitectonic mapping of the reticular formation in the mammalian series. That an investigation of this type may reveal quite considerable species differences seems not unlikely in view of the wide variations which Walberg (1952) found to exist even for one particular group, the lateral reticular nucleus.

There is no need to give any lengthy description of the subdivision of the reticular formation from a cytoarchitectonic point of view. It will be sufficient to mention a few points, which are relevant to the following account. The data given (see Text-fig. 1) refer particularly to the cat which has formed the subject for most of the experimental work that will be discussed.

Only the more conspicuous reticular groups are indicated in Text-fig. 1 and most of the minor subdivisions of Olszewski and his collaborators are neglected. Since detailed accounts of the cytoarchitecture of the nucleus reticularis lateralis and of the nucleus reticularis tegmenti pontis have been published elsewhere (Brodal, 1943; Walberg, 1952; and Brodal and Jansen, 1946, respectively) these nuclei are shown in outline only in the diagram, but appear in more detail in Text-figs. 2 and 4.

The *lateral reticular nucleus* (N.r.l. in Text-fig. 1) or the nucleus of the lateral funiculus[1] is situated lateral and inferior to the inferior olive. Dorsally it fuses with the remainder of the reticular formation, but it is fairly well circumscribed otherwise. There are three types of cells present and according to the grouping of these, three, or in some species only two, subdivisions may be distinguished (Brodal, 1943; Walberg, 1952).

The *nucleus reticularis tegmenti pontis of Bechterew* (N.r.t. in Text-fig. 1) is topographically closely related to the pontine nuclei proper and is situated immediately dorsal to them. It is characterized by a reticular structure and a high proportion of large multipolar cells (see Brodal and Jansen, 1946).

The *paramedian reticular nucleus* is a small group of cells, large, medium sized and small, situated near the midline, dorsal to the inferior olive. It was only recognized as a separate nucleus on the basis of its cell loss following decerebellations (Brodal, 1953*a*). It may be subdivided into three smaller groups, a dorsal, a ventral and an accessory group (d, v and a in Text-fig. 1).

The *nucleus reticularis gigantocellularis* (R.gc. in Text-fig. 1) in the rabbit and cat occupies approximately the medial two-thirds of the entire reticular formation lying dorsal to the rostral half of the olive and extending cranially to the level of the facial nucleus. In addition to its content of giant cells, responsible for its name, it contains large, medium sized and small cells. Its

[1] This term is used in the sense employed here by several authors. It is unfortunate, therefore, that Olszewski and his collaborators use the same name for another part of the reticular formation (R.l. in Text-fig. 1).

Abbreviations employed in Text-figs. 1, 5-11, 13, 14 and 17

a: Accessory group of paramedian reticular nucleus.
Br.c.: Superior cerebellar peduncle. (Brachium conjunctivum.)
Br.p.: Middle cerebellar peduncle. (Brachium pontis.)
C.i.: Inferior colliculus.
Coe.: Nucleus coeruleus.
C.r.: Inferior cerebellar peduncle. (Restiform body.)
C.s.: Superior colliculus.
d: Dorsal group of paramedian reticular nucleus.
Dec.br.conj.: Decussation of superior cerebellar peduncle (brachium conjunctivum).
F.l.m.: Medial longitudinal fasciculus.
h: Region poor in cells (Meessen and Olszewski) surrounding the motor trigeminal nucleus.
k: Cell group "k" of Meessen and Olszewski.
L.: left.
m: Cell group "m" of Meessen and Olszewski.
N.c.: Cochlear nuclei.
N.c.e.: External (accessory) cuneate nucleus.
N.c.t.: Nucleus of corpus trapezoideum.
N.d.: Dentate nucleus.
N.f.: Fastigial nucleus.
N.f.c.: Nucleus cuneatus.
N.f.g.: Nucleus gracilis.
N.ic.: Nucleus intercalatus.
N.in.: Nucleus interpositus.
N.i.p.: Nucleus interpeduncularis.
N.l.l.: Nuclei of lateral lemniscus.
N.m.X.: Dorsal motor (parasympathetic) nucleus of vagus.
N.mes.V.: Mesencephalic trigeminal nucleus.
N.n.V.: Sensory trigeminal nuclei.
N.r.: Red nucleus.
N.r.l.: Lateral reticular nucleus (nucleus of lateral funiculus).
N.r.p.: Nucleus reticularis paramedianus.
N.r.t.: Nucleus reticularis tegmenti pontis.
N.t.d.: Dorsal tegmental nucleus.
N.tr.sp.V.: Spinal nucleus of trigeminal nerve.
N.t.v.: Ventral tegmental nucleus.
N. III, V, VI, VII, X, XII: Root fibres of cranial nerves.
Ol.i.: Inferior olive.
Ol.s.: Superior olive.
P.: Pontine nuclei.
p.Br.: Nucleus parabrachialis.
P.c.: Basis Pedunculi (Crus Cerebri).
P.g.: Periaqueductal grey.
P.h.: Nucleus praepositus hypoglossi.
Py.: Pyramid.
R.: Right.
R.gc.: Nucleus reticularis gigantocellularis.
R.l.: Nucleus reticularis lateralis (Meessen and Olszewski).
R.mes.: Reticular formation of the mesencephalon.
R.n.: Nucleus of the raphe.
R.p.c.: Nucleus reticularis pontis caudalis.
R.pc.: Nucleus reticularis parvicellularis.
R.p.o.: Nucleus reticularis pontis oralis.
R.v.: Nucleus reticularis ventralis.
S.n.: Substantia nigra.
T.: Trapezoid body.
Tr.sp.V: Spinal tract of trigeminal nerve.
T.s.: Tractus solitarius surrounded by nucleus of solitary tract.
v.: Ventral group of paramedian reticular nucleus.
V.d.: Inferior (descending) vestibular nucleus.
V.l.: Lateral vestibular nucleus.
V.m.: Medial vestibular nucleus.
V.s.: Superior vestibular nucleus.
III, IV, V, VII, X and XII: Motor nuclei of cranial nerves (**X:** Nucleus ambiguus).

TEXT-FIGURE 1

A series of equally spaced drawings of transverse Nissl-stained sections through the brain stem of the cat to show the groupings of cells in the reticular formation. The drawings have been made by means of a projection apparatus and have subsequently been checked under the microscope and the details filled in. In the right half of the drawings dots of different sizes indicate the distribution of cell types according to size. The broken lines in the left half give the approximate borders between major cellular groups (reticular nuclei) which can be outlined on a cytoarchitectonic basis. These are in agreement with Meessen and Olszewski's (1949) atlas of the rabbit brain stem, though many of their minor cell groups have been omitted. The terms nucleus reticularis tegmenti pontis (N.r.t.) and nucleus reticularis lateralis (N.r.l.) are used for the groups which Meessen and Olszweski label ppl. and L.c.mc. and pc. respectively. Details concerning these nuclei are shown in Text-figs. 2 and 4.