On Cerebral Homologies in Vertebrates and Invertebrates. By Professor Owen, C.B., M.R.S., V.L.S., &c. By Professor Owen, C.B., M.R.S., V.L.S.

(Read November 16, 1882)

In a study of the homologies of the divisions of the Vertebrate brain with Nerve-centres in Invertebrates the subjects of comparison should be the best-developed anterior and special-sense-masses in the latter and the least developed ones in the former subkingdom.

Par) In many fishes - Lepidosteus, Anguilla, e.g. -[1] the neural masses in direct relation to nerves of special sense are as large as or larger than those not so related bearing the names of 'cerebrum' and 'cerebellum'; these being the homologues of those

1/ 'Anatomy of Vertebrates', 8vo, Vol. i, (1866), p. 275, figs. 174, 175./

those centres which receive, in higher Vertebrates, such vast accessions of grey and white neurine as to represent, or seemingly compose, the whole organ known as 'the brain', in Man and most Mammals.

Par/ The chief accumulation rises and expands from the parial nerve-tracts, or 'crura'; between those portions of the tracts which, in front of the cerebral hemispheres, develope the masses or ganglia related to the sense of 'Smell' and those behind the hemispheres related to the sense of 'Sight'. Next, in retral succession, are enlargements related to the sense of 'Taste' & movements of parts of the mouth; & behind the 'trigeminal' centres are those subserving the sense of Hearing: above these centres rises the ~~[illegible]~~ 'cerebellum'.

(Par) Thus the central masses of the neural axis in relation to the 'special senses' run in longitudinal sequence from before backward, and

and might be called the 'ganglions' of smell, sight, taste & hearing.

(Par) These several sense-centres are not in contact with one another in all Vertebrates. The olfactory ganglia are connected by long chords with the optic ganglia in many fishes, Cyprinoids, e.g.,[1] The intercommunicating tracts, with the trigeminal lobes recall the corresponding ones known as 'œsophageal chords' in Mollusks and Insects. Short and thick in all Vertebrates, or 'medulla oblongata' are the tracts of the macromyelon connecting the gustatory with the auditory nerve-centres, but all are reckoned parts of the ~~tebrate~~ 'Brain'.

(Par) The condition which affects the length & tenuity of the tracts connecting the optic (ib. b) with the oral nerve-centres in Invertebrates is the course of the alimentary canal, (ib. c, d) neurad[2], along the interspace between the premoral and

such centres with superadded masses

(diags. a. f.)

[1] Tom. cit. p. 275, figs. 177, 178. [2] Ib. p. 276, fig. 179 (chorda).

[2] See also, Figure 3, 'On the Homology of the Cotyloid-hypophysial tract,' Journal of the Linnean Society – Zoology – Vol. XVI, p. 135 ff

and the next neural centres.

Par) The elongated homologues of the vertebrate 'crura cerebri' ~~with nucleated interganglionic connecting tracts~~ are termed by Lyonnet (with sound homological views) "conduits de la moelle epinière";

Par) by later Anatomists, rejecting his views, 'œsophageal chords' or 'commissures'.

Par.) In illustration of the present suggestions of the homologies in question I propose to take, from the group of Arthropods, the nervous system of the Locust. 2/

Par) The foremost, first commonly neural 'ganglionic mass', fig. a, which, by the course of

1/ 'Traité Anatomique de la Chenille qui ronge le bois du Saule' 4to, 1762.

2/ As represented in Caloptenus femur-rubrum, ~~and~~ Cal. spretus and Cal. bivittatus, by the exemplary dissections and microscopic sections by W. M. Burgess and Mason, described and figured by Prof. Packard in the 'Second Report of the U. S. Entomological Commission', 1880, p.p. 223–242, Pls. IX–XV.

of the œsophagus, in Mollusks & Articulates, is turned to the hæmal aspect of the alimentary canal, is that which is usually designated the 'supra-œsophageal ganglion', or, after Lyonnet & Cuvier, 1/ 'the brain'.

1/ "le cerveau proprement dit." Leçons d'Anat. Comparée Ed. 1845, tom. iii, p.p. 305, 335.

Par. This consists of a pair of neural masses, or 'hemispheres', confluent mesially for one half of their longitudinal extent, before and behind which confluent tract, they are free. Each moiety presents three lobes or enlargements, the smallest of which receives the 'antennal nerve', fig. 1, c, a second — the largest — the optic nerve, f, the third ~~and smallest~~ the ocellar nerve, g. 1/. From the œsophageal surface of each moiety proceeds the tract or 'commissure', d, which, traversing it's own side of the gullet, converges to & ~~unite with~~, with it's fellow, & expands into the neural mass termed the 'sub-œsophageal ganglion', b.

Par. With mesial 1/ I omit the filaments connecting the foremost minute ganglia ~~each of the hemispheres~~ of the 'sympathetic' or 'stomato-gastric' system, with the above cerebral masses. /

With this neural mass are connected by origin or insertion the nerves to the trophi; i.e. the labrum, the mandibles, the maxillæ, & labium with its tongue-like extension, and the sense-organs called 'maxillary' and 'labial palpi', together with the complex muscles of these several parts.

Par) The properties of the vertebrate mouth viz. taste and motions may be reasonably assigned to the foregoing invertebrate oral organs: accordingly the nerves connected therewith, ~~and~~ owning the mouth with the same characteristic powers and properties for testing, seizing & comminuting alimentary substances, I deem, with their neural centres, to be homologous with those in the vertebrate animals.

Par) The part of the vertebrate brain to which, therefore, the so-called 'subœsophageal ganglion', in invertebrates, is analogous, and I conceive ~~is I deem~~, also, homologous, is the basis of the

epencept

encephalon known as the 'medulla oblongata' (macromyelon); or so much of that myelencephalous tract as may be in connection with the trigeminal and hypoglossal nerves — the neural machinery, to wit, for the sensations and motions of the parts forming or being lodged within a vertebrate or furnishing secretions to, the mouth.

Pon) Through the different course of the gullet, in relation to certain nerve-centres in Vertebrates and Invertebrates,[1] a greater degree of juxtaposition and concentration of those centres connected with the 'special senses', and the neural mechanism relating to the reception and conception of their impressions, is possible, in the group in which the 'brain', or sum of such centres, is not traversed by the alimentary canal.

We

[1] 'Linnean Society's Journal', Vol. XVI, p. 135, figs. 2 & 3.

We are thus prepared for the conception, that, as the oral nerve-centres, in Invertebrata, are so far removed from the narial nerve-centres, so the ear-organs and their centres may be correspondingly remote from the oral ones.

Var) Johannes Müller ~~and in~~ recognized a structure in the fore-leg of the Gryllus hieroglyphus, which von Siebold detected in other Orthoptera, and this structure was by both regarded as the true seat of the auditory sense. Vesicle, in connection with a quasi tympanic membrane closing an orifice in the fore leg, receives ~~one~~ two unusually large nerves from the foremost Thoracic ganglion; these nerves accompanying the tracheal branch of the vesicle: the lesser nerve attaches itself to the vesicular dilatation & there expands into a flattened tract, displaying a structure akin to that of the acoustic nerve-lining of the semicircular canals in Vertebrata. This interpretation

is

is accepted by the experienced Anatomist of the Arthropoda, Prof. Packard, who writes:-
"In the green grasshoppers, such as the Katydids (and their allies, whose ears are situated in (their fore legs, the 'first thoracic ganglion' is a complexone"; /- such 'auditory nerves' communicating therewith.

Par / Although, physiologically, the remoter neural maps may be compared with the part of the epencephalon in connection with the auditory organ, it may be too much to look for consent to a corresponding homology. - And, if such be denied, yet the retral remoter of a sense-character beyond the gnatal one to the foremost or even a remoter thoracic nerve-map ~~ganglion~~ may not, consequentially, affect the ground for

/ 'Second Report', &c., p. 225. /

for homologizing both the so-called 'supra-œsophageal ganglia' (which are constant in regard to their special sense-nerves, and 'sub-œsophageal ganglia') with the parts of the vertebrate brain similarly distinguished by relations to nerves of special sense.

Par. Conclusions, counter to these homologies, either limit the term 'brain' to what is called the 'supra-œsophageal ganglia' in Invertebrates; or, more consistently, sketch a negation of the homology of any part of the central neural system in Invertebrates, with any part of that system in Vertebrates.

Par. The latest Neurotomist of the Arthropoda, for example, concludes, emphatically, as follows:— "It should be remembered that the word "brain" is applied to the compound (supra-œsophageal) ganglia simply by courtesy and as a matter of convenience, as it does not correspond with to the brain of a vertebrate animal, the brain of the horse or man being composed of several distinct pairs of ganglia. Moreover, the brain and nervous cord of the fish or man is fundamentally different, or not homologous with that of the lower or invertebrate animals.'— 'The nervous cord of the insect con-

'consists of a chain of ganglia connected by nerves or com-
'-missures."[1]

~~several distinct pairs of ganglia~~

(Poulton) The 'nervous cord' here signifies the central tracts – ganglionic or otherwise – occupying, in Invertebrates, what is held to be, and is described as, 'the ventral region' of the body-cavity.

The structural phenomena cited in support of the foregoing negation are:– "The entire brain of an insect is
'white, as are all the ganglia:"[2] while "the spinal cord
of the fish or man consists of two kinds of substances or tissues, called
"gray" and "white substance".[3]

But the associated microscopical investigators and manipulators, Burgess & Mason, found in the entire brain (my 'fore-brain', ~~'cerebrum' or 'cerebral hemisphere'~~ or phaseal
'centre.') ~~'Brain of Prof. Packard'~~: "I. An outer,
'slightly darker, usually pale grayish white portion,
'made up of "cortical cells":[3] (The medullary or
'inner part of the brain consists of matter which remains
'white or unstained after the preparation has remained
'thoroughly exposed to the action of carmine. It consists
'of minute granules and interlacing fibres. The
'latter and: "II.

[1] Packard, 'Second Report', &c., p. 224. [2] Ib. ib.
[3] Ib. p. 226.

'latter often forms a fine irregular net-work in-
'closing masses of finely granulated nerve matter."[1]

Par. Remembering the transposition of the grey & white neurine in different parts of the vertebrate neural axis I cannot ~~assign~~ give the ~~same~~ value ~~to such~~ to a similar transposition in parts of the invertebrate neural axis ~~as~~ which Professor Packard assigns thereto.

Par. The eyes of the cuttle fish are the homologues of those of the lamp fish, as are the optic nerves and the cerebral masses superadded, in both, to the centre receiving the impressions of those nerves. Such homology legitimately extends from Cephalopods to Invertebrates in which a homologue of the vertebrate hemispheres may not be so largely developed or superadded

Par. Accordingly, I conclude that the collective neural centres and their intercommunicating tracts in ~~vertebrates~~ Invertebrates are the homologues of those centres and tracts, called 'brain & Spinal chord' in Vertebrates; and that such 'neural axis' marks, in both grades of the Animal series, the same position in the body, & the same local relations to the vascular centre and the alimentary canal. As a corollary, the neural axis, or 'ganglionic chord' in Arthropods, denotes

1/ Ib. ib. p. 227.

denotes the neural position, (supports the inference) and that its foremost portion is simply displaced by the course of the gullet through the brain in order to open by a mouth upon the neural aspect of the body. The suppression of such trans-cerebral tract in Vertebrates allows the continuation of the alimentary canal forwards to an oral opening on the hæmal aspect of the body. Hence the œsophagus offers no obstacle to the approximation of the main cerebral centres to each other — the fore-brain to the hind-brain: hence that juxtaposed collocation of the primary encephalic divisions, ~~which~~ associated with the progressive accumulations of grey and white neurine, which the cerebrum & cerebellum present, in

, in relation to the centres subservient to the ingoing conductors of sensations & the outgoing ones of motions, ~~presents~~ as we pass in their contemplation from the fish to the ape and to man.

Par. The so-called 'brain' in the Locusts answers to a part only of the brain of a fish: moreover, it is not a 'supra-œsophageal ganglion' but a 'sub-' or 'hæm-œsophageal' one.

Par. The next neural mass in the brain of the Locust answers to the epencephalon of the fish: it is not a 'sub-œsophageal ganglion' but a 'supra-' or 'neur-œsophageal' one, and the foremost of that series of the neural centres or 'ganglions'.

Par. The homologue of the vertebrate myelon in Invertebrates is not protected by a special bony case or 'vertebral column'. The 'ganglionic chord'

is

is, nevertheless, the most precious as it is the most delicate and crushable of an insect's organs.

Hence it has been, so to speak, ordained, that the part of the body's surface to which the neural axis is nearest should not be, as in the beast, along the part most exposed and liable to blows. By a modified flexure of the limb-segments of a beetle or lobster the trunk is turned so as to hold the same relative position to the ground as does the part of the beast's body least exposed to injuries.

Par) The aspects of the trunk in locomotion are no primary or essential characters of a natural group. Some insects, indeed, swim with their neural surface upwards as does the fish.

Active Binaua, in the aspects of the trunk, differ from both beasts and beetles: when a man stands his body is at right angles to the ground & the limbs are in the same line with the trunk.

Par) But

But the heart, in Man, indicates the 'hæmal' aspect, the myelon the 'neural' aspect, as in the animals of lower grade whether vertebrate or invertebrate.

Rat The restriction by Cuvier of cerebral homologies to the so-called 'suprasœsophageal ganglion' in the latter leads me to add a few remarks on what may be derived from the Molluscous Subkingdom in illustration of my present subject. In this group, indeed, the great Anatomist admitted an exception in favor of the highest Cephalopoda.

zoological division

Op. cit., tom. iii, p. 297

In fact, the encephalon in the Dibranchiate order resembles that of Vertebrates in the mutual proximity of the 'fore-' and 'hind-brains'; so approximated, they are both also protected partially by a cartilaginous case, which is analogous to, if not homologous with, the vertebrate cranium.

But the cephalopodic brain retains the invertebrate condition of giving passage to the gullet along the tract or part answering to the third ventricle; only the lateral boundaries or crural tracts are much shorter and thicker than in inferior Mollusks or in Articulates.

Rat Stk

Still it is plain that the nervous mass on one side of the gullet answers to the 'supra-oesophageal ganglion' and that on the opposite side to the 'sub-oesophageal ganglion' of lower Invertebrates.

The latter sends off the acoustic nerves and is continued into the chords which endow the muscles and skin of the trunk with the motory and sensory powers. A closer resemblance than is usually seen in Invertebrates to the Vertebrate myelon is moreover manifested by the conspicuous ganglions developed on the sensory tracts or chords of the trunk[1], and the non-ganglionic continuation of the motory division of the body-chords continued from the Cephalopod's brain.

From the beginning of the short and thick side-tracts which indicate, if they do not represent, the parts of the vertebrate brain intervening between the 'pros'- and 'epencephala', the large optic nerves are given off.

I need not repeat their well-known characters and devel-

[1] 'Anatomy of the Pearly Nautilus', 4to, 1832, p. 38, plate 7, fig. 3.

developments in relation to the large and complex eyes of the Dibranchiates.

Beyond the origin of the optic nerves each side-tract terminates in a 'subœsophageal' mass, divided into two portions and supplying the parts corresponding with those in Vertebrates which send and receive their nervous influences through the 'medulla oblongata' (macromyelon) and the 'Spinal chord' (myelon).

The dibranchiate homologue of the supraœsophageal ganglion moreover, supports a part of the vertebrate cerebrum, less manifestly, if at all, shown in other Invertebrates; it is a superposed mass of a whiter colour than the rest

than the rest of the encephalic centres, with an indication of a division into a lateral pair of lobes, and, in *Sepia*, presenting a subtriangular form, with the apex anterior.

From the deeper seated part of the 'superœsophageal' mass are sent off, besides smaller filaments, a pair of nerves, or 'crura'; which converge and are lost in a more anterior ganglionic mass – the 'ganglion sus-buccal,' or the superoral ganglion, of Cuvier, which distributes nerves to the delicate membranous folds and processes developed from the interspaces of the cephalic arms, and to the plicated and papillose lips which surround the beak, and project anterior to beak, and which soft and lubricous parts we may reasonably suppose to receive from their superœsophageal, or cerebral, centres the faculty of judging of the odorous qualities of the substances to be seized by the ~~horal~~ beak.

Par / From the anterior portion of the larger subœsophageal mass, are sent off nerves to the rasping and gustatory organs within the mouth, and the larger nerves which supply the eight ~~brach~~ cephalic acetabuliferous arms, and tentacles. From the posterior division of the subœsophageal mass are sent off the moto-sensory nerves of the trunk, already noticed, & also ~~& with the same division of the brain the~~ visceral nerves, ~~vagal & sympathetic~~ ~~– are connected~~ 1/

Par/ In the Tetrabranchiate Cephalopods, the pore-

1/ Memoir on the Pearly Nautilus, 4to, 1832, p. 37, pl. 7, fig. 3 ~~[illegible]~~

The presumed literary character of Editors of Journals

Names of Journals – the very profession, literary of Editors & Supporters might lead one to expect them to give a name to the channel or medium of their lucubrations which would bear derivative (harmony) criticism.

a proper one – (i) by a one-sided aim (2)

Both Editors and Writers on the Periodical supported by the 'Society that they ~~these Editors~~ belong to the τα ζωα: ~~the~~ Species, ~~Ass~~ with – that they are of the same pains & maladies they would arrest & prevent the cure

If this be to protect animals rather than other τα ζωα the progress of the Healing art as applied to the Human Species, insofar as it depends on experiments on the lower animals, should be injured – they for call themselves 'Zoophilists' – tis true that for daily sustenance of their own species they object not or raise no voice against the skull-smashing, throat-cutting operations – not in relation to occasional luxuries to the skinning alive (eels) & boiling alive (lobster – some) shrimps until stewed to breakfast – But they ought to know better than call their journal the 'Zoophilist',

But, limiting their denunciations to such sections as Harvey & Hunter needed to make, in their benevolent relations to mankind, 'Theriophylist' it is properly the 'Beastiarian' — The higher Zoa – animals, are those whose torments it wants to perpetuate – noblest of the animalia or zoa of the Author of Natural History

If they will flaunt a classical epithet, is that exclusively to which, alone, they are entitled – But a better name for the periodical published under the auspices of the Victoria Street Society would be the 'Bestiarian'. The species whose tormenting maladies the Society seek to perpetuate are the highest & ought to be the

the foregoing primary divisions and functions of the brain are simplified and so are more clearly manifested. The cartilaginous defensive case protects only the homologue of the 'sub-' or rather 'neur-' œsophageal ganglion, which is more distinctly divided into a fore and hind mass. The first supplies the anterior or cephalic muscular and tegumentary parts, the second the posterior or corporal ones; and from this division of cerebral centre are derived the nerves of the acoustic organs developed in or imbedded in the corresponding supporting cartilage. /

Par) The super (hom-) œsophageal body develops no peripheral lobe, is in the form of a thick chord which sends forward nerves to oral parts suggestive of an olfactory function, and laterally, the large short chords swelling into ganglions subserving the retinal supply of the pedunculate eyes.

The brain-space traversed by the gullet is wider than

/ Macdonald, Anat: of the Nautilus umbilicatus. /

thon in the Dibranchiates, the connectant tracts between the 'supra'- and 'sub'-œsophageal masses are longer: but their resemblance to the œsophageal chord in the Articulates is still closer in the modifications of the cephalopodal type of the nervous system - especially of its encephalic centres which are seen in Aplysia and all lower Mollusca.

Par/ And here I need only to refer to the rich series of Monographs on this branch of Comparative Neurology ~~(communicated)~~ for which we are indebted ~~(published)~~ to our Fellow-Member & Labourer, Mr. Robert Garner of Stoke upon Trent [1], still in enjoyment of health & intellectual vigour; also ~~and~~ to another whose loss we lament, the late Dr. Albany Hancock, F.R.S. [2].

Par/ But, to

2/ By Monographs in the Publications by the Ray Society; in the Annals of Natural History, and in the 'Philosophical Transactions': with his associate Workers Embleton and Alder.

1/ See his beautifully illustrated Memoirs [in the 'Transactions of the Linnean Society Vol. XVII, 1837, and in the 'Transactions of the Zoological Society', Vol. II (1835).

But, to resume, my contention here is, that the homologies of the primary divisions of the brain in Mollusks are the parts known in Articulates as the 'supra-' and 'sub-œsophageal ganglions with their commissural or annectant chords, or œsura. That the topical relations of these parts to the gullet are the same in both great divisions of Invertebrates, and that the homologies of the aforesaid parts with the primary divisions of the Vertebrate brain are affected solely by the altered relation thereto of the gullet & mouth.

For The homologies of the Dibranchiate brain, notwithstanding the œsophageal and oral differences and a non-appreciation of their essential nature and cause, were recognized and affirmed by the Father of the Anatomy of the Mollusca. (They are clearly expressed in the first of his immortal 'Memoires' on that subject, and are briefly

1/ 'Mémoires pour servir à l'Histoire et l'Anatomie des Mollusques', 4to, 1816. Mem. 1re. Sur la Poulpe (Octopus Vulgaris).—

briefly summarized in the "Leçons d'Anatomie Comparée". After describing the 'sub-' & 'supra-Oesophageal centres Cuvier affirms:- "On pourrait comparer le premiere au cervelet, l'autre au cerveau des Vertébres". If for 'cerebellum' one writes 'epencephalon' the defined correspondence ~~with the brains of the Vertebrata, except the Lephas~~ of the brain of the highest Mollusks with that of the lowest Vertebrates would square with my own convictions. But, now, I am driven to ask:- Why did Cuvier refuse to extend his views - whether homologeal or analogical - of the answerable parts of the brain in Vertebrates and Invertebrates beyond the 'supercesophageal mass or ganglion' in Mollusks & Articulates? Because he declined to extend those views in relation to the Vertebrate & Invertebrate encephalic centres beyond or below the higher order of Cephalopoda; and he, logically

logically pronounced, at the conclusion of his admirable anatomical Monograph of the 'Poulpe' (Octopus vulgaris), that the class of which it was the type — my Cephalopoda dibranchiata — "formed not the passage to any other group, & that they have not resulted from the development of other animals, and that their own development has produced nothing superior to them."[1] It must be remembered, however, that at that date, the transitional modifications of the Tetrabranchiate Cephalopods had not been made known.

But if, however the cerebral homologies may be traced, with the guidance of the Pearly Nautilus, to the still lower, more simplified, Mollusca, my next contention is that these homologies may be predicated of the modifications of the brain in the Articulata.

So plain, so obvious, indeed, seem to me the grounds for such homologies, that I think I should have shrunk from urging them before my fellow-labourers of this Society were not views, very analogous to the restricted ones of Cuvier, maintained and asserted by the most accomplished and experienced comparative anatomist, especially of Invertebrate Animals, in the United States, to whose valuable Monographs[2] I have already referred.

[1] 'Mémoire sur le Poulpe,' Op. cit., p. 43.

[2] Ante p. .

referred.

I gladly, however, welcome the alliance of my Master in predicating corresponding parts of the nervous centres in the whole series of brain-possessing animals, so far as he felt himself justified to go.

And I avail myself of this concordance to define, agreeably with our common views, the aspects of the body in the adult Cephalopod, but in the terms which have been suggested by conclusions as to the essential conditions and wide extent of a possible predication of neural homologies.

Par. The side of the body of a Cuttlefish or Squid, denoted by the 'near-æsophageal' (so called 'sub-æsophageal') brain-part with the chief nervous extensions therefrom along the trunk, is the neural aspect; its

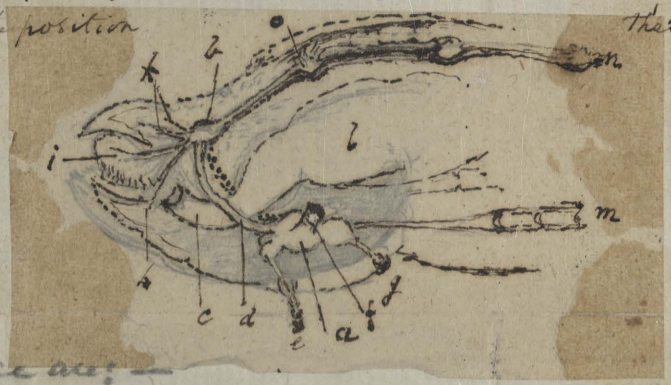
'neural aspect', its superficies ~~is~~ the 'neural surface'.
The side of the body to which the 'hæmal cæsophageal'
~~or~~ (so called 'supra-cæsophageal') brain-part has been turned by the curve of the gullet ~~to the~~
~~mouth~~, is the 'hæmal aspect', its superficies is
the 'hæmal surface'. The 'narrow space inclosed
by the arms, which contains the mouth', together
with the entire acetabular surface of those cephalic
arms, is the anterior or 'oral surface', answering
to that so termed in all other Invertebrates, ~~and is~~ as the
homologous part in all Vertebrates. The opposite end of the body, with
its ~~appendages~~ appended fins, is the posterior or
caudal end: what is usually called the upper
surface, in adult Cephalopods ~~as in~~ all lower Mollusks,
and in Articulates, is the 'hæmal one'; the opposite
surface is the 'neural' one. As here defined,
and as illustrated & named in a former contribution to the Society[1]
there can be, at least, no doubt as to the answerable aspects and
surfaces ~~so defined~~ in any Invertebrate possessing
comparable centres and chord of the nervous system,
with comparable centres or heart, of the vascular system.

[1] Journal of the Linnean Society, (Zoology), January, 1882,
p. 132, figs. 2, 3, 7, 8, 11.

system.

So, the heart in Man indicates the 'hæmal' aspect of his body, the myelon the 'neural' aspect, as in the animals below him whether vertebrate or invertebrate. ///

Profile diagram of head and brain of Insect, with fore-part of the neural & hæmal tracts or centres, in the position thereby indicated.



The letters of reference are:—

a. Hæmæsophageal centre, or 'ganglion' = fore-brain.
b. Neuræsophageal centre, or 'ganglion' = hind-brain.
c Æsophagus traversing the crura cerebri, or connecting chords, d, in its course hæmal, to the neural
e Nerve (olfactory?), to antenna.
f Optic nerve.
g Ocellar nerve.
h Mandibular nerve.
i Lingual nerve.
k Maxillary & labial palpal nerves.
l. Stomach, or alimentary axis.
m Heart, or hæmal axis.
n Ganglionic chords, or neural axis = myelon.
o Foremost thoracic centre, or ganglion.

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