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II. Wissenschaftliche Mittheilungen.

1. The Structure and Homologies of the Cranial Nerves of the Amphibia as determined by their Peripheral Distribution and Internal Origin.

By Oliver Strong, M.A., University Fellow in Biology, Princeton, U.S.A. eingeg. 13. September 1890.

My ultimate object in this investigation is to resolve each of the cranial nerves into its several component parts and to ascertain both

the internal origin and peripheral distribution of these parts. This is a slow but exact method of settling the many mooted questions regarding the homologies of the cranial nerves. The research was suggested to the writer by Prof. Osborn who found the very indefinite knowledge of the homologies and peripheral distribution of the nerves limited his investigations upon the internal structure of the Amphibian brain.

The forms observed are Spelerpes ruber, Desmognathus fusca, Tadpoles of common Frogs, Chorophilus triseriatus (?) and Bufo lentiginosus. The third and fourth species have been worked out most completely and are to be understood as referred to unless it is otherwise specified.

The method has been that of serial sections through the entire heads of small Amphibians, in order to observe the finer anatomical relations which elude gross dissection and to determine the precise nature of the fibres of the various nerves.

Although the investigation is not yet completed, I have thought it best to communicate some of the results which have been obtained thus far.

1. The Oculo-Motor Group.

A small sensory intracranial twig was observed to arise from the IV, nerve.

The fibres of the VI. can be traced through the Gasserian ganglion, preserving their continuity, but cannot always be easily distinguished beyond this from the Ophthalmicus trigemini, with which they are merged.

The Ciliary Ganglion. — Extirpation of the ciliary nerves was followed by nearly complete degeneration of the ganglion, only a few scattered cells on the III. remaining. In *Desmognathus* there appears to be no well defined ciliary ganglion — only scattered ganglion cells.

2. The Trigeminus and Facial.

Trigeminus. — The fibres of the Trigeminus are of varying sizes, the majority being small but with a number of large fibres among them. I find that while (a) some of the latter are motor, entering the muscles supplied by the Trigeminus, (b) a number of the large fibres can be followed out in all the main branches of the Trigeminus until they are seen to have a cutaneous distribution. Although not traced out, there can be little doubt but that the (a) motor fibres are from the Trigeminal motor nucleus, forming the minor root of the V. which is here,

however, but little separated from the rest of the V. As to the large (b) cutaneous fibres, they can be traced caudad in the ascending Trigeminal tract to the posterior columns of the cord and are thus continuous with the large fibres found in these columns.

Facial. — Some of the most interesting discoveries have been made in connection with this nerve.

The Facial of the Amphibia is divisible into two parts, very different from each other: a ventral part which persists in the higher Vertebrates and corresponds, in part at least, to the Facial of Mammalia; and a dorsal part, representing in *Chorophilus* and tadpoles the diminished remnant of a nerve, or group of nerves, which are much more important in the *Urodela* and remaining *Ichthyopsida*.

a) The ventral VII., or Facial of the higher Vertebrata, using the former term for clearness, is given off close beneath the Auditory. It arises by two roots: a fine-fibred root, VII. aa, from the Fasciculus communis¹ of Osborn and a coarse-fibred root, VII. ab, more ventral which appears to be connected with a nucleus similar to that of the minor Trigeminus. The root apparently corresponding to this in Urodela, however, Osborn has ascertained to be derived from the posterior longitudinal fasciculus. It may, perhaps, have a double origin.

After its exit, the ventral VII. (VII. a) proceeds forwards, is reënforced by one-half the coarse-fibred dorsal VII. (VII. b, see below) and just before coming in contact with the Gasserian ganglion, divides into two parts, a coarse and a fine-fibred. The latter breaks up in the ventral part of the Gasserian ganglion and emerges as the fine-fibred Palatine. It is reënforced here by fibres of the Sympathetic and also contains a considerable number of ganglion cells somewhat smaller than those of the Gasserian ganglion. In Ecker's Anatomy of the Froga this is spoken of as if mainly a branch of the Ophthalmicus trigemini reënforced by the Facial (3, p. 169). I believe, rather, that the majority, if not all, of its fibres are from the Facial and not from the Trigeminus, which opinion is further supported by the fact that this

¹ See ¹10). This tract first becomes conspicuous in the posterior horn of the medulla shortly cephalad of the opening of the IV. ventricle. It is fine-fibred and contributes to the X., IX. and VII. or VIII. nerves in *Urodela* according to the observations of Osborn which are confirmed by those of Miller (10 and 9). I have verified these in *Anura* but have shown that it goes to the VII. and not the VIII. Köppen (8) seems to have observed this tract but fallen into the error of assigning it to the V. instead of the VII. It is probably identical with the tract described by Goronowitsch (7) as found in the Lobus vagi of *Acipenser*.

nerve does not come into connection with the Gasserian ganglion in Urodela.

The important point here established is that the Fasciculus communis enters the Palatine branch of the Facial, a nerve to the roof of the mouth. According to Stirling (12), this branch is composed of fibres to the mucous epithelium, to glands and to blood-vessels. Eliminating the fibres of the Sympathetic, it would be afferent and it follows that the Fasciculus communis tract is, in all probability, afferent. This view is further supported by its internal position in the dorsal part of the medulla and by the fact that it constitutes the bulk of the Glossopharyngeal.

The other, coarse-fibred, division of the ventral VII. is the Hyomandibular. Although it is for a short distance imbedded in the outer ventral part of the Gasserian ganglion, it retains its continuity throughout. In the Urodele forms examined and in those described by Fischer (5), neither this nerve nore the Palatine comes into contact with the Gasserian ganglion. Its position in *Anura* is not improbably due to the greater development of the Auditory capsule, which pushes it forward. As the Hyomandibular leaves the Gasserian ganglion, it receives a number of the fine Palatine fibres. This is probably also the case in Urodele forms and is likewise inferred by Ewart as probable in Elasmobranchs from macroscopic appearances (4).

Thus the Hyomandibular consists of three components: one from the ventral root of the ventral VII. (VII. ab), coarse-fibred, one from the dorsal VII. (VII. b), coarse-fibred and sensory, and one ultimately from the Fasciculus communis (VII. aa), fine-fibred and sensory. Unfortunately the ultimate distribution of these parts is complicated by the fact that the Hyomandibular receives a communicating branch from the IX. + X. group. It would seem highly probable, however, that the Ramus mandibularis, which is fine-fibred and supplies parts of the oral cavity, derives its fibres from the Fasciculus communis component (VII. aa). The dorsal VII. (VII. b) component must be regarded (see below) as supplying cutaneous branches. From the joint nerve formed by the Hyomandibular and the communicating branch from the IX. + X. are also given off a number of motor branches. I believe these are, in part at least, supplied by the remaining component, i. e. VII. ab, especially as this has the position and characteristics of a motor root.

3. The Nerves of the Lateral Sense Organs.

b) The dorsal VII. (»V.—VII. urla of Osborn). This is given off from the dorsal part of the medulla immediately above the Auditory

exit. It separates and passes forwards, about half of its fibres soon passing downwards to reënforce the ventral VII. (VII. a) as described above. The remaining fibres proceed along the dorsal side of the Gasserian cancilion and divide, one part receiving a filament of the Symnathetic and proceeding outwards to bend forwards under the eye while the other part proceeds upwards, pierces the cranium by a separate foramen and runs directly forward along the top of the head. Both of these parts, a short distance from the Gasserian ganglion, fuse for a small part of their course with branches from the Trigeminus. They are both cutaneous and seem to follow the lines of the lateral sense organs seen in the Tadpole to which I believe they belong. The fibres of the dorsal VII, are coarse and very uniform in size. In Desmognathus and Spelernes, the above description also holds good essentially except that the Fasciculus communis is given off above the Auditory and therefore immediately below the dorsal VII., which agrees with Osborn's account of Cryptobranchus.

The dorsal VII. is largest in *Urodela*, is reduced in Tadpoles of *Anura* and is entirely wanting in the full grown Frog and Toad. This disappearance accounts for the apparent discrepancy between Osborn's account of the Facial as mainly dorsal to the Auditory in *Urodela* and the usual account according to which it is ventral to the Auditory in *Anura* and higher forms.

In some Urodele forms examined, the nerve VII. $a + \frac{1}{2}$ VII. b was seen to have two ganglia, one immediately below the Auditory ganglion and probably belonging to the Palatine (Fasciculus communis) portion and the other further outwards on the Hyomandibular. In Anurous forms examined, including Tadpoles, no ganglion cells seem to occur on the VII. until its connection with the Gasserian ganglion. This being the case, it is evident that the Gasserian ganglion in Anura is very complex, consisting not only of the ganglia of the Maxillomandibularis and the Ophthalmicus trigemini but also of the Palatine and of the branches of the dorsal VII., if the latter have ganglia, as long as they persist.

The anterior root of the Glossopharyngeal and Vagus group.

This arises usually some distance cephalad of the other roots and also much more dorsally. Its fibres can be tolerably well traced through the ganglia of the IX. +X. and all its branches appear to have a cutaneous distribution. It is to be regarded as the Lateral nerve and in respect to the origin of its fibres, their character and distribution, it agrees with the dorsal VII.

This system of nerves arising by the dorsal VII. root and the first root of the IX. + X. is to be distinguished, judging by the size and origin of its fibres, from the sensory Trigeminus. This conclusion is supported, I find, from the standpoint of distribution, by the investigations of Ewart and Allis. The former assigns only the Facial and Lateral to the mucous canals in Elasmobranchs (4) and likewise Allis, in his thorough work on Amia (2), says: "the Facial is the first one of the cranial nerves that takes any part in supplying the regular organs of the lateral canals".

It is obvious that the connection of the dorsal VII. with the lateral sense organs affords an explanation of its disappearance in adult *Anura* and also that a careful study of the relations of the internal tracts of this system to those of the Auditory may throw some light upon the primitive relations between the lateral and auditory sense organs.

4. Glossopharyngeal and Vagus.

The second main root (IX.) of this group is supplied largely by the Fasciculus communis (see also 10 and 9). There is also a small ventral rootlet, probably motor. Applying the results obtained above concerning the Fasciculus communis, we conclude that the fine-fibred Ramus lingualis must be composed of fibres from this tract, although the fibres cannot be continuously traced out.

The third and fourth roote (X.a + X.b) come off close together and likewise receive a large supply from the Fasciculus communis which may be regarded as entering branches to the mucous epithelium of the alimentary canal and its outgrowths (Rami gastrici et pulmonales). There are ventral rootlets present here also.

The fifth root (X.c) receives either a very small or no supply from the Fasciculus communis and is mainly derived from the Fasciculus solitarius (also 10 and 9) which is an ascending lateral fasciculus and, reasoning by elimination, must be considered efferent.

Shore (11) has insisted upon the division of the Vagus into a coarse-fibred lateral and a fine-fibred visceral portion. This holds good in the main, but the splanchnic motor fibres of the Vagus are, in many cases, at least, coarse constituting an exception to this distinction.

5. Hypoglossus.

This nerve has in *Chorophilus* a fine dorsal root and a ganglion. This appears to be also the case in early Tadpole stages but in an older Tadpole examined, no dorsal root could be found although there was a ganglion. It seems, however, when present, to break up in the ganglion and reappear as the non-medulated com-

municating branch with the Sympathetic. From observations on the first and second cervical nerves, I am inclined to think that the fibres of the communicating branch are derived mainly from the dorsal root. Gaskell has already suggested that this may be the case. If the ganglion belongs to the dorsal root, it must then be regarded as a detached portion of the splanchnic ganglionated efferent (Sympathetic) system.

The following tables must be regarded as incomplete and largely tentative, especially the homologous. For the meaning of Nuclei »series $A\alpha$ and »series $B\alpha$ see the Summary.

Table showing the Function, Origin, and Homologies of the Cranial Nerves. (Preliminary.)

	1		II .1
Nerve	Function	Internal Origin	Homologous internal Tracts in Fishes and Uro- dela
III., IV.	somatic non-gang.	Nuclei, series A	
VII. + XII.	(except ciliary nerves)		
V. major	somatic afferent	Ascending tract from post. spinal col.	Ascending tract in Petro- myzon (1), Acipenser (7), Aniurus (13) and Crypto- branchus (10)
V. minor	splanchnic non- gang. efferent	Nucleus, series B (and post, long. fasc.?)	"Transverse« from nucleus of large cells in Petromy- zon (1), "Transverse« in Amiurus from? (13), Motor nucleus in Cryptobranchus (10)
Dorsal VII. $(VII. b)$	somatic afferent	Ascending and descending dorsal tracts	Dorso-lateral tract in Acipenser (7), Tuberculum acusticum in Amiurus (13), Tract traced to sensory nucleus in Cryptobranchus (10)
Ventral VII. (VII. aa)	splanchnic afferent	Fasciculus communis	Tract in Lobus vagi in Aci- penser (7), Dorsal genicu- lated in Lobus Trig. in Amiurus? (13), Fasciculus communis in Crypto- branchus (10)
(VII, ab)	splanchnic non- gang. efferent	Nucleus, series B	Motor cells corresponding to ant. horn in Acipenser (7), (also post. long. fasc.), see 2. a for Cryptobranehus

Nerve	Function	Internal Origin	Homologous internal Tracts in Fishes and <i>Uro-</i> <i>dela</i>	
First root of IX. + X.	somatic afferent		Dorso-lateral tract in Acipenser (7), Tuberculum acusticum in Amiurus (13)	
IX. + X. (IX.)	splanchnic afferent	Fasciculus communis	Tract in Lobus vagi in Acipenser (7), Fasciculus communis in Cryptobranchus (10)	
	splanchnic non- gang. efferent	Nucleus, series B	Motor cells corresponding to ant. horn in Acipenser (7)	
$(\mathbf{X}.a)$ and $(\mathbf{X}.b)$	same as (IX.)			
(X. c)		Nucleus, series B Fasciculus solitarius		

The following I am inclined to believe are the homologies of the branches of the dorsal VII. in Amia.

Tadpole and Chorophilus	Amia
Branch along top of the head (see 3.) Branch under the eye Branch uniting with Hyomandibular	Ophthalmicus superficialis Buccalis and Oticus Mandibularis facialis externus

Summary.

The following is a summary of the principal results:

1) That while the calibre of the fibres composing the nerves often affords valuable indications for tracing different tracts, there is no general law whereby function can be inferred from size, e. g. —

III., IV. and VI.	motor	mainly coarse-fibred
major V.	sensory	small with a few large fibres
minor V.	motor	coarse
VII.b	sensory	coarse
VII. aa	sensory	fine-fibred
VII. ab	motor	coarse
VIII.	sensory	partly very coarse and partly fine
Ist root of IX. + X.	sensory	coarse
IX. + X.	motor	all branches fine-fibred, including the Laryn-
		geals to striated muscles, except those
		branches entering the Petrohyoid, Intertrans-
		versarius and Trapezius muscles

- 2) That the large sensory root of the Facial, dorsal to the Auditory (dorsal VII.) together with the anterior root of the Glossopharyngeal form a distinct group by themselves, differentiated from the others by their internal origin and by the character of their fibres and belonging distinctly to the organs of the lateral canals. It is possible that the Auditory may have some relation to this system of nerves.
- 3) That the Amphibia are transition types since in them we can trace the disappearance of the above group of nerves, so characteristic of the Fishes. The *Urodela* approach the piscine condition with their large dorsal sensory VII., the *Anura* approach the higher vertebrates with the dorsal sensory VII. wanting and the ventral motor VII. consequently more prominent. The remaining portion of the Facial, that arising from the Fasciculus communis, is possibly the homologue of the Portio intermedia.
- 4) That, as observed by Osborn, we have in the medulla at least two series of motor nuclei: (A) one series those of the III., IV., VI. and XII. nerves, (B) and the other series, those of the motor V., ventral motor VII. and of a number of ventral rootlets of the IX. + X., which latter rootlets may, I believe, be regarded as homologous with the medullary portion of the XI.
- 5) It is the second series which, in position and in the size of the cells, seems to correspond most closely with the large cells in the anterior horn of the spinal cord of the Frog.
- 6) That in the medulla we have a remarkable concentration of certain tracts. This has been mentioned by Gaskell and should be extended to include the Fasciculus communis and those tracts connected with the organs of the lateral line.
- 7) That the Fasciculus communis, of Osborn, is an afferent splanchnic tract supplying parts of the epithelium of the mouth and alimentary canal.

Princeton, Aug. 28., 1890.

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2. Die Richtungskörperchen von Balanus.

Von Dr. Bernh. Solger, Greifswald.

eingeg. 24. September 1890.

Das Vorkommen eines »Richtungsbläschens« bei Balanus wurde schon im Jahre 1876 von Hoek festgestellt, und zwar an den aus dem Mantelraum von B. balanoides entnommenen Eiern, an deren stumpfem Pol zwischen Dotter und Eihülle es sich vorfand. Balfour verhielt sich in seinem bekannten Handbuche dieser Beobachtung gegenüber ziemlich reserviert, — mit Unrecht, wie wir jetzt sagen können, denn neuerdings wurde von Weismann und Ischikawa die Angabe von Hoek bestätigt. An seiner Deutung ist um so weniger zu zweifeln, als Weismann und Ischikawa außerdem in Ovarialeiern von Balanus die erste Richtungsspindel, in deren »Äquatorialplatte vier Doppel-Chromatinelemente von Körnerform enthalten sind«, entdeckten. Der Nachweis eines zweiten Richtungskörperchens konnte aus Mangel an Material nicht erbracht werden.

Ich habe nun im Laufe des Sommers bei Balanus improvisus, einer Form, die an der Mündung des Ryckflusses außerordentlich häufig vorkommt, die Abschnürung beider Richtungskörperchen, sowie das gleichzeitige Vorhandensein zweier solcher Gebilde an einer großen Anzahl lebender Eier feststellen können, nachdem ich dieselben in besamtes Wasser gebracht hatte. Auch hier spielt sich der Proceß, wie bei B. balanoides am stumpfen Eipole ab. Während der Abschnürung

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